Plant and Vegetation 18

Geraldo Alves Damasceno-Junior
Arnildo Pott *Editors*

Flora and Vegetation of the Pantanal Wetland

MOREMEDIA

Springer

Plant and Vegetation

Volume 18

Series Editor
Marinus J. A. Werger, Section Plant Ecology & Biodiversity, Utrecht University,
Padualaan, Utrecht, The Netherlands

Plant and Vegetation is a new Springer series comprising a series of books that present current knowledge and new perspectives on world vegetation. Examining the ecology of plants and vegetation at all scales – from plant to landscape – and covering key issues such as globalization, invasive species, climate change and the dynamics of plant biodiversity, this book series draws together a wide range of material of interest to plant ecologists, vegetation scientists, and geographers around the world.

The series provides a valuable resource for both graduate students and researchers in environmental and biological sciences, as well as for landscape planners and policy makers involved in land-use and restoration projects at local, regional and international levels.

More information about this series at http://www.springer.com/series/7549

Geraldo Alves Damasceno-Junior • Arnildo Pott
Editors

Flora and Vegetation of the Pantanal Wetland

Springer

Editors
Geraldo Alves Damasceno-Junior
Instituto de Biociências
Federal University of Mato Grosso do Sul
Campo Grande, Mato Grosso do Sul, Brazil

Arnildo Pott
Instituto de Biociências
Federal University of Mato Grosso do Sul
Campo Grande, Mato Grosso do Sul, Brazil

ISSN 1875-1318 ISSN 1875-1326 (electronic)
Plant and Vegetation
ISBN 978-3-030-83374-9 ISBN 978-3-030-83375-6 (eBook)
https://doi.org/10.1007/978-3-030-83375-6

© Springer Nature Switzerland AG 2021
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, expressed or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

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 km^2 of which some 140,000 km^2 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

Contents

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 km^2 (Silva and Abdon 1998), similar to a previous estimate of 137,000 km^2 (Hamilton et al. 1996). It extends into Paraguay (5,000 km^2) and Bolivia (15,000 km^2) (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 km^2, including 363,442 km^2 in Brazil and 132,558 km^2 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.

G. A. Damasceno-Junior (✉) · A. Pott
Laboratório de Ecologia Vegetal, Instituto de Biociências, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_1

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 km^2 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.

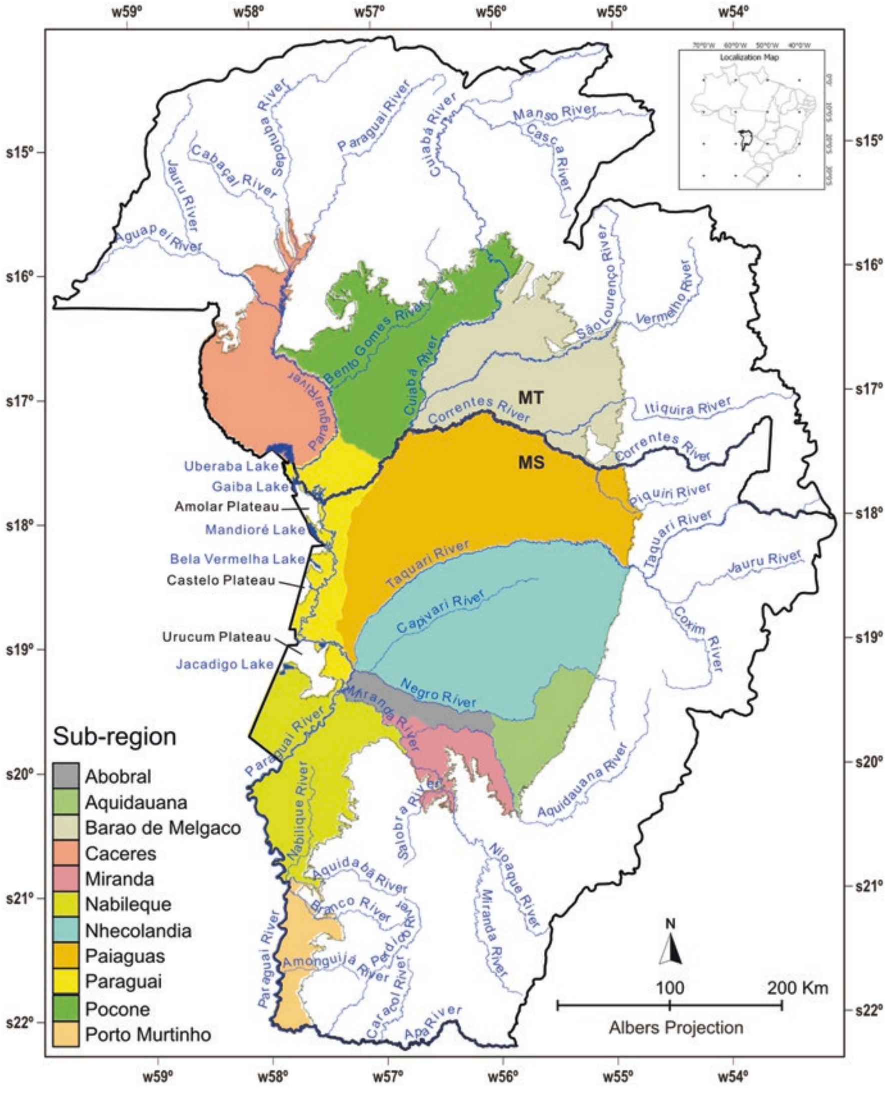


Fig. 1.2 The Brazilian Pantanal, showing its location in the map of Brazil, and its subdivision into 11 subregions and main rivers. Map by João dos Santos Vila da Silva (According to Silva and Abdon 1998)

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

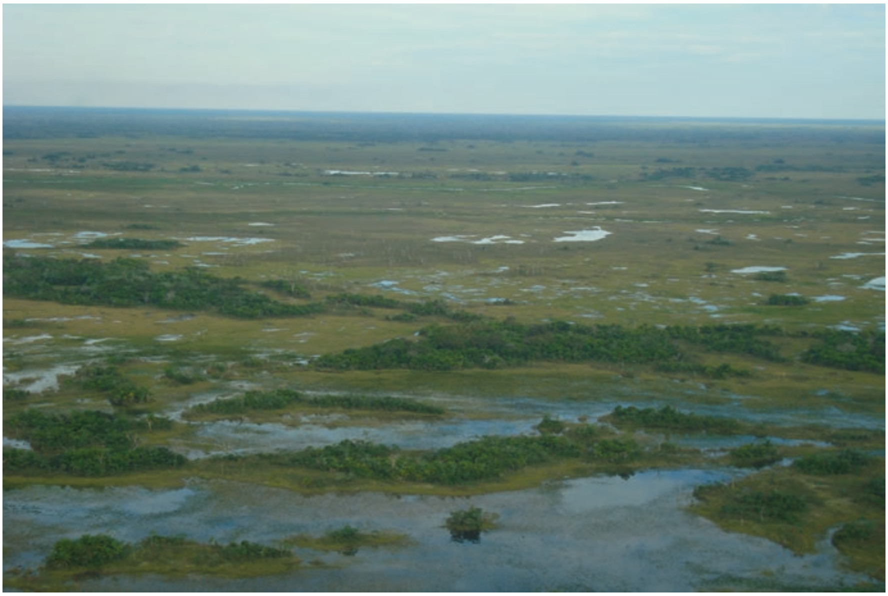


Fig. 1.3 Aerial photo showing the Pantanal of the Paiaguas landscape with *cordilheiras* (long-lined forested areas) and seasonally flooded grasslands. (Photo by Geraldo Alves Damasceno Junior)

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 25ºC 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 dendrochronological 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 km^2 and a minimum of 11,000 km^2 in rainy years (1979-1987) of higher floods (Hamilton et al. 1996), compared with a maximum of 52,900 km^2 and a minimum of 5,500 km^2 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

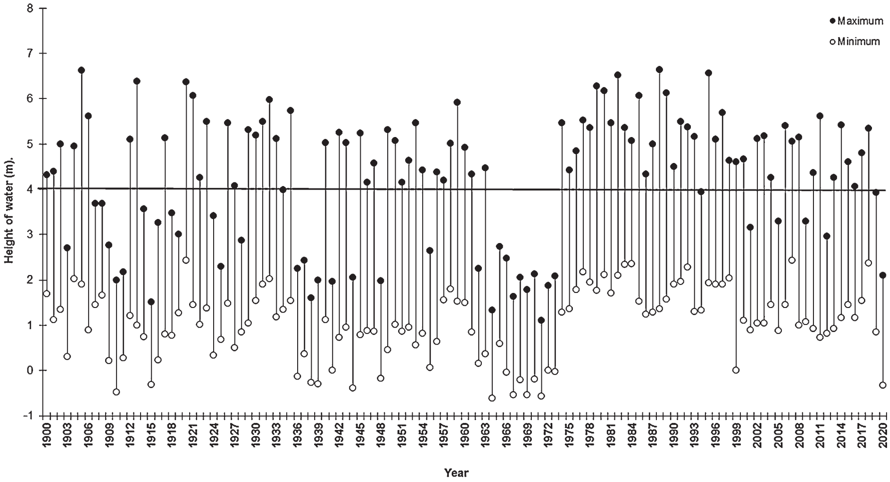


Fig. 1.4 Yearly maximum and minimum levels of the Paraguay River from 1900 to 2020 in Ladário. The 4 m line marks the upward limit for river overflow. (Data provided by the Brazilian Navy)

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 werneri*, 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 peripherical, 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.

References

Ab'Sáber AN (1988) O Pantanal Mato-Grossense e a Teoria dos Refúgios. Rev Bras Geogr 50:1–28

Adámoli J (1982) O Pantanal e suas relações fitogeográficas com os cerrados. Discussão sobre o conceito do "Complexo do Pantanal." XXXII Congr Nac Botânica 109–119

Alfonsi RR, de Camargo MBP (1986) Condições climáticas para a região do Pantanal mato-grossense. In: SIMPÓSIO SOBRE RECURSOS NATURAIS E SÓCIO-ECONÔMICOS DO PANTANAL, I. Embrapa Pantanal, Brasília, pp 29–42

Alvarenga SM, Brasil AE, Del'Arco DM (1982) Geomorfologia. In: Brasil. Ministério das Minas e Energia (ed) Projeto RADAMBRASIL. Folha SE.20. Campo Grande (Levantamento de Recursos Naturais, 28). Ministério das Minas e Energia, Rio de Janeiro, pp 125–184

ANA (2003) Implementação de práticas de gerenciamento integrado de bacia hidrográfica para o Pantanal e Bacia do Alto Paraguai-Elaboração do Diagnóstico Analítico do Pantanal e Bacia do Alto Paraguai-DAB Relatório Final Diagnóstico analítico do Pantanal e Bacia do Alto Paraguai. Brasilia

Assine ML, Macedo HA, Stevaux JC, Bergier I, Padovani CR, Silva A (2015a) Avulsive Rivers in the Hydrology of the Pantanal Wetland. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal Wetland in South America. Springer Verlag, Berlin Heidelberg, pp 83–110

Assine ML, Merino ER, Do Nascimento Pupim F, De Azevedo MH, Dos Santos MGM (2015b) The Quaternary alluvial systems tract of the Pantanal Basin. Brazilian J Geol 45

Assine ML, Merino ER, Pupim FN, Warren LV, Guerreiro RL, McGlue MM (2015c) Geology and Geomorphology of the Pantanal Basin. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal Wetland in South America. Springer, Berlin Heidelberg, pp 23–50

Assis ELM, Labiak PH (2009a) Polypodiaceae da borda oeste do Pantanal sul-matogrossense, Brasil. Rev Bras Bot 32:233–247. https://doi.org/10.1590/s0100-84042009000200004

Assis ELM, Labiak PH (2009b) Lycophyta from the western Pantanal, Mato Grosso do Sul State, Brazil. Acta Bot Brasilica 23:703–712. https://doi.org/10.1590/s0102-33062009000300009

Bergier I, Assine ML (2016) Dynamics of the Pantanal Wetland in South America. Springer, Berlin Heidelberg

Brasil (1982a) Folha SE.21 Corumbá e parte da Folha SE.20. Geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Vol 27. Ministério de Minas e Energia, Departamento Nacional de Produção Mineral. Projeto RADAMBRASIL, Rio de Janeiro

Brasil (1982b) Folha SF 21 Campo Grande. Geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Vol. 28. Ministério de Minas e Energia, Departamento Nacional de Produção Mineral. Projeto RADAMBRASIL, Rio de Janeiro

Câmara PEAS, Vital DM (2004) Briófitas do município de Poconé, Pantanal de Mato Grosso, MT, Brasil. Acta Bot Brasilica 18:881–886. https://doi.org/10.1590/S0102-33062004000400019

Camara PEAS, Vital DM (2006) Briófitos de Cáceres, Pantanal de Matogrosso, Brasil, con nuevos registros para el estado y el País. Bryophyt Divers Evol 27:1–8. https://doi.org/10.11646/bde.27.1.2

Cunha NG, Pott A, Gonçalves AR (1985) Solos calcimórficos da sub-região do Abobral, Pantanal Mato-Grossense. Embrapa Corumbá, Circ Técnica 19:52

Del'Arco JO, Silva RH, Tarapanoff L, Freire FA, Pereira LGM, Souza SL, Luz LG, Palmeira RCB, Tassianri CCG (1982) Geologia. In: Brasil Ministério das Minas e Energia (ed) Projeto RADAMBRASIL Folha SE. 21 Corumbá e parte da Folha SE.20 (Levantamento de Recursos Naturais, 27). Ministério das Minas e Energia, Rio de Janeiro, pp 21–160

Fortes CF, Nunes-da-Cunha C, Rosa SA, Paixão E, Junk WJ, Schöngart J, Paixão E, Junk WJ (2018) Dendrochronological records of a pioneer tree species containing ENSO signal in the Pantanal, Brazil. Brazilian J Bot 41:167–174. https://doi.org/10.1007/s40415-017-0434-8

Gris D, Paixão E, Arruda RCO, Ishii IH, Marques MR, Damasceno-Junior GA (2020) Growth and establishment of monodominant stands affected by ENSO and flooding in the Pantanal. Sci Rep 10:1–13. https://doi.org/10.1038/s41598-020-60402-x

Guerra A, Roque F d O, Garcia LC, Ochao-Quintero JM, de Oliveira PTS, Guariento RD, IMD R (2020) Drivers and projections of vegetation loss in the Pantanal and surrounding ecosystems. Land Use Pol 91:104388. https://doi.org/10.1016/j.landusepol.2019.104388

Hamilton SK, Sippel SJ, Melack JM (1996) Inundation patterns in the Pantanal Wetland of South America determined from passive microwave remote sensing. Arch für Hydrobiol 137:1–23

Heckman CW (1998) The Pantanal of Poconé, biota and ecology in the northern section of the world's largest pristine wetland. Springer, The Netherlands

IMASUL (2021) Reserva Particular do Patrimônio Natural - RPPN. https://www.imasul.ms.gov.br/reserva-particular-do-patrimonio-natural-rppn/. Accessed 11 Apr 2021

Irion G, Buchas H, Junk JW, Nunes da Cunha C, Morais JO, Kasbohm J (2011) Aspects of geological and sedimentological evolution of the Pantanal plain. In: Junk JW, Da Silva CJ, Nunes da Cunha C, Wantzen KM (eds) The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia-Moscow, pp 47–70

Junk W, Nunes da Cunha C (2012) Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction? Wetl Ecol Manag 20:111–122. https://doi.org/10.1007/s11273-011-9246-y

Junk WJ, Bayley PB, Sparks RE (1989) The flood-pulse concept in river-floodplain systems. In: Dodge DP (ed) Proceedings of the International Large River Symposium. pp 110–127

Junk WJ, Silva CJ, Nunes da Cunha C, Wantzen KM (2011) The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia-Moscow

Marsh WM, Kaufman MM (2013) Physical Geography. Great Systems and Global Environments. Cambrige University Press, New York

Nunes da Cunha C, Junk WJ (2014) A Classificação dos Macrohabitats do Pantanal Matogrossense. In: Nunes da Cunha C, Piedade MT, Junk WJ (eds) Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats. EdUFMT, Cuiabá, pp 83–130

Oliveira JE (1996) Guató: Argonautas do Pantanal. EDIPUCRS, Porto Alegre

Padovani CR (2010) Dinâmica Espaço-Temporal Das Inundações Do Pantanal. Esc Super Agric "Luiz Queiroz" Cent Energ Nucl na Agric 174

Peixoto JL, de Arruda AA (2015) Interação regional dos grupos indígenas pré-coloniais que ocuparam a região das Grandes Lagoas do Pantanal e da Chiquitania. In: Alconini S, Betancourt CJ (eds) En el corazón de América del Sur 3 (Arqueología de las tierras bajas de Bolivia y zonas limítrofes). Imprenta 2E, Santa Cruz de la Sierra, pp 41–66

Schmitz PI, Rogge JH, Rosa AO, Beber MV, de Freitas EAV (2009) Aterros da Tradição Pantanal nas fazendas Sagrado Coração de Jesus e Bodoquena, Corumbá, MS. Pesqui Antropol 67:321–374

Schmitz PI, Rogge JH, Beber MV, Rosa AO (2014) Arqueologia do Pantanal do Mato Grosso do Sul - Projeto Corumbá. Tellus 0:11–26. https://doi.org/10.20435/TELLUS.V0I1.2

Silva JSV, Abdon MM (1998) Delimitação do Pantanal brasileiro e suas sub-regiões. Pesq. Agropec. Bras. 33:1703–1711

Soriano BMA (1997) Caracterização climática de Corumbá. Embrapa-CPAP (Bol. de Pesquisa, 11), Corumbá. 25p

Thielen D, Schuchmann KL, Ramoni-Perazzi P, Marquez M, Rojas W, Quintero JI, Marques MI (2020) Quo vadis Pantanal? Expected precipitation extremes and drought dynamics from changing sea surface temperature. PLoS One 15:1–25. https://doi.org/10.1371/journal.pone.0227437

Tricart J (1982) El Pantanal: un ejemplo del impacto geomorfologico sobre el ambiente. Inf Geogr 29:81–97

Chapter 2
Classification and Mapping of the Vegetation of the Brazilian Pantanal

João dos Santos Vila da Silva, Arnildo Pott, and Jô Vinícius Barrozo Chaves

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 km^2) and the Pantanal floodplain (138,183 km^2) considering the aspects of floods, relief, soils, and vegetation (Fig. 2.1). However, IBGE (2004) delimited the Pantanal as a biome (150,335 km^2), a divergence arisen from different conceptual criteria, field observations, and the adopted scale. The term "biome" is considered by the governmental

---

J. dos Santos Vila da Silva (✉)
Embrapa Agricultura Digital, Pesquisa & Desenvolvimento, Campinas, SP, Brazil
e-mail: joao.vila@embrapa.br

A. Pott
Laboratório de Ecologia vegetal, Instituto de Biociências, Universidade Federal de mato Grosso do Sul, Campo Grande, MS, Brazil

J. V. B. Chaves
Pós-graduação em Sistema de Infraestrutura Urbana, Pontifícia Univesidade Católica de Campinas Rua João Bissoto Filho, Valinhos, SP, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_2

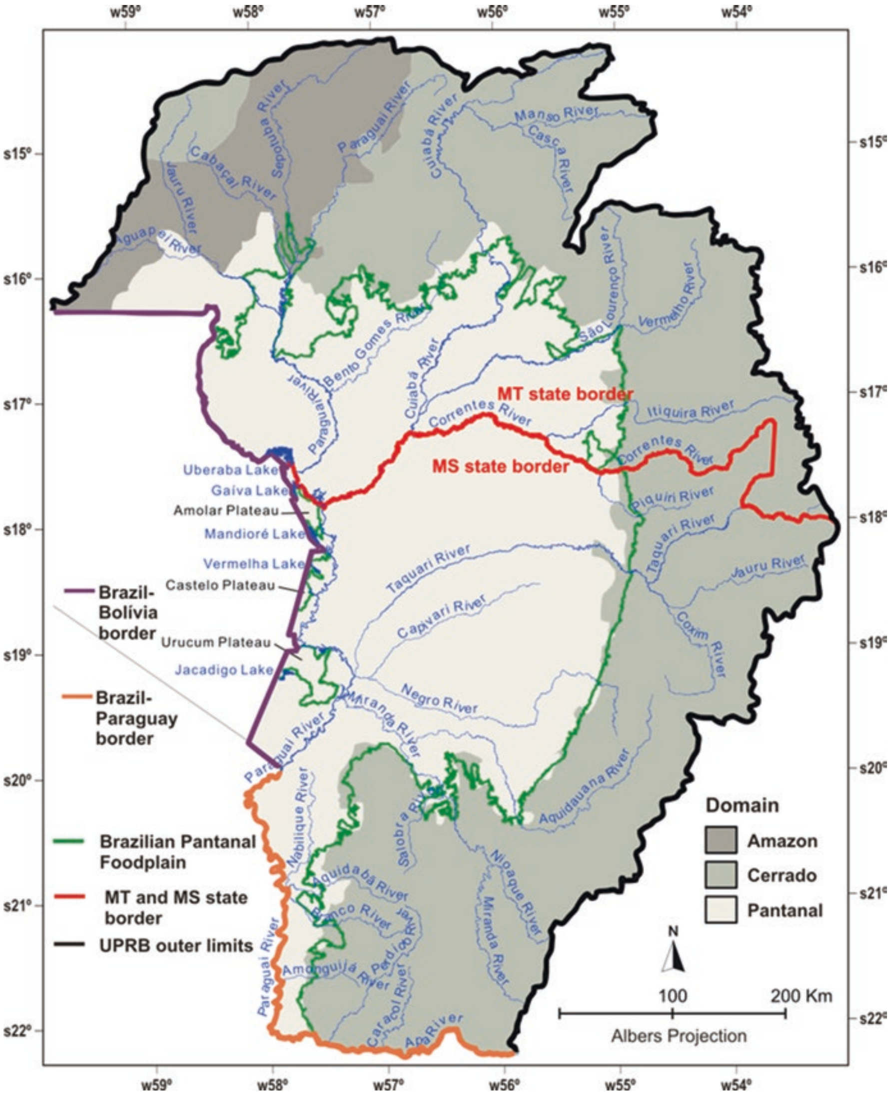


Fig. 2.1 Delimitation of the Pantanal floodplain and its phytogeographic domains (plain: in light gray) and its upper hydrographic basin or UPRB (Upper Paraguay River Basin) (dark gray and light brown) in Brazilian territory. MT = state of Mato Grosso; MS = state of Mato Grosso do Sul. Source: Silva and Abdon (1998), Silva et al. (2011a, b, c), and Pott and Silva (2015)

organs as the phytogeographic domain, despite the concepts not being synonymous (Coutinho 2016).

The first region-wide survey of the Pantanal landscape was made in the 1970s and 1980s using aerial photographs (1:60,000) obtained in 1964–1966 by the US Air Force, useful to distinguish woody vegetation from savanna, but difficult to interpret further. Such information can be found in the topographic maps of Brazil. Then, EDIBAP (Brasil 1979), a set of integrated studies on the UPRB, made a broad preliminary study on natural resources, including brief information on the vegetation. Adámoli (1982) distinguished four main phytogeographic influences in the Pantanal. After the 1980s, the classification and mapping of Pantanal vegetation became better known, generated mainly by the regional survey for environmental planning based on geotechnology products and field survey (Silva and Carlini 2015). Those authors highlight three great such governmental initiatives in the 1980s and the 1990s. The RadamBrasil program (Amaral et al. 1982; Furtado et al. 1982; Loureiro et al. 1982) produced the first regional mapping for the vegetation of the region in the scale 1:250,000 with the use of images of airborne side-looking radar obtained in 1976. Mato Grosso do Sul (1989) elaborated, together with others, maps of vegetation cover and land use at the 1:250,000 scale, including the Southern Pantanal in that state, using analog images from the Landsat 5 obtained in 1984–1985. Also utilizing analogical images from Landsat 5 of the year 1994, Pott et al. (1997) and Silva et al. (1997) mapped the vegetation of the UPRB, also at the 1:250,000 scale, under the aegis of the project known as PCBAP – Conservation Plan for the Upper Paraguay River Basin. That project adopted the Brazilian System of Vegetation Classification, described in the Technical Handbook of the Brazilian Vegetation Adapted to the Universal System (IBGE 1992). An aerial survey using small aircraft estimated the frequency of vegetation classes applying a grid over the entire Pantanal (Silva et al. 2000).

At the beginning of the twenty-first century, two important mapping initiatives occurred in the region. The first, reported by Abdon and Silva (2006), Abdon et al. (2007), and Silva et al. (2007a, b), refers to the mapping of the Pantanal based on Landsat digital orbital satellite images of the year 2002, at the scale 1:250,000, induced by the Ministry of Environment (MMA) by means of the project "Mapping of the remnants of vegetation in the Brazilian biomes," as part of the actions of PROBIO – Project of Conservation and Sustainable Use of the Brazilian Biological Diversity. The second initiative was the mapping of the vegetation cover and land use of the State of Mato Grosso do Sul, at the scale 1:100,000, for which details can be found in Silva et al. (2011b, c) and Silva and Carlini (2015). That mapping, within the scope of the Project GeoMS (Georeferenced Information System as support to decision making – study case: State of Mato Grosso do Sul), utilized digital images of the CBERS satellite from the year 2007 and aimed to start monitoring deforestation and to implement the environmental regularization of the rural properties of the state of Mato Grosso do Sul.

Those studies constitute the basis of knowledge about the spatial patterns of the vegetation in the region and replaced the older concept of the "Pantanal Complex" which had long appeared on Brazilian maps. Nevertheless, Coutinho (2016) considered the term "complex" to be valid since the Pantanal is not a true biome. Nowadays it is recognized that the Upper Paraguay River Basin (UPRB) is composed of the intersection of four large phytoecological regions: seasonal deciduous forest, seasonal semideciduous forest, savanna (*Cerrado*), and Stepic savanna (Chaco). According to Silva et al. (2011a), the UPRB also contains elements of Ombrophylous

Forest, typical of the Amazon. In addition, there are the floristic contacts and the pioneer (early successional) formations.

Based on both cultural and environmental aspects, the Pantanal has been variably portrayed as distinct subregions (Fig. 2.2), sometimes called *pantanals*. The subregions traditionally known as Cáceres, Poconé, Barão de Melgaço, and part of the Paraguai subregion are located in the State of Mato Grosso and occupy 48,865 km^2

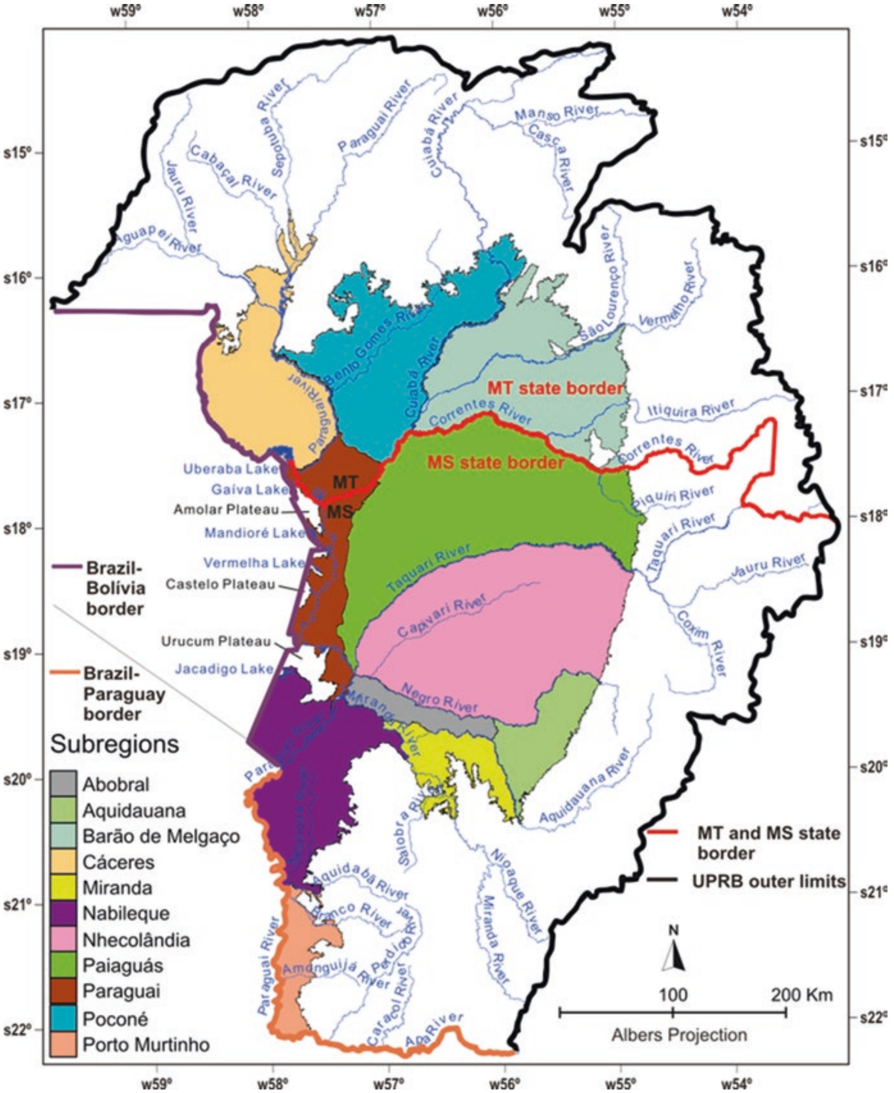


Fig. 2.2 Subregions of the Brazilian Pantanal wetland and main rivers. Areas in white: Upper Paraguay River Basin. MT = State of Mato Grosso; MS = State of Mato Grosso do Sul. Source: based on Silva and Abdon (1998) and Silva et al. (2011a, b, c)

(35.36%) of the floodplain; the other subregions are in the State of Mato Grosso do Sul and occupy 89,318 km^2 (64.64%). Figure 2.2 will be useful to interpret the distribution of the main vegetation types occurring in the Pantanal, as well as to associate them with the various subregions and also with the upland areas adjacent to the western border. Other subdivisions have been proposed for various purposes. Brasil (1979) and Adámoli (1982) accepted the traditional subregions, except Porto Murtinho. Hamilton et al. (1996) took into account the geomorphology and flooding hydrology to propose a more hydrogeomorphological delineation of subregions. Mioto et al. (2012) divided the Pantanal into 18 subregions, employing the Normalized Difference Vegetation Index derived from satellite imagery as a photo-interpretation tool: Alto Barão do Melgaço, Apa-Amonguijá Aquidabã, Aquidauana, Baixo Barão do Melgaço, Cabeceira do Pantanal, Cáceres, Canoeira, Entorno Pantaneiro, Miranda-Abobral, Nabileque, Negro, Nhecolândia, Paiaguás, Paraguai, Poconé, Taboco, Taquari, and Tuiuiú. Assine et al. (2015) considered hydrosedimentology as a criterion.

Vegetation mapping in the Pantanal is not an easy task because of mixtures of types, mosaic patterns, and dynamics. The distribution of the vegetation along flood gradients in the Pantanal has been the subject of several studies (e.g., Nunes da Cunha and Junk 2001; Pott and Silva 2015). The components of the vegetation mosaic often have abrupt limits, sometimes coinciding with changes in the depth and duration of flooding and with the type of sediment. An interesting case is the recently investigated lineament coinciding with a geological fault in the northern part of the Pantanal (Almeida et al. 2019), between the subregions Paiaguás (Mato Grosso do Sul) and Poconé (Mato Grosso).

2.2 Main Vegetation Types

Four phytoecological regions (Adámoli 1982; Mato Grosso do Sul 1989) or phytogeographic domains occur in the Pantanal: savanna (*Cerrado*), Stepic savanna (Chaco), seasonal deciduous forest, and seasonal semideciduous forest, plus areas of pioneer formations, floristic contacts, vegetational refuges, and anthropic areas. Considering the occurrence of various formations and subformations, as well as mixtures, 56 classes have been distinguished in the region. The Pantanal vegetation types were shown in single maps in earlier publications (e.g., Pott et al. 2011; Pott and Silva 2015), but, for didactic reasons, in this chapter, we present the vegetation in separate maps for each type. We aggregated the vegetation into seven main sets: (1) forest formations, (2) Arboreal *Cerrado* (woody savanna and park savanna), (3) Herbaceous *Cerrado* (grassy-woody savanna), (4) Chaco (Stepic woody savanna and Stepic grassy-woody savanna), (5) monodominant formations (pioneer formations and Stepic park savanna), (6) vegetational mixtures, floristic contacts (ecotones and enclaves), and vegetational refuges, and (7) anthropic areas. A list of the mentioned species is given below (Table 2.1), with their authors and the main vegetation types.

Table 2.1 List of cited plant species with family and scientific names with author(s) and main vegetation types

Family	Genus and species	Vegetation type						
		Ce	S	R	Ch	G	M	O
Alismataceae	*Echinodorus* spp.					X		
Anacardiaceae	*Anacardium humile* A.St.-Hil.	X						
	Astronium fraxinifolium Schott	X	X					
	Astronium urundeuva (M. Allemão) Engl.	X	X					
	Schinopsis brasilensis Engl.		X					
	S. balansae Engl.				X			
	Spondias mombin L.		X					
	Tapirira guianensis Aubl.			X				
Annonaceae	*Annona* spp.	X						
	Duguetia furfuracea (A.St.-Hil.) Saff.	X						
	Unonopsis guatterioides (A.DC.) R.E.Fr.			X				
	Xylopia aromatica (lam.) Mart.	X						
	X. emarginata Mart.			X				
Apocynaceae	*Aspidosperma australe* Müll.Arg.							
	A. cylindrocarpon Müll.Arg.		X					
	A. pyrifolium Mart.		X					
	A. quebracho-blanco Schtdl.				X			
	A. subincanum Müll.Arg.							
	Hancornia speciosa Gomes	X						
Arecaceae	*Acrocomia totai* Mart.			X				
	Attalea phalerata Mart. *ex* Spreng.		X	X				
	A. speciosa Mart. *ex* Spreng.						X	
	Copernicia alba Morong				X		X	
	Mauritia flexuosa L.f.			X			X	
	Syagrus oleracea (Mart.) Becc.		X					
Asteraceae	*Aspilia grazielae* U.Santos							X
	A. latissima Malme			X		X		
Bignoniaceae	*Handroanthus heptaphyllus* Mattos			X			X	
	H. impetiginosus Mattos		X					
	H. ochraceous (Cham.) Mattos	X	X					
	Tabebuia aurea (Silva Manso) Benth. & Hook.f. *ex* S.Moore	X				X	X	
	T. insignis (Miq.) Sandwith			X				X
	T. nodosa (Griseb.) Griseb.				X			
	T. roseoalba (Ridl.) Sandwith	X	X					
Boraginaceae	*Cordia americana* (L.) Gottschling & J.S.Mill.		X					
	C. glabrata DC.		X					
	C. sellowiana Cham.		X					
	C. trichotoma (Vell.) Arráb. *ex* Steud.		X					
Bromeliaceae	*Deuterochonia meziana* Kuntze *ex* Mez							X
	Dyckia spp.							X

(continued)

Table 2.1 (continued)

Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand			X				
	Cereus spp.				X			
	Cleistocactus spp.				X			
	Echinopsis rhodotricha K.Schum.				X			
	Gymnocalycium anisitsii (K.Schum.) Britton & Rose				X			
	Frailea spp.				X			
	Harrisia spp.				X			
	Opuntia spp.				X			
	Stetsonia coryne (Salm-Dyck) Britton & Rose				X			
Calophyllaceae	*Calophyllum brasiliense* Cambess.		X	X				
Cannabaceae	*Celtis* spp.		X					
	Trema micrantha (L.) Blume		X					
Capparaceae	*Anisocapparis speciosa* (Griseb.) Cornejo & Iltis		X					
	Crateva tapia L.			X				
Caricaceae	*Jacaratia spinosa* (Aubl.) A.DC.		X					
Caryocaraceae	*Caryocar brasiliense* Cambess.	X						
Celastraceae	*Salacia elliptica* (Mart.) Peyr.			X				
Chrysobalanaceae	*Couepia uiti* (Mart. & Zucc.) Benth.			X				
	Leptobalanus parvifolius (Hub). Sothers & Prance.			X			X	
	Kielmeyera spp.	X						
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi			X				
Combretaceae	*Combretum* spp.						X	
	Terminalia argentea Mart.	X						
	Terminalia corrugata (Ducke) Gere & Boatwr.	X						
Connaraceae	*Rourea induta* planch.	X						
Convolvulaceae	*Ipomoea carnea* Jacq.						X	
Cyperaceae	*Cyperus giganteus* L.						X	
Dilleniaceae	*Curatella americana* L.	X					X	
	Davilla elliptica A.St.-Hil.	X						
Erythroxylaceae	*Erythroxylum anguifugum* Mart.			X				
	E. suberosum A.St.-Hil.	X						
Euphorbiaceae	*Alchornea castaneifolia* (Willd.) A.Juss.			X				
	Croton urucurana Baill.			X				
	Mabea paniculata Spruce *ex* Benth.			X				
	Sapium obovatum Klotzsch *ex* Müll.Arg.			X				
Fabaceae	*Acosmium cardenasii* H.S.Irwin & Arroyo		X					
	Albizia inundata (Mart.) Barneby & J.W.Grimes			X				

(continued)

Table 2.1 (continued)

	A. niopoides (Spreng.) Burk.			X				
	Amburana cearensis (Allemão) A.C.Sm.		X					
	Anadenanthera colubrina (Vell.) Brenan		X					
	A. falcata (L.) Speg.	X						
	Andira cujabensis Benth.	X						
	A. humilis Benth.	X						
	A. inermis Kunth			X				
	A. vermifuga (Mart.) Benth.	X						
	Bauhinia bauhinioides McBr.						X	
	Bowdichia virgilioides Kunth	X						
	Calliandra parviflora Benth.	X						
	Cassia grandis L.			X				
	Copaifera langsdorffii Desf.	X	X					
	C. martii Hayne	X						
	Dimorphandra mollis Benth.	X						
	Dipteryx alata Vogel	X						
	Diptychandra aurantiaca Tul.	X						
	Enterolobium contortisiliquum (Vell.) Morong	X	X					
	Erythrina fusca Lourt.			X			X	
	Holocalyx glaziovii Taub. *ex* Glaz.		X					
	Hymenaea courbaril L.		X					
	H. martiana Hayne		X					
	Hymenaea stigonocarpa Mart. *ex* Hayne	X						
	Inga vera Willd.			X				
	Leptolobium elegans Vogel	X						
	Libidibia paraguariensis (D.Parodi) G.P.Lewis				X			
	Machaerium aculeatum Raddi	X	X					
	Microlobius foetidus var. *paraguensis* (Benth.) M.Sousa & G.Andrade				X			
	Mimosa hexandra Michele				X			
	Ormosia arborea (Vell.) Harms			X				
	Parapiptadenia rigida (Benth.) Brenan		X					
	Parkinsonia praecox (Ruiz & Pav.) Hawkins				X			
	Peltophorum dubium Tul.		X					
	Plathymenia reticulata Benth.	X						
	Prosopis rubriflora Hassl.				X			
	P. ruscifolia Griseb.				X			
	Pterocarpus santalinoides L'Hér *ex* Benth.			X				
	Pterodon emarginatus Vogel	X						
	Pterogyne nitens Tul.		X					
	Samanea tubulosa (Benth.) Barneby & J.W. Grimes		X					

(continued)

Table 2.1 (continued)

	Senegalia tenuifolia (L.) Britton & Rose		X					
	Stryphnodendron rotundifolium Mart.	X						
	Swartzia jorori Harms							
	Tachigali aurea Tul.	X						
	Vachellia farnesiana (L.) Wright & Arn.		X		X			
	Zygia spp.			X				
Lamiaceae	*Vitex cymosa* Bert.			X				
Lauraceae	*Nectandra amazonum* Nees			X				
	Ocotea diospyrifolia (Meisn.) Mez			X				
Lecythidaceae	*Cariniana estrellensis* (Raddi) Kuntze		X					
Lythraceae	*Lafoensia pacari* A.St.-Hil.	X						
Magnoliaceae	*Magnolia ovata* (A.St.-Hil.) Spreng.			X				
Malpighiaceae	*Byrsonima orbignyana* A.Juss.						X	
Malvaceae	*Byttneria filipes* Mart. *ex* K.Schum.						X	
	Eriotheca gracilipes (K.Schum) A.Robyns	X						
	Luehea paniculata Mart.	X						
	Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	X						
	Pseudobombax marginatum (A.St.-Hil.) A.Robyns	X	X					
Marantaceae	*Thalia geniculata* L.						X	
Melastomataceae	*Mouriri elliptica* Mart.	X						
	M. guianensis Aubl.			X				
Meliaceae	*Cabralea canjerana* (Vell.) Mart.		X					
	Cedrela fissilis Vell.		X					
	Guarea guidonea (L.) Sleum.			X				
	Trichilia elegans A.Juss.		X					
Moraceae	*Maclura tinctoria* (L.) Don *ex* Steud.		X					
Myrtaceae	*Campomanesia xanthocarpa* (Mart.) O.Berg		X					
	Eugenia spp.							
Nyctaginaceae	*Pisonia zapallo* Griseb.		X					
Oleaceae	*Priogymnanthus hasslerianus* (Chodat) P.S.Green		X					
Onagraceae	*Ludwigia nervosa* (Poir.) H.Hara						X	
Phyllanthaceae	*Hieronyma alchorneoides* Allemão			X				
	Phyllanthus chacoensis Morong				X			
Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms		X	X				
Poaceae	*Andropogon bicornis* L.					X		
	A. hypogynus Hack.					X		
	Axonopus purspusii (Mez) Chase					X		
	Elionurus muticus (Spreng.) Kuntze	X				X		
	Guadua paniculata Munro	X						
	Leersia hexandra Sw.					X		
	Mesosetum chaseae Luces					X		
	Oryza spp.					X		

(continued)

Table 2.1 (continued)

	Paspalum carinatum Humb. & Bonpl. *ex* Flüggé					X		
	P. fasciculatum Willd. *ex* Flüggé					X		
	P. lineare Trin.					X		
	P. virgatum L.					X		
	P. wrightii Hitchc. & Chase					X		
	Steinchisma laxum (Sw.) Zuloaga					X		
Polygonaceae	*Coccoloba cuyabensis* Wedd.			X				
	Polygonum spp.					X		
	Ruprechtia laxiflora Meisn.		X					
	R. triflora Griseb.		X					
	Triplaris americana L.			X				
Pontederiaceae	*Eichhornia azurea* (Sw.) Kunth					X		
	E. crassipes (Mart.) Solms					X		
	Pontederia sp..					X		
Rhamnaceae	*Rhamnidium elaeocarpum* Reiss.	X	X					
	Sarcomphalus mistol (Griseb.) Hauenschild				X			
Rubiaceae	*Alibertia edulis* (Rich.) A.Rich.	X						
	Calycophyllum multiflorum Griseb.		X					
	Cordiera sessilis (Vell.) K.Schum.	X						
	Genipa americana L.			X				
	Simira rubescens (Benth.) Bremek. *ex* Steyrm.			X				
Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl.		X					
	Zanthoxylum caribaeum Lam.		X					
	Z. fagara. (L.) Sarg.		X		X			
	Z. rigidum Lam.	X						
Salicaceae	*Banara arguta* Briq.			X				
	Casearia spp.							
	Salix humboldtiana Willd.			X	X			
Sapindaceae	*Diplokeleba floribunda* N.E.Br.				X			
	Magonia pubescens A.St.-Hil.	X						
	Melicoccus lepidopetalus Radlk.				X			
	Sapindus saponaria L.		X					
	Talisia esculenta (A.St.-Hil.) Radlk.		X					
Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichl. *ex* Miq.) Engl.		X					
	C. marginatum (Hook. & Arn.) Radlk.	X	X	X				
	Pouteria glomerata (Miq.) Radlk.			X				
	Sideroxylon obtusifolium (Roem. & Schult.) Penn.		X					
Selaginellaceae	*Selaginella sellowii* Hieron.				X			X
Simaroubaceae	*Castela coccinea* Griseb.				X			
	Simarouba versicolor A.St.-Hil.	X						
Solanaceae	*Solanum lycocarpum* A.St.-Hil.	X						

(continued)

Table 2.1 (continued)

Typhaceae	*Typha domingensis* Pers.					X	X	
Ulmaceae	*Phyllostylon rhamnoides* (J.Poiss.) Taub.		X					
Urticaceae	*Cecropia pachystachya* Trécul			X				
Velloziaceae	*Vellozia variabilis* Vell.							X
Verbenaceae	*Cytharexylum myrianthum* Cham.			X				
Vochysiaceae	*Callisthene fasciculata* Mart.	X						
	Qualea spp.	X						
	Vochysia cinnamomea Pohl	X						
	V. divergens Pohl			X			X	
	V. haenkeana Mart.	X						
	V. rufa Mart.	X						

Ce Cerrado, S seasonal forest, Ch Chaco, V ciliary vegetation, G grassland and aquatic plants, M modominant formation, O other than the previous types) of the Pantanal

2.2.1 Forest Formations

As forests, we grouped the seasonal semideciduous forest (Alluvial and Submontane), the seasonal deciduous forest (alluvial, lowlands, and submontane), and the forested savanna (*Cerradão*) with its mixed classes. Figure 2.3 shows that these formations have a wide distribution in the Pantanal, occurring in all subregions.

The tropical **seasonal forests** occur in areas where the annual rainfall is ≤1600 mm, and there is a dry season of 5–6 months. Within the Pantanal floodplains, where the rainfall is lower than that on the upload plateaus, such formations occur on soil with better fertility but still experiencing seasonal water limitation, generally within the savannic matrix (Prado 2000). According to the occurrence of seasonal climate that determines semideciduidad of the foliage of the forest cover, they are classified in seasonal semideciduous forests, which can drop 20–50% of the leaves in the dry period, and seasonal deciduous forests, which lose ≥50% (IBGE 1992). In terms of physiognomy and floristic composition, there is a *continuum* between the semideciduous formations and the areas of forested savanna (*Cerradão*), which can be considered as an intermediate stage between forest and savanna (Silva et al. 2011b).

The **alluvial forest or ciliary vegetation** is located on the margins of watercourses and is tolerant of seasonal soil saturation or flooding, typically growing on alluvial loamy, clayey, or sandy-clayey soils. Its structure is different from a alluvial forest or gallery forest typical since, besides the arboreal vegetation named forest, 10–17 m tall, this vegetation can present different physiognomies such as wet grasslands, shrubby, and floating vegetation, making the term "ciliary vegetation" more appropriate and comprehensive, instead of alluvial seasonal semideciduous forest, as it encompasses other forms than just forest. The Brazilian legislation contains the term "ciliary," widely used in Brazil. Nunes da Cunha and Junk (2014) called it polyspecific forest. There is a succession of colonization of sediments, from herbaceous plants, followed by pioneer woody species and last the actual forest, which can be seen in a chronosequence of banks of cut-off oxbow lakes along the winding rivers (Pott and Ratter 2011; Pott et al. 2011). On slightly higher ground grow forest

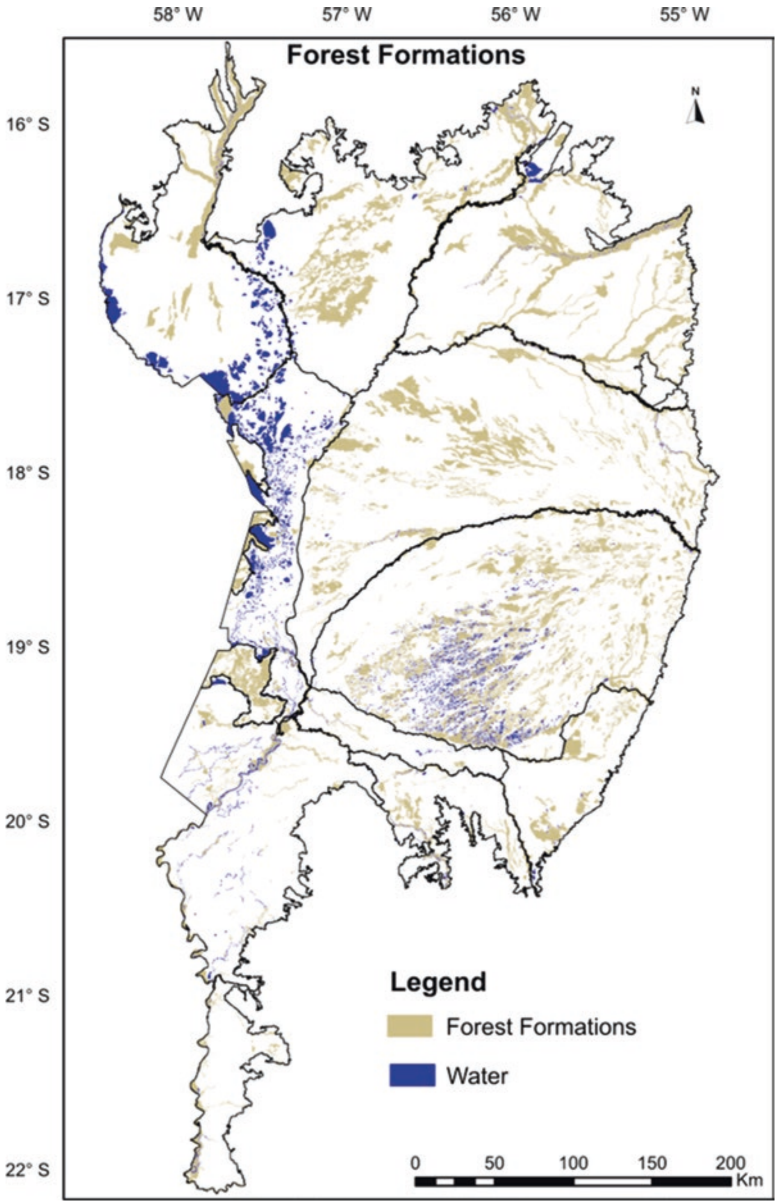


Fig. 2.3 Distribution of the forest formations [seasonal forests (seasonal semideciduous and seasonal deciduous) + forested savanna (*Cerradão*)] in the Brazilian Pantanal

islets (*capões*) with riverine trees such as *Calophyllum brasiliense*. All these physiognomies were mapped within a single class.

Along the rivers and old riverbeds (*corixos*) of the Pantanal plain, the most frequent trees are *Albizia inundata*, *A. niopoides*, *Alchornea castaneifolia*, *Andira* *inermis*, *Banara arguta*, *Calophyllum brasiliense*, *Cassia grandis*, *Cecropia pachystachya*, *Coccoloba cuyabensis*, *Couepia uiti*, *Crateva tapia*, *Erythrina fusca*, *Erythroxylum anguifugum*, *Eugenia* spp., *Genipa americana*, *Handroanthus heptaphyllus*, *Inga vera*, *Mabea paniculata*, *Mouriri guianensis*, *Ocotea diospyrifolia*, *Nectandra amazonum*, *Pouteria glomerata*, *Pterocarpus santalinoides*, *Garcinia gardneriana*, *Salacia elliptica*, *Sapium obovatum*, *Simira rubescens*, *Triplaris americana*, *Unonopsis guatterioides*, *Vitex cymosa*, *Vochysia divergens*, and *Zygia* spp.

The **submontane seasonal semideciduous forest** is characterized by 20–50% leaf loss in winter. It presents trees between 15 and 20 m or more in height, generally on clayey-sandy soils, at altitudes between 130 and 600 m. They are the forests related to the Atlantic Forest, whose remnants occur in the Urucum range (near the town of Corumbá), associated with deposits of iron and manganese ores. They are the taller forests near the Pantanal plain. Typical trees are *Aspidosperma australe*, *A. cylindrocarpon*, *Balfourodendron riedelianum*, *Cabralea canjerana*, *Campomanesia xanthocarpa*, *Cariniana estrellensis*, *Casearia* spp., *Cedrela fissilis*, *Chrysophyllum gonocarpum*, *Cordia americana*, *C. sellowiana*, *C. trichotoma*, *Enterolobium contortisiliquum*, *Handroanthus impetiginosus*, *H. ochraceous*, *Holocalyx glaziovii*, *Jacaratia spinosa*, *Nectandra* spp., *Parapiptadenia rigida*, *Peltophorum dubium*, *Protium heptaphyllum*, *Ruprechtia triflora*, and *Spondias mombin*.

The **submontane seasonal deciduous forest** predominates on limestone hills in the vicinity of Corumbá and on the Amolar and Castelo. Generally, they are located at 100–600 m altitude. This physiognomy is regionally known as dry forest or calcareous forest, for occurring on terrains composed of carbonate rocks (calcareous soils). Its main characteristic is the leaf loss in the winter of over 50% of the whole canopy. It presents trees between 15 and 20 m in eight or more. Two trees to recognize the dry forest on slopes near the plain are *Ceiba pubiflora* and *Cenostigma pluviosa*, besides many cacti, e.g., *Cereus bicolor*. This same *C. bicolor* does not indicate dry forest within the Pantanal, as in dry years it can grow even in grasslands. According to Damasceno Junior et al. (2009), on the plain, there are a few areas of deciduous forests, such as Mata do Cedro (*mata* means forest), Mata do Fuzil, and Mata do Bebe, the largest one (protected in the private preserve SESC). The typical trees are: *Acosmium cardenasii*, *Amburana cearensis*, *Anisocapparis speciosa*, *Aspidosperma australe*, *A. pyrifolium, A. subincanum*, *Astronium brasiliense*, *Calycophyllum multiflorum*, *Combretum leprosum*, *Dilodendron bipinnatum*, *Diplokeleba floribunda*, *Gallesia integrifolia*, *Machaerium aculeatum*, *Maclura tinctoria*, *Astronium urundeuva*, *Phyllostylon rhamnoides*, *Pisonia zapallo*, *Priogymnanthus hasslerianus*, *Pterogyne nitens*, *Rhamnidium elaeocarpum*, *Ruprechtia laxiflora*, *Spondias mombin*, *Samanea tubulosa*, *Sapindus saponaria*, *Senegalia tenuifolia*, *Sideroxylon obtusifolium*, *Swartzia jorori*, *Talisia esculenta*, and *Zanthoxylum caribaeum* (Damasceno Junior et al. 2009; Pott and Ratter 2011). Most of these trees are widely distributed over the Pleistocene arch of dry forests in South America (Prado 2000). Another type peculiar to the Pantanal are *capões* or forest islets with deciduous forest in the middle and semideciduous on the outer belt, distinguishable on satellite images, but too small to be mapped at the present scale.

The structure of the **forested savanna** resembles a forest, as the tree canopies are close together, with shrubby and herbaceous strata and lianas, but the species belong to the flora of *cerrados*. The most frequent trees are *Anadenanthera falcata*, *Andira cujabensis*, *A. vermifuga*, *Caryocar brasiliense*, *Cordiera sessilis*, *Couepia grandiflora*, *Dipteryx alata*, *Diptychandra aurantiaca*, *Eriotheca gracilipes*, *Hymenaea stigonocarpa*, *Leptolobium elegans*, *Luehea paniculata*, *Plathymenia reticulata*, *Pseudobombax longiflorum*, *Qualea* spp., *Simarouba versicolor*, *Tabebuia aurea*, *Terminalia argentea* and *Vochysia cinnamomea*. These trees include some of those present in ≥50% of Cerrado areas in Brazil (Ratter et al. 2003). Generally, the height of the trees varies between 8 and 15 m. It occurs mostly on poor sandy soils, known as dystrophic *cerradão*, with some species losing the leaves, mainly in winter. Yet, on more fertile and/or rocky soils, the *cerradão* can be deciduous. On calcium-rich soils, of medium fertility, occurs the mesotrophic *cerradão*, very frequent in Mato Grosso do Sul (Ratter et al. 2003). In the Pantanal, this *cerradão* is common on sandy ridges (*cordilheiras*) 1–3 m above the grassland, with trees such as *Agonandra brasiliensis*, *Anadenanthera colubrina*, *Astronium fraxinifolium*, *Attalea phalerata*, *Callisthene fasciculata*, *Cordia glabrata*, *Magonia pubescens* and *Pseudobombax marginatum*. Because of the occurrence of *Astronium urundeuva* and *Tabebuia roseoalba*, some *cerradões* are actually ecotones and can be confounded with seasonal semideciduous forest, with some species of trees reaching heights up to 20 m of (e.g., *Pterodon emarginatus*). The bamboo *Guadua paniculata* is frequent.

2.2.2 Arboreal Cerrado

The Arboreal *Cerrado* encompasses the woody savanna with and without gallery forest and the park savanna without gallery forest (Fig. 2.4). In the wood savanna are included physiognomies regionally known as *cerrado* grassland, *cerrado* and open *cerrado*, while the park savanna has stands of *Byrsonima cydoniifolia* and *Curatella americana*. The Arboreal *Cerrado* occurs practically throughout the Pantanal, except in the Nabileque and Porto Murtinho subregions.

The **woody savanna** is the *cerrado* stricto sensu, with various regional names (open *cerrado*, closed *cerrado*, dense *cerrado*), depending on the density or size of the woody plants. The tree stratum is discontinuous; i.e., the trees are scattered, tortuous, 7–12 m tall, with shrubs, subshrubs, and herbs (grasses and others). It occurs on sandy or rocky soils and has wide occurrence, being common on the Pantanal plain in areas less subjected to flooding. Among the most common woody species occur *Alibertia edulis*, *Anacardium humile*, *Annona* spp., *Bowdichia virgilioides*, *Terminalia corrugata*, *Byrsonima* spp., *Campomanesia* spp., *Cordiera sessilis*, *Curatella americana*, *Davilla elliptica*, *Dimorphandra mollis*, *Duguetia furfuracea*, *Erythroxylum suberosum*, *Hancornia speciosa*, *Kielmeyera* spp., *Lafoensia pacari*, *Magonia pubescens*, *Mouriri elliptica*, *Pseudobombax*

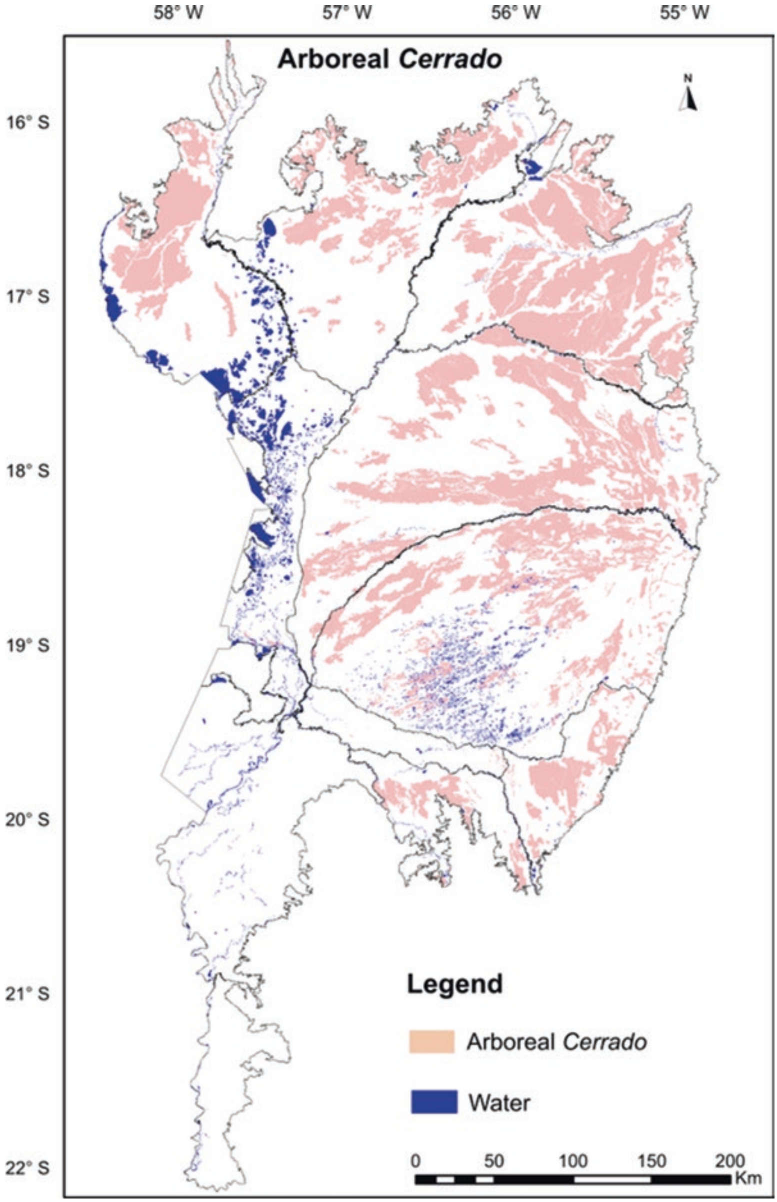


Fig. 2.4 Distribution of the Arboreal *Cerrado* (woody savanna + park savanna) in the Brazilian Pantanal

gracilipes, *Rourea induta*, *Simarouba versicolor*, *Solanum lycocarpum*, *Stryphnodendron* spp., *Vochysia rufa*, and *Xylopia aromatica*.

Park savanna is a *cerrado* physiognomy of grassland with interspersed trees varying between 3 and 8 m tall. It is widely distributed throughout the Pantanal plain, such as the savannas dominated by *Curatella americana* or *Byrsonima cydoniifolia*, on seasonally flooded sandy soils. Sometimes the trees grow on small elevations (earthmounds), named *murundus*, although this vegetation is different from the *campos de murundu* occurring in the region of Araguaia and Xingu. Besides these two main species, also occur *Terminalia corrugata*, *Ocotea diospyrifolia*, *Simarouba versicolor*, *Sorocea saxicola*, *Swartzia jorori*, *Tachigali aurea*, *Zanthoxylum rigidum*, and *Xylopia aromatica*. It is a physiognomy difficult to to be mapped since it can be confounded with grassland. The *Tabebuia aurea* savanna used to be classified as such, but owing to the soil with calcium carbonate concretions and associated species from the Chaco it was reframed as Chaco (stepic savanna) (Silva et al. 2011b). In areas covered with *cerrados* on the Pantanal edge, park savanna also occurs, mainly on rocky soils, such as on the Serra do Amolar, between grassland and *cerradão*, with trees such as *Copaifera langsdorffii*, *Hancornia speciosa*, and *Hymenaea stigonocarpa*.

2.2.3 *Herbaceous* Cerrado

The Herbaceous *Cerrado* refers to grassy-woody savanna with and without gallery forest (Fig. 2.5) and encompasses the phytophysiognomies regionally known as grassland, open grassland, shrubby grassland, *Elionurus* grassland, *Campina*, and flooded grassland. It has a wide distribution in the Pantanal, in the *Cerrado* domain, widespread in the Paiaguás and Nhecolândia subregions. It does not occur in the Nabileque and Porto Murtinho subregions.

The **grassy-woody savanna** is a form of grassland with or without sparse or dense shrubs and subshrubs. In general, the higher the flood level, the fewer the shrubs. The *Elionurus* grassland is an almost flood-free zone with dominance of the tussock grass *Elionurus muticus*, typical of the Nhecolândia subregion and other sandy areas of the Pantanal, whereas in the eastern part, without ponds, there are grasslands with other tall and tough grasses, such as *Paspalum carinatum*/*P. lineare*, with intermingled earthmounds supporting short trees such as *Curatella americana*, *Mouriri elliptica*, and *Stryphnodendron rotundifolium*. Other frequently dominant species are *Axonopus purpusii*, *Mesosetum chaseae*, and *Andropogon bicornis*. This class encompasses open grassland, shrubby grassland, *Elionurus* grassland, and flooded grassland.

2.2.4 *Chaco*

When the field team of vegetation survey of the Radambrasil project first saw the spiny woodlands in Porto Murtinho, the famous botanist Murça Pires was called to help and he started to collect to identify this very different flora (Furtado et al. 1982). Since then, a great volume of work has been done there (e.g., Sartori et al.

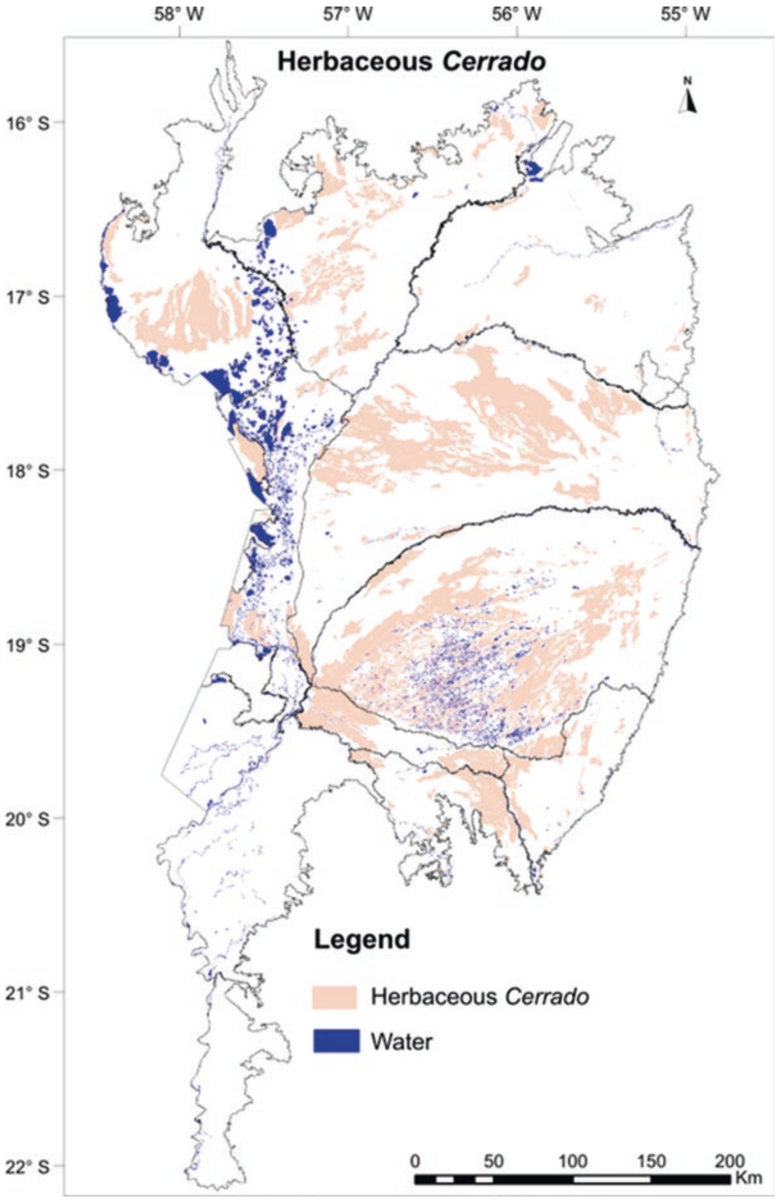


Fig. 2.5 Distribution of the Herbaceous *Cerrado* (grassy-woody savanna; grassland, open grassland, shrubby grassland, *Elionurus* grassland, and flooded grassland) in the Brazilian Pantanal

2018). The Chaco depicted in this chapter is composed of the woody steppic savanna with and without gallery forest and of the grassy-woody steppic savanna with and without gallery forest (Fig. 2.6). The woody steppic savanna is regionally known as open Chaco and the grassy-woody steppic savanna as open grassland, shrubby

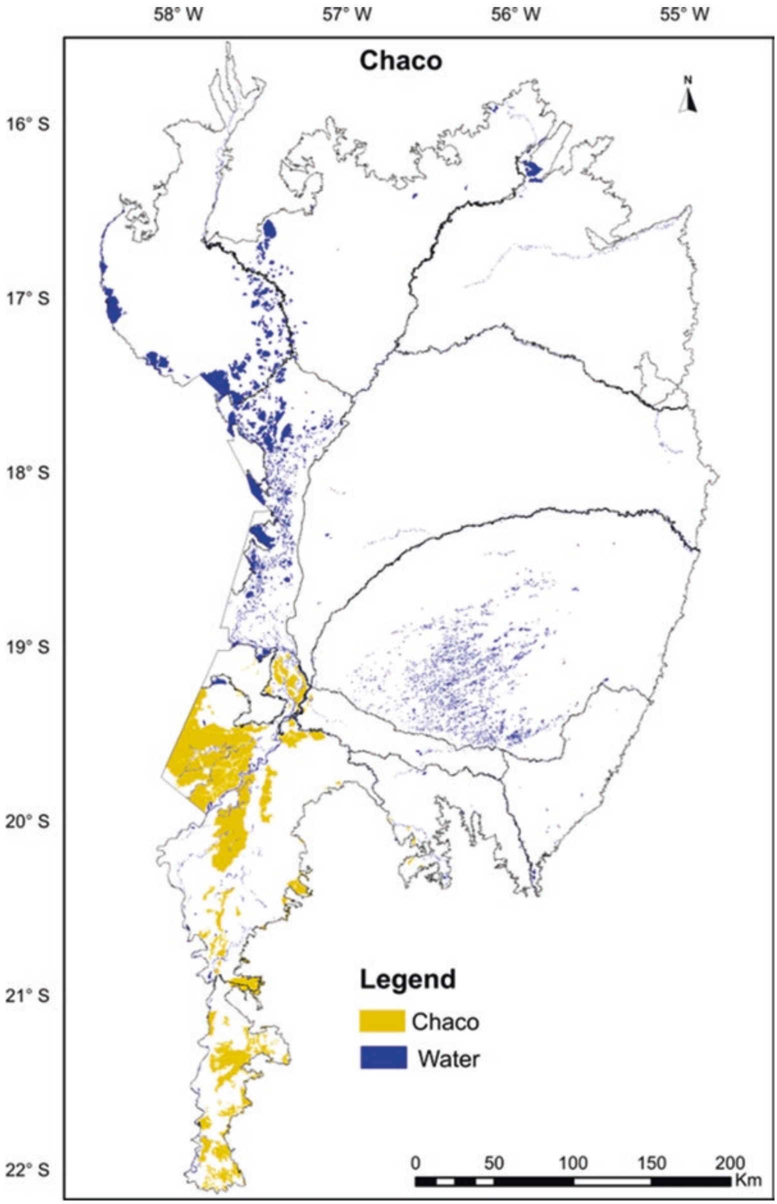


Fig. 2.6 Distribution of Chaco (woody steppic savanna and grassy-woody steppic savanna) in the Brazilian Pantanal

grassland, *campina*, and flooded grassland. True Chaco occurs only in the southern part of the Pantanal, in the Paraguai, Miranda, Nabileque, and Porto Murtinho subregions.

The Chaco is formed by woody, low, and spiny vegetation, associated with grassland (also called *campina*). When the woody vegetation is tall, similar to the structure of *Cerradão* or forest, the grassland is practically absent. This vegetation is typical of the southern part of the Pantanal, in the Miranda, Nabileque, and Porto Murtinho subregions, where we observed large areas of *Copernicia alba* and *Tabebuia aurea*, growing on clayey soils with high sodium content (mapped in the topic monodominant formations). This is the only region of true Chaco in Brazil, connected to the Chaco of Paraguay and Bolivia, and extending into Argentina, forming a phytogeographic province of 800 thousand km^2. The Chaco resembles the Caatinga vegetation for the spiny plants with small, deciduous leaves, often green bark, with the presence of cacti, although both floras have a low similarity in species composition. Common trees in the Brazilian Chaco are *Aspidosperma quebracho-blanco*, *Copernicia alba*, *Libidibia paraguariensis*, *Melicoccus lepidopetalus*, *Parkinsonia praecox*, *Prosopis rubriflora*, *P. ruscifolia*, *Ruprechtia triflora*, *Schinopsis balansae*, *Tabebuia aurea*, *T. nodosa*, and *Sarcomphalus mistol* (Prado 2000; Sartori et al. 2018). In Porto Murtinho there are areas with alternation of seasonal deciduous forest and Chaco, the first on higher and the latter on lower parts of the microrelief, within distances as short as 10 m, and it can be difficult to tell them apart in the dry season without being well acquainted with the species.

The **woody steppic savanna (open Chaco)** is composed of sparse, spiny, small-leaved trees and treelets, with continuous herbaceous cover; however, the tree stems are not as tortuous as in the *Cerrado* and the soils are clayey, alkaline, and often salty. The vegetation has quite evenly spaced trees (*Phyllanthus chacoensis*, *Castela coccinea*, *Diplokeleba floribunda*, *Microlobius foetidus* var. *paraguensis*, *Prosopis rubriflora*, *Sarcomphalus mistol*), 4–10 m tall, many spiny shrubs (*Mimosa hexandra*, *Vachellia farnesiana*), and columnar (*Cereus* spp., *Stetsonia coryne*), scandent (*Harrisia* spp.) and small cacti (*Cleistocactus* spp., *Echinopsis rhodotricha*, *Frailea* spp., *Gymnocalycium anisitsii*, *Opuntia* spp.). The ground cover is composed of short grasses and *Selaginella sellowii*, which becomes gray and seems dead at drought, but it is dormant, turning green again after rain.

The **grassy-woody steppic savanna (Grassland)** is the grassland form of Chaco, formed by grasses and herbs intermingled with small shrubs, mostly on clayey soils. They are the most floodable savannas in the region, generally close to the Paraguay River and its branch Nabileque River, in floodplains subject to riverine inundation. They are tall grasslands, with aquatic plants (*Echinodorus* spp., *Oryza* spp.) in the flood season. The main grasses are *Andropogon hypogynus*, *Paspalum fasciculatum*, *P. virgatum*, and *P. wrightii*, forming dense clonal stands, mixed with slender species such as *Leersia hexandra* and *Steinchisma laxum*. In this class, we include open grassland, shrubby grassland, grassland with *Copernicia alba* (*Campina de Carandá*), and flooded grassland.

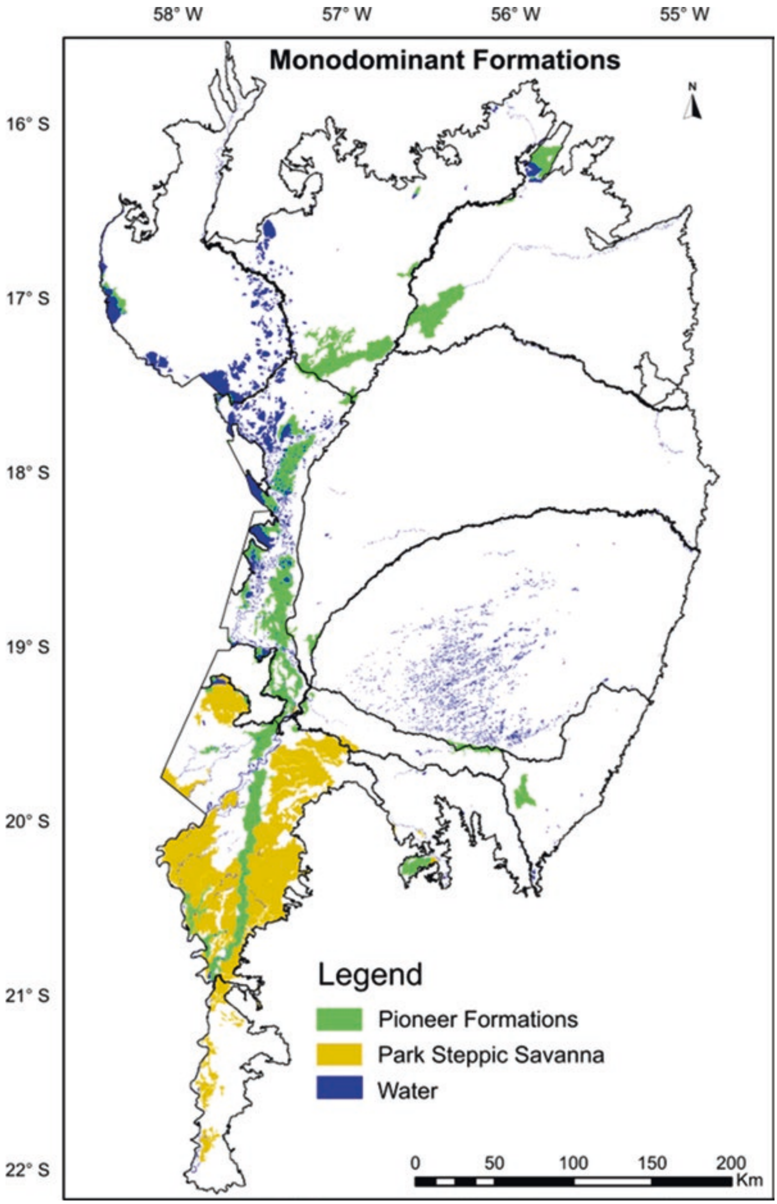


Fig. 2.7 Distribution of the monodominant formations (pioneer formations and park steppic savanna (continuum *Copernicia alba* palm tree, *Copernicia* grassland and *Tabebuia aurea*)] in the Brazilian Pantanal

2.2.5 Monodominant Formations

The monodominant formations (see the chap. 8 for more details (Chap. 8)) are represented by the pioneer formations (Fig. 2.7 – green) and part of the Chaco formed by the park steppic savanna (Fig. 2.7 – yellow). The pioneer formations occur close to rivers in the subregions of Barão de Melgaço, Poconé, Cáceres, Paraguai, Nabileque, Aquidauana (*brejo do Taboco*, a swamp where the rivers Taboco and Negro spread out from their channels and almost disappear), and Miranda (*brejo do Salobra*). Park steppic savanna occurs in the southern Pantanal. On sandy ridges in parts of the Nhecolândia subregion occur dense monodominant patches of *Attalea speciosa*, with few other trees, e.g., *Astronium fraxinifolium*; but they rather are a forest type similar to the babassu forest in the state of Maranhão.

The **pioneer formations** are under constant succession and colonize young and/or unstable terrains generally on alluvial riverine and lacustrine soils subject to disturbance by flooding, derived from sandy to clayey sediments. They are floodplain communities reflecting the effects of floods and of annually flooded depressions, encompassing from aquatic vegetation to support herbs, shrubs, and trees tolerant of inundation. The most widespread is the woodland of *Vochysia divergens* (see the chapter on encroachment (Chap. 11)), trees that are often 10–20 m tall, reaching 25 m. This tree is typical of amazon wetlands, e.g., Araguaia floodplains. Other pioneer thickets are composed of *Alchornea castaneifolia*, *Combretum* spp., *Couepia uiti* and *Leptobalanus parvifolius*, the latter two trees having broad canopies, around 5 m high. The spiny scrub is composed of entangled *Bauhinia bauhinioides*, *Byttneria filipes*, and lianas, around 2–4 m tall. There are also herbaceous-subshrubby monodominant stands of *Cyperus giganteus* (giant sedge); *Thalia geniculata* (fireflag), *Aspilia latissima*, *Ipomoea carnea*, *Polygonum* spp., and *Typha domingensis*; swamps with aquatic plants; and floating mats of *Eichhornia azurea*, *E. crassipes* and *Pontederia* spp. The floating meadow is a floating islet, with floating organic soil, and when not drifted away or does not dry out, it grows thicker and can sustain shrubs and treelets such as *Cecropia pachystachya*, *Ludwigia nervosa*, and *Tabebuia insignis*.

The **park steppic savanna** is formed by grassland vegetation with scattered trees, generally dominated by a single species and with a continuous grass cover, on clayey soil. In Mato Grosso do Sul, this phytophysiognomy occurs in floodable grassland and shows two main types, depending on the dominant tree: *Copernicia alba* palm tree and *Tabebuia aurea*. The *C. alba* area is a floodable park steppic savanna, 4–15 m tall, called *carandazal*, or *campina de carandá* when spaced and is known as *carandeiro* when the palms are particulary dense. The *T. aurea* area, called *paratudal*, contains practically just this single species of tree, mostly on anthill mounds. Tree height is around 5–10 m but can reach 17 m on less flooded ground or on patches of sandy soil. Because *T. aurea* also grows in the *cerrado*, though not as monodominant, this vegetation had been previously considered as *cerrado* (Loureiro et al. 1982). Instead of *cerrado*, in view of the vertic clays, absent in the *cerrado*, and of the associated species belonging to the Chaco (e.g. *Phyllanthus chacoensis*, *Prosopis rubriflora* etc.), the *T. aurea* park steppic savanna was classified as Chaco (Silva et al. 2011b). Indeed, the *T. aurea* park steppic savanna is a continuum with similar vegetation in Paraguay and Bolivia.

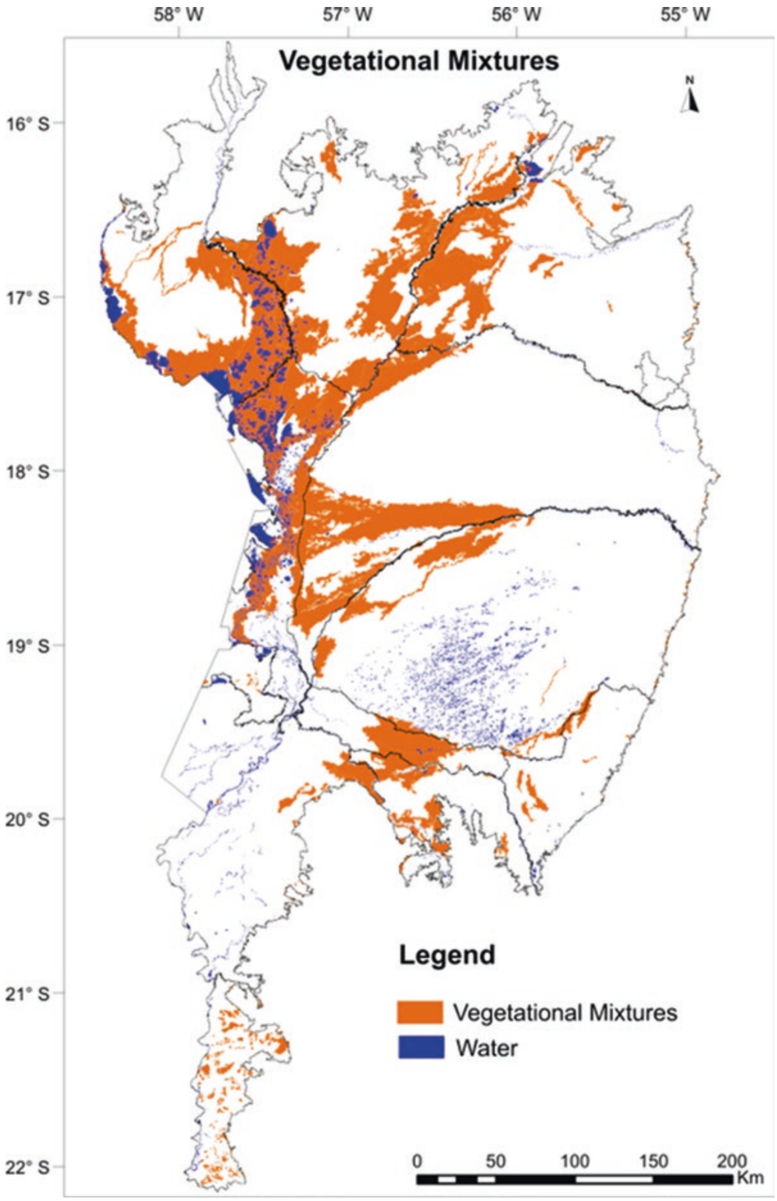


Fig. 2.8 Distribution of the vegetational mixtures [floristic contacts (ecotone and enclave) + vegetational refuges] in the Brazilian Pantanal

2.2.6 Vegetational Mixtures

The vegetational sixtures are formed by the floristic contacts (ecotones and enclaves) and by the submontane refuges, shown in Fig. 2.8 They occur in all subregions but are almost nonexistent in the Aquidauana and Nabileque subregions. The refuges only occur on the Urucum range, on the western edge of the Pantanal near the city of Corumbá. We note that the floristic contacts mapped now in the Porto Murtinho subregion, formerly (Mato Grosso do Sul 1989) were mapped as forested steppic savanna.

The **floristic contacts** are areas where two or more phytoecological regions meet and intermix, constituting the floristic transitions of the ecotone type (species from different regions that mix) or enclaves (species from different phytogeographic origins that do not mix). In general, in Mato Grosso do Sul, the contacts predominate in the Pantanal, while the enclaves are more frequent on the upland.

The **ecotone** constitutes a transition area between two types of neighbouring vegetation, where species mix or grow side by side, from distinct floras such as *Cerrado* and seasonal semideciduous forest, and such ecotones are common in the Pantanal. On *cordilheiras* (ancient levees), the mixture or the transition *cerradão*/seasonal dry forest within a few meters is very frequente, as a continuum from riparian forest to dry forest to *cerradão* (Pott and Silva 2015). The presence of species common to two phytogeographic origins can confound the interpretation of such vegetation type, as for example, the association of *Anadenanthera colubrina*, *Astronium fraxinifolium*, and *Dilodendron bipinnatum*. When the physiognomic structures are similar (seasonal forest/forested savanna), a floristic survey is essential for the identification of this formation. Because of the flooding dynamics of the Pantanal, we mapped the ecotones on the plain, occurring on sandy and sandy-clayey soils. We point out that in the Pantanal it is practically impossible to keep a Cerrado/forest ecotone protected from fires long enough for it to evolve to Forest (see the chapter on Fire (Chap. 18)). The earlier mentioned SESC reserve has had wildfires in spite of intense surveillance.

The **enclaves** are the floristic transitions, where the floras from different phytogeographic domains are intermixed, constituting a physiognomy where the species do not mix; i.e., they are disjunct areas in contact. They can be linked to edaphic contacts, but not necessarily. Their occurrences are located, most often on slopes, generally on drainage lines and on the edge of plateaus; however, they can be found on other than steep terrain such as in the Porto Murtinho subregion. Although associated with other vegetation, their areas can be mapped and distinguished if evaluated at a more detailed scale. The soils vary from sandy to clayey.

The **vegetational refuges** (relict communities) are vegetation types totally different from the surroundings, either floristically or for the physiognomy and maintenance of ecological processes in small areas. One type is the *canga* vegetation, found on the lateritic outcrops (ferruginous concretions), situated at 200–300 m on the foot of Urucum-Jacadigo hills. The laterite is covered with bromeliads (*Dyckia*, *Deuterochonia*), small cacti (e.g., *Discocactus ferricola*), ephemeral annual herbs (e.g., *Portulaca* spp.), and some shrubs where a bit more soil is held (Pott et al. 2000). Another type, on tops of the ranges (*serras*) known as Amolar and Urucum, was mapped as montane herbaceous refuge (grassland), because of the grassland structure and altitudes above 600 m, except the laterite. On the Urucum range, there

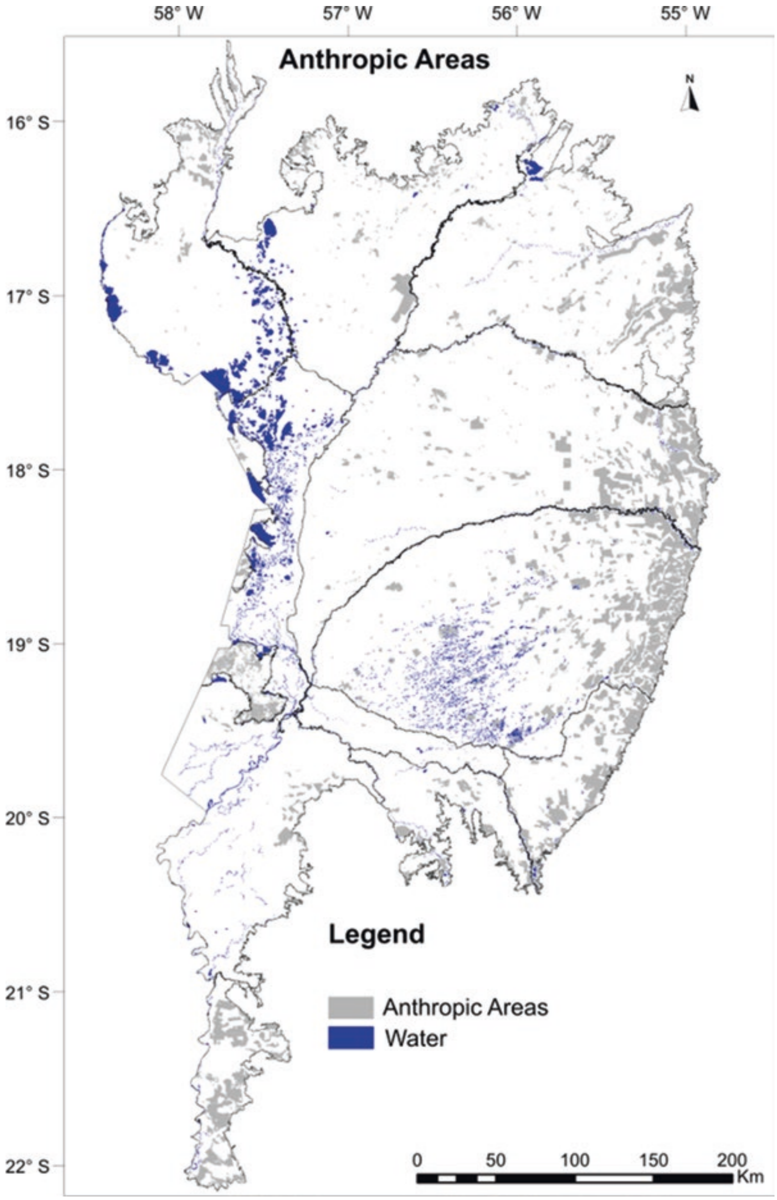


Fig. 2.9 Distribution of anthropic areas (secondary vegetation, agriculture, pasture, mining and urban influence) in the Brazilian Pantanal

are species endemic to the iron-rich geology, e.g., *Aspilia grazielae*, named in honour of the great botanist born in Corumbá, Graziela Maciel Barroso. At the highest elevations of the Serra do Amolar range, then on arenitic rocks, *Vellozia variabilis*, an element of rupestrian grassland, can occur, as well as bromeliads, cacti, and other xerophytes.

2.2.7 Anthropic Areas

The anthropic areas (Fig. 2.9) are composed of secondary vegetation, annual agriculture, cultivated pasture, mining areas, and urban areas. Over 95% of the anthropic areas are cultivated pasture for beef cattle, existing in all subregions. The pastures are more widespread in the eastern edge of the Pantanal and in the Porto Murtinho subregion. Only two cities (Corumbá and Ladário) are within the analysed area, near the Urucum-Jacadigo ranges. We observed secondary vegetation mostly in the Porto Murtinho subregion, while annual agriculture resumes to irrigated rice, concentrated in one farm in the Miranda subregion, on the left margin of the Miranda river.

Secondary vegetation is any natural vegetation that recolonizes an area after clearing, i.e., from regeneration (see the chapter on Regeneration (Chap. 20)), in various phases of succession, with variable size, located in areas where human intervention occurred for some use and then the land was abandoned. There can occur a return of *Cerrado* or a forest can start to develop in cleared areas. In general, plants considered weeds of degraded pasture can become dominant of the early succession stage. The regional name for such vegetation is *capoeira*, or *capoeirão* when more developed, though these terms are preferred for forest regeneration. In sites of previous *Cerrado*, succession can bring back species such as *Andira humilis*, *Annona* spp., *Byrsonima* spp., *Calliandra parviflora*, *Curatella americana*, *Duguetia furfuracea*, *Qualea* spp., *Xylopia aromatica*, and *Zanhoxylum rigidum*, mostly from underground resprouting. Where the original vegetation was deciduous and semideciduous forest, there is often a return of *Acrocomia totai*, *Attalea phalerata*, cacti, *Celtis* spp., *Astronium urundeuva*, *Trema micrantha*, *Vachellia farnesiana*, and *Zanhoxylum rhoifolium*, mainly from seed. In areas of previous alluvial or riparian forest, tend to return *Albizia inundata*, *Cecropia pachystachya*, *Crateva tapia*, *Handroanthus heptaphyllus*, *Genipa americana*, *Inga vera*, *Sapium obovatum*, and *Vitex cymosa*.

Annual agriculture or temporary crops have a short life between sowing/planting and harvest, generally less than a year. In the Pantanal very little land is used for cropping, just one farm grows irrigated rice, the rest are tiny patches of cassava and orchard for domestic consumption, negligible to map, but important because it is shift cultivation and after a few years new areas are slashed and burned.

Cultivated pasture is plantation of perennial forages for grazing of beef cattle. The suppressed native vegetation is replaced by grasses (rarely legumes), with height varying from nearly bare ground to 2 m. The most utilized species are

Megathyrsus maximus, *Urochloa decumbens*, *U. brizantha*, and *U. humidicola*. Often cultivated pasture replacing native grassland is difficult to distinguish, as there are no straight limits like after deforestation. It is worth mentioning that the natural vegetation is not easily invaded by these exotic grasses, in contrast with other savannas in Brazil.

Urban areas are areas where residential, commercial, or industrial buildings predominate, represented by towns and some villages, mostly on the edges of the floodplains. The mapped area covers urban nuclei and its surroundings with signs of urban expansion.

Mining areas refer to surface mining of iron ore, located in the Urucum range, in the municipality of Corumbá. The iron ore washed and transported to the port of Ladário on the Paraguay River for export. On the same hills, manganese is mined in tunnels. Less extensive mining activity includes limestone for cement from calcareous rocks formation, on lower hills.

The Table 2.1 shows the list of the mentioned plant species, with their authors, and main vegetation type.

References

Abdon MM, Silva JSV (2006) Fisionomias da vegetação nas sub-regiões do Pantanal brasileiro. São José dos Campos: INPE; Campinas: Embrapa Informática Agropecuária. 1 CD-ROM

Abdon MM, Silva JSV, Souza IM, Romon VT, Rampazzo J, Ferrari DL (2007) Desmatamento no bioma Pantanal até o ano 2002: relações com a fitofisionomia e limites municipais. Revista Brasileira de Cartografia, Rio de Janeiro 59(1):17–24

Adámoli J (1982) O Pantanal e sua relação fitogeográfica com os cerrados; discussão sobre o conceito de "Complexo do Pantanal". In: Anais do XXXII Congresso Nacional de Botânica, Teresina, pp 109–119

Almeida ITR, Amaral CH, Botelho M, Ribeiro EF, Penatti NC (2019) Geobotany in a fault in world's largest continuous wetland. Wetl Ecol Manag. https://doi.org/10.1007/s11273-018-9650-7

Amaral DL, Fonzar BC, Oliveira Filho LC (1982) Vegetação. As regiões fitoecológicas, sua natureza e seus recursos econômicos.1982. In: BRASIL. Ministério das Minas e Energia. Projeto Radambrasil. geologia, geomorfologia, solos, vegetação e uso potencial da terra. Folha SD.21 Cuiabá. Rio de Janeiro: DNPM. 416 p. (Levantamento de Recursos Naturais, vol 26). pp 401–452

Assine ML, Merino E, Pupim F, Warren L, Guerreiro R, Mcglue M (2015) Geology and geomorphology of the Pantanal Basin. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal Wetland in South America. Springer, Cham

BRASIL (1979) Ministério do Interior. Estudo de Desenvolvimento Integrado da Bacia do Alto Paraguai. Relatório de 1ª. fase. EDIBAP (ed). Brasília: Superintendência do Desenvolvimento da Região Centro-Oeste (SUDECO), t.2, 235p

Coutinho LM (2016) Biomas brasileiros. Oficina de Textos, São Paulo

Damasceno Junior GA, Pott A, Pott VJ, Silva JSV (2009) Florestas estacionais no Pantanal: considerações florísticas e subsídios para conservação. Geografia vol 34, Número Especial, pp 697–707. https://www.geopantanal.cnptia.embrapa.br/publicacoes/2geo/Cap-6.pdf

Furtado PP, Guimarães JG, Fonzar BC (1982) Vegetação. In: BRASIL. Ministério das Minas e Energia. Projeto Radambrasil. Folha SF.21 Campo Grande: geologia, geomorfologia, solos, vegetação e uso potencial da terra. Rio de Janeiro: DNPM (Levantamento de Recursos Naturais, v.28), pp 281–333

Hamilton SK, Sippel SJ, Melack JM (1996) Inundation patterns in the Pantanal wetland of South America determined from passive microvawe remote sensing. Arch Hydrobiol 137(1):1–23

IBGE (1992) Manual técnico da vegetação brasileira adaptada a um sistema universal. IBGE, Rio de Janeiro, 92 p

IBGE (2004) Mapa de Biomas do Brasil: primeira aproximação. IBGE, Rio de Janeiro

IBGE (2006) Manual Técnico de Uso da Terra. Rio de Janeiro: IBGE, 91 p. (n 7, 2ª ed.)

Loureiro RL, Lima JPS, Fonzar BC (1982) Vegetação. In: BRASIL. Ministério das Minas e Energia. Projeto Radambrasil. Folha SE.21 Corumbá e parte da Folha SE.20: geologia, geomorfologia, solos, vegetação e uso potencial da terra. Rio de Janeiro: DNPM. (Levantamento de Recursos Naturais, v. 27), pp 329–372

Mato Grosso Do Sul (1989) Secretaria de Planejamento. Macrozoneamento geoambiental do Estado de Mato Grosso do Sul. SEPLAN/FIPLAN, Campo Grande, 242 p

Mioto CL, Paranhos-Filho AC, Albrez EA (2012) Contribuição à caracterização das sub-regiões do Pantanal. Revista Entre-Lugar 8:165–180

Nunes Da Cunha C, Junk WJ (2001) Distribution of woody plant communities along the flood gradiente in the Pantanal of Poconé, Mato Grosso. Braz Int J Ecol Environ Sci 27:63–70

Nunes Da Cunha C, Junk WJ (2014) Classificação dos macrohabitats do Pantanal Matogrossense. In: Nunes Da Cunha C, Piedade MTF, Junk WJ (eds) Classificação e delineamento das Áreas Úmidas brasileiras e seu macrohabitats. EdUFMT, Cuiabá

Pott A, da dos Silva JSV (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal wetland in South America. Handbook of environmental chemistry, vol 37. Springer, Cham, pp 111–132

Pott A, Ratter JA (2011) Species diversity of terrestrial plants and human impacts on the vegetation of the Pantanal. In: Junk WJ, silva CJ, Nunes Da Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large tropical seasonal wetland. Pensoft, Sofia, pp 282–300

Pott A, Silva JSV, Abdon MM, Pott VJ, Rodrigues LMR, Salis SM, Hatschbach GG (1997) Vegetação. In: Programa Nacional Do Meio Ambiente (Brasil). Plano de Conservação da Bacia do Alto Paraguai – PCBAP: diagnóstico dos meios físico e biótico. Brasília: Ministério do Meio Ambiente, dos Recursos Hídricos e da Amazônia Legal, vol 2, pp 1–179, t.1. Subcomponente Pantanal

Pott A, Silva JSV, Salis SM, Pott VJ, Silva MP (2000) Vegetação e uso da terra. In: Silva JSV (Org.) Zoneamento ambiental da borda oeste do Pantanal. Maciço do Urucum e adjacências. Brasília: Embrapa. pp 111–132

Pott A, Oliveira AKM, Damasceno-Junior GA, Silva JSV (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71(1, Supl):265–273

Prado DE (2000) Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. Edinb J Bot 57(3):437–461

Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinb J Bot 60:57–109

Sartori ALB, Pott VJ, Pott A, Carvalho FS (2018) Check-list das Angiospermas do Chaco de Mato Grosso do Sul. Iheringia Botânica 73(Supl):22–33

Silva JSV, Abdon MM (1998) Delimitação do Pantanal brasileiro e suas sub-regiões. Pesq Agrop Brasileira 33:1703–1712

Silva JSV dos da, Carlini F (2015) Vegetation cover of the Upper Paraguai Basin in Mato Grosso do Sul state: comparison between Pantanal wetland and the plateau. Geografia, Rio Claro, vol 40, Número Especial, pp 211–226

Silva JSV, Abdon MM, Pott A, Ribeiro LM (1997) Vegetação da bacia do Alto Paraguai – Pantanal brasileiro – detectada por satélite. (CD-ROM). In: Simpósio Latino Americano de Percepcion Remota, 8, Mérida, Venezuela, 2-7 novembro. Anais… Memórias do VIII Simpósio Latino Americano de Percepción Remota, Caracas: Editado pela SELPER/Unidade Técnica de Sistemas. Instituto de Ingeneria. Monitoreo de Recursos Naturales (CD-ROM: RCN_006.doc)

Silva MP, Mauro RA, Mourão G, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Rev Bras Bot 23(2):123–152

Silva JSV, Abdon MM, Pott A, Mauro RA (2003) Fragile ecosystem: the Brazilian Pantanal Wetland, in regional sustainable development review: Brasil. In: Sanchez LE (ed) Encyclopedia of Life Support Systems (EOLSS), developed under the Auspicies of the UNESCO, Eolss Publishers, Oxford, 31p. http://www.eolss.net, http://www.eolss.net/sample-chapters/c16/e1-58-49-00.pdf

Silva JSV, Abdon MM, Pott A (2007a) Cobertura vegetal do Bioma Pantanal em 2002. In: Congresso Brasileiro De Cartografia, 23, 2007, Rio de Janeiro. Anais… Rio de Janeiro: SBC. pp 1030–1038. 1 CD.ROM

Silva JSV, Abdon MM, Silva AM, Souza LA (2007b) Banco de dados de vegetação do projeto Probio-Pantanal. In: Congresso Brasileiro De Cartografia, 23, Rio de Janeiro. Anais… Rio de Janeiro: SBC. pp 1643–1652. 1CD.ROM

Silva J dos SV da, de Abdon, MM; da Silva, SMA, de Moraes JA (2011a) Evolution of deforestation in the Brazilian Pantanal and surroundings in the timeframe 1976–2008. Geografia, Rio Claro, vol 36, Número Especial, pp 35–55

Silva J d SV d, Pott A, Abdon MM, Pott VJ, dos Santos KR (2011b) Projeto GeoMS: cobertura vegetal e uso da terra do Estado de Mato Grosso do Sul. Embrapa Informática Agropecuária, Campinas, 64 p

Silva J d SV d, Speranza EA, Vendrusculo LG, Esquerdo JCDM, de Mauro RA, Bianchini SL, de Florence RO (2011c) Projeto GeoMS: melhorando o sistema de licenciamento ambiental do Estado de Mato Grosso do Sul. Embrapa Informática Agropecuária, Campinas, 64 p

Silva J d SV d, Speranza EA, Vendrusculo LG, Esquerdo JCDM, de Mauro RA, Bianchini SL, de Florence RO (2011d) Projeto GeoMS: melhorando o sistema de licenciamento ambiental do Estado de Mato Grosso do Sul. Embrapa Informática Agropecuária, Campinas, 64 p

Chapter 3
Flora of the Pantanal

Arnildo Pott and Vali Joana Pott

3.1 Introduction

The contents in this chapter give taxonomic support to all others, in which we quote plants cited without their nomenclatural authority, aiming at an easier reading. Our checklist is the result of 40 years of collecting throughout the Pantanal, documented in herbaria, as well as collaboration from specialists, in addition to the consultation of virtual herbaria.

Sampaio (1916) described the history of scientific expeditions that explored the Pantanal flora, having started in1788, by European botanists who collected plants on the plains. However, they worked mainly in the surroundings of fluvial ports, e.g., Corumbá and Cuiabá, because access to the inland was more difficult at that time. Later, Brazilian botanists travelled and published their findings, one of the most active being Frederico C. Hoehne, from the Instituto de Botânica de São Paulo; he and J.G Kuhlmann joined the telegraph line construction by Marechal Rondon through the Pantanal (Hoehne 1923; Hoehne and Kuhlmann 1951). The next relevant publications were produced by Guarim Neto (1981), Prance and Schaller (1982), and Conceição and Paula (1986). Slowly the number of local botanists increased; they strengthened various regional herbaria (CPAP at Embrapa Pantanal, COR at UFMS-CPAN, CGMS at UFMS, and UFMT that later partly was lost), while boosting the floristic investigation of the Pantanal.

Several specialists contributed to identifying the plants we collected in the region; initially, mainly José F.M. Valls (CEN, Embrapa Genetic Resources and

---

A. Pott (✉)
Laboratório de Ecologia Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

V. J. Pott
Herbário CGMS, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_3

Biotechnology) and the team lead by Antonio Krapovickas (CTES, Instituto de Botánica del Nordeste, Argentina) played a major role in the taxonomic activity. An outstanding book on the Pantanal grasslands was the result of a comprehensive survey by Allem and Valls (1987), whose specimens are stored in the Herbarium CEN, with some duplicates in CPAP. Later, Schessl (1997) described grasslands of the Poconé subregion, already with our assistance. One of the richest collections was made by Gert Hatschbach, from MBM, Curitiba Botanic Garden. Compiled from MBM and European herbaria labels, Dubs (1998) published the first annotated checklist of the states of Mato Grosso and Mato Grosso do Sul (though only Mato Grosso is in the title), including several angiosperms from the Pantanal. Two books were published with colorful pictures of Pantanal plants (Pott and Pott 1994; Pott and Pott 2000). Also, there is a growing number of articles on the Flora (e.g. Pott et al. 2011, Sartori et al. 2018a), Plant Taxonomy (e.g. Pott 1998; Souza-Lima et al. 2017; Guglieri-Caporal et al. 2018; Sartori et al. 2018a, b), Phytogeography of woody species (Pott and Ratter 2011), and many on the vegetation as cited in other chapters (e.g. Pott et al. 2011; Pott and Silva 2015).

The compilation of a checklist is usually an endless task because new occurrences can be found as new sites are explored throughout the vast Pantanal, especially from areas that are difficult to access. The added records to the previous list of 1863 plants (Pott and Pott 1999) come mostly from our regular collecting activity, and many from the southernmost subregion of Porto Murtinho (Chaco), in addition to some collected by other botanists in the largest private preserve called SESC Pantanal, in the northeastern Barão de Melgaço subregion.

This census is a compiled list of all known species of angiosperms occurring in the Pantanal as per herbaria holdings. Our criterion was to include only species deposited in herbaria and recorded from the Pantanal sedimentary plain as delineated by Silva and Abdon (1998). Otherwise, the list would be endless and it would mix with the flora of the hills and surrounding highlands. But we are aware that often the distinction between Pantanal plain, i.e., sensu stricto, and Pantanal basin is not clear in the literature. Even in Flora do Brasil (Flora do Brasil 2020), several species ascribed to the Pantanal occur only in the proximity or at the upper watershed instead of on the plain, and many publications follow this information, which is inaccurate in our view. Therefore, we preferred to select specimens revised by specialists (credits shown in Table 3.1), plus those we were able to check personally at the RBGE Herbarium and some at Kew. Other collections were selected mainly from the platform Species Link, as well as virtual herbaria such as Jabot, INCT, Flora do Brasil (2020), GBIF, NYBG, Mobot, RBGE, Kew (Royal Botanic Gardens Kew), and visited the herbaria, CGMS, MBM, CEN, CPAP, HPAN (Herbário do Pantanal Vali Joana Pott), COR, UFMG, and UFMT.

We included exotic cultivated plants because they may indicate environmental conditions and, more important, they can become naturalized. Also, most cultivated plants are visited by frugivores and pollinators. Some had no recorded voucher, but they are well-known species. We did not include potted plants.

In case it was difficult to ascertain whether or not a species is native or naturalized, we followed indications from Flora do Brasil (Flora do Brasil 2020).

Table 3.1 Checklist of Angiosperms of the Pantanal wetland

Family, genus, species	Identified by	Voucher	Habit	Polli.	Dispers.	Distribution	Endem.
Acanthaceae							
Aphelandra longiflora (Lindl.) Profice	C. Kameyama	A. Pott 2606	Ss	E	Au	CO, N, S, SE	
*,***Asystasia gangelica* (L.) T.Anderson	C. Ezcurra	M.G. Caxambu 1573	H	E	Au	CO, SE	
Elytraria imbricata (Vahl) Pers.	A. Pott	A. Pott 15545	H	E	Au	CO, SE, N, NE	
Hygrophila costata Nees	A. Pott	A. Pott 4754	H	E	Au, Hy	CO, N, NE, S, SE	
H. guianensis Nees ex Benth.	V.J. Pott	V.J. Pott 3581	H	E	Au, Hy	CO, N, NE, S, SE	
H. laevis (Nees) Lindau	V.J. Pott	A. Pott 2043	H	E	Au, Hy	CO	
Justicia comata (L.) Lam.	A. Pott	V.J. Pott 3289	H	E	Au	CO, N, NE, S, SE	
J. dumetorum Morong	D.M. Braz	G.A. Damasceno Jr. 2375	H	E	Au	CO	
J. glaziovii Lindau	A. Pott	A. Pott 4330	Ss	E	Au	CO, NE, SE	
J. goudotii V.A.W.Graham	A. Pott	V.J. Pott 8676	Ss	E	Au	CO, SE	
J. hassleri (Lindau) V.A.W.Graham	A. Pott	A. Pott 4850	Ss	E	Au	CO	
J. laevilinguis (Nees) Lindau	A. Schinini	A. Pott 4490	H	E	Au, Hy	CO, N, NE, S, SE	Brazil
J. lavandulifolia (Pohl ex Nees) Wassh.	D.C. Wasshausen	M. Schessl 103/1-1	H	E	Au, Hy	CO, N	
***J. pectoralis* Jacq.	D.M. Braz	C.D.O. Cabral 35	H	E		CO, N, NE	

(continued)

Table 3.1 (continued)

J. thunbergioides (Lindau) Leonard	D.C. Wasshausen	G. Hatschbach 60771	H	E	Au	CO, NE, SE	
J. tocantina (Nees) V.A.W.Graham	J.R.I. Wood	G. Schaller 23	Ss	E	Au	CO, SE	
Lepidagathis alopecuroides (Vahl) R.Br. ex Griseb.	U.G. Fernandes	A. Pott 5442	H	E	Au	CO, N	
L. floribunda (Pohl) Kameyama	C. Kameyama	A. Pott 11168	Ss	E	Au	CO, N, NE, SE	
L. sessilifolia (Pohl) Kameyama ex Wassh. & J.R.I.Wood	C. Kameyama	A. Pott 7135	Ss	E	Au	CO, N, NE	
Mendoncia puberula Mart.	C. Kameyama	A. Pott 4106	L	E	Au	CO, N, SE, S	
Pachystachys velutina (W.Bull) A.L.A.Côrtes	A. Pott	A. Pott 4953	Ss	Z	Au	CO, N	
Pseuderanthemum congestum (S. Moore) Wassh.	A. Pott	A. Pott 4953	Ss	E	Au	CO, N, NE	
Ruellia angustiflora (Nees) Lindau ex Rambo	A. Pott	A. Pott 15400	Ss	E, O	Au	CO, S, SE	
R. bahiensis (Nees) Morong	A. Pott	A. Pott 5442	Ss	E	Au	CO, NE, SE	Brazil
R. brevifolia (Pohl) C. Ezcurra	C. Kameyama	C.J. Silva 37	Ss	E, O	Au	CO, N, S, SE	
R. bulbifera Lindau	U.G. Fernandes	A.Pott 3815	H	E	Au	CO, S, SE	
R. erythopus (Nees) Lindau	D.C. Wasshausen	A.C. Cervi 3240	H	E	Au	CO, S, SE	

R. geminiflora Kunth	A. Pott	A. Pott 1466	H	E	Au	CO, N, NE, S, SE	
R. hygrophila Mart.	A. Pott	A. Pott 3865	H	E	Au	CO	
R. multifolia (Nees) Lindau	D.C. Wasshausen	G. Hatschbach 74204	H	E	Au	CO, S, SE	
R. nobilis (S.Moore) Lindau	V.J. Pott & A. Pott	A. Pott 16755	Ss	E	Au	CO	
R. simplex C.Wright	C. Ezcurra	G. Hatschbach 49293	H	E	Au	CO, NE, S, SE	
Staurogyne diantheroides Lindau	A. Pott	V.J. Pott 5755	H	E	Au	CO, N	
Stenandrium diphyllum Nees	D.C. Wasshausen	B. Dubs 1093	H	E	Au	CO, S, SE	
S. dulce (Cav.) Nees	D.C. Wasshausen	G. Hatschbach 74038	H	E	Au	CO, S	
S. pohlii Nees	C. Kameyama	A. Pott 1555	H	E	Au	CO, S, SE	
Thyrsacanthus boliviensis (Nees) A.Côrtes & Rapini	A.L.A. Côrtes	E.R. Salviani 25	Ss	E, O	Au	CO, N	
Achatocarpaceae							
Achatocarpus praecox Griseb.	A. Schinini; O.S. Ribas	A. Pott 2427	T	E	O	CO, S, SE	
Alismataceae							
Echinodorus aschersonianus Graebn.	L.Q. Matias	J.U. Santos 585	H	E	Hy	CO, N, S, SE	
E. cordifolius (L.) Griseb.	R.R. Haynes; S. Lehtonen & L. Myllys	V.J. Pott 538	H	E	Hy	CO	
E. cylindricus Rataj	S. Lehtonen & L. Myllys	V.J. Pott 402	H	E	Hy	CO, N	Brazil

(continued)

Table 3.1 (continued)

E. glaucus Rataj	V.J. Pott; S. Lehtonen & L. Myllys	V.J. Pott 739	H	E	Hy	CO, N	
E. grandiflorus (Cham. & Schltr.) Micheli	S. Lehtonen & L. Myllys	V.J. Pott 3333	H	E	Hy	CO, N, NE, S, SE	
E. longipetalus Micheli	V.J. Pott	V.J. Pott 3925	H	E	Hy	CO, N, S, SE	
E. paniculatus Micheli	V.J. Pott	V.J. Pott 3941	H	E	Hy	CO, N, NE, S, SE	
E. scaber Rataj	R.R. Haynes; S. Lehtonen & L. Myllys	V.J. Pott 4756	H	E	Hy	CO, N, NE, S, SE	
E. subulatus (Mart.) Griseb.	R.R. Haynes	A. Pott 5255	H	E	Hy	CO, N, NE, SE	
Helanthium bolivianum (Rusby) Lehtonen & Myllys	V.J. Pott; S. Lehtonen & L. Myllys	V.J. Pott 3215	H	E	Hy	CO, N, NE, S, SE	
H. tenellum (Mart.) Britton	V.J. Pott; S. Lehtonen & L. Myllys	V.J. Pott 889	H	E	Hy	CO, N, NE, S, SE	
Hydrocleys nymphoides (Willd.) Buchenau	V.J. Pott	V.J. Pott 2982	H	E	Hy	CO, N, NE, S, SE	
H. parviflora Seub.	C.D.K. Cook	A. Pott 4736	H	E	Hy	CO, NE, SE	
Limnocharis flava (L.) Buchenau	V.J. Pott	V.J. Pott 2981	H	E	Hy	CO, N, NE, S, SE	
L. laforesti Duchass. ex Griseb.	V.C. Souza	A. Pott 5519	H	E	Hy	CO, N, NE	
Sagittaria guayanensis Kunth	V.J. Pott	V.J. Pott 2649	H	E	Hy	CO, N, NE, SE	
S. montevidensis Cham. & Schltdl.	V.J. Pott	V.J. Pott 3074	H	E	Hy	CO, N, S, SE	
S. planitiana G.Agostini	V.J. Pott	V.J. Pott 2167	H	E	Hy	CO, NE	

S. rhombifolia Cham.	V.J. Pott	V.J. Pott 2700	H	E	Hy	CO, N, NE, S, SE	
Alstroemeriaceae							
Alstroemeria psittacina Lehm.	A. Schinini	A. Pott 5510	H	E	Au	CO, S, SE	Brazil
Amaranthaceae							
**Achyranthes aspera* L.	G.M. Barroso; T.M. Pedersen	A. Pott 2690	Ss	E	Z	CO, N, NE, SE	
Alternanthera aquatica (D.Parodi) Chodat	J.C. Siqueira	V.J. Pott 1859	H	E	Hy	CO, N, NE, S, SE	
**A. blitum* L.	T.M. Pedersen	A.Pott 2275	H	E	Au, Z	CO, NE, S	
**A. brasiliana* (L.) Kuntze	J.C. Siqueira	J.A. Silva 45	Ss	E	Au	CO, N, NE, S, SE	
A. kurtzii Schinz	L. Senna	G. Hatschbach 73315	Ss	E	Au	CO, NE, S, SE	
**A. paronychioides* A.St.-Hil.	J.C. Siqueira	A. Pott 3859	H	E	Au	CO, N, NE, S, SE	
A. philoxeroides (Mart.) Griseb.	V.J. Pott	V.J. Pott 851	H	E	Au	CO, N, NE, S, SE	
**A. pungens* Kunth	J.C. Siqueira	G. Hatschbach 21865	H	E	Au, Z	CO, N, NE, S, SE	
A. reineckii Briq.	T.M. Pedersen	V.J. Pott 1698	H	E	Au, Hy	CO, N, S, SE	
A. tenella Colla	T.M. Pedersen	A. Pott 2642	H	E	Au	CO, N, NE, S, SE	
**Amaranthus deflexus* L.	A. Pott	A. Pott 2155	H	E	Au, Z	CO, S, SE	
**A. spinosus* L.	A. Pott	A. Pott 1658	H	E	Au, Z	CO, N, S, SE	

(continued)

Table 3.1 (continued)

**A. viridis* L.	A. Pott	A. Pott 3699	H	E	Au, Z	CO, N, NE, S, SE	
***Celosia argentea* L.	I.M. Bortolotto	I.M. Bortolotto 15-4-1996	H	E	Au	CO, N, NE, S, SE	
**Dysphania ambrosioides* (L.) Mosyakin & Clements	A. Pott & V.J. Pott	A.Pott 1742	H	E	Au	CO, N, NE, S, SE	
Froelichia procera (Seub.) Pedersen	T.M. Pedersen	A. Pott 5869	Ss	E	Au, An	CO, N, S, SE	
Gomphrena arborescens L.f.	T.M. Pedersen; M.C.H. Mamede	D.F.R. Bommer 49	H	E	Au, An	CO, NE, SE	
**G. celosioides* Mart.	M.C.H. Mamede	V.J. Pott 1938	H	E	Au, An	CO, N, NE, S, SE	
G. elegans Mart.	J.C. Siqueira	A.Pott 4720	H	E	Au, Hy	CO, N, NE, S, SE	Brazil
G. gardneri Moq.	E.F. Guimarães	G. Martinelli 18629	Ss	E	Au	C, N, NE	Brazil
G. mattogrossensis Suess.	J.C. Siqueira	A. Pott 5301	H	E	Au	CO, SE	Brazil
G. vaga Mart.	J.C. Siqueira	A. Pott 3852	H	E	Au	CO, N, NE, S, SE	Brazil
Hebanthe eriantha (Poir.) Pedersen	A. Furlan	L. Rossi & I. Cordeiro no n.	Ss	E	Au, An	CO, N, NE, S, SE	
H. pulverulenta Mart.	J.C. Siqueira	S.A. Rego 609	Ss	E	Au, An	CO, SE	
Iresine diffusa Humb. & Bonpl. ex Willd.	T.M. Pedersen	A. Pott 2722	L	E	An	CO, N, NE, SE, S	
Pedersenia macrophylla (R.E. Fr.) Holub	T.M. Pedersen	A. Pott 5102	L	E	An	CO	
Pfaffia acutifolia (Moq.) O. Stützer	J.C. Siqueira	A. Pott 2624	E	E	Au	Co, N, NE, SE	

***P. iresinoides* (Kunth) Spreng.	V.J. Pott	V.J. Pott 1735	H	E	Au	CO	
P. glomerata (Spreng.) Pedersen	T.M. Pedersen	A. Pott 3258	Ss	E	Au, Hy	CO, N, NE, S, SE	
Quaternella confusa Pedersen	J.C. Siqueira	G. Hatschbach 73313	Ss	E	Au	CO, NE	Brazil
Amaryllidaceae							
***Allium fistulosum* L.		V.J. Pott 1788	H	E		Exotic	
**Crinum americanum* L.	T.R.F. Sinani	T.R.F. Sinani 418	H	E	Au	CO, N, NE, S, SE	
Zephyranthes lactea S.Moore	J. Dutilh	V.J. Pott 6541	H	E	Au	CO, NE, S, SE	
Z. pantanalensis (Ravenna) R.S. Oliveira & Dutilh	P.F. Ravenna	A. Pott 3633 (Typus)	H	E	Au	CO	Brazil
Hippeastrum elegans (Spreng.) H.E.Moore	P.F. Ravenna	G. Hatschbach 23043	H	E	Au	CO, N, NE, SE	
H. puniceum (Lam.) Kuntze	A. Pott	A. Pott 3827	H	E	Au	CO, N, NE, S, SE	
Anacardiaceae							
Anacardium humile A.St.-Hil.	J.A. Ratter	A. Pott 4380	S	E	Z	CO, N, NE, S, SE	
*,***A. occidentale* L.	J.D. Mitchell	A.C. Allem 148	T	E	Z	CO, N, NE, SE	
Astronium fraxinifolium Schott	J.A. Ratter	A. Pott 3426	T	E	An	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

A. urundeuva (M.Allemão) Engl.	J.A. Ratter	A. Pott 3308	T	E	An	CO, N, NE, S, SE	
*,***Mangifera indica* L.	E.P. Seleme	E.P. Seleme s/n	T	E	Z	Exotic	
Schinopsis balansae Engl.	D.E. Prado	A. Pott 4613	T	E	An	CO	
S. brasiliensis Engl.	D.E. Prado	A.Pott 4637	T	E	An	CO, NE, SE	
***Spondias cytherea* Sonn.			T	E	Z	Exotic	
S. mombin L.	A. Pott	V.J. Pott 1985	T	E	Z	CO, N, NE, SE	
***S. purpurea* L.	E.P. Seleme	E.P. Seleme 453	T	E	Z	Exotic	
Tapirira guianensis Aubl.	A. Pott	A. Pott 4394	T	E	Z	CO, N, NE, S, SE	
T. obtusa (Benth.) J.D.Mitch.	J.R. Pirani	A. Pott 5600	T	E	Z	CO, N, NE, SE	
Annonaceae							
Annona aurantiaca Barb. Rodr.	J.A. Ratter	A. Pott 4787	S	E	Z	CO, N, NE	Brazil
***A. cherimola* Mill.			T	E	Z	Exotic	
***A. cherimola* Mill. x *A. squamosa* L.			T	E	Z	Exotic	
A. coriacea Mart.	V.F. Mansano	D.T. Azevedo 37	T	E	Z	CO, N, NE, S, SE	
A. cornifolia A.St.-Hil.	J.Y. Tamashiro	A. Pott 4547	S	E	Z	CO, S, SE	
A. crassiflora Mart.	A. Pott	A. Pott 6547	T	E	Z	CO, N, NE, S, SE	
A. dioica A.St.-Hil.	J.A. Ratter	A. Pott 4467	S	E	Z	CO, N, NE, S, SE	

A. emarginata (Schtdl.) H.Rainer	J.Y. Tamashiro	A. Pott 4528	T	E	Z	CO, NE, S, SE	
A. nutans (R.E.Fr.) R.E.Fr.	A. Pott	A. Pott 2347	S	E	Z	CO, SE	
***A. squamosa* L.	I.M. Bortolotto	I.M. Bortolotto 11-12-1998	T	E	Z	Exotic	
A. sylvatica A.St.-Hil.	J.C. Lopes	G.A. Damasceno Jr. 3132	T	E	Z	CO, NE, S. SE	Brazil
Bocageopsis mattogrossensis (R.E.Fr.) R.E.Fr.	A. Pott	T.H. Stefanello 302	T	E	Z	CO, N, S	
Duguetia furfuracea (A.St.-Hil.) Saff.	J.A. Ratter	A.Pott 5072	S	E	Z	CO, N, NE, S, SE	
D. marcgraviana Mart.	P. He & P.J.M. Maas	G. Schaller 153	T	E	Z	CO, N, NE	
D. phaeoclados (Mart.) Maas & H.Rainer	W. Morawetz; P. He; J.M. Maas	A. Pott 3481	S	E	Z	CO	
Unonopsis guatterioides (A.DC.) R.E.Fr.	J.A. Ratter	A. Pott 5035	T	E	Z	CO, N, NE, S, SE	
Xylopia aromatica (Lam.) Mart.	A. Pott	A. Pott 4396	T	E	Z	CO, N, NE, S, SE	
Apiaceae							
**Cyclospermum leptophyllum* (Pers.) Sprague	A. Pott & V.J. Pott	I.P.P. Araújo 22	H	E	Au	CO, NE, S, SE	
***Coriandrum sativum* L.	A. Pott	A. Pott 17932	H	E	Au	Exotic	

(continued)

Table 3.1 (continued)

Eryngium ebracteatum Lam.	V.J. Pott	A. Pott 4416	H	E	Au, Hy	CO, NE, S, SE	
E. elegans Cham. & Schltdl.	V.J. Pott	A. Pott 3580	H	E	Au	CO, S, SE	
***E. foetidum* L.	M.A. Carniello	M.A. Carniello 489	H	E	Au	CO, N, NE, S, SE	
E. pristis Cham. & Schltdl.	P. Fiaschi	A. Pott 1590	H	E	Au	CO, N, S, SE	
***Petroselinum sativum* L.			H	E	Au	Exotic	
Apocynaceae (included Asclepiadaceae)							
***Adenium obesum* Balf.			Ss	E		Exotic	
Allamanda angustifolia Pohl	A. Rapini	W.W. Thomas 4559	S	E	An	CO, N, NE, SE	Brazil
***A. cathartica* L.	A. Pott	S.S. Moura 160	T	E		CO, N, NE, S, SE	
Araujia brachystephana (Griseb.) Fontella & Goyder	A.O. Simões	J.A. Ratter 6111	L	E	An	CO, S	Brazil
A. odorata (Hook. & Arn.) Fontella & Goyder	J. Fontella	A. Pott 1189	L	E	An	CO, S	
A. plumosa Schltr.	T. Konno	J. Cordeiro 3183	L	E	An	CO, S, SE	
A. stormiana Morong	M.A. Farinaccio	M.A. Farinaccio 963	L	E	An	CO	
A. stuckeriana (Kurtz ex Heger) Fontella & Goyder	M.A. Farinaccio	M.A. Farinaccio 934	L	E	An	CO	
A. variegata (Griseb.) Fontella & Goyder	A. Rapini	A. Pott 1189	L	E	An	CO	

**Asclepias curassavica* L.	R.R. Silva	R.R. Silva 30	H	E	An	CO, N, NE, S, SE	
A. mellodora A.St.-Hil.	A. Pott	A.Pott 3485	H	E	An	CO, N, NE, S, SE	
Aspidosperma australe Müll.Arg.	D.J. Machate	A. Pott 7971	T	E	An	CO, NE, S, SE	
A. cuspa (Kunth) S.F.Blake	G.A. Damasceno Jr.	L.V.S. Campos 381	T	E	An	CO, N, NE, SE	
A. cylindrocarpon Müll. Arg.	C.N. Cunha	A.Pott 5220	T	E	An	CO, N, NE, S, SE	
A. macrocarpon Mart.	D.J. Machate	A. Pott 4961	T	E	An	CO, N, NE, SE	
A. parvifolium A.DC.	S.M. Gomes	A. Pott 3549	T	E	An	CO, N, NE, S, SE	
A. pyrifolium Mart. & Zucc.	A. Pott	A. Pott 2020	T	E	An	CO, N, NE, SE	
A. quebracho-blanco Schtdl.	D.E. Prado	A. Pott 6960	T	E	An	CO	
A. quirandy Hassl.	W. Marcondes-Ferreira	T.B. Breier 1330	T	E	An	CO	
A. tomentosum Mart.	J.A. Ratter	A. Pott 3427	T	E	An	CO, N, NE, S, SE	
A. triternatum Rojas Acosta	D.E. Prado	A. Pott 5293	L	E	An	CO	
Blepharodon pictum (Vahl) W.D.Stevens	M.A. Farinaccio	M.A. Farinaccio 879	L	E	An	CO, N, NE, S, SE	
**Calotropis procera* (Aiton) W.T.Aiton	A. Pott & V.J. Pott	V.J. Pott 3390	S	E	An	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

**Catharanthus roseus* (L.) Don	M.A. Carniello	M.A. Carniello 4733	E	E	An	CO, N, NE, S, SE	
Cynanchum montevidense Spreng.	V.J. Pott; M.A. Farinaccio	A. Pott 1756	L	E	An	CO, N, NE, S, SE	
C. rioparanaense E.Sundell	M.A. Farinaccio	V.J. Pott 4412	L	E	An	CO, S, SE	
Echites rubrovenosus Linden (illegitimate name)	A. Pott	A. Pott 4731	L	E	An	?	
Forsteronia pubescens A.DC.	J.A. Ratter	A. Pott 3844	L	E	An	CO, NE, S, SE	
Funastrum clausum (Jacq.) Schltr.	J. Fontella	A. Pott 3573	L	E	An	CO, N, NE, S, SE	
Hancornia speciosa Gomes	A. Pott	A. Pott 2038	T	E	Z	CO, N, NE, S, SE	
Himatanthus obovatus (Muell.Arg.) Woodson	J.A. Ratter	A. Pott 4582	T	E	An	CO, N, NE, SE	
Gonolobus rotratus (Vahl) R.Br. ex Shult.	A. Rapini	L.E.A.M. Lescano	T	E	An	CO, N, NE, S, SE	Brazil
Mandevilla angustifolia (Malme) Woodson	M.A. Farinaccio	M.A. Farinaccio 994	L	E	An	CO	
M. petraea (A.St.-Hil.) Pichon	A.L. Scudeler	A.Pott 3830	Ss	E	An	CO, S, SE	
M. pohliana (Stadelm.) A.H.Gentry	G. Hatschbach	A.Pott 5876	Ss	E	An	CO, N, NE, S, SE	
M. rugosa (Benth.) Woodson	M.A. Farinaccio	V.J. Pott 4412	L	E	An	CO, N, NE	

Marsdenia altissima (Jacq.) Dugand	M.A. Farinaccio	M.A. Farinaccio 932	L	E	An	CO, N, NE, SE	
M. macrophylla (Humb. & Bonpl. ex Schult.) E. Fourn.	M.A. Farinaccio	A. Pott 3260	L	E	An	CO, N, NE, S, SE	
Mesechites mansoanus (A.DC.) Woodson	A. Rapini	A. Pott 4508	L	E	An	CO, N, SE	
M. trifidus (Jacq.) Müll. Arg.	A.O. Simões	V.J. Pott 1190	L	E	An	CO, N, SE	
Odontadenia hypoglauca Müll.Arg.	A.O. Simões	A.G. Boaretto 294					
O. lutea (Vell.) Markgr.	A. Pott & V.J. Pott	A. Pott 2044	L	E	An	CO, N, NE, SE	
O. nitida (Vahl) Müll. Arg.	A.L. Scudeler	A. Pott 4819	L	E	An	CO, N	
Oxypetalum arnottianum H.Buek. ex E.Fourn.	A.J.M. Leeuwenberg	V.J. Pott 3769	H	E	An	CO, S, SE	
O. balansae Malme	V.J. Pott	A. Pott 3217	L	E	An	CO, N, S, SE	
***Plumeria rubra* L.			T	E	An	Exotic	
Prestonia coalita (Vell.) Woodson	G. Hatschbach	A. Pott 4508	L	E	An	CO, N, NE, S, SE	
P. erecta (Malme) J.F.Morales	A. L. Scudeler	A. Pott 4477	Ss	E	An	CO, N, NE, S, SE	
P. lagoensis (Muell. Arg.) Woodson	I. Koch	G.A. Damasceno Jr. 832	L	E	An	CO, NE, SE	
P. quinquangularis (Jacq.) Spreng.	M.C.S. Rio	A.C. Araújo 1021	L	E	An	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

P. tomentosa R.Br.	I. Koch	A. Pott 13070	L	E	An	CO, N, NE, S, SE	
Rauvolfia ligustrina Willd.	I. Koch	V.J. Pott 1204	S	E	An	CO, N, NE, SE	
Rhabdadenia madida (Vell.) Miers	S.G. Tressens; I. Koch	A. Pott 3171	L	E	An	CO, N, S, SE	
Schubertia grandiflora Mart. & Zucc.	J. Fontella	A. Pott 1807	L	E	An	CO, N, NE, S, SE	
Secondatia densiflora A.DC.	J.A. Ratter	A. Pott 5174	L	E	An	CO, N, NE, SE	
Tabernaemontana flavicans Willd. ex Roem. & Schult.	L. Kinoshita	A.C. Cervi 3343	S	E	Z	CO, N, NE, SE	
T. siphilitica (L.f.) Leeuwenb.	S. Tressens	A. Pott 4945	S	E	Z	CO, N, NE	
Tassadia berteroana (Spreng.) W.D.Stevens	J. Fontella	A. Pott 4690	L	E	An	CO, N, S, SE	
Telminostelma corymbosum (Decne.) Fontella & K.Schum.	J. Fontella	A. Pott 1756	L	E	An	CO, N	
Thevetia bicornuta Müll. Arg.	J.A. Ratter	A. Pott 5941	S	E	An	CO	
***T. peruviana* (Pers.) K. Schum.	A.O. Simões	T. Stefanello 28	S	Z	An	CO, N, NE, SE	
Tweedia brunonis Hook. & Arn.	A. Pott & V.J. Pott	A. Pott 3898	L	E	Na	CO	
Aquifoliaceae							
Ilex affinis Gardner	V.J. Pott	S.N. Moreira 1563	T	E	Z	CO, N, NE, S, SE	

Araceae (including Lemnaceae)							
Anthurium plowmanii Croat	E.G. Gonçalves	A. Pott 5294	H	E	Z	CO, N	
Dieffenbachia aglaonematifolia Engl.	E.G. Gonçalves	V.J. Pott 2156	H	E	Z	CO, N, NE, S, SE	
***D. amoena* Hort. ex Gentil	E.P. Seleme	E.P. Seleme 436	H	E		Exotic	
Dracontium margaretae Bogner	E.G. Gonçalves	V.J. Pott 3045	H	E	Z	CO, N	
***Epipremmum aureum* (L.) Engl.			L	E	Z	Exotic	
Lemna aequinoctialis Welw.	V.J. Pott; E. Landolt	V.J. Pott 2295	H	E	Hy	CO, N, NE, S, SE	
L. minuta Kunth	V.J. Pott; E. Landolt	V.J. Pott 1833	H	E	Hy	CO, N, NE, S, SE	
L. valdiviana Phil.	V.J. Pott; E. Landolt	V.J. Pott 2124	H	E	Hy	CO, N, NE, S, SE	
Philodendron megalophyllum Schott	E.E. Gonçalves	A. Pott 5046	T/S	E	Z	CO, NE, SE	
Pistia stratiotes L.	V.J. Pott	V.J. Pott 2918	H	E	Hy	CO, N, NE, S, SE	
Spathicarpa hastifolia Hook.	J.A. Ratter	A. Pott 3822	H	E	Z	CO, S, SE	
Spirodela intermedia W.Koch	V.J. Pott; E. Landolt	V.J. Pott 2532	H	E	Hy	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Taccarum weddellianum Brongn ex Schott	V.J. Pott; E.G. Gonçalves	A. Pott 7700	H	E	Z	CO, N. NE	
Urospatha sagittifolia (Rudge) Schott	V.J. Pott; E.G. Gonçalves	V.J. Pott 2679	H	E	Hy	CO, N, NE, SE	
Wolffia brasiliensis Wedd.	V.J. Pott; E. Landolt	V.J. Pott 2135	H	E	Hy	CO, N, NE, S, SE	
W. columbiana Karst.	V.J. Pott; E. Landolt	V.J. Pott 2238	H	E	Hy	CO, NE, S, SE	
Wolffiella lingulata (Hegelm.) Hegelm.	V.J. Pott; E. Landolt	V.J. Pott2302	H	E	Hy	CO, N, NE, S, SE	
W. oblonga (Phil.) Hegelm.	V.J. Pott; E. Landolt	V.J. Pott 1992	H	E	Hy	CO, N, NE, S, SE	
W. welwitschii (Hegelm.) Monod	V.J. Pott; E. Landolt	V.J. Pott 2305	H	E	Hy	CO, N, NE, SE	
Xanthosoma aristeguietae (G.S.Bunting) Madison	V.J. Pott; E.G. Gonçalves	V.J. Pott 3350	H	E	Z, Hy	CO, N	
X. helleborifolium (Jacq.) Schott	M.N. Coelho	A. Pott 5250	H	E	Z	CO, N, NE, SE	
X. pottii E.G.Gonç.	E.G. Gonçalves	A. Pott 7685 (Typus)	H	E	Z	CO	
X. striatipes (Kunth & Bouché) Madison	V.J. Pott; E.G. Gonçalves	V.J. Pott 3043	H	E	Z, Hy	CO, N, NE, SE	
Araliaceae (including part of Apiaceae)							
Hydrocotyle pusilla A. Rich.	V.J. Pott	S.N. Moreira 1562	H	E	Au	CO, NE, S, SE	
H. ranunculoides L.f.	B.E. Irgang	V.J. Pott 1842	H	E	Hy	CO, NE, S, SE	
H. verticillata Thunb.	B.E. Irgang	A.C. Cervi 4247	H	E	Au	Co, S, SE	
***Heptapleurum actinophyllum* (Endl.) Lowry & G.M. Plunkett			T	E		Exotic	

Arecaceae							
Acrocomia corumbaensis S.A.Vianna	S.A. Vianna	S.A. Vianna 27 (Typus)	T	E	Z	CO	Brazil
A. totai Mart.	S.A. Vianna	V.J. Pott 2408	T	E	Z	CO, N, NE, S, SE	
Allagoptera leucocalyx (Drude) Kuntze	J.A. Ratter	A. Pott 4306	S	E	Z	CO, NE, S, SE	
Astrocaryum vulgare Mart.	A. Pott & V.J. Pott	V.J. Pott 8365	T	E	Z	CO, N, NE	
Attalea phalerata Mart. ex Spreng.	J.A. Ratter	A. Pott 4427	T	E	Z	CO, N, SE	
A. speciosa Mart. ex Spreng.	A. Pott	A. Pott 6454	T	E	Z	CO, N, NE	
Bactris brongniartii Mart.	G.A. Elias	G.A. Damasceno Jr. 3032	S	E	Z, Hy	CO, N, NE	
B. glaucescens Drude	A. Pott	A. Pott 4513	S	E	Z, Hy	CO, N	
B. major Jacq.	M. Moraes R.	G.A. Damasceno Jr. 2392	S	E	Z, Hy	CO, N, NE	
B. riparia Mart.	M. Moraes R.	G.A. Damasceno Jr. 2344	T	E	Z, Hy	CO, N	
***Cocos nucifera* L.			T	E	Z	Exotic	
Copernicia alba Morong ex Morong & Britton	A. Pott	A. Pott 1880	T	E	Z	CO	
Desmoncus horridus Splitg. ex Mart.	A.J. Henderson	M. Schessl 2299	L	E	Z	CO, N, NE	
D. orthacanthus Mart.	M. Moraes R.	A. Pott 2609	L	E	Z	CO, NE, S, SE	
***Euterpe oleracea* Mart.			L	E	Z	CO, N, NE	

(continued)

Table 3.1 (continued)

Mauritia flexuosa L.f.	V.J. Pott	A. Pott 5430	T	E	Z	CO, NE, S, SE	
***Roystonea regia* (Kunth) O.F. Cook			T	E	Z	Exotic	
Syagrus flexuosa (Mart.) Becc.	J.A. Ratter	A. Pott 4389	S	E	Z	CO, NE, S, SE	Brazil
Trithrinax schizophylla Drude	I.H. Ishii	I.H. Ishii 780	T	E	Z	CO	
Aristolochiaceae							
Aristolochia arcuata Mast.	L.Z. Ahumada	G. Hatschbach 21904	L	E	Au	CO, S, SE	Brazil
A. esperanzae Kuntze	A. Pott	A. Pott 3411	L	E	Au	CO, SE	
A. holostylis F.González	A. Pott	A. Pott 13666	Ss	E	Au	CO, N, NE	
A. labiata Willd.	A. Pott	L.V.S. Campos 55	L	E	Au	CO, N, NE, S, SE	
A. odoratissima L.	A. Pott	A. Pott 4073	L	E	Au	CO, N, NE, S, SE	
A. ridicula N.E.Brown	A. Pott	A. Pott 3419	L	E	Au	CO, SE	
A. rojasiana (Chodat & Hassl.) Hosseus	A. Pott	A. Pott 12692	L	E	Au	CO, SE	
A. urupaensis Hoehne	A. Pott	L.V.S. Campos 696	L	E	Au	CO, N, SE	
Asparagaceae							
***Asparagus aethiopicus* L.			L	E		Exotic	
***Cordyline fruticosa* (L.) A.Chev.			S	E		Exotic	

***Furcraea gigantea* Vent,			H	E		Exotic	
Herreria salsaparilha Mart.	A. Pott & V.J. Pott	A. Pott 12879	L	E	An	CO, SE	Brazil
***Sansevieria cylindrica* Bojer			H	E		Exotic	
***S. trifasciata* Prain	M.A. Carniello	M.A. Carniello 03/06-2011	H	E		Exotic	
***Yucca elephantipes* Hort. ex Regel			S	E		Exotic	
Asteraceae							
**Acanthospermum australe* (Loefl.) Kuntze	G.M. Barroso	G. Hatschbach 21867	H	E	Z	CO, N, NE, S, SE	
**A. hispidum* DC.	A. Pott	A. Pott 1661	H	E	Z	CO, NE, S, SE	
Achyrocline gertiana Deble & Marchiori	L.P. Deble	F. Chagas e Silva 767	H	E	An	CO, SE	
A. satureioides (Lam.) DC.	A. Pott	A. Pott 2052	H	E	An	CO, NE, S, SE	
Acilepidopsis echitifolia (Mart. ex DC.) H. Rob.	R.L. Esteves; G. Heiden	V.J. Pott 2077	H	E	An	CO, SE	
**Acmella alpestris* (Griseb.) R.K.Jansen	H. Robinson	G. Hatschbach 74633	H	E	Au	CO	
A. decumbens (Sm.) R.K.Jansen	H. Robinson	G. Hatschbach 76331	H	E	Au	CO, NE, S, SE	
**A. grisea* (Chodat) R.K.Jansen	H. Robinson	G. Hatschbach 76212	H	E	Au	CO, S	

(continued)

Table 3.1 (continued)

Ageratum conyzoides L.	A. Pott	V.J. Pott 3493	H	E	An	CO, N, NE, S, SE	
**Ambrosia elatior* L.	A. Pott	A. Pott 5773	H	E	Au	S, SE	
**Artemisia verlotorum* Lamotte	A. Pott	A. Pott 7891	H	E	Au	CO, N, NE, S, SE	
Aspilia elata Pilg.	G.M. Barroso	A. Pott 1115	H	E	Au	CO, NE, SE	Brazil
A. floribunda (Gardner) Baker	B. Loeuille	A. Pott 3885	H	E	Au	CO, N, NE, S, SE	Brazil
A. foliacea (Spreng.) Baker	J.N. Nakajima	V.J. Pott 8528	H	E	Au	CO, N, S, SE	Brazil
A. latissima Malme	V.J. Pott & A .Pott	A. Pott 4485	Ss	E	Au, Hy	CO, S	Brazil
A. montevidensis (Spreng.) Kuntze	G.M. Barroso	A. Pott 2679	H	E	Au	CO, NE, S, SE	
A. silphioides (Hook. & Arn.) Benth. & Hook.	H. Robinson	J.M. Silva 4875	H	E	Au	CO	
Baccharis dracunculifolia DC.	G. Heiden	L.E.A.M. Lescano	S	E	An	CO, NE, S, SE	
B. glutinosa Pers.	M.G. Lopez; G. Heiden	A. Pott 4743	H	E	An	CO, NE, S, SE	
B. pingraea DC.	G.M. Barroso	G. Hatschbach 22026	Ss	E	An	CO, S	
Barrosoa candolleana (Hook. & Arn.) R.M.King & H.Rob.	N.I. Matzenbacher	V.J. Pott 3899	H	E	An	CO, S, SE	
Bidens gardneri Baker	A. Pott	A. Pott 1524	H	E	Z	CO, N, SE	
**B. pilosa* L.	V.J. Pott	S.S. Moura 137	H	E	Z	CO, S	
**B. subalternans* DC.	A. Pott	A. Pott 16891	H	E	Z	CO, S	
Calea candolleana Baker	G.H. Silva	A. Pott 12.897	H	E	Au	CO, N, NE, SE	Brazil

C. papposa Malme	J.N. Nakajima	A. Pott 6316	Ss	E	Au	CO	
C. reticulata Gardner	J.N. Nakajima	A. Pott 7615	H	E	Au	CO, N	
C. rupicola Chodat	H. Robinson	J.M. Silva 5294	H	E	Au	CO	
Campuloclinium macrocephalum (Less.) R.M King & H.Rob.	G.M. Barroso	A. Pott 4562	H	E	An	CO, N, NE, S, SE	
C. riedelii (Baker) R.M.King & H.Rob.	R.E. Esteves	A. Pott 4562	Ss	E	An	CO, S, SE	
**Centratherum punctatum* Cass.	A. Pott	A. Pott 17305	H	E	An	CO, N, NE, S, SE	
Chaptalia integerrima (Vell.) Burkart	A.M. Teles	L.E.A.M. Lescano 17		E	An	CO, NE, S, SE	
C. nutans (L.) Polak.	M.G. López	A. Pott 1243	H	E	An	CO, N, NE, S, SE	
Chromolaena arnottiana (Griseb.) R.M.King & H.Rob.	G.M. Barroso	A.Pott 1895	Ss	E	An	CO	
C. christieana (Baker) K.M.King & H.Rob.	M.G. López	A. Pott 4599	Ss	E	An	CO, S	
C. ivifolia (L.) K.M.King & H.Rob.	R.L. Esteves	A. Pott 1895	Ss	E	An	CO, N, S, SE	
C. laevigata (Lam.) K.M.King & H Rob.	A. Pott	A. Pott 13057	S	E	An	CO, N, NE, S, SE	
C. lilacina (Hieron.) R.M.King & H.Rob.	A. Pott	S.N. Moreira 848	Ss	E	An	CO	Brazil

(continued)

Table 3.1 (continued)

C. maximilianii (Schrad. ex DC.) K.M.King & H. Rob.	A.C. Fernandes	A.C. Araújo 1176	S	E	An	CO, N, NE, S, SE	
C. odorata (L.) K.M.King & H.Rob.	C.L. Cristóbal	A. Pott 1833	S	E	An	CO, N, NE, S, SE	
C. orbignyana (Klatt) R.M.King & H.Rob.	A.M. Teles	A. Pott 12840	S	E	An	CO, N	
C. picta (Gardner) R.M. King & H.Rob.	A.M. Teles	L.E.A.M. Lescano 213	S	E	An	CO, SE	Brazil
C. squalida (DC.) K.M.King & H.Rob.	A.C. Fernandes	A. Pott 1090	Ss	E	An	CO, N, NE, S, SE	
Chrysolaena cognata (Less.) Dematt.	G.M. Barroso	M. Schessl 275/1-4	Ss	E	An	CO, S, SE	
C. propinqua (Hieron.) H. Rob.	B. Loeuille	A. Pott 4077	Ss	E	An	CO, S, SE	
Clibadium armani (Balb.) Sch. Bip. ex O.E.Schulz	V.J. Pott	V.J. Pott 8386	Ss	E	An	CO, N, NE, S, SE	
Conyza bonariensis (L.) Cronquist	N.I. Matzenbacher	A. Pott 4653	H	E	An	CO, N, NE, S, SE	
**Cosmos caudatus* Kunth	A. Pott & V.J. Pott	A. Pott 4775	H	E	Au, Z	CO, NE, SE	
Critonia megaphylla (Baker) R.M.King & H.Rob.	V.C. Souza	V.C. Souza 32443	S	E	Au	CO, S, SE	
Cyrtocymura cincta (Griseb.) H.Rob.	B. Loeuille	A. Pott 2902	Ss	E	An	CO	
Dimerostemma apense (Chodat) M.D.Moraes	M.D. Moraes	M.D. Moraes 614	S	E	Au	CO	

D. goyazense (Gardner) D.M.Moraes	J.N. Nakajima	G.P. Nunes 177	Ss	E	Au	CO, SE	Brazil
D. indutum (Chodat) M.D.Moraes	H. Robinson; M.D. Moraes	G. Hatschbach 17179	Ss	E	Au	CO	
D. paneroi M.D.Moraes	J.N. Nakajima	J.M. Resende 938	Ss	E	Au	CO	Brazil
D. virgosum H. Rob.	M.D. Moraes	A. Pott 8009	Ss	E	Au	CO	Brazil
Eclipta prostrata (L.) L.	H. Robinson	G. Hatschbach 60939	H	E	Au	CO, N, NE, S, SE	
**Elephantopus mollis* Kunth	A. Pott	A. Pott 5597	H	E	Au	CO, N, NE, S, SE	
E. palustris Gardner	V.J. Pott	S.N. Moreira 832	H	E	Au	CO, N, NE, S, SE	
**Emilia forsbergii* Nicolson	V.J. Pott	V.J. Pott 2051	H	E	An	CO, N, NE, S, SE	
**E. sonchifolia* (L.) DC. ex Wight	V.J. Pott	V.J. Pott 3570	H	E	An	CO, N, NE, SE	
Enhydra anagallis Gardner	C.D.K. Cook	V.J. Pott 3194	H	E	Hy	CO, S, SE	
Erechtites hieracifolius (L.) Raf. ex DC.	V.J. Pott	V.J. Pott 1072	H	E	An	CO, N, NE, S, SE	
**Galinsoga parviflora* Cav.	A. Pott	L.V.S. Campos 27	H	E	Au	CO, N, NE, S, SE	
**Gamochaeta americana* (L.) Wedd.	A. Pott	A. Pott 2068	H	E	An	CO, NE, S, SE	
G. pensylvanica (Willd.) Cabrera	G.M. Barroso	A. Pott 2779	H	E	An	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

**Gnaphalium spathulatum* Burm.f.	J.N. Nakajima	A. Pott 5631	H	E	An	Exotic	
***Gymnanthemum amygdalinum* (Delile) Sch.Bip. ex Walp.	G.M. Barroso; B. Loeuille	A. Pott 5099	S	E	An	Exotic	
Gymnocoronis spilanthoides (Hook. & Arn.) DC.	V.J. Pott	V.J. Pott 6238	H	E	An, Hy	CO, N, NE, S, SE	
Isostigma hoffmannii Kuntze	J.N. Nakajima; G. Heiden	A.L.B. Sartori 1079	H	E	Au	CO	
Lagascea mollis Cav.	H. Robinson	G. Hatschbach 72312	H	E	An	CO, NE, SE	
Lepidaploa amambaia H. Rob.	B. Loeuille	C.S. Souza 29	H	E	Na	CO	Brazil
L. balansae (Chodat) H.Rob.	B. Loeuille	A. Pott 2881	Ss	E	An	CO, S, SE	
L. helophila (Mart. ex DC.) H.Rob.		L.E.A.M. Lescano 18	Ss	E	An	CO, NE, SE	
L. muricata (DC.) H Rob.	A.L.B. Sartori	F.J. Kochanowski 471	S	E	An	CO, SE	
L. reflexa (Gardner) H. Rob.	J.N. Nakajima	D.K. Noguchi 35	Ss	E	An	NE, SE	Brazil
L. remotiflora (L.C.Rich.) H.Rob.	G. Heiden	A. Pott 1834	Ss	E	An	CO, N, NE, S, SE	
Lessingianthus brevifolius (Less.) H.Rob.	G.M. Barroso	A. Pott 4624	H	E	An	CO, S, SE	
L. grandiflorus (Less.) H.Rob.	G. Heiden	A.Pott 7689	Ss	E	An	CO, S, SE	

L. rubricaulis (Humb. & Bonpl.) H.Rob.	G.M. Barroso	V.J. Pott 3128	Ss	E	An	CO, S, SE	
Lycoseris retroflexa Koster	G.M. Barroso	G. Hatschbach 21906	Ss	E	An	CO	
Melanthera latifolia (Gardner) Cabrera	C.L. Cristóbal	A. Pott 3093	H	E	Au, Hy	CO, N, NE, S, SE	
Mesanthophora rojasii (Cabrera) H.Rob.	B. Loeuille	A. Pott 3645	Ss	E	An	CO	
Mikania capricorni H.Rob.	N.I. Matzenbacher	A. Pott 4292	L	E	An	CO, S, SE	
M. cordifolia (L.f.) Willd.	G.M. Barroso	N.C. Bueno 21	L	E	An	CO, N, NE, S, SE	
M. cynanchifolia Hook. & Arn. ex B.L.Rob.	R.L. Esteves	V.J. Pott 1011	L	E	An	CO, S	
M. malacolepis B.L Rob.	N.I. Matzenbacher	A. Pott 1943	L	E	An	CO, S	Brazil
M. micrantha Kunth	G.M. Barroso	V.J. Pott 1011	L	E	An	CO, N, NE, S, SE	
M. parodii Cabrera	G.M. Barroso	A. Pott 2678	L	E	An	CO, S	
M. stenophylla W.C.Holmes	G. Heiden	V.J. Pott 3344	L	E	An	CO	X
Moquiniastrum barrosoae (Cabrera) G. Sancho	J.N. Nakajima	A. Pott 11414	S	E	An	CO, NE, S, SE	
Orthopappus angustifolius (Sw.) Gleason	N.I. Matzenbacher	A. Pott 1548	H	E	An	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Pacourina edulis Aubl.	V.J. Pott	V.J. Pott 2520	H	E	Au, Hy	Co, N, SE	
**Parthenium hysterophorus* L.	A. Pott	A. Pott 2117	H	E	An	CO, N, NE, S, SE	
Pectis gardneri Baker	J.N. Nakajima	A.Pott 11404	H	E	Au	CO, NE	Brazil
P. odorata Griseb.	H. Robinson	G. Hatschbach 76571	H	E	Au	CO	
P. stella Malme	H. Robinson	G. Hatschbach 21968	H	E	Au	CO, NE	Brazil
P. substriata Rusby	A. Pott	A. Pott 177475	H	E	Au	CO	
Plagiocheilus tanacetoides Haenk. ex DC.	C.L. Cristóbal	A. Pott 5122	H	E	Au	CO	
Pluchea sagittalis (Lam.) Cabrera	N.I. Matzenbacher	A. Pott 3766	H	E	An	CO, N, NE, S, SE	
**Porophyllum lanceolatum* DC.	C.L. Cristóbal	A.Pott 1767	H	E	An	CO, N, NE, S, SE	
**P. ruderale* (Jacq.) Cass.	A. Pott & G.A. Damasceno Jr.	F.S. Carvalho 132	H	E	An	CO, N, NE, S, SE	
Praxelis clematidea (Griseb.) R.M.King & H.Rob.	A. Pott	A. Pott 5036	H	E	An	CO, N, NE, S, SE	
P. diffusa (Rich.) Pruski	R.L. Esteves	B. Dubs 516	H	E	An	CO, N, NE, S, SE	
P. kleinioides (Kunth) R.M.King & H.Rob.	J.N. Nakajima	V.J. Pott 4118	H	E	An	CO, N, NE, S, SE	
P. ostenii (H.Rob.) R.M.King & H.Rob.	H. Robinson	G. Hatschbach 76215	H	E	An	CO, NE, S	
P. pauciflora (Kunth) R.M.King & H Rob.	A.C. Fernandes	G.A. Damasceno Jr. 2312	H	E	An	CO, N, NE, S	

Pterocaulon alopecuroides (Lam.) DC.	O.S. Ribas	A. Pott 7027	H	E	An	CO, N, NE, S, SE	
**P. lanatum* Kuntze	A. Pott	A. Pott 7925	Ss	E	An	CO, S, SE	
P. lorentzii Malme	O.S. Ribas	A. Pott 1743	H	E	E	CO, S, SE	
P. purpurascens Malme	C.L. Cristóbal	A. Pott 6815	H	E	An	CO	
Salmea scandens (L.) DC.	M.A.G. Magenta	A.Pott 4909	S	E		CO, SE	
Solidago chilensis Meyen	N.I. Matzenbacher	A. Pott 3862	H	E	An	CO, NE, S, SE	
Sphagneticola brachycarpa (Baker) Pruski)	C.L. Cristóbal	A. Pott 1863	H	E	Au, Hy	CO	
S. trilobata (L.) Pruski	B. Loeuille	I.M. Bortolotto 1612	H	E	Au	CO, N, S, SE	
Stilpnopappus pantanalensis H.Rob.	H. Robinson	G. Hatschbach 60918	H	E	An	CO	Pantanal
**Synedrellopsis grisebachii* Hieron. & Kuntze	A. Pott	A. Pott 6236	H	E	Au	CO, NE, SE	
**Tagetes minuta* L.	B. Loeuille	A. Pott 6355	H	E	Au	CO, NE, S, SE	
Tilesia baccata (L.f.) Pruski	E.K.O. Hattori	G. Hatschbach 73085	H	E	Z	CO, N, NE, S, SE	
***Tithonia diversifolia* (Hemsl.) A.Gray			S	E	Au	Exotic	
Trichospira verticillata (L.) S.F.Blake	T.M. Pedersen	A. Pott 5441	H	E	Au, Hy	CO, N, NE, S	

(continued)

Table 3.1 (continued)

**Tridax procumbens* L.	H. Robinson	G. Hatschbach 52492	H	E	An	CO, N, NE, S, SE	
Trixis antimenorrhoea (Schrank) Kuntze	A. Pott	A. Pott 2008	S	E	An	CO, NE, S, SE	
**Unxia kubitzkii* H. Rob.	M.A. Carniello	M.A. Carniello 195	H	E	Au	CO, N	Brazil
Urolepis hecatantha (DC.) K.M.King & H Rob.	M.G. López	A. Pott 4001	H	E	An	CO, S, SE	
Vernonanthura brasiliana (L.) H.Rob.	G.M. Barroso; G. Heiden	A. Pott 5093	S	E	An	CO, N, NE, S, SE	
V. ferruginea (Less.) H. Rob.	A. Pott; G. Heiden	A. Pott 4274	S	E	An	CO, N, NE, S, SE	
V. membranacea (Gardner) H.Rob.	B. Loeuille	A. Pott 8026	Ss	E	An	CO, N, SE	
V. petiolaris (DC.) H. Rob.	J.N. Nakajima	L.E.A.M. Lescano 288	S	E	An	CO, NE, SE	Brazil
V. polyanthes Vega & M Dematt.	H.F. Leitão F.; G. Heiden	A. Pott 2189	S	E	An	CO, NE, SE	
V. tweediana (Baker) H. Rob.	G.M. Barroso	A. Pott 1874	S	E	An	CO, NE, S, SE	
Wedelia brachylepis Griseb.	H. Robinson	G. Hatschbach 76562	H	E	Au	CO	
W. calycina Rich.	T.S. Mendes	G. Martinelli 18618	Ss	E	Au	CO, N. NE	
W. pilosa Baker	H. Robinson	W.W. Thomas 4267	H	E	Au	CO, SE	Brazil
W. subvelutina DC.	A.A. Saenz	A. Pott 3358	H	E	Au	CO, N, S, SE	Brazil
W. trichostephia DC.	J.N. Nakajima	L.E.A.M. Lescano 94	Ss	E	Au	CO, N, NE, S	
Balanophoraceae							

Helosis cayennensis (Sw.) Spreng.	A. Pott	A. Pott 16306	Hp	E	Z	CO, N, NE, S, SE	
Langsdorffia hypogaea Mart.	A.M. Radovancich	A. Pott 2931	Hp	E	Z	CO, N, NE, S, SE	
Lophophytum mirabile Schott & Endl.	V.J. Pott	V.J. Pott 7819	Hp	E	Z	CO, N, NE, S, SE	Brazil
Basellaceae							
**Basella alba* L.	R.A.S. Campos	R.A.S. Campos	L			Exotic	
Begoniaceae							
Begonia cucculata Wiild.	V.J. Pott	V.J. Pott 5785	H	E	An, Hy		
B. lindmanii Brade	V.J. Pott	V.J. Pott 6326	H	E	An	CO	Brazil
Bignoniaceae							
Adenocalymma nodosum (Silva Manso) L.G.Lohmannn	L.H.M. Fonseca	A. Pott 2298	T	E	An	CO, N, NE, SE	Brazil
Amphilophium crucigerum (L.) L.G.Lohmann	A. Pott	A. Pott 4305	L	E	An	CO, N, NE, S, SE	
Anemopaegma brevipes S.Moore	M.M. Arbo, M.M. Silva-Castro	A. Pott 6216	L	E	An	CO	Brazil
A. longipetiolatum Sprague	M.M. Silva-Castro	A. Pott 4636	Ss	E	An	CO, NE, SE	
Bignonia corymbosa (Vent.) L.G.Lohmann	C.E.B. Proença	A. Pott 3660	L	E	An	CO, N, NE, SE	
B. decora (S.Moore) L.G.Lohmann	A.H. Gentry; A.R. Zuntini	G. Schaller 83	L	E	An	CO, S, SE	

(continued)

Table 3.1 (continued)

Callichlamys latifolia (Rich.) K.Schum.	C.E.B. Proença	A. Pott 4702	L	E	An	CO, N, NE, SE	
***Crescentia cujete* L.			T	E	An	CO, N, NE, SE	
Cuspidaria lateriflora (Mart.) DC.	C.E.B. Proença	A. Pott 4964	L	E	An	CO, N, NE, SE	
Dolichandra cynanchoides Cham.	A. Pott	A. Pott 12873	L	E	An	CO, S	
D. quadrivalvis (Jacq.) L.G.Lohmann	M.M. Arbo	A. Pott 4455	L	E	An	CO, N, NE, S, SE	
D. uncata (Andrews) L.G.Lohmann	L.H.M. Fonseca	A. Pott 5435	L	E	An	CO, N, NE, S, SE	
D. unguis-cati (L.) L.G.Lohmann	C.E.B. Proença	A. Pott 3641	L	E	An	CO, N, NE, S, SE	
Fridericia candicans (Rich.) L.G.Lohmann	M.M. Arbo	A. Pott 4824	L	E	An	CO, N	
F. conjugata (Vell.) L.G.Lohmann	J. Semir	G.A. Damasceno Jr. 728	L	E	An	CO, N, NE, S, SE	
F. dichotoma (Jacq.) L.G.Lohmann	J.E.Q. Faria	A. Pott 3653	L	E	An	CO, N, NE, SE	
F. fagoides (Cham.) L.G.Lohmann	A.H. Gentry	G. Schaller 77	L	E	An	CO, SE	
F. florida (DC.) L.G.Lohmann	A. Pott	A. Pott 5525		E	An	CO, N, NE, S, SE	
F. patellifera (Schltdl.) L.G.Lohmann	N.Y. Sandwith	G. Hatschbach 62742	L	E	An	CO, N	
F. platyphylla (Cham.) L.G.Lohmann	N. Saddi	N. Saddi 1007	L	Ean		CO, N, NE, S, SE	

F. pubescens (L.) L.G.Lohmann	A.H. Gentry	G. Hatschbach 21926	L	E	An	CO, N, NE, SE	
F. triplinervia (Mart. ex DC.) L.G.Lohmann	A. Pott	A. Pott 8818	L	E	An	CO, N, NE, S, SE	
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	A. Pott	A. Pott 13029	T	E, O	An	CO, NE, S, SE	
H. heptaphyllus (Vell.) Mattos	A. Pott	A. Pott 3225	T	E, O	An	CO, NE, S, SE	
H. impetiginosus (Mart. ex DC.) Mattos	J.A. Ratter	A. Pott 1395	T	E, O	An	CO, N, NE, SE	
H. ochraceus (Cham.) Mattos	J.A. Ratter	A. Pott 4326	T	E, O	An	CO, N, NE, S, SE	
H. serratifolius (A.H.Gentry) S.Grose	B.T.M. Walter	A. Pott 13199	T	E, O	An	CO, N, NE, S, SE	
H. umbellatus (Sond.) Mattos	R. Farias	A. Pott 7596	T	E, O	An	CO, NE, S, SE	
Jacaranda cuspidifolia Mart.	J.A. Ratter	A. Pott 3641	T	E, O	An	CO, SE	
J. decurrens Cham.	A. Pott	A. Pott 6492	S	E, O	An	CO, SE	
J. ulei Bureau & K. Schum.	A. Pott	A. Pott 13602	S	E, O	An	CO, NE, SE	Brazil
Perianthomega vellozoi Bureau	J.C. Gomes Jr.	E. Pereira 192	S	E	An	CO, SE	
Pleonotoma melioides (S.Moore) A.H.Gentry	B.M. Gomes	M. Nadruz 415	L	E	An	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

***Spathodea nilotica* Seem			T	E		Exotic	
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore	A. Pott	A. Pott 3281	T	E, O	An	CO, N, NE, S, SE	
T. insignis (Miq.) Sandwith	A. Pott	V.J. Pott 4417	T	E, O	An	CO, N, SE	
T. nodosa (Griseb.) Griseb.	A. Pott	A. Pott 4402	T	E, O	An	CO	
***T. rosea* (Bertol.) Bertero ex A.DC.	F.M. Alves		T	E, O	An	Exotic	
T. roseoalba (Ridl.) Sandwith	V.J. Pott	V.J. Pott 2138	T	E, O	An	CO, N, NE, SE	
Tanaecium jaroba Sw.	G.A. Damasceno Jr.	G.A. Damasceno Jr. 2904	L	E	An	CO, N	
T. mutabile (Bureau ex K.Schum.) L.G.Lohmann	A. Frazão	A. Pott 4377	L	E	An	CO, S, SE	
T. pyramidatum (Rich.) L.G.Lohmann	A. Pott	A. Pott 3660	L	E	An	CO, N, NE, S, SE	
T. selloi (Spreng.) L.G.Lohmann	A.H. Gentry	G. Hatschbach 49.249	L	E	An	CO, NE, S, SE	
***Tecoma stans* (L.) Juss. ex Kunth			L	E	An	Exotic	
Xylophragma pratense (Bureau & K. Schum.) Sprague	A.H. Gentry	B. Dubs 1035	L	E	An	CO, N, NE, S, SE	
Bixaceae							
Bixa orellana L.	A. Pott	A. Pott 6252	T	E	Z	CO, N, NE, S, SE	

Cochlospermum regium (Mart. ex Schrank) Pilg.	A. Pott	A. Pott 4373	S	E	An	CO, N, NE, S, SE	
Boraginaceae							
Cordia alliodora (Ruiz & Pav.) Cham.	A. Pott	A. Pott 2270	T	E	An	CO, N, NE	
C. brasiliensis (I.M.Johnst.) Gottschilng & J.S.Mill.	V.C. Souza	H. Lorenzi 14448	T	E	An	CO	Brazil
C. glabrata (Mart.) A. DC.	J.A. Ratter	A. Pott 3823	T	E	An	CO, N, NE, SE	
C. insignis Cham.	A. Pott	A. Pott 4776	S	E	An	CO, NE, SE	
C. naidophila I.M.Johnst.	C.N. Cunha	A. Pott 5155	T	E	An	CO, N	
C. sellowiana Cham.	J.N. Nakajima	V.J. Pott 3940	T	E	Z	CO, N, NE, SE	
C. tetrandra Aubl.	M.N.S. Stapf	A. Pott 2970	T	E	Z	CO, N, NE	
C. trichotoma (Vell.) Arráb. ex Steud.	A. Pott	A. Pott 2270	T	E	An	CO, NE, S, SE	
Euploca filiformis (Lehm.) J.I.M.Melo & Semir	R.L. Degen N.	A. Pott 5151	H	E	Au	CO, N, NE, SE	
E. hassleriana (Chodat) J.I.M.Melo & Semir	J.I.M. Melo	A.C. Allem 13	H	E	Au	CO	
E. lagoensis (Warm.) Diane & Hilger	D.C. Daly	G. Schaller 255A	H	E	Au	CO, N, NE, SE	
E. pallescens (I.M.Johnst.) J.I.M.Melo & Semir	J.I.M. Melo	A. Pott 3634	H	E	Au	CO	

(continued)

Table 3.1 (continued)

E. paradoxa (Mart.) J.I.M.Melo & Semir	A. Pott	M. Schessl 2322	H	E	Au	CO, NE	Brazil
E. pottii J.I.M.Melo & Semir	J.I.M. Melo	A. Pott 1397 (Type)	H	E	Au	CO	Pantanal
E. procumbens (Mill.) Diane & Hilger	R.L. Degen N.	A. Pott 3322	H	E	Au	CO, N, NE, S, SE	
Heliotropium indicum L.	A. Pott	A. Pott 4475	H	E	Au	CO, N, NE, S, SE	
Myriopus paniculatus (Cham.) Feuillet	A. Pott	A.Pott 5402	L	E	Z	CO, NE, S, SE	
Varronia chacoensis (Chodat) Borhidi	A. Schinini	A.Pott 2911	S	E	Z	CO	
V. curassavica Jacq.	A. Schinini	A. Pott 1698	Ss	E	Z	CO, N, NE, S, SE	
V. polycephala Lam.	V.J. Pott	V.J. Pott 3427	S	E	Z	CO, N, NE, SE	
Brassicaceae							
***Brassica oleracea* L.			H	E	Au	Exotic	
**Cardamine bonariensis* Pers.	A. Pott	A. Pott 13439	H	E	Au	Exotic	
***Eruca vesicaria* (L.) Cav.	M.A. Carniello	M.A. Carniello 4730	H	E	Au	Exotic	
**Lepidium virginicum* L.			H	E	Au	CO, NE, S, SE	
***Raphanus sativus* L.			H	E	Au	Exotic	
Bromeliaceae							
Aechmea distichantha Lem.	T. Wendt	A. Pott 4412	H	E	Au, An	CO, S, SE	

Ananas ananassoides (Baker) L.B.Sm.	J.F.M. Valls	A. Pott 4382	H	E	Z	CO, N, NE, S, SE	
A. bracteatus (Lindl.) Schult. & Schult.f.	M. Alves	A. Pott 8700	H	E	Z	CO, NE, S, SE	
*******A. comosus* (L.) Merril			H	O	Z	NE	Brazil
Billbergia zebrina (Herb.) Lindl.	V.J. Pott	A. Pott 10947	H	O	An	CO, S, SE	
Bromelia balansae Mez	V.J. Pott	V.J. Pott 714	H	E	Z	CO, N, S, SE	
B. hieronymi Mez	R.F. Monteiro	A.L.B. Sartori 1115	H	E	Z	CO	
B. interior L.B.Sm.	R.F. Monteiro	Castellanos & Strang 22472	H	E	Z	CO, NE, SE	
B. sylvicola S.Moore	G. Martinelli	G. Martinelli 18665	H	Z	Z	CO	Brazil
Dyckia leptostachya Baker	E. Leme	A. Pott 2022	H	O	An	CO, S	
Encholirium lymanianum E.Pereira & Martinelli	M. Moreli	M. Moreli 200	H	O	Au	CO	Brazil
Pseudananas sagenarius (Arruda) Camargo	T. Wendt	T. Wendt 262	H	O	Z	CO, NE, S, SE	
Tillandsia bryoides Griseb. ex Baker	A. Pott	A. Pott 15541	H	E	An	CO	
T. didisticha (E. Morren) Baker	V.J. Pott	V.J. Pott 1525	Ep	E	An	CO, S	
T. duratii Vis.	J.F.M. Valls; T. Wendt	V.J. Pott 829	Ep	E	An	CO	
T. geminiflora Brong.	V.J. Pott	A. Pott 16123	Ep	E	An	CO, NE, S, SE	
T. loliacea Mart. ex Schult. & Schult.f.	A. Pott	A. Pott 2019	Ep	E	An	CO, NE, S, SE	

(continued)

Table 3.1 (continued)

T. pohliana Mez	V.J. Pott	V.J. Pott 6044	Ep	E	An	CO, NE, S, SE	
T. recurvifolia Hook.	R.C. Tardivo	E. Barboza 1537	Ep	E	An	CO, S, SE	Brazil
T. streptocarpa Baker	T. Wendt	V.J. Pott 4318	Ep	E	An	CO, NE, S, SE	
T. stricta Sol.	R.F. Monteiro	A.K.D. Salomão 442	Ep	E	An	CO, NE, S, SE	Brazil
T. tenuifolia L.	M. Alves	M. Morelli 190	Ep	E	An	CO, NE, S, SE	
T. tricholepis Baker	J.V.C.	A. Pott 7094	Ep	E	An	CO, NE, S, SE	
T. vernicosa Baker	G.M. Paggi	G.M. Paggi 3	Ep	E	An	CO, NE	
Burmanniaceae							
Burmannia bicolor Mart.	J. van Benthem & P.J.M. Maas	Castellanos 22474	H	E	Au, Hy	CO, N, NE, SE	
B. capitata (Walter ex J.F.Gmel.) Mart.	V.J. Pott	A. Pott 2917	H	E	Au, Hy	CO, N, NE, SE	
C. flava Mart.	V.J. Pott	A. Pott 5563	H	E	Au, Hy	CO, N, NE, S, SE	
Burseraceae							
Commiphora leptophloeos (Mart.) J.B.Gillet	G.A. Damasceno Jr.	M.A.O. Bezerra 15	T	E	Z	CO, N, NE, SE	
Protium heptaphyllum (Mart.) Marchand	J. Tamashiro	A. Pott 1292	T	E	Z	CO, N, NE, SE	
Cabombaceae							
Cabomba furcata Schult. & Schult.f.	V.J. Pott	V.J. Pott 3177	H	E	Hy	CO, N, NE, SE	
C. haynesii Wiersema	V.J. Pott	A. Pott 1826	H	E	Hy, Z	CO, SE	
Cactaceae							

Brasiliopuntia brasiliensis (Wild.) A. Berger	G. A. Damasceno Jr.	G.A. Damasceno Jr. 2668	T	E, Q	Z	CO, N, NE, S, SE	
Cereus bicolor Rizzini & A.Mattos	G. A. Damasceno Jr.	A. Pott 5725	T	E, Q	Z	CO	Brazil
C. kroenleinii N.Taylor	N.P. Taylor	A. Pott 12036	S	E, Q	Z	CO	
C. saddianus (Rizzini & Mattos) P.J.Braun	N.P. Taylor	V.J. Pott 4904	S	E, Q	Z	CO	Brazil
C. stenogonus K.Schum.	D. Zappi	J.A. Siqueira-F. 2809	Ss	E, Q	Z	CO	
Cleistocactus baumannii (Lem.) Lem.	V.J. Pott	V.J. Pott 11689	Ss	O	Z	CO	
C. samaipatanus (Cárdenas) D.R.Hunt	V.J. Pott	V.J. Pott 9379	Ss	O	Z	CO	
Discocactus catinguicola Buining & Brederoo	D. Zappi	M.R. Santos 60	H	E	Z	CO, NE, S, SE	Brazil
Echinopsis rhodotricha K.Schum.	V.J. Pott	V.J. Pott 11690	H	E, Q	Z	CO	
Epiphyllum phyllanthus (L.) Haw.	D. Villarroel	M. Moraes 26	Ep	E, Q	Z	CO, N, NE, S, SE	
Frailea cataphracta (Dams) Britton & Rose	D. Zappi	V.J. Pott 7090	H	E, Q	Z	CO	
F. schilinzkyana (K.Schum.) Britton & Rose	D. Zappi	V.J. Pott 11884	H	E	Z	CO, S	

(continued)

Table 3.1 (continued)

Gymnocalycium anisitsii (K.Schum.) Britton & Rose	N.P. Taylor	V.J. Pott 6996	H	E	Z	CO	
G. marsoneri Y.Itô	D. Zappi	A.K.D. Salomoão 383	H	E	Z	CO	
Harrisia balansae (K.Schum.) N.P.Taylor & Zappi	N.P. Taylor	V.J. Pott 433	Ss	E, Q	Z	CO	
H. tortuosa (J.Forbes ex Otto & A.Dietr.) Britton & Rose	V.J. Pott; D. Zappi	P.R. Souza 5/2013	Ss	E, Q	Z	CO	
Hylocereus setaceus (Salm-Dyck) R.Bauer	V.J. Pott	V.J. Pott 11849	Ep	E	Z	CO, N, NE, S, SE	
Lepismium lumbricoides (Lem.) Borthlott	D. Zappi	V.N. Gomes 5	Ep	E, Q	Z	CO, S, SE	
Opuntia elata Salm-Dyck	V.J. Pott	V.J. Pott 11691	Ss	E	Z	CO, S	
O. monacantha Haw.	D. Zappi	V.J. Pott 435	Ss	E	Z	CO, NE, S, SE	
O. retrorsa Speg.	J.A. Lombardi	V.J. Pott 432	Ss	E	Z	CO	
Pereskia sacharosa Griseb.	A. Pott	A. Pott 5306	S, T	E	Z	CO	
Praecereus euchlorus (F.A.C.Weber) N.P.Taylor	D. Zappi	G.P. Nunes 293	Ss	E, Q	Z	CO, S, SE	
P. saxicola (Morong) N.P.Taylor	N.P. Taylor	B.H.S. Ferreira	L	E, Q	Z	CO	
Rhipsalis baccifera (J.F.Muell.) Stearns	A. Pott	A. Pott 11422	Ep	E	Z	CO, N, NE	
R. floccosa Salm-Dyck ex Pfeiff.	N.P. Taylor	J.A. Siqueira F. 2819	Ep	E	Z	CO, NE, S, SE	

Stetsonia coryne (Salm-Dyck) Britton & Rose	V.J. Pott	V.J. Pott 7530	T	E, Q	Z	CO	
Calophyllaceae (partly including Clusiaceae)							
Calophyllum brasiliense Cambess.	C.N. Cunha; A.M. Radovancich	A. Pott 4462	T	E	Z	CO, N, NE, S, SE	
Kielmeyera coriacea Mart. & Zucc.	A. Pott	A. Pott 2166	T	E	An	CO, N, NE, S, SE	
K. rubriflora Cambess.	A. Pott	A. Pott 2167	T	E	An	CO, N, NE, SE	
Campanulaceae							
Centropogon cornutus (L.) Druce	V.J. Pott	A.Pott 6575	H	O	Au, Z, Hy	CO, N, NE, SE	
Lobelia aquatica Cham.	V.J. Pott	V.J. Pott 3728	H	E	Au, Hy	CO, N, NE, S, SE	
L. nummulariodes Cham.	V.J. Pott	A. Pott 3363	H	E	Au, Hy	CO, S, SE	
Cannabaceae (partly including Ulmaceae)							
Celtis eherenbergiana (Klotzsch) Liebm.	M.H. Nee	J.E. Paula 1724	T	E	Z	CO, NE, SE	
C. iguanaea (Jacq.) Sarg.	J.A. Ratter	A. Pott 3787	T	E	Z	CO, N, NE, S, SE	
Trema micrantha (L.) Blume	A. Pott	A. Pott 5390	T	E	Z	CO, N, NE, SE	
Cannaceae							
Canna glauca L.	V.J. Pott	V.J. Pott 2150	H	E	Au, Hy	CO, N, NE, SE	
**C. indica* L.			H	E	Au	Exotic	

(continued)

Table 3.1 (continued)

C. paniculata Riuz & Pav.	V.J. Pott	V.J. Pott 10488	E	E	Au	CO, NE, S, SE	
Capparaceae							
Anisocapparis speciosa Cornejo & Iltis	D.E. Prado; A.M. Radovancich	A. Pott 4449	T	E	Z	CO	
Capparicordis tweediana (Eichler) Iltis & Cornejo	V.J. Pott	A. Pott 4451	S	E	Z	CO, NE, S, SE	
Capparidastrum osmanthus (Diels) Cornejo & Iltis		J.A. Ratter 6114	S	E	Z	CO	
Crateva tapia L.	A. Pott	A. Pott 6971	T	E	Z	CO, N, NE, SE	
Cynophalla declinata (Vell.) Iltis & Cornejo	H.H. Iltis	J.A. Ratter 5950	T	E	Z	CO, NE, S, SE	Brazil
C. mattogrossensis (Pilg.) Cornejo & Iltis	G.A. Damasceno Jr.	G.A. Damasceno Jr. 436	T	E	Z	CO, NE	Brazil
C. retusa (Griseb.) Cornejo & Iltis	D.E. Prado	A. Pott 4450	T	E	Z	CO	
Caricaceae							
*,***Carica papaya* L.	I.M. Bortolotto	I.M. Bortolotto 15-4-1998	T	E	Z	Exotic	
Jacaratia corumbensis Kuntze	J.A. Ratter	V.J. Pott 29	S, T	E	Z	CO, N, NE, SE	
Caryocaraceae							
Caryocar brasiliense Cambess.	J.F.M. Valls	J.F.M. Valls 9218	T	Q	Z	CO, N, SE	
Caryophyllaceae							
Paronychia communis Cambess.	J.A. Siqueira	A. Pott 2192	H	E	Au	CO, S, SE	
Polycarpaea corymbosa (L.) Lam.	V.J. Pott	T.H.D. Leandro 100	H	E	Au	CO, N, NE, S, SE	

Polycarpon depressum Nutt.	T.M. Pedersen	A. Pott 5267	H	E	Au	CO, N, SE	
Celastraceae (including Hippocrateaceae)							
Anthodon decussatum Ruiz & Pav.	J.A. Lombardi	L.V.S. Campos 676	L	E	An	CO, N, NE, SE	
Hippocratea volubilis L.	J.A. Ratter; A.M. Radovancich	A. Pott 3074	L	E	An	CO, N, NE, S, SE	
Monteverdia evonymoides (Reissek) Biral	J.A. Ratter	J.A. Ratter 7541	S	E	Z	CO, S, SE	
M. ilicifolia (Mart. ex Reissek) Biral	A.L.B. Sartori	F. Matos-Alves 453	S	E	Z	CO	Brazil
Peritassa campestris (Cambess.) A.C.Sm.	J.A. Lombardi	A. Pott 2278	S	E	Z	CO, N, NE, SE	
P. ducis (Benth.) Miers	J.A. Lombardi	G. Martinelli no n.	S	E	Z	CO, N, NE, SE	
Pristimera nervosa (Miers) A.C.Sm.	J.A. Lombardi	A. Pott 4144	L	E	An	CO, N, NE, SE	
Salacia arborea (Schrank) Peyr.	E.F .Guimarães	G. Martinelli 18648	S	E	Z	CO, NE, SE	
S. elliptica (Mart. ex Schult.) G. Don	J.A. Ratter; L. Biral	A. Pott 6752	T	E	Z	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Tontelea micrantha (Mart. ex Schult.) A.C.Sm.	J.A. Lombardi	A. Krapovickas 43125	S	E	Z	CO, N, NE, SE	
Ceratophyllaceae							
Ceratophyllum demersum L.	V.J. Pott	A. Pott 2259	H	Hy	Hy	CO, S, SE	
C. submersum L. var. *echinatum* (A.Gray) Wilmot-Dear	V.J. Pott	V.J. Pott 2526	H	Hy	Hy	CO, N	
Chrysobalanaceae							
Couepia grandiflora Benth.	J.A. Ratter	A. Pott 4376	T	E	Z	CO, N, NE, SE	
C. uiti (Mart. & Zucc.) Benth.	A. Pott	A. Pott 3762	T	E	Z	CO, N, SE	
Hirtella glandulosa Spreng.	J.A. Ratter; C.E.B. Proença	A. Pott 6511	S	E	Z	CO, N, SE	
H. gracilipes (Hook.f.) Prance	A. Pott	A. Pott 7663	T	E	Z	CO, N, NE, SE	
Leptobalanus apetalus (E.Mey.) Sothers & Prance	L.P. Queiroz	A. Pott 4277	T	E	Z	CO, N, NE, SE	
L. gardneri (Hook.f.) Sothers & Prance	G.T. Prance	A. Pott 4277	T	E	Z	CO, N, NE, SE	
L. humilis (Cham. & Schltdl) Sothers & Prance	E.F. Guimarães	G. Martinelli 16654	T	E	Z	CO, N, NE, SE	
Moquilea minutiflora Sagot	J.A. Ratter	A. Pott 3456	T	E	Z	CO, N, NE	

L. parvifolius (Huber) Sothers & Prance	C.N. Cunha	A. Pott 4463	T	E	Z	CO, N, NE	
***M. tomentosa* Benth.			T	E	Z	CO, NE, SE	
Cleomaceae (dismembered from Capparaceae)							
Cleoserrata paludosa (Willd. ex Eichler) Iltis	L.P. Queiroz	A.Pott 3857	Ss	E	Au	CO, NE, SE	
**Gynandropsis gynandra* (L.) Briq.	V.J. Pott	A.Pott 16087	H	E	Au	CO, NE, SE	
Physostemon guianense (Aubl.) Malme	A. Schinini	A.Pott 4132	H	E	Au	CO, N, NE, SE	
**Tarenaya aculeata* (L.) Soares Neto & Roalson	M.B. Costa e Silva	A.Pott 5344	H	E	Au	CO, N, NE, SE	
T. hassleriana (Chodat) H.H.Iltis	R. Tsuji	E.R. Salviani 595	Ss	E	Au	CO, NE, S, SE	
T. spinosa (Jacq.) Raf.	L.P. Queiroz	A. Pott 2684	H	E	Au	CO, N, NE, SE	
Clusiaceae							
Garcinia gardneriana (Planch. & Triana) Zappi	V.C. Souza	V.C. Souza 32282	T	E	Z	CO, N, NE, S, SE	
Combretaceae							
Terminalia grandis Ducke) Gere & Boatwr	N. Marquete	G.A. Damasceno Jr. 9454	T	E	Z	CO, N, NE	
T. oxycarpa Mart.	C.A. Stace	G.T. Prance 26243	T	E	Z	CO, N, NE	
T. tetraphylla (Aubl.) Gere & Boatwr	A. Pott	A. Pott 6998	T	E	Z	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

T. corrugata (Ducke) Gere & Boatwr	J.A. Ratter	A. Pott 5088	T	E	Z	CO, N, NE, SE	
Combretum duarteanum Cambess.	V.J. Pott	A. Pott 6332	T	E	An	CO, N, NE, SE	
C. fruticosum (Loefl.) Stuntz	G.A. Damasceno Jr.	G.A. Damasceno Jr. 2906	T	E	An	CO, N, NE, S, SE	
C. lanceolatum Pohl	A. Pott	A. Pott 2963	L	E	An	CO, N, NE, SE	
C. laxum Jacq.	A. Schinini	A. Pott 3265	L	E	An	CO, N, NE, S, SE	
C. leprosum Mart.	C.A. Stace	A. Pott 5450	T	E	An	CO, N, NE, SE	
C. mellifluum Eichler	A. Pott	A. Pott 6422	S	E	An	CO, N, NE, SE	
***Quisqualis indica* L.	V.C. Souza	V.C. Souza 32287	L	E	An	Exotic	
Terminalia argentea Mart.	J.A. Ratter	A. Pott 3236	T	E	An	CO, N, NE, S, SE	
***T. catappa* L.	E.P. Seleme	E.P. Seleme 447	T	E	Z	Exotic	
T. fagifolia Mart.	N.M.F. Silva	D.T. Azevedo 44	T	E	An	CO, NE, SE	
Commelinaceae							
Callisia filiformis (M.Martens & Galeotti) D.R.Hunt	R.C. Barreto	A. Pott 4706	H	E	Au	CO, NE	
**Commelina benghalensis* L.	V.J. Pott	V.J. Pott 6107	H	E		CO, N, NE, S, SE	
C. diffusa Burm.f.	L.Y.S. Aona	F.S. Carvalho 149	H	E	Au	CO, N, NE, S, SE	
C. erecta L.	R.C. Barreto	V.J. Pott 1656	H	E	Au	CO, N, NE, S, SE	
C. longicaulis Jacq.	R.B. Faden; G. Hassemer	V.J. Pott 3195	H	E	Au, Hy	CO, NE	Brazil

C. obliqua Vahl	L.Y.S. Aona	A. Pott 10915	H	v	Au	CO, N, NE, S, SE	
C. platyphylla Klotzsch ex Seub.	R.B. Faden	A. Pott 4472	H	E	Au	CO	
C. rufipes Seub.	L.Y.S. Aona; G. Hassemer	A. Pott 11065	H	E	Au		
Gibasis geniculata (Jacq.) Rohweder	L.Y.S. Aona	A. Pott 12864	H	E	Au	CO, N, NE, S, SE	
Dichorisandra hexandra (Aubl.) C.B.Clarke	R.C. Barreto	V.J. Pott 6133	H	E	Au	CO, N, NE, S, SE	
D. villosula Mart. ex Schult.f.	L.Y.S. Aona	G.A. Damasceno Jr. 3121	H	E	Au	N, SE	
Floscopa glabrata (Kunth) Hassk.	A. Pott	L.V.S. Campos 66z	H	E	Au	CO, N, NE, S, SE	
Murdannia engelsii M.Pell. & Faden	R.B. Faden; M. Pellegrin	V.J. Pott 595 (Paratypus)	H	E	Au, Hy	CO, N, NE, SE	Brazil
M. nudiflora (L.) Brenan	R.B. Faden; L.Y.S. Aona	A. Pott 4706	H	E	Au	CO	
M. semifoliata (C.B.Clarke ex S.Moore) G.Brückn.	L.Y.S. Aona	V.J. Pott 4112	H	E	Au	CO	Brazil
***Tradescantia pallida* (Rose) D.R.Hunt	G. Hassemer	S.S. Moura 185	H			Exotic	
Tripogandra glandulosa (Seub.) Rohweder	R.B. Faden	A. Pott 4133	H	E	Au	CO, N, NE, SE	
Connaraceae							

(continued)

Table 3.1 (continued)

Connarus suberosus var. *fulvus* (Planch.) Forero	J.A. Ratter	A. Pott 3831	T	E	Z	CO, N, NE	Brazil
R. induta Planch.	J.A. Ratter	A. Pott 5063	T	E	Z	CO, N, NE, SE	Brazil
R. puberula Baker	E. Forero	A. Pott 132684	S, L	E	Z	CO, N	
Convolvulaceae							
Aniseia martinicensis (Jacq.) Choisy	A. Pott	A. Pott 4165	L	E	Au	CO, N, NE, SE	
Bonamia balansae Hallier f.	A. Pott	A. Pott 4596	L	E	Au	CO	
Camonea umbellata (L.) A.R.Simões & Staples	V.J. Pott	A. Pott 5090	L	E	Au, Hy	CO, N, NE, S, SE	
Cuscuta cf. *obtusiflora* Kunth	V.J. Pott	V.J. Pott 3719	P	E	Au	CO, SE	
Distimake aturensis (Kunth) A.R.Simões & Staples	R. Simão-Bianchini; G. Staples	V.J. Pott 6313	L	E	Au	CO, N, SE	
D. cissoides (Lam.) A.R.Simões & Staples	V.J. Pott	A. Pott 2610	L	E	Au	CO, N, NE, S, SE	
D. dissectus (Jacq.) A.R.Simões & Staples	V.J. Pott	A. Pott 3436	L	E	Au	CO, N, NE, S, SE	
D. tuberosus (L.) A.R.Simões & Staples	R. Simão-Bianchini	A. Pott 2629	L	E	Au	CO, NE, S, SE	
Evolvulus convolvuloides (Willd. ex Schult.) Stearn	A. Pott	V.J. Pott 3075	H	E	Au	CO, SE	
Evolvulus filipes Mart.	R. Simão-Bianchini	A. Pott 7914	H	E	Au	CO, N, NE, S, SE	

E. glomeratus Nees & Mart.	R. Simão-Bianchini	A. Pott 7793	H	E	Au	CO, N, NE, S, SE	
E. gypsophiloides Moric.	R.T. Queiroz	R.T. Queiroz 1431	H	E	Au	CO, NE, SE	Brazil
E. nummularius (L.) L.	A. Pott	A. Pott 5198	H	E	Au	CO, N, NE, S, SE	
E. phyllanthoides Moric.	R. Simão-Bianchini	V.J. Pott 3083	H	E	Au	CO, N, NE, SE	Brazil
E. pterygophyllus Mart.	A. Pott	A. Pott 5875	H	E	Au	CO, N, NE, SE	
E. saxifragus Mart.	R. Simão-Bianchini	A. Pott 4628	H	E	Au	CO, NE, SE	
E. sericeus (Kunth) Ooststr.	R. Simão-Bianchini	A. Pott 1462	H	E	Au	CO, N, NE, SE	
Ipomoea alba L.	A. Pott	A. PottP 3021	L	E	Au	CO, N, NE, S, SE	
I. amnicola Morong	A. Krapovickas	A. Pott 3405	L	E	Au	CO, NE, SE	
**I. aristolochiifolia* G.Don	V.J. Pott	A. Pott 1635	L	E	Au	CO, N, NE, S, SE	
I. asarifolia (Desr.) Roem. & Schult.	A. Krapovickas	A. Pott 2436	L	E	Au	CO, N, NE, SE	
***I. batatas* (L.) Lam.			H	E		CO, N, NE	
I. bonariensis Hook.	R. Simão-Bianchini	A. Pott 8103	L	E	Au	CO, NE, S, SE	
**I. cairica* (L.) Sweet	V.J. Pott		L	E	Au	CO, NE, S, SE	
I. burchellii Meisn.	T.S. Mendes	G. Martinelli 18682	L	E	Au	CO, N, NE, SE	
I. carnea ssp. *fistulosa* (Mart. & Choisy) Austin	V.J. Pott	A. Pott 5176	S	E	Hy	CO, N, NE, S, SE	
I. cheirophylla O'Donell	J.R.I. Wood	A. Pott 4837	L	E	Au	CO	
I. chiliantha Hall.	R. Simão-Bianchini	V.J. Pott 3920	L	E	Au	CO	

(continued)

Table 3.1 (continued)

I. cordatotriloba Dennst	R. Simão-Bianchini	V.J. Pott 7522	L	E	Au	CO, S	
I. cuneifolia Meisn.	A. Krapovickas	A. Pott 5576	L	E	Au	CO, N, NE	Brazil
I. crinicalyx S. Moore	V.J. Pott	W. Fava 162	L	E	Au	CO	
I. haenkeana Choisy	G. Staples	A. Pott 11094	Ss	E	Au	CO, SE	
I. hederifolia L.	B.O. Bruel	S.R. Zaniolo 281	L	E	Au	CO, N, NE, S, SE	
I. cf. *hieronymi* (Kuntze) O'Donell	G. Staples	R.S. Arruda 26	L	E	Au	CO	
I. maurandioides Meisn.	G. Staples	L.E.A.M. Lescano 132	L	E	Au	CO, N, NE, S, SE	
I. megapotamica Choisy	J.R.I. Wood	A. Pott 5558	L	E	Au	CO, NE, SE	
**I. nil* (L.) Roth	G. Staples	V.J. Pott 5289	L	E	Au	CO, N, NE, S, SE	
I. paludicola J.R.I.Wood & R.W.Scotland	G. Staples	V.J. Pott 579	L	E	Au	CO	
I. paludosa O'Donell	J.R.I.Wood	A. Pott 5576	L	E	Au	CO	
I. pantanalensis J.R.I. Wood & C. Urbanets	J.R.I. Wood	A. Pott 5475 (Typus)	L	E	Au	CO	Pantanal
I. philomega (Vell.) House	A. Krapovickas	A. Pott 5558	L	E	Au	CO, N, NE, S, SE	
I. piresii O'Donell	R. Simão-Bianchini	A. Pott 7955	L	E	Au	CO, N, NE, SE	Brazil
**I. quamoclit* L.	A. Pott	A. Pott 1789	L	E	Au	CO, N, NE, S, SE	
I. cf. *ramosissima* (Poir.) Choisy	G. Staples	A.C. Araújo 927	L	E	Au	CO, N, NE, S, SE	
I. rubens Choisy	A. Krapovickas	V.J. Pott 2032	L	E	Au	CO, N, SE	
I. setifera Poir.	A. Krapovickas	V.J. Pott 3648	L	E	Au	CO, N, NE, S, SE	

I. squamosa Choisy	J.R.I. Wood	A. Pott 4163	L	E	Au	CO, N, NE	
I. subrevoluta Choisy	A. Krapovickas; R.S. Bianchini	V.J. Pott 855	L	E	Au	CO, N, S, SE	
I. tenera Meisn.	V.J. Pott	A. Pott 4498	L	E	Au	CO, NE	Brazil
I. tiliacea (Willd.) Choisy	T.S. Mendes	G. Martinelli 18619	L	E	Au	N, NE, S, SE	
I. wrightii A.Gray	T.S.Mendes	G. Martinelli 18598	L	E	Au	CO, N, NE, SE	
Iseia luxurians (Moric.) O'Donell	R. Simão-Bianchini	G.A. Damasceno Jr. 2307	L	E	Au	CO, N, NE, S, SE	
Jacquemontia blanchetii Moric.	G. Staples	A. Pott 12848	L	E	Au	CO, N, NE, S, SE	
J. evolvuloides (Moric.) Meisn.	R. Simão-Bianchini; G. Staples	A. Pott 6817	L	E	Au	N, NE, SE	
J. ferruginea Choisy	E.F.Guimarães	G. Martinelli 18688	L	E	Au	N, NE, S, SE	Brazil
J. heterantha (Nees & Mart.) Hallier f.	M.T. Strong	P. Acevedo-Rodriguez 16671	L	E	Au	CO, NE, SE	
J. linoides (Choisy) Meisn.	M. Pastore	A.L. Prado 3181	H	E	Au	CO, NE	Brazil
J. parviflora Choisy	R. Simão-Bianchini	A. Pott 8020	L	E	Au	CO	Brazil
J. sphaerostigma (Cav.) Rusby	A. Pott	A. Pott 1910	L	E	Au	CO, N, NE, S, SE	
J. tamnifolia (L.) Griseb.	R. Simão-Bianchini	A. Pott 3829	L	E	Au	CO, N, NE, S, SE	
Operculina hamiltonii (G.Don) D.F.Austin & Staples	A. Krapovickas	A. Pott 7090	L	E	Au	CO, N, NE	

(continued)

Table 3.1 (continued)

Turbina cordata (Choisy) D.F.Austin & Staples	R. Simão-Bianchini	S.R. Zaniolo 248	L	E	Au	CO, N, NE, SE	Brazil
Costaceae							
Costus arabicus L.	A. Pott	A. Pott 4672	H	E	Z	CO, N, NE, S, SE	
***C. spiralis* (Jacq.) Roscoe	A. Pott	S.S. Moura 192	H	E	Z	CO, N, NE, S, SE	
Crassulaceae							
***Kalanchoe pinnata* (Lam.) Pers.	C.T. Rampin	C.D.O Cabral 12	H	E	Z	Exotic	
***Sedum dendroideum* Moc. & Sessé			H			Exotic	
Cucurbitaceae							
Cayaponia citrullifolia (Griseb.) Cogn.	V.J.G. Klein	A. Pott 7996	L	E	Z	CO, N	
C. cruegeri (Naudin) Cogn.	V.J.G. Klein	A. Pott 5829	L	E	Z	CO, N	
C. hilariana Cogn.	C. Jeffrey	G. Hatschbach 21930	L	E	Z	CO	
C. podantha Cogn.	D.M. Kearns; V.L.G. Klein	A. Pott 3407	L	E	Z	CO, N, NE, S	Brazil
C. tayuya (Vell.) Cogn.	G.A. Damasceno Jr.	G.A. Damasceno Jr. 5143	L	E	Z	CO, N, NE, S, SE	Brazil
Ceratosanthes hilariana Cogn.	V.J.G. Klein	N. Saddi 2920	L	E	Z	CO, S, SE	
C. multiloba Cogn.	A. Pott	A. Pott 4470	L	E	Z	CO, NE, S, SE	

*******Citrulus lanatus* (Thunb.) Matsum. & Nakai			H	E	Z	Exotic	
*,***Cucumis anguria* L.	G. Hatschbach	G. Hatschbach 49227	H	E	Z	CO, N, NE, SE	
***Cucurbita maxima* Duchesne ex Lam.			H	E	Z	Exotic	
***C. moschata* (Duchesne) Duchesne ex Poir.			H	E	Z	Exotic	
***C. pepo* L.	V.J.G. Klein	M.A. Carniello 1265	L	E	Z	Exotic	
Cucurbitella duriaei (Naudin) Cogn.	C. Jeffrey	G. Hatschbach 49245	L	E	Z	CO	
Cyclanthera hystrix (Gill.) Arn.	V.J. Pott	V.J. Pott 3203	L	E	Au, Hy	CO, S, SE	
Echinopepon racemosus Naudin	A. Pott	A. Pott 15565	L	E	Z	CO, N, NE, SE	
***Lagenaria siceraria* (Mol.) Standl.						Exotic	
*,***Luffa cylindrica* (L.) M.Roem.			L	E	Au, Hy	Exotic	
**L. operculata* (L.) Cogn.	A. Pott	A. Pott 14385	L	E	Au	CO, N, NE, SE	
Melothria candolleana Cogn.	V.J.G. Klein	A. Pott 1395	L	E	Z	CO, N	
M. cucumis Vell.	V.J.G. Klein	A. Pott 6338	L	E	Z	CO, NE, S, SE	
M. hirsuta Cogn.	V.J.G. Klein	A. Pott 2922	L	E	Z	CO, S, SE	Brazil

(continued)

Table 3.1 (continued)

M. pendula L.	V.J.G. Klein	A. Pott 3740	L	E	Z	CO, N, NE, S, SE	
M. warmingii Cogn.	V.J.G. Klein	A. Pott 3742	L	E	Z	CO, N, NE, S, SE	
**Momordica charantia* L.	A. Pott	A. Pott 16904	L	E	Z	CO, N, NE, S, SE	
Psiguria ternata (M.Roem.) C.Jeffrey	V.J.G. Klein	A. Pott 4588	L	E	Z	CO, N, NE, S, SE	
***Sicana odorifera* (Vell.) Naudin	A. Pott	A. Pott 2959	L	E	Z	CO, NE, SE	
Siolmatra brasiliensis (Cogn.) Baill.	D.M. Kearns	A. Pott 5275	L	E	Z	CO, N, NE, SE	
Cyperaceae							
Abildgaardia ovata (Burm.f.) Kral	A. Pott	A. Pott 3911	H	An	Au	CO, N, NE, S, SE	
Bulbostylis capillaris (L.) C.B.Clarke	L.T. Eiten	F.R. Bommer 25	H	An	Au, Hy	CO, N, NE, S, SE	
B. conifera (Kunth) C.B.Clarke	V.J. Pott	A. Pott 2366	H	An	An	CO, N, NE, S, SE	
B. hirtella (Schrad.) Urb.	V.J. Pott	V.J. Pott 3369	H	An	Au	CO, NE, S, SE	
B. junciformis (Kunth) C.B.Clarke	L.T. Eiten	E.F. Nienstedt 314	H	An	Au	CO, N, NE, S, SE	
B. paraensis (Schrad. ex Nees) C.B.Clarke	V.J. Pott	V.J. Pott 1542	H	An	Hy	CO, N, SE	
B. scabra (J.Presl. & C.Presl.) C.B.Clarke	T.M. Pedersen	A. Pott 8035	H	An	Au	CO, N, NE, S, SE	Brazil
B. sphaerocephala (Boeckeler) C.B.Clarke	M.G. Lopez	A. Pott 5870	H	An	Au	CO, NE, S, SE	

Calyptrocarya glomerulata (Brongn.) Urb.	V.J. Pott	L.V.S. Campos 621	H	An	Au	CO, N, NE, S, SE	
Cladium mariscus subsp. *jamaicense* (Crantz) Kük.	T.M. Pedersen	A. Pott 3891	H	An	Au, Hy	CO, NE, S, SE	
Cyperus aggregatus (Willd.) Endl.	T.M. Pedersen	A. Pott 2612	H	An	Au	CO, N, NE, S, SE	
C. articulatus L.	T.M. Pedersen; L. Pereira-Silva	V.J. Pott 11677	H	An	Au	CO, N, NE, SE	
C. blepharoleptos Steud.	T.M. Pedersen; L. Pereira-Silva	S.N. Moreira 874	H	An	Au	CO, N, NE, S, SE	
C. brasiliensis (Kunth) Bauters	L. Pereira-Silva	V.J. Pott 7902	H	An	Au	CO, N, NE, S, SE	
C. brevifolius (Rottb.) Endl. ex Hassk.	V.J. Pott	A. Pott 1060	H	An	Au	CO, N, NE, S, SE	
C. compressus L.	T.M. Pedersen	V.J. Pott 5357	H	An	Au	CO, N, NE, S, SE	
C. cornelli-ostenii Kük.	T.M. Pedersen	A. Pott 1505	H	An	Au	CO, SE	
C. corymbosus Rottb.	V.J. Pott	A. Pott 8915	H	An	Au	CO, S	
C. digitatus Roxb.	T.M. Pedersen	V.J. Pott 2859	H	An	Au, Z	CO, N, NE, S	
C. distans L.	M.A. Carniello	M.A. Carniello 3505	H	An	Au	CO, N, NE, S, SE	
C. entrerianus Boeckeler	T.M. Pedersen	A. Pott 2663	H	An	Au	CO, NE, S, SE	
C. eragrostis Lam.	S.M. Hefler	A. Pott 4148	H	An	Au	CO, NE, S, SE	
C. esculentus L.	T.M. Pedersen	A. Pott 4505	H	An	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

C. flavescens L.	E.R. Guaglianone	A. Pott 1650	H	An	Au	CO, N, NE, S, SE	
C. gardneri Nees	T.M. Pedersen	V.J. Pott 1051	H	An	Hy	CO, NE	Brazil
C. giganteus Vahl	V.J. Pott	V.J. Pott 1550	H	An	Au, Hy	CO, N, NE, S, SE	
C. haspan L.	T.M. Pedersen	A. Pott 3300	H	An	Au, Hy	CO, N, NE, S, SE	
C. hermaphoditus (Jacq.) Standl.	M. Alves	D.C. Souza 8/6/2009	H	An	Au, Hy	CO, N, NE, S, SE	
C. hortensis (Salzm. ex Steud.) Dorr	L. Pereira-Silva	V.J. Pott 3766	H	An	Au	CO, N, NE, S, SE	
C. imbricatus Retz.	S.M. Hefler	V.J. Pott 5023	H	An	Au	CO, N, NE, S, SE	
C. incomptus Kunth	S.M. Hefler; L. Pereira-Silva	V.J. Pott 6058	H	An	Au	CO, S, SE	
C. iria L.	V.J. Pott	V.J. Pott 2904	H	An	Au	CO, N, NE, S, SE	
C. lanceolatus Poir.	V.J. Pott	V.J. Pott 3779	H	An	Au	CO, N, NE, S, SE	
C. laxus Lam.	L. Pereira-Silva	A. Pott 1250	H	An	Au	CO, N, NE, S, SE	Brazil
C. ligularis L.	S.M. Hefler	V.J. Pott 6045	H	An	Au	CO, N, NE, S, SE	
C. luzulae (L.) Retz.	V.J. Pott	V.J. Pott 2470	H	An	Au	CO, N, NE, S, SE	
C. macrostachyos Lam.	L. Pereira-Silva	F. Bao 59	H	An	Au	CO, N, NE, SE	
C. meyenianus Kunth	T.M. Pedersen	A. Pott 5832	H	An	Au	CO, NE	

C. obtusatus (J.Presl. & C.Presl.) Mattf. & Kük.	M. Schessl	M. Schessl 2806	H	An	Au	CO, N, NE, S, SE	
C. ochraceus Vahl	V.J. Pott	V.J. Pott 4168	H	An	Au	CO, N, NE, S, SE	
C. odoratus L.	S.M. Hefler	V.J. Pott 2360	H	An	Au	CO, N, NE, S, SE	
C. papyrus L.	M. Alves	W.W. Thomas 4585	H	An	Au, Hy	CO, N, NE, S, SE	
C. polystachyos Rottb.	T.M. Pedersen	V.J. Pott 862	H	An	Au	CO, N, NE, S, SE	
C. prolixus Kunth	V.J. Pott	S.N. Moreira 828	H	An	Au, Hy	CO, NE, S, SE	
C. reflexus Vahl	L. Pereira-Silva	A. Pott 3227	H	An	Au	CO, S, SE	
C. rigens C. Presl.	V.J. Pott	M. Rocha 32	H	An	Au, Hy	CO, N, NE, S, SE	
**C. rotundus* L.	L. Pereira-Silva	S. Sousa no n.	H	An	Au	CO, N, NE, S, SE	
C. salzmannianus (Steud.) Bauters	V.J. Pott	V.J. Pott 8019	H	An	Au	CO, N, NE, SE	Brazil
C. schomburgkianus Nees	T.M. Pedersen	A. Pott 2401	H	An	Au	CO, N, NE, SE	
C. sellowianus (Kunth) T.Koyama	S. M. Costa	A. Pott 3693	H	An	Au	CO, N, NE, S, SE	
C. sesquiflorus (Torrey) Mattf. & Kük.	A. Pott	A. Pott 1061	H	An	Au	CO, N, NE, S, SE	
C. sphacelatus Rottb.	T.M. Pedersen	V.J. Pott 2993	H	An	Au	CO, N, NE, S, SE	
C. squarrosus L.	S.M. Hefler	A. Pott 7906	H	An	Au, Hy	N, NE	

(continued)

Table 3.1 (continued)

C. subsquarrosus (Muhl.) Bauters	T.M. Pedersen	V.J. Pott 1530	H	An	Hy	CO, N, NE, S, SE	
C. surinamensis Rottb.	T.M. Pedersen	V.J. Pott 1083	H	An	Au	CO, S, SE	
C. unicolor Boeckeler	V.J. Pott	V.J. Pott 1163	H	An	Au	CO, NE	
C. unioloides R.Br.	V.J. Pott	V.J. Pott 2469	H	An	Au	CO, N, NE, S, SE	
C. virens Michx.	S.M. Hefler	V.J. Pott 3708	H	An	Hy	CO, N, NE, S, SE	
Eleocharis acutangula (Roxb.) Schult.	T.M. Pedersen; F. Mereles	V.J. Pott 3152	H	An	Hy	CO, NE, SE	
E. barrosii Svenson	T.M. Pedersen	A. Pott 3304	H	An	Au, Hy	CO, S	
E. contracta Vahl	T.M. Pedersen	N.C. Bueno 324	H	An	Au, Hy	CO, N, NE, S, SE	
E. elegans (Kunth) Roem. & Schult.	F. Mereles	V.J. Pott 3094	H	An	Au, Hy	CO, N, NE, S, SE	
E. filiculmis Kunth	F. Mereles	V.J. Pott 2252	H	An	Au	CO, N, NE, S, SE	
E. geniculata (L.) Roem. & Schult.	F. Mereles	V.J. Pott 3168	H	An	Hy	CO, N, NE, S, SE	
E. hatschbachii R. Trevis.	R. Trevisan	V.J. Pott 3364 (Paratypus)	H	An	Hy	CO	
E. interstincta (Vahl) Roem. & Schult.	F. Mereles	V.J. Pott 3120	H	An	Hy	CO	
E. jelskiana Boeckeler	V.J. Pott	S.M. Salis 545	H	An	Hy	CO, S	
E. maculosa (Vahl) Roem. & Schult.	T.M. Pedersen; F. Mereles	V.J. Pott 3148	H	An	Au, Hy	CO, N, NE, S, SE	
E. minima Kunth	T.M. Pedersen; F. Mereles	G. Lima Jr. 281	H	An	Hy	CO, N, NE, S, SE	

E. montana Kunth) Roem. & Schult.	T.M. Pedersen	V.J. Pott 3159	H	An	Au	CO, N, NE, S, SE	
E. mutata (L.) Roem. & Schult.	T.M. Pedersen	A. Pott 2135	H	An	Au, Hy	CO, N, NE, S, SE	
E. nana Kunth	V.J. Pott	T.H.D. Leandro 98	H	An	Au, Hy	CO	
E. nudipes (Kunth) Palla	T.M. Pedersen; R. Trevisan	V.J. Pott 8302	H	An	Hy	CO, N, NE, S, SE	
E. plicarhachis (Griseb.) Svenson	R. Trevisan	V.J. Pott 7893	H	An	Hy	CO, S	
E. viridans Kük. ex Osten	M. Schessl	M. Schessl 4154	H	An	Au	CO, N, NE, S, SE	
Fimbristylis aestivalis Vahl	T.M. Pedersen	A. Pott 6563	H	An	Au, Hy	CO, N	
F. autumnalis (L.) Roem. & Schult.	T.M. Pedersen	V.J. Pott 8732	H	An	Au, Hy	CO, N, NE, S, SE	
F. complanata (Retz) Link	T.M. Pedersen	V.J. Pott 1556	H	An	Au, Hy	CO, N, NE, S, SE	
F. cymosa R.Br.	L. Pereira-Silva	V.J. Pott 11827	H	An	Au, Hy	N, NE, S, SE	
F. dichotoma (L.) Vahl	T.M. Pedersen	V.J. Pott 3389	H	An	Au, Hy	CO, N, NE, S, SE	
F. littoralis Gaudich.	T.M. Pedersen	V.J. Pott 2543	H	An	Au, Hy	CO, N, NE, S, SE	
F. squarrosa Vahl	M. Alves	V.J. Pott 1062	H	An	Au, Hy	CO, N, NE, S, SE	
Fuirena umbellata Rottb.	T.M. Pedersen; A.P. Prata	V.J. Pott 752	H	An	Au, Hy	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Rhynchospora armerioides J.Presl. & C.Presl.	K. Camelbeke	M. Schessl 3101	H	An	Au	CO, N, NE, SE	
R. asperula (Nees) Steud.	P.J.S. Silva Filho	V.J. Pott 4399	H	An	Au, Hy	CO, NE, S, SE	
R. brevirostris Griseb.	V.J. Pott	V.J. Pott 3479	H	An	Au	CO, N, NE, SE	
R. ciliata Kük.	P.J. Silva F.	A. Pott 1543	H	An	Au	CO, NE	
R. corymbosa (L.) Britton	T.M. Pedersen	V.J. Pott 2795	H	An	Au, Hy	CO, N, NE, SE	
R. emaciata (Nees) Boeckeler	M. Alves	V.J. Pott 6302	H	An	Au	CO, N, NE, S, SE	
R. eximia (Nees) Boeckeler	T.M. Pedersen	A. Pott 1811	H	An	Au	CO, N, NE, S, SE	
R. globosa (Kunth) Roem. & Schult.	T.M. Pedersen	A. Pott 1976	H	An	Au	CO, N, NE, S, SE	
R. hirta (Nees) Boeckeler	A.C. Araújo	A. Pott 2502	H	An	Au	CO, N, NE, SE	
R. holoschoenoides (L.C.Rich.) Herter	T.M. Pedersen	V.J. Pott 2077	H	An	Au	CO, N, NE, S, SE	
R. nervosa (Vahl) Boeckeler	T.M. Pedersen	V.J. Pott 2973	H	An	Au	CO, N, NE, S, SE	Brazil
R. riparia (Nees) Boeckeler	M. Alves	A. Pott 13861	H	An	Au, Hy	CO, N, NE, S, SE	
R. rugosa (Vahl) Gale	E.R. Guaglianone	V.J. Pott 3685	H	An	Au	CO, N, NE, S, SE	
R. scutellata Griseb.	V.J. Pott	A.P. Oliveira 53	H	An	Au	CO, N, NE, S, SE	
R. tenerrima Nees ex Spreng.	E.R. Guaglianone	V.J. Pott 3407	H	An	Au	CO, N, NE, S, SE	
R. tenuis Link	T.M. Pedersen	A. Pott 1719	H	An	Au, Hy	CO, N, NE, S, SE	

R. triflora Vahl	T.M. Pedersen; E.R. Guaglianone	S.M. Salis 691	H	An	Au	CO, N, NE, SE	
R. trispicata (Nees) Schrad. ex Steud.	T.M. Pedersen; E.R. Guaglianone	V.J. Pott 3181	H	An	Au, Hy	CO, N, CO	
R. velutina (Kunth) Boeckeler	T.M. Pedersen; E.R. Guaglianone	A. Pott 3879	H	An	Au	CO, N, NE, S, SE	
Schoenoplectiella supina (L.) Lye	E.R. Guaglianone	V.J. Pott 1081	H	An	Au, Hy	CO, S	
Scleria flagellum-nigrorum P.J.Bergius	W.W. Thomas	W.W. Thomas 4615	H	An	Au	CO, N	
S. gaertneri Raddi	T.M. Pedersen	V.J. Pott 1877	H	An	Hy	CO, N, NE, S, SE	
S. hirtella Sw.	M. Alves	V.J. Pott 3141	H	An	Au	CO, N, NE, S, SE	
S. lacustris C.Wright	A.C. Araújo	V.J. Pott 10529	H	An	Hy	N, NE	
S. latifolia Sw.	M. Alves	J. Arieira 17-77-2017	H	An	Au, Hy	CO, N, NE, S, SE	
S. leptostachya Kunth	T.M. Pedersen	M. Schessl 125	H	An	Au	CO, N, NE, S, SE	
S. lithosperma (L.) Sw.	V.J. Pott	S.N. Moreira 838	H	An	Au, Hy	CO, N	
S. macrophylla J.Presl & C.Presl	T.M. Pedersen; M. Alves	V.J. Pott 3182	H	An	Au, Hy	CO, N, NE, SE	
S. microcarpa Nees ex Kunth	T.M. Pedersen	V.J. Pott 1877	H	An	Au	CO, N, NE, S, SE	
S. pusilla Pilg. (*S. minima*)	T.M. Pedersen	M. Schessl 3158	H	An	Au	CO, N	
S. reticularis Michx. ex Willd.	T.M. Pedersen	M. Schessl 130	H	An	Au	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

S. secans (L.) Urb.	T.M. Pedersen	V.J. Pott 3182	H	An	Au	CO, N, NE, S, SE	
S. vaginata Steud.	A.C. Araújo	M. Schessl 3006	H	An	Au	CO, NE	
S. variegata (Nees) Steud.	V.J. Pott	V.J. Pott 6392	H	An	Au	CO, NE, S	
Dilleniaceae							
Curatella americana L.	A. Pott	A. Pott 11815	T	E	Z	CO, N, NE, SE	
Davilla elliptica A.St.-Hil.	J.A. Ratter	A. Pott 1357	L	E	Z	CO, N, NE, SE	
D. nitida (Vahl) Kubitszi	A. Pott	S.N. Moreira 834	L	E	Z	CO, N, NE, SE	
Doliocarpus dentatus (Aubl.) Standl.	A. Schinini	A. Pott 4316	L	E	Z	CO, N, NE, S, SE	
D. kubitzkii Aymard	S.F. Smith	G. Hatschbach 60870	L	E	Z	CO	
D. major G.F. Gmel.	C.N. Fraga	H.N. Borges 283	L	E	Z	CO, N, NE, SE	
Tetracera willdenowiana Steud.	C.N. Fraga	J.S. Silva 156	L	E	Z	CO, N, NE, S, SE	
Dioscoreaceae							
Dioscorea aesculifolia R.Knuth	M. Kirizawa	G.A. Damasceno Jr. 3118	L	E	An	CO, SE	Brazil
D. chondrocarpa Griseb.	G. Pedralli	A. Pott 5201	L	E	An	CO, N, NE, S, SE	
D. corumbensis R.Knuth	M. Kirizawa	G.A. Damasceno Jr. 2880	L	E	An	CO, N, NE	Brazil
D. hassleriana Chodat	G. Pedralli	A. Pott 5553	L	E	An	CO, N, NE, S, SE	Brazil
D. orthogoneura Uline ex Hochr.	G. Pedralli; G. Heiden	A. Pott 2189	L	E	An	CO, N, NE, SE	
Droseraceae							

Drosera communis A.St.-Hil.	V.J. Pott	S.N. Moreira 1549	H	E	Au	CO, N, NE, S, SE	
D. sessilifolia A.St.-Hil.	T.R.S. Silva	A. Pott 14170	H	E	Au	CO, N, NE, S, SE	
Ebenaceae							
Diospyros brasiliensis Mart. ex Miq.	J.A. Ratter	A. Pott 4460	T	E	Z	CO, SE	
D. dalyom B.Walln.	M.T. Strong	P. Acevedo-Rodriguez 16674	T	E	Z	CO, N	
D. inconstans Jacq.	B. Wallnöfer	W.W. Thomas 4619	T	E	Z	CO, N, NE, S, SE	
D. lasiocalyx (Mart.) B. Walln.	B. Wallnöfer	V.J. Pott 4223	S	E	Z	CO, N, NE, S, SE	
Elaeocarpaceae							
Sloanea guianensis (Aubl.) Benth.	M. Sampaio	A. Pott 5640	T	E		CO, N, NE, S, SE	
S. porphyrocarpa Ducke	G. Guarim Neto	G. Guarim Neto 1981	T	E		N, NE	
S. terniflora (DC.) Standl.	M. Sampaio	C.P. Collior 924	T	E		CO, N, NE, SE	
Eriocaulaceae							
Paepalanthus chiquitensis Herzog	P. Sano	A. Pott 2232	H	E	Au	CO, N, NE, SE	
P. lamarckii Kunth	A.M. Giulietti	A. Pott 1064	H	E	Au	CO, N, NE	
Syngonanthus caulescens (Poir.) Ruhland	A.M. Giulietti	A. Pott 5601	H	E	Au	CO, N, NE, S, SE	
S. cuyabensis (Bong.) Giul., Hensold & L.P.Parra	V.J. Pott	A. Pott 2208	H	E	Au, Hy	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

S. gracilis (Bong.) Ruhland	A.M. Giulietti	A. Pott 1957	H	E	Au	CO, N, NE, S, SE	
Erythroxylaceae							
Erythroxylum anguifugum Mart.	A. Pott	A. Pott 3490	T	E	Z	CO, N, NE, S, SE	Brazil
E. cuneifolium (Mart.) O.E.Schulz	A. Pott	A. Pott 14190	T	E	Z	CO, N, NE, S, SE	
E. daphnites Mart.	M.I.B. Loiola	T.H. Stefanello 289	T	E	Z	CO, N, NE, SE	
E. deciduum A.St.-Hil.	J.A. Ratter	A. Pott 4552	Ss	E	Z	CO, S, SE	
E. patentissimum O.E.Schulz	A. Pott	A. Pott 12843	T	E	Z	CO	
E. pelleterianum A St.-Hil.	J.A. Ratter	J.A. Ratter R5146	T	E	Z	CO, N, NE, S, SE	
E. suberosum A.St.-Hil.	A. Pott	A. Pott 2288	T	E	Z	CO, N, NE, S, SE	
Euphorbiaceae							
**Acalypha arvensis* Poepp.	G.L. Webster	A. Pott 1481	H	E	Au	CO, N	
A. communis Müll.Arg.	G.L. Webster	A. Pott 4279	Ss	E	Au	CO, S, SE	
***A. hispida* Willd.				E	Au	Exotic	
A. villosa Jacq.	A. Pott	A. Pott 13647	Ss	E	Au	CO, NE, S, SE	Brazil
Adelia membranifolia (Muell.Arg.) Chodat & Hassl.	A. Pott & V.J. Pott	A. Pott 2324	T	E	Au	CO, NE, SE	
Alchornea castaneifolia (Willd.) A. Juss.	V.J. Pott	V.J. Pott 4329	T	E	Z, Hy	CO, N, NE	
A. discolor Poepp.	G.L. Webster; M. Pompert	A. Pott 3825	T	E	Z	CO, N, NE	

Astraea lobata (L.) Klotzsch	G.L. Webster; I. Cordeiro	A. Pott 1500	H	E	Au	CO, N, NE, S, SE	
A. paulina Didr.	I. Cordeiro	A. Pott 5675	Ss	E	Au	CO, N, NE, SE	
Bernardia multicaulis Müll.Arg.	J.F. Carrón R.	G.P. Nunes 120	Ss	E	Au	CO, S, SE	
Caperonia castaneifolia (L.) A.St.-Hil.	V.J. Pott	V.J. Pott 3126	H	E	Hy	CO, N, NE, S, SE	
C. palustris (L.) A. St.-Hil.	A. Pott & V.J. Pott	A. Pott 4496	Ss	E	Au	CO, N, NE, SE	
Cnidoscolus albomaculatus (Pax) I.M.Johnst.	A. Pott	A. Pott 1501	Ss	E	Au	CO	
C. appendiculatus (Pax & K.Hoffm.) Pax & K Hoffm.	G.L. Webster	A. Pott 2546	Ss	E	Au	CO	
C. cervii Fern. Casas	J.F. Fernández Casas	A.C. Cervi 3271	Ss	E	Au	CO	Brazil
C. cnicodendron Griseb.	A. Pott	A. Pott 5485	Ss	E	Au	CO, SE	
C. urens L.	I. Cordeiro	A.C. Araújo 795	S	E	Au	CO, N, NE, SE	
C. tridentifer Fern.Casas & J.M.Pizarro	J.F. Fernández Casas	A.C. Allem 128	S	E	Au	CO	Brazil
C. vitifolius (Mill.) Pohl	J.F. Fernández Casas	G. Hatschbach 21883	S	E	Au	CO, N, NE, SE	
***Codiaeum variegatum* Blume			S			Exotic	
Croton andinus Müll. Arg.	L.R. Lima	G.A. Amador 145	Ss	E	Au	CO	
C. betaceus Baill.	R.C. Sodré	A. Pott 2139	SS	E	Au	CO, N, NE, SE	
C. blanchetianus Baill.	I. Cordeiro	A. Pott 16876	S	E	Au	CO, NE, SE	

(continued)

Table 3.1 (continued)

C. bonplandianus Baill.	R.C. Sodré; I. Cordeiro	A. Pott 8912	H	E	Au	CO, S	
C. campestris A St.-Hil.	I. Cordeiro	F. Matos-Alves 390	Ss	E	Au	CO, N, NE, SE	
C. corumbensis S.Moore	G.L. Webster	G.L. Webster 25357	Ss	E	Au	CO	Brazil
C. cuneatus Klotzsch	I. Cordeiro	A. Pott 8714	Ss	E	Au	CO, N, NE, BR	
C. cuyabensis Pilg.	G.L. Webster	A. Pott 4333	Ss	E	Au	CO, N, NE, BR	
C. didrichsenii G.L.Webster	I. Cordeiro	A.C. Allem 165	Ss	E	Au	CO, N, NE, S, SE	
C. doctoris S.Moore	I. Cordeiro	A. Pott 14175	S	E	Au	CO	
C. glandulosus L.	R.C. Sodré	F. Bao 83	Ss	E	Au	CO, N, NE, S, SE	
C. glyptospermus Müll. Arg.	I. Cordeiro	V.F. Kinupp 1086	S	E	Au	CO, SE, BR	
C. gracilipes Baill.	M.B.R. Caruzo	A. Pott 8884	S	E	Au	CO, S, SE	
C. grandivelus Baill.	G.L. Webster; M.B.R. Caruzo	G.L. Webster 23350	Ss	E	Au	CO, N, NE, S, SE	
C. heliotropiifolius Kunth	V.J. Pott; I. Cordeiro	A. Pott 15406	Ss	E	Au	CO, NE, SE	
C. linearifolius Müll.Arg.	D.S. Carneiro-Torres	J.A Siqueira-F. 2798	Ss	E	Au	NE, S	
C. lundianus (Didr.) Müll.Arg.	V.J. Pott	A. Pott 16258	Ss	E	Au	CO, N, NE, S, SE	
C. micans Sw.	I. Cordeiro	A. Pott 12414	S	E	Au	CO	
C. paucistamineus Müll. Arg.	R.C. Sodré	A. Pott 13534	Ss	E	Au	CO	Brazil
C. pedicellatus Kunth	G.L. Webster; M.B.R. Caruzo	G.L. Webster 25349	Ss	E	Au	CO, N, NE, S, SE	
C. roraimensis Croizat	R.C. Sodré	J. Arieira 122	T	E	Au	CO, N	
C. sanctae-crucis S.Moore	I. Cordeiro	A. Pott 13228	Ss	E	Au	Co, SE, BR	

C. sarcopetaloides S.Moore	G.L. Webster	G.L. Webster 2.343	S	E	Au	CO, BR	
C. sellowii Baill.	I. Cordeiro	G.A. Damasceno Jr. 2316	Ss	E	Au	CO, NE	Brazil
C. trinitatis Millsp.	R.C. Sodré	A. Pott 8594	H, Ss	E	Au	CO, N, NE, S, SE	
C. triqueter Lam.	M.B.R. Caruzo; I. Cordeiro	A. Pott 12442	Ss	E	Au	CO, NE, S, SE	
C. urucurana Baill.	M.B.R. Caruzo	A.C. Araújo 1156	T	E	Au	CO, N, NE, S, SE	
C. vulnerarius Baill.	M.B.R. Caruzo	A. Pott 4918	S	E	Au	S, SE	Brazil
Dalechampia ficifolia Lam.	I. Cordeiro	E. Pereira 299	L	E	Au	CO, NE, S, SE	Brazil
D. humilis Müll.Arg.	I. Cordeiro	A.C. Allem 709	Ss	E	Au	CO, SE	
D. scandens L.	A. Pott	A. Pott 5038	L	E	Au	CO, NE, S, SE	
Ditaxis montevidensis (Didr.) Pax	A. Pott	A. Pott 3896	Ss	E	Au	CO, N, S	
D. purpurascens (S.Moore) Pax & K. Hoffm.	I. Cordeiro	A. Pott 5088	Ss	E	Au	CO	
D. salina Pax & K. Hoffm.	J. Kühlkamp	A. Pott 8878	Ss	E	Au	CO	
**Euphorbia comosa* Vell.	I. Cordeiro	G. Hatschbach 22023	H	E	Au	CO, N, NE, S, SE	
**E. heterophylla* L.	I. Cordeiro	J.S. Silva 267	H	E	Au	CO, N, NE, S, SE	
**E. hirta* L.	V.J. Pott	V.J. Pott 376	H	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

E. hirtella Boiss.	J.A. Kalunki	G. Schaller 261	H	E	Au	CO, N, NE, SE	
E. hyssopifolia L.	G.L. Webster	A. Pott 3525	H	E	Au	CO, N, NE, S, SE	
***E. millii* Des Moul. ex Boiss.			Ss	E		Exotic	
E. prostrata Aiton	O.L.M. Silva	T.H. Stefanello 114	H	E	Au	CO, NE, S, SE	
***E. pulcherrima* Willd. ex Klotzsch			S	E		Exotic	
E. potentilioides Boiss.	O.L.M. Silva	M. Schessl 29-10-1992	H	E	Au	CO, N, NE, S, SE	
E. sciadophila Boiss.	O.L.M. Silva	A. Pott 2328	H	E	Au	CO, N, NE, S, SE	
E. serpens Kunth	O.L.M. Silva	A.P. Oliveira 28	H	E	Au	CO, N, NE, S, SE	
E. thymifolia L.	G.L. Webster	A. Pott 5382	H	E	Au	CO, N, NE, S, SE	
***E. tithymaloides* L.			S	E	Au	Exotic	
***E. tirucalli* L.			S	E	Au	Exotic	
Gymnanthes discolor (Spreng.) Müll.Arg.	A. Pott	A. Pott 12871	T	E	Au	CO, NE, SE	
Jatropha breviloba (Morong) Pax & K. Hoffm.	F.J. Fernández Casas	G. Hatschbach 49252	Ss	E	Au	CO	Brazil
**J. curcas* L.	M. Mendoza	T.S. Conceição s/n	T	E	Au	CO, N, NE, S, SE	
J. elliptica (Pohl) Oken	A.C. Allem	A. Pott 2293	Ss	E	Au	CO, N, NE, SE	
J. gossypiifolia L.	G.L. Webster; M.Mendoza	A. Pott 1452	Ss	E	Au	CO, N, NE, S, SE	

Jatropha hieronymi Kuntze	A. Pott	A. Pott 12887	S	E	Au	CO	
J. intermedia (Chodat & Hassl.) Pax	F.J. Fernández Casas	B. Dubs 3-5-1987	Ss	E	Au	CO	
J. ribifolia (Pohl) Baill.	G.L. Webster	G.L. Webster 25338	Ss	E	Au	CO, NE, SE	
J. thyrsantha Pax & K.Hoffm.	F.J. Fernández Casas	G. Hatschbach 49252		E		CO	
J. weddelliana Baill.	G.L. Webster	A. Pott 4956	Ss	E	Au	CO	
Mabea fistulifera Mart.	C.A. Conceição	C.A. Conceição 2301	T	E	Au	CO, N, NE, SE	
M. paniculata Spruce ex Benth.	A. Pott	A. Pott 11816	T	E	Au	CO, N	
Manihot anomala Pohl	M. Mendoza	A. Pott 2458	Ss	E	Au	CO, N, NE, SE	
M. caerulescens Pohl	A. Pott	L.V.S. Campos 471	S	E	Au	CO, N, NE, SE	
M. carthagenensis (Jacq.) Müll.Arg.	A.C. Allem	A.C. Allem 4314	Ss	E	Au	CO, N, NE, SE	
***M. esculenta* Crantz	A.C. Allem	A.C. Allem 90	Ss	E	Au	CO, N, NE, SE	
M. guaranitica Chodat & Hassl.	M. Mendoza	A.C. Allem 1311	Ss	E	Au	CO	
M. tripartita (Spreng.) Müll.Arg.	A.C. Allem	A.C. Allem 164	Ss	E	Au	CO, N, NE, SE	Brazil
M. xavantinensis D.J.Rogers & Appan	W. Punt	B. Dubs 1433	Ss	E	Au	CO	Brazil
Maprounea guianensis Aubl.	A. Pott	A.Pott 16457	T	E	Au	CO, N, NE, S, SE	
Microstachys bidentata (Mart. & Zucc.) Esser	A. Schinini	A. Pott 1266	H	E	Au	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

M. corniculata (Vahl) Griseb.	I. Cordeiro	V.F. Kinupp 1094	Ss	E	Au	CO, N, NE, S, SE	
M. daphnoides (Mart.) Müll.Arg.	I. Cordeiro	A. Pott 11027	SS	E	Au	CO, NE, SE	
M. glandulosa (Mart. & Zucc.) Esser & M.J.Silva	W. Punt	G. Hatschbach 60873	Ss	E	Au	CO, NE, SE	
M. hispida (Mart.) Govaerts	A.C. Allem	A.C. Allem 1162	Ss	E	Au	CO, NE, S, SE	
Pleradenophora membranifolia (Müll. Arg.) Esser & A.L.Melo	O.L.M.Silva	C.P. Callari 15-7-2008	T	E	Au	CO, SE	
Plukenetia volubilis L.	A. Pott	A. Pott 11056	L	E	Au	CO, N	
Romanoa tamnoides (A.Juss.) Raadci.-Sm.	I. Cordeiro	G.A. Damasceno Jr. 2287	L	E	Au	CO, NE, S, SE	
**Ricinus communis* L.			S	E	Au	Exotic	
Sapium glandulosum (L.) Morong	I. Cordeiro	A.C. Allem 2265	T	E	Z	CO, N, NE, S, SE	
S. haematospermum Müll.Arg.	G.L. Webster	A. Pott 1450A	T	E	Z	CO, S, SE	
S. obovatum Klotzsch ex Müll.Arg.	G.L. Webster	A. Pott 4468	T	E	Z, Au, Hy	CO, N, NE, SE	
S. pallidum (Müll. Arg.) Huber	L. Senna-Valle	N. Saddi 7756	T	E	Au	CO, N, NE	Brazil
Sebastiania brasiliensis Spreng.	I. Cordeiro	A. Pott 14207	T	E	Au	CO, S, SE	
Tragia bahiensis Müll. Arg.	A.C. Allem	A.C. Allem	E	E	Au	CO, NE, S, SE	
T. melochioides Griseb.	G.L. Webster	G.L. Webster 25358	L	E	Au	CO, S	

T. volubilis L.	A. Pott	A. Pott 3821	L	E	Au	CO, N, NE, SE	
Fabaceae (Leguminosae)							
***Adenanthera pavonina* L.			T	E	Au	Exotic	
Aeschynomene americana L.	R. Vanni	A. Pott 13852	H, Ss	E	Au	CO, N, NE, S, SE	
A. ciliata Vogel	R. Vanni; L.C.P. Lima	V.J. Pott 3136	Ss	E	Hy	CO, N, NE, SE	
A. evenia C.Wright & Sauvalle	L.C.P. Lima	A.L.B. Sartori 1113	H	E	Hy	CO, N, NE, S, SE	
A. fluminensis Vell.	R. Vanni; L.C.P. Lima	V.J. Pott 839	Ss	E	Au	CO, N, NE, SE	
A. magna Rudd	L.C.C. Antunes	F.M. Leme 55	SS	E	Au, Hy	CO	
A. montevidensis Vogel	L.C.P. Lima	V.J. Pott 7088	Ss	E	Hy	CO, S	
A. rudis Benth.	V.J. Pott; L.C.P. Lima	V.J. Pott 2546	Ss	E	Hy	CO, N, NE, SE	
A. sensitiva Sw.	V.J. Pott; L.C.P. Lima	V.J. Pott 5504	Ss	E	Hy	CO, N, NE, SE	
Albizia inundata (Mart.) Barneby & J.W.Grimes	D.E. Prado	A. Pott 3605	T	E	Au, Hy	CO, N, NE, S, SE	
***A. lebbek* (L.) Benth.	A. Pott	V.J. Pott 1387	T	E	Au	Exotic	
A. niopoides (Spruce ex Benth.) Burkart	J.A. Ratter	A. Pott 4283	T	E	Au, An	CO, N, NE, S, SE	
A. subdimidiata (Splitg.) Barneby & J.W. Grimes	V.C. Souza	V.C. Souza 32324	T	E	Au, Hy	CO, N, NE	
**Alysicarpus ovalifolius* (Schumach) J. Léonard	G. Hassemer	S.M. Faria & A. Pott 956	T	E	Au, Z	Exotic	
Amburana cearensis (Allemão) A.C.Sm.	J.A. Ratter	A. Pott 4634	H	E	Au	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

Anadenanthera colubrina var. *cebil* (Griseb.) Altschul	J.A. Ratter	A. Pott 5946	T	E	Au	CO, NE, SE	
Ancistrotropis peduncularis (Kunth) A. Delgado	R. Vanni	A. Pott 4309	T	E	Z	CO, N, NE, S, SE	
Andira cujabensis Benth.	J.A. Ratter; R. Vanni	A. Pott 4688	L	E	Z	CO, N, NE	
A. humilis Mart. ex Benth.	A. Pott	A. Pott 13464	T	E	Z	CO, N, NE, S, SE	Brazil
A. inermis (W.Wright) DC.	A. Pott	A. Pott 3612	T	E	Z	CO, N, NE, S, SE	Brazil
A. vermifuga (Mart.) Benth.	A. Pott	A. Pott 1769	H	E	Z	CO, N, NE, SE	
Arachis appressipila Krapov. & W.C.Greg.	A. Krapovickas	A. Krapovickas 30007	H	E	Geo	CO	Pantanal
A. cryptopotamica Krapov. & W.C.Greg.	A. Krapovickas; J.F.M. Valls	A. Pott 2191	H	E	Geo	CO	Brazil
A. diogoi Hoehne	J.F.M. Valls	V.J. Pott 5012	H	E	Geo	CO	
A. glabrata Benth.	J.F.M. Valls	A. Pott 12687	H			CO, SE	
A. helodes Mart. ex Krapov. & Rigoni	J.F.M. Valls; R.T. Queiroz	J.F.M. Valls 13789	H	E	Geo	CO	Brazil
A. hermannii Krapov. & W.C.Greg.	J.F.M. Valls	J.F.M. Valls 7555	H	E	Geo	CO	Brazil
A. hoehnei Krapov. & W.C.Greg.	J.F.M. Valls	V.J. Pott 4801	H	E	Geo	CO	Pantanal
A. kretschmeri Krapov. & W.C.Greg.	J.F.M. Valls	A. Pott 13888	H	E	Geo	CO	Brazil
A. kuhlmannii Krapov. & W.C.Greg.	J.F.M. Valls	A. Pott 1782	H	E	Geo	CO	Brazil

A. lignosa (Chodat & Hassl.) Krapov. & W.C.Greg.	J.F.M. Valls	A. Pott 12021	H	E	Geo	CO	
A. linearifolia Valls et al.	J.F.M. Valls	J.F.M. Valls 12080	H	E	Geo	CO	Pantanal
A. lutescens Krapov. & Rigoni	J.F.M. Valls	J.F.M. Valls 8740	H	E	Geo	CO, SE	Brazil
A. major Krapov. & W.C.Greg.	J.F.M. Valls	A. Pott 1255	H	E	Geo	CO	
A. matiensis Krapov. et al.	J.F.M. Valls	J.F.M. Valls 12084	H	E	Geo	CO	
A. microsperma Krapov. et al.	J.F.M. Valls	F.J. Kochanowski 354	H	E	Geo	CO	
A. nitida Valls et al.	J.F.M. Valls	V.J. Pott 9099	H	E	Geo	CO	
A. oteroi Krapov. & W.C.Greg.	J.F.M. Valls	A.C. Allem 169	H	E	Geo	CO	Brazil
A. paraguariensis Chodat & Hassl.	J.F.M. Valls	A. Pott 12033	H	E	Geo	CO	
A. subcoriacea Krapov. & W.C.Greg.	J.F.M. Valls	J.F.M. Valls 13706	H	E	Geo	CO	Brazil
A. valida Krapov. & W.C.Greg.	A. Krapovickas	A. Krapovickas 30011-Typus	H	E	Geo	CO	Pantanal
A. vallsii Krapov. & W.C.Greg.	R.T. Queiroz	J.F.M. Valls 7635 -Typus	H	E	Geo	CO	Pantanal
Ateleia guaraya Herzog	D.N.S. Machado	G. Martinelli 18739	T	E	An	CO, N, NE	
Bauhinia argentinensis Burkart	A.M.S.F. Vaz	J.J.M. Rodrigues	L	E	Au	CO	

(continued)

Table 3.1 (continued)

B. bauhinioides (Mart.) J.F.Macbr.	A.M.S.F. Vaz; R. Vanni; G.P. Lewis	A. Pott 2444	S	Q	Au	CO, NE, SE	
B. bicolor (Bong.) Steud.	F. Matos-Alves	F. Matos-Alves 626	S	Q	Au	CO	Brazil
B. brevipes Vogel	V.J. Pott	A. Pott 13927	S	Q	Au	CO, N, NE, SE	
B. cheilantha (Bong.) Steud.	G.M. Silva	A. Pott 7931	S	Q	Au	CO, NE, SE	
B. corniculata Benth.	A.M.S.F. Vaz; R. Fortunato; G.M. Silva	A. Pott 3062	S	Q	Au	CO, N	
B. curvula Benth.	A.L.B. Sartori	G.P. Nunes 71	S	Q	Au	CO, NE, SE	Brazil
B. cuyabensis (Bong.) Steud.	R. Fortunato	V.J. Pott 1513	S	Q	Au	CO, N, NE	
B. glaziovii Taub.	A.M.S.F. Vaz	A. Pott 7714	S	Q	Au	CO, NE, SE	Brazil
B. hagenbeckii Harms	A.M.S.F. Vaz	G.M. Silva 113	S	Q	Au	CO	
B. marginata (Bong.) Steud.	F.Matos-Alves	F. Matos-Alves 607	S	Q	Au	CO, SE	
B. mollis (Bong.) D.Dietr.	J.A. Ratter; A.M.S.F. Vaz	A. Pott 1843	S	Q	Au	CO, NE, SE	
B. pentandra (Bong.) D. Dietr.	J.A. Ratter; A.M.S.F. Vaz	A. Pott 4842	T	Q	Au	CO, N, NE, SE	
B. rufa (Bong.) Steud.	J.A. Ratter; R. Vanni	A. Pott 3209	T	Q	Au	CO, SE	
B. ungulata L.	G.M. Silva	A. Pott 13048	T	E	Au	CO, N, NE, SE	
Betencourtia scarlatina (Mart. ex Benth.) L.P.Queiroz	A.L.B. Sartori	A.L.B. Sartori 377	L	E	Au	CO, N, SE	
Bowdichia virgilioides Kunth	R. Vanni; J.A. Ratter	A. Pott 1951	T	E	An	CO, N, NE, S, SE	
***Caesalpinia pulcherrima* (L.) Sw.	M.C. Henrique	J.S. Silva 120	S	E	Au	exot	

Caetangil paraguariensis (Chodat & Hassl.) L.P.Queiroz	R. Vanni	A. Pott 3173	L	E	Au	CO, S	
***Cajanus cajan* (L.) Huth	V.J. Pott	V.J. Pott 507	S	E	Au	exot	
Calliandra parviflora (Hook. & Arn.) Speg.	J.A. Ratter	A. Pott 4293	S	E	Au	CO, N, NE, S, SE	
Calopogonium caeruleum (Benth.) C.Wright	A. Pott	A. Pott 3667	L	E	Au	CO, N, NE, S, SE	
C. mucunoides Desv.	A. Pott	A. Pott 1249	L	E	Au	CO, N, NE, S, SE	
Canavalia mattogrossensis (Barb. Rodr.) Malme	R. Vanni	A. Pott 4433	L	E	Au	CO, S	
Cassia grandis L.f.	A. Pott	A. Pott 5156	T	E	Au, Hy	CO, N, NE, S, SE	
Cenostigma marginatum (Tul.) E.Gagnon & G.P.Lewis	E. Gagnon	A. Pott 4600	Ss	E	Au	CO	
C. pluviosum (DC.) E. Gagnon & G.P.Lewis	A. Pott	A. Pott 7932	T	E	Au	CO, N, NE, S, SE	
Centrosema angustifolium (Kunth) Benth.	D.N.S. Machado	G. Martinelli 18625	T	E	Au	CO, N, NE, S, SE	
C. brasilianum (L.) Benth.	J.F.M. Valls	A. Pott 1739	L	E	Au	CO, N, NE, S, SE	
C. pascuorum Mart. ex Benth.	R.R. Silva	U.M. Resende 487	L	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

C. pubescens Benth.	R. Vanni; J.F.M. Valls	A. Pott 4166	L	E	Au	CO, N, NE, S, SE	
C. sagittatum (Humb. & Bonpl. ex Willd.) Brandegee	J.F.M. Valls	A. Pott 2128	L	E	Au	CO, NE, S, SE	
C. schottii Schum.	R. Vanni; J.F.M. Valls	A. Pott 3087	L	E	Au	CO, N	
C. vexillatum Benth.	R. Vanni; J.F.M. Valls	J.S. Silva 189	L	E	Au	CO, N, NE, SE	
C. virginianum (L.) Benth.	J.F.M. Valls	A. Pott 12912	L	E	Au	CO, N, NE, S, SE	
Cerradicola diversifolia (Benth.) L.P.Queiroz	R. Fortunato	S.J. Silva 170	Ss	E	Au	CO, SE	Brazil
C. elliptica (Desv.) L.P. Queiroz	R. Vanni	A. Pott 3085	Ss	E	Au	CO, N, NE, S, SE	
Chaetocalyx brasiliensis (Vogel) Benth.	V.J. Pott	A. Pott 8027	L	E		CO, N, NE, S, SE	
Chamaecrista campestris H.S.Irwin & Barneby	G. Hatschbach	A. Pott 1640	Ss	E	Au	CO, N, SE	
C. cordistipula (L.) H.S.Irwin & Barneby	R.T. Queiroz	R.T. Queiroz 1443	Ss	E	Au	CO, SE	
C. desvauxii (Collad.) Killip	A. Pott	A. Pott 1163	Ss	E	Au	CO, N, NE, SE	
C. flexuosa (L.) Greene	A. Pott; G. Hatschbach	A. Pott 4365	Ss	E	Au	CO, N, NE, S, SE	
C. kunthiana (Schltdl. & Cham.) H.S.Irwin & Barneby	M. Cota	A.L. Prado 2569	Ss	E	Au	CO, N, NE, SE	
C. nictitans (L.) Moench	G. Hatschbach	A. Pott 2698	Ss	E	Au	CO, N, NE, S, SE	

C. rotundifolia (Pers.) Greene	A.O. Souza	A. Pott 8645	H	E	Au	CO, N, NE, S, SE	
C. serpens (L.) Greene	A. Pott	A. Pott 4549	H	E	Au	CO, N, NE, SE	
C. viscosa (Kunth) H.S.Irwin & Barneby	F. Matos-Alves	F. Matos-Alves 636		E	Au	CO, N, NE, SE	
Chloroleucon chacoense (Burkart) Barneby & J.W.Grimes	R.L.C. Bortoluzzi	R.R. Silva 48	T	E	Au	CO	
C. foliolosum (Benth.) G.P.Lewis	A.L.B. Sartori	A. Pott 15673	T	E	Au	CO, N, NE, SE	
C. laxiflorum (Tul.) Gagnon & G.P. Lewis	F. Matos-Alves	T.C. Piva 56	S	E	Au	CO, NE	
C. mangense (Jacq.) Britton & Rose	F. Matos-Alves	F. Matos-Alves 637	T	E	Au	CO, N, NE	
C. tenuiflorum (Benth.) Barneby & J.W.Grimes	A.L.B. Sartori	A.L.B. Sartori 2000	T	E	Au	CO, N, SE	
C. tortum (Mart.) Pittier	A. Pott	A. Pott 4332	T	E	Au, Z	CO, N, NE, SE	Brazil
Clitoria falcata Lam.	J.F.M. Valls	A. Pott 4663	L	E	Au	CO, N, NE, S, SE	
***C. fairshildiana* R.A.Howard			T	E	Au	CO, N, NE, S, SE	
C. guianensis (Aubl.) Benth.	A.L. Prado	A.L. Prado 2003	Ss	E	Au	CO, N, NE, S, SE	
C. stipularis Benth.	A. Pott	A. Pott 2512	Ss	E	Au	CO, N, NE	Brazil
**C. ternatea* L.	A. Pott	S.S. Moura 194	L	E	Au	CO, N, NE, SE	
Copaifera langsdorffii Desf.	G.A. Damasceno Jr.	D.T. Azevedo 23	T	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

C. malmei Harms	J.S. Costa	B. Dubs 338	S	E	Au	CO	
C. martii Hayne	J.A. Ratter	A. Pott 3237	S	E	Au	CO, N, NE	
Coursetia hassleri Chodat	A. Pott	A. Pott 1918	L	E	Au	CO	
Cratylia argentea (Desv.) Kuntze	G.P. Lewis	A. Pott 4817	L	E	Au	CO, N, NE, SE	
**Crotalaria incana* L.	A. Pott	A. Pott 5447	Ss	E	Au	CO, N, NE, S, SE	
**C. lanceolata* E.Mey.	A. Pott	A. Pott 8058	H	E	Au	CO, N, NE, S, SE	
**C. maypurensis* Kunth	A. Pott	V.J. Pott 1284	H	E	Au	CO, N, NE, S, SE	
C. micans Link	R. Vanni	A. Pott 1755	Ss	E	Au	CO, N, NE, S, SE	
**C. pallida* Aiton	A. Pott	V.J. Pott 3426	Ss	E	Au	CO, N, NE, S, SE	
C. pilosa Mill.	A. Pott	A.Pott 13865	H	E	Au	CO, N, NE, SE	
C. retusa L.	A. Pott & V.J. Pott	V.J. Pott 6052	Ss	E	Au	CO, N, NE, S, SE	
C. sagittalis L.	A. Flores	A.L. Prado 3220	H	E	Au	CO, N	
C. stipularia Desv.	A. Pott	A. Pott 2350	H	E	Au	CO, N, NE, SE	
**C. vitellina* Ker Gawl.	A.C. Allem	A.C. Allem 1673	Ss	E	Au	CO, N, S, SE	
Ctenodon brevipes (Benth.) D.B.O.S. Cardoso, P.L.R. Moraes & H.C. LIma	L.C.P. Lima	G.P. Nunes 215	H	E	Au	CO, NE	

C. denticulatus (Benth.) D.B.O.S. Cardoso, P.L.R. Moraes & H.C. LIma	V.J. Pott; L.C.P. Lima	A. Pott 6302	Ss	E	Hy	CO, N, NE, S, SE	
C. falcatus (Poir.) D.B.O.S. Cardoso, P.L.R. Moraes & H.C. LIma	R. Vanni	V.J. Pott 6025	Ss	E	Au	CO, NE, S, SE	
C. histrix (Poir.) D.B.O.S. Cardoso, P.L.R. Moraes & H.C. Lima	R. Vanni; L.C.P. Lima	A. Pott 2159	Ss	E	Au	CO, N, NE, SE	
C. molliculus (Kunth) D.B.O.S. Cardoso, P.L.R. Moraes & H.C. LIma	L.C.P. Lima	L.E.A.M. Lescano 144	Ss	E	Au	CO, NE, SE	
C. paniculatus (Willd. ex Vogel) D.B.O.S. Cardoso, P.L.R. Moraes & H.C. Lima	R. Vanni; L.C.P. Lima	A. Pott 1015	Ss	E	Au	CO, N, NE, SE	
Cynometra bauhiniaefolia Benth.	A. Pott	V.J. Pott 2008	T	E	Au, Hy	CO, N, NE	
Dalbergia cuiabensis Benth.	G.P. Lewis	A. Pott 4327	S	E	Au	CO	
D. riedelii (Benth.) Sandwith	G.P. Lewis	V.J. Pott 1494	T	E, O		CO, N	

(continued)

Table 3.1 (continued)

*, ***Delonix regia* (Bojer ex Hook.) Raf.			T	E	Au	Exotic	
Desmanthus virgatus (L.) Willd.	A. Pott	A. Pott 3475	Ss	E	Au	CO, N, S, SE	
Desmodium affine Schltdl.	L.C.P. Lima	A. Pott 15582	H	E	Z	CO, N, NE, S, SE	
D. album (Schindl.) J.F.Macbr.	L.C.P. Lima	A.C. Araújo 1130	Ss	E	Z	CO, S	
D. axillare (Sw.) DC.	V.J. Pott	A. Pott 15601	H	E	Z	CO, N, NE, S, SE	
D. barbatum (L.) Benth.	A. Pott; R. Vanni; L.C.P. Lima	A. Pott 1708	H	E	Z	CO, N, NE, S, SE	
D. cajanifolium (Kunth) DC.	L.C.P. Lima	S.N. Moreira 859	Ss	E	Z	CO, N, NE, S, SE	
**D. cuneatum* Hook. & Arn.	L.C.P. Lima	V.J. Pott 1162	Ss	E	Z	CO, S, SE	
D. distortum (Aubl.) J.F.Macbr.	A.M.G.A. Tozzi; L.C.P. Lima	A. Pott 13858	Ss	E	Z	CO, N, NE, SE	
D. guaraniticum (Chodat & Hassl.) Malme	L.C.P. Lima	A. Pott 5466	Ss	E	Z	CO, S, SE	
D. incanum DC.	A. Pott	A. Pott 1242	H, Ss	E	Z	CO, N, NE, S, SE	
D. juruenense Hoehne	A.M.G.A. Tozzi	A.L. Prado 3094	Ss	E	Z	CO, N	Brazil
D. leiocarpum (Spreng.) G.Don	D.N.S Machado	G. Martinelli 18708	Ss	E	Z	CO, NE, S, SE	
D. procumbens (Mill.) Hitchc.	L.C.P. Lima	A. Pott 15.101	H	E	Z	CO, N, NE, S, SE	
D. sclerophyllum Benth.	L.C.P. Lima	VJP 6112	Ss	E	Z	CO, N, NE, SE	

D. scorpiurus (Sw.) Desv.	L.C.P. Lima	L.C.P. Lima 126	Ss	E	Z	CO, NE, S, SE	
D. tortuosum (Sw.) DC.	L.C.P. Lima	V.J. Pott 6053	Ss	E	Z	CO, N, NE, S, SE	
**D. triflorum* (L.) DC.	L.C.P. Lima	V.J. Pott 9368	H	E	Z	CO, N, NE, S, SE	
Dimorphandra mollis Benth.	A. Pott	A. Pott 2579	T	E	Au	CO, N, NE, SE	
Dioclea burkartii R.H.Maxwell	A. Pott; L.P. Queiroz	A. Pott 1317	L	E	Au	CO	
Dipteryx alata Vogel	A. Pott	A. Pott 2393	T	E	Z	CO, N, NE, SE	
Diptychandra aurantiaca Tul.	J.A. Ratter; G.P. Lewis	A. Pott 4387	T	E	Hy	CO, N, NE, SE	
Discolobium leptophyllum Benth.	R. Vanni	M.F. Loureiro 06	Ss	E	Hy	CO	Brazil
D. psoraliaefolium Benth.	R. Vanni	A. Pott 5507	Ss	E	Hy	CO, S	
D. pulchellum Benth.	V.J. Pott; R. Vanni	A. Pott 1037	Ss	E	Au	CO	
Dolichopsis paraguariensis (Benth.) Hassl.	J.F.M. Valls	A. Pott 4495	H	E	Au	CO	
Entada polystachya (L.) DC.	J.A. Ratter	V.J. Pott 1751	L	E	Au	CO, N, NE	
Enterolobium contortisiliquum (Vell.) Morong	J.A. Ratter	A. Pott 6970	T	E	Au	CO, NE, S, SE	
Eriosema crinitum (Kunth) G.Don	A.C.M. Cristaldo	A. Pott 4124	Ss	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

E. platycarpon Micheli	R. Vanni; A.C.M. Cristaldo	A. Pott 5690	Ss	E	Au	CO, SE	
E. rufum (Kunth) G.Don	R. Fortunato; A.C.M. Cristaldo	A. Pott 1710	Ss	E	Au	CO, N, NE, S, SE	
E. simplicifolium (Kunth) G.Don	A.C.M. Cristaldo	A. Pott 13625	Ss	E, O	Au	CO, N, NE, SE	
E. mulungu Mart.	A. Pott	A. Pott 4954	T	E, O	Au	CO, SE	
E. fusca Lourt.	A. Pott	A. Pott 3408	T	E	Au	CO, N	
Galactia benthamiana Micheli	R.T. Queiroz	J.F.M. Valls 9117	H	E	Au	CO	
G. glaucescens Kunth	A. Pott	A. Pott 4369	Ss	E	Au	CO, N, NE, SE	
G. jussiaeana Kunth	F.B. Ceolin	A.C. Allem 125	L	E	Au	CO, N, NE	
G. latisiliqua Desv.	F.B. Ceolin	A.Pott 6821	L	E	Au	SE	
G. striata (Jacq.) Urb.	R.R. Silva	A. Pott 6821	T	E	Z	CO, N, NE, S, SE	
Geoffoea spinosa Jacq. (G. striata)	D.E. Prado	A. Pott 4620	T	E	Au	CO, NE	
Gleditsia amorphoides (Griseb.) Taub.	A. Pott	A. Pott 8958	T	E	Au	CO, S	
Guibourtia chodatiana Hassl.	A.L.B. Sartori	A.L.B. Sartori 1019	T	E	Au	CO, NE, SE	
Hydrochorea corymbosa (Rich.) Barneby & J.W.Grimes	A. Pott	A. Pott 9393	T	E	Au, Hy	CO, N, NE	
Hymenaea courbaril L.	A. Pott	A. Pott 5206	T	E	Z	CO, N, NE, S, SE	
H. martiana Hayne	R.B. Pinto	A. Pott 7973	T	E	Z	CO, N, NE, S, SE	

H. stigonocarpa Mart. ex Hayne	A. Pott	A. Pott 2750		E	Z	CO, N, NE, SE	
Indigofera asperifolia Bong. ex Benth.	A.L.B. Sartori	U.M. Resende 551	H	E	Au	CO, S, SE	
I. campestris Bong. ex Benth.	A. Pott	A. Pott 1010	Ss	E	Au	CO, NE, S, SE	
I. guaranitica Hassl.	S. Eisinger	J.A. Comastri Filho 3	Ss	E	Au	CO, SE	
**I. campestris* Bong.	A. Pott	A. Pott 1010	Ss	E	Au	CO, N, NE, S, SE	
I. lespedezioides Kunth	A. Pott	A. Pott 2140	Ss	E	Au	CO, N, NE, SE	
I. microcarpa Desv.	L.C.P. Lima	A.C. Araujo 736	Ss	E	Au	NE, SE	
I. pascuorum Griseb.	R. Duré	G. Hatschbach 21964	H	E	Au	CO, N, NE, S, SE	
I. sabulicola Benth.	A. Pott	A. Pott 4989	Ss	E	Au	CO, NE, S, SE	
I. spicata Forssk.	F. Matos-Alves	F. Matos-Alves 373	Ss	E	Au	CO	
**I. suffruticosa* Mill.	A. Pott	A. Pott 15469	Ss	E	Au	CO, N, NE, S, SE	
**I. truxillensis* Kunth	A.L.B. Sartori	A.L.B. Sartori 379	Ss	E	Z	CO, SE	Brazil
Inga disticha Benth.	F. Garcia	A. Pott 5134	T	E, O	Z	CO, N	
I. laurina (Sw.) Willd.	F. Garcia	A. Pott 2005	T	E, O	Z	CO, N, NE, S, SE	
I. nobilis Willd.	J.W. Grimes	W.W. Thomas 4632	T	E, O	Z	CO, N, NE, SE	
I. vera subsp. *affinis* (DC.) T.D.Penn.	R. Vanni; F. Garcia	A. Pott 5808	T	E	An	CO, N, NE, S, SE	
Lachesiodendron viridiflorum (Kunth) P.G.Ribeiro et al.	R. Vanni; G.P. Lewis	A. Pott 4926	T	E	Au	CO, NE, SE	

(continued)

Table 3.1 (continued)

Leptolobium dasycarpum Vogel	A. Pott	A. Pott 1187	T	E	An	CO, N, NE, SE	
L. elegans Vogel	J.A. Ratter	A. Pott 4314	T	E	Au	CO, S, SE	
Leptospron adenanthum (G.Mey.) A.Delgado	R. Vanni	A. Pott 2686	T	E	Au	CO, N, NE, S, SE	
**Leucaena leucocephala* (Lam.) de Wit	A. Pott	A. Pott 4631	T	E	Au, An	Exotic	
Libidibia paraguariensis (D.Parodi) G.P.Lewis	D.E. Prado	A. Pott 4631	T	E	Au, Z	CO	
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	M.J. Silva	G.O. Romão 1086	T	E	Au	CO, N, NE, S, SE	
L. pluvialis Rusby	M.J. Silva	F. Matos-Alves 154	T	E	Au	CO, SE	
L. sericeus (Poir.) Kunth ex DC.	G.P. Lewis	A. Pott 4649	T	E	Au	CO, N, NE, S, SE	
Machaerium aculeatum Raddi	J.A. Ratter	A. Pott 3418	T	E	An	CO, NE, SE	Brazil
M. acutifolium Vogel	J.A. Ratter	A. Pott 4282	T	E	An	CO, N, NE, S, SE	
M. amplum Benth.	G.P. Lewis	A. Pott 4773	T	E	An	CO, N, NE, SE	
M. eriocarpum Benth.	A.L.B. Sartori	A.L.B. Sartori 453	T	E	An	CO	
M. hirtum (Vell.) Stellfeld	J.A. Ratter; C.A. Polido	A. Pott 3267	T	E	An	CO, N, NE, S, SE	
M. isadelphum (E.Mey.) Amshoff	C.A. Polido	C.R. Lehn 1/7/2006	L	E	An	CO, N, NE	
M. paraguariense Hassl.	R. Vanni	V.J. Pott 474	T	E	Au	CO, NE, S, SE	
Macropsycanthus glaber L.P. Queiroz & Snak	A. Pott	A. Pott 4308	T	E	Au	CO, N, NE, SE	Brazil

Macroptilium atropurpureum (Sessé & Moc. ex DC.) Urb.	L.P. Queiroz	G. Hatschbach 49246	L	E	Au	CO, N, NE, S, SE	
M. bracteatum (Nees & Mart.) Maréchal & Baudet	J.L.A. Moreira	A. Pott 3810	L	E	Au	CO, NE, S, SE	
M. lathyroides (L.) Urb.	A. Pott	A. Pott 2984	H	E	Au	CO, N, NE, S, SE	
M. martii (Benth.) Maréchal & Baudet	L.C.P. Lima	D.K. Noguchi 130	Ss	E	Au	CO, NE	
M. sabaraense (Hoehne) V.P. Barbosa	J. Cordeiro & E.C. Nardin	M.G. Caxambu 4220	T	E	Au	CO, NE, SE	
Microlobius foetidus var. *paraguensis* (Benth.) M. Sousa & G.Andrade	J.F.M. Valls; G.P Lewis	A. Pott 1871	T	E	Au, Z	CO	
Mimosa acutistipula (Mart.) Benth.	O.S. Ribas	G. Hatschbach 74955	Ss	E	Au	CO, N, NE	
M. adenocarpa Benth.	R. Vanni	A. Pott 4657	Ss	E	Au	CO, N, NE, SE	Brazil
M. alleniana Morong	O.S. Ribas	A. Pott 10583	Ss	E	Au	CO, SE	
M. apodocarpa Benth.	J.S. Silva	A. Pott 13033	S	E	Au	CO	Brazil
M. bimucronata (DC.) Kuntze	R.R. Silva	A. Pott 7900	T	E	Au	CO, NE, S, SE	
M. brevipes Benth.	R.R. Silva	A. Pott 13854	Ss	E	Au	CO, SE	
M. candollei R.Grether	R. Barneby	G. Hatschbach 49251	H	E	Au	CO, N, NE, S, SE	
M. centurions Barneby	M. Morales	F.M. Alves 25	H	E	Au	CO	

(continued)

Table 3.1 (continued)

M. debilis Humb. & Bonpl. ex Willd.	R. Fortunato; R.R. Silva	V.J. Pott 2065	Ss	E	Au	CO, N, NE, S, SE	
M. diplotricha C.Wright ex Sauville	R. Barneby	E.P. Heringer	Ss	E	Au	CO, N, NE, S, SE	
M. distans Benth.	O.S. Ribas	A. Pott 10584	Ss	E	Au	CO, N, NE, S, SE	
M. diversipila M.Micheli	M. Morales	G. Hatschbach 74625	Ss	E	Au	CO	
M. dolens Vell.	J.S. Silva	G.P. Nunes 76	Ss	E	Au	CO, S, SE	
M. gemmulata Barneby	F. Garcia	S.R. Zaniolo 241	S	E	Au	CO, NE, SE	
M. glutinosa Malme	O.S. Ribas	A. Pott 4591	T	E	Au, Hy	CO	
M. gracilis (Poepp. ex Benth) Urb.	H.C. Lima	G. Martinelli 18676	L	E	Au	CO, S, SE	
M. hexandra Micheli	M. Morales	A. Pott 12878	S	E	Au, Hy	CO, NE, SE	
M. invisa Mart. ex Colla	F. Garcia	S.R. Zaniolo 232	Ss	E	Au	CO, N, NE, S, SE	
M. laticifera Rizzini & A.Mattos	A. Pott	A. Pott 6512	T	E	Au	CO, NE, SE	Brazil
M. paludosa Benth.	R. Barneby	M. Schessl 3384	S	E	Au	CO, N, SE	
M. pellita Humb. & Bonpl. ex Willd.	R. Fortunato; R.R. Silva	V.J. Pott 871	S	E	Au, Hy	CO, N, NE, SE	
M. pigra L.	R.R. Silva	V.J. Pott 1049	S	E	Au, Hy	CO, N, NE, S, SE	
M. polycarpa Kunth	R. Vanni	A. Pott 2998	S	E	Au	CO, N, S, SE	
M. pudica L.	A. Pott	A. Pott 7928	Ss	E	Au	CO, N, NE, S, SE	
M. sensibilis Griseb.	M. Morales	E.P. Seleme 317	S	E	Au	CO	
M. somnians Humb. & Bonpl. ex Willd.	R.R. Silva	A. Pott 7697	S	E	Au	CO, N, NE, S, SE	

M. supravisa Barneby	R. Barneby	A.G. Fernandes no n.	S	E	Au	CO, N, NE, SE	Brazil
M. vellosiella Herter	A. Pott	A. Pott 5342	S	E	Au	CO	
M. velloziana Mart.	N.A.G. Escobar	G.A. Damasceno Jr. 2372A	S	E	Au	CO, N, NE, S, SE	
M. weddelliana Benth.	R. Barneby	G. Hatschbach 60853	S	E	Au	CO, NE, SE	
M. xanthocentra Mart.	M. Morales	A. Pott 13229	S	E	Au	CO, N, NE, S, SE	
M. xavantinae Barneby	O.S. Ribas	G. Hatschbach 70880	T	E	Au	CO	Brazil
Muellera filipes (Benth.) M.J Silva & A.M.G.Azevedo	G.P. Lewis	J.A. Ratter 5945	T	E	Au	CO, SE	Brazil
M. nudiflora (Burkart) M.J.Silva & A.M.G.Azevedo	R. Barneby	A. Pott 4453	T	E	Au, Hy	CO	
M. sericea (Micheli) M.J Silva & A.M.G.Azevedo	J.F.M. Valls	A. Pott 4930	T	E	Au, Hy	CO	
Neptunia oleracea Lourt.	R. Vanni	A. Pott 5268	H	E	Au, Hy	CO, N, NE	
N. plena (L.) Benth.	R. Barneby	G. Hatschbach 60910	H, Ss	E	Au, Hy	CO, N, NE	
N. pubescens Benth.	J.F.M. Valls	A. Pott 3504	Ss	E	Au	CO	
Nissolia fruticosa Jacq.	R. Vanni	A. Pott 7075	L	E	Au	CO, N	
Parapiptadenia rigida (Benth.) Brenan	R. Vanni	A. Pott 7044	T	E	Au	CO, S, SE	
Parkinsonia aculeata L.	V.J. Pott	V.J. Pott 323A	T	E	Au	CO, N, NE, S, SE	
P. praecox (Ruiz & Pav.) Hawkins	A. Pott	A. Pott 11392	T	E	An	CO	

(continued)

Table 3.1 (continued)

Peltogyne confertiflora (Mart. ex Hayne) Benth.	A. Pott	L.V.S. Campos 426	T	E	An	CO, N, NE, SE	
Peltophorum dubium (Spreng.) Taub.	A.M.S.F. Vaz; R. Fortunato	A. Pott 5016	L	E	An	CO, NE, S, SE	
Periandra pujlu Emmerich & L.Senna	L.G. Silveira	M. Sazima & C.N. Cunha 12639A	T	E	Au	CO, NE, SE	
***Phanera purpurea* (L.) Benth.			T	O	Au	exot	
**Phaseolus lunatus* L.	J.L.A. Moreira	A. Pott 3068	T	E	Au	Exotic	
Plathymenia reticulata Benth.	A. Pott	A. Pott 4366	T	E		CO, N, NE, S, SE	
Platypodium elegans Vogel	A. Pott	A. Pott 1970	T	E	An	CO, N, NE, S, SE	
Poecilanthe parviflora Benth.	D.M. Neves	D.M. Neves 1940	T	E	AU, Hy	CO, S, SE	
Prosopis affinis Spreng.	R. Barneby	G. Hatschbach 51648	S	E		CO, S	
P. alba Griseb.	A.L.B. Sartori	F. Matos-Alves 600	T	E	Z	CO	
P. nigra (Griseb.) Hieron.	A.L.B. Sartori	A.L.B. Sartori 1108	T	E	Z	CO, S	
P. rubriflora Hassler	J.F.M. Valls	A. Pott 4603	T	E	Au	CO	
P. ruscifolia Griseb.	J.F.M. Valls; D.E. Prado	A. Pott 4404	T	E	Au	CO, NE	
Pterocarpus rohrii Vahl	V.E. Rudd	W.W. Thomas 4588	T	E	Hy	CO, N, NE, S, SE	
P. santalinoides L'Hér. ex DC.	A.L.B. Sartori	U.M. Resende	T	E	Hy	CO, N, NE	
Pterodon emarginatus Vogel		not collected	T	E	An	CO, N, NE, SE	
Pterogyne nitens Tul.	A. Pott	V.J. Pott 774	T	E	Au	CO, NE, S, SE	

Rhynchosia balansae Micheli	A.C.M. Cristaldo	A. Pott 1007	T	E	Au	CO	
R. burkartii Fortunato	R. Fortunato	A. Pott 1920	L	E	Au	CO	
R. edulis Griseb.	A.C.M. Cristaldo	A. Pott 1692	L	E	Au	CO, NE, S, SE	
R. minima (L.) DC.	A.C.M. Cristaldo	A.L.B. Sartori 465	L	E	Au	CO, N, NE, S, SE	
Riedeliella graciliflora Harms	G.P. Lewis	A. Pott 5590	S	E	Au	CO, NE, SE	
Samanea tubulosa (Benth.) Barneby & J.W.Grimes	R.C. Barneby	A. Pott 3786	T	E	Au	CO, N	
Schnella glabra (Jacq.) Dugand	A.M.S.F.Vaz; R.Fortunato; J.L.A. Moreira	A. Pott 5016	L	E	Au	CO, N, NE	
Senegalia lasiophylla (Benth.) Seigler & Ebinger	P.G. Ribeiro	F. Matos-Alves 489	T	E	Au	CO, SE	Brazil
S. loretensis (J.F.Macbr.) Seigler & Ebinger	D.S. Seigler	G. Martinelli 18637	T	E	Au	CO, N, NE	
S. martii (Benth.) Seigler & Ebinger	P.G. Ribeiro	A. Pott 4948	T	E	Au	CO, SE	
S. multipinnata (Ducke) Seigler & Ebinger	V. Terra dos Santos	W.W. Thomas 4654	T	E	Au	N, NE	
S. polyphylla (DC.) Britton & Rose	E. S. Souza-Lima	E.P. Seleme 243	T	E	Au	CO, N, NE, S, SE	
S. praecox (Griseb.) Seigler & Ebinger	D.E. Prado; P.F. Ribeiro	A. Pott 4614	T	E	Au	CO	

(continued)

Table 3.1 (continued)

S. riparia (Kunth) Britton & Rose ex Britton & Killip)	G.A. Damasceno Jr.	G.A. Damasceno Jr. 5161	T	E	Au	N, NE, SE	
S. rostrata (Humb. & Bonpl. ex Willd.) Seigler & Ebinger	P.G. Ribeiro	A. Pott 9454	T	E	Au	N	
S. tenuifolia (L.) Britton & Rose	P.G. Ribeiro	A. Pott 13644	T	E	Au	CO, N, NE, S, SE	
S. tucumanensis (Griseb.) Seigler & Ebinger	F. Matos Alves	F. Matos-Alves 406	L	E	Au	CO, S	
S. velutina (DC.) Seigler & Ebinger	P.G. Ribeiro	A.L.B. Sartori 362	L	E	Au	NE, S, SE	
Senna aculeata (Pohl ex Benth.) H.S.Irwin & Barneby	A. Pott	A. Pott 5092	S	E	Au, Hy	CO, N, NE, SE	
S. alata (L.) Roxb.	A. Pott	V.J. Pott 1292	S	E	Au	CO, N, NE, S, SE	
S. hirsuta (L.) H.S.Irwin & Barneby	A. Pott	A. Pott 15585	Ss	E	Au	CO, N, NE, S, SE	
***S. macranthera* (DC. ex Collad.) H.S.Irwin & Barneby			T	E	Au	CO, N, NE, S, SE	
S. mucronifera (Mart. ex Benth.) H.S.Irwin & Barneby	R.C. Barneby	G. Schaller 300B	T	E	Au	CO, N, NE, SE	
**S. obtusifolia* (L.) H.S.Irwin & Barneby	J.O.R. Miranda	A. Pott 4654	Ss	E	Au	CO, N, NE, S, SE	
**S. occidentalis* (L.) Link	A. Pott	A. Pott 2554	Ss	E	Au	CO, N, NE, S, SE	

S. paradyction (Vogel) H.S.Irwin & Barneby	A. Burkart	G. Hatschbach 21922	Ss	E	Au	CO, SE	
S. pendula Humb. & Bonpl. ex (Willd.) H.S.Irwin & Barneby	A. Pott	A. Pott 4928	S	E	Au	CO, N, NE, S, SE	
S. pilifera (Vogel) H.S.Irwin & Barneby	R. Vanni	A. Pott 3097	Ss	E	Au,Hy	CO, N, NE, S, SE	
S. reticulata (Willd.) H.S. Irwin & Barneby	R.C. Barneby	B. Dubs 1251	S	E	Au	CO, N, NE, SE	
***S. siamea* (Lam.) H.S.Irwin & Barneby			T	E	Au, An	Exotic	
S. silvestris (Vell.) H.S.Irwin & Barneby	G. Hatschbach	A. Pott 4816	S	E	Au	CO, N, NE, S, SE	
S. spinescens (Hoffmanns. ex Vogel) H.S.Irwin & Barneby	A. Pott	A. Pott 9396	Ss	E	Au	CO, N	
S. splendida (Vogel) H.S.Irwin & Barneby	G. Hatschbach	A. Pott 5552	Ss	E	Au	CO, NE, S, SE	
S. velutina (Vogel) H.S.Irwin & Barneby	J.O.R. Miranda	V.J. Pott 2058	S	E	Au	CO, N, NE, SE	
Sesbania emerus (Aubl.) Urb.	V.J. Pott	V.J. Pott 4314	Ss	E	Au,Hy	CO, NE, SE	
S. exasperata Kunth	V.J. Pott	A. Pott 4717	S	E	Au,Hy	CO, N, NE, S, SE	
S. sesban (L.) Merr.	D.N.S. Machado	G. Martinelli 18612	S	E	Au,Hy	CO, N, NE, S, SE	
S. virgata (Cav.) Pers.	A. Pott	A. Pott 2997	T	E	Hy	CO, NE, S, SE	

(continued)

Table 3.1 (continued)

Stryphnodendron rotundifolium Mart.	R. Vanni	A. Pott 1237	T	E	Au	CO, N, NE, S, SE	
Stylosanthes acuminata M.B.Ferreira & Souza Costa	J.F.M. Valls	A. Pott 5274	Ss	E	Au, Z	CO, N, NE, S, SE	
S. grandifolia M.B.Ferreira & Souza Costa	L.C. Costa	A. Pott 13851	Ss	E	Au, Z	CO, N, NE, S, SE	
S. guianensis (Aubl.) Sw.	A. Pott	A. Pott 2348	Ss	E	Au, Z	CO, N, NE, SE	
S. hamata (L.) Taub.	L.C. Costa	A. Pott 12969	H	E	Au, Z	CO, NE	
S. humilis Kunth	F. Matos-Alves	J.S. Silva 871	H	E	Au, Z	CO, N, NE, SE	
S. maracajuensis Sousa Costa & Van den Berg	L.C. Costa	D.K. Noguchi 114	Ss	E	Au, Z	CO	
S. scabra Vogel	L.C. Costa	A. Pott 13208	Ss	E	Au, Z	CO, N, NE, S, SE	
Swartzia jorori Harms	A. Pott	A. Pott 4481	T	E	Au	CO, N	
Sweetia fruticosa Spreng.	J.A. Ratter	A. Pott 5079	T	E	An	CO, NE, S, SE	
Tachigali aurea Tul.	J.A. Ratter	A. Pott 1198	T	E	Au	CO, N, NE, SE	
***Tamarindus indica* L.		S.S. Moura 130	T	E	Z	Exotic	
Tephrosia adunca Benth.	A. Pott; R. Vanni	A. Pott 4310	H	E	Au	CO, N, NE, S, SE	
T. chaquenha R.T. Queiroz & A.M.G.Azevedo	R.T. Queiroz	R.T. Queiroz 1439	Ss	E	Au	CO	
T. cinerea (L.) Pers.	L.P. Queiroz	F. Matos-Alves 568		E	Au	CO, N, NE, S, SE	
T. pseudoadunca (Hassl.) R.T. Queiroz & A.M.G.Azevedo	R.T. Queiroz	A.K.D. Salomão 467	Ss	E	Au	CO	

Teramnus volubilis Sw.	J.F.M. Valls	A. Pott 5100	L	E	Au	CO, N, SE	
Vachellia caven (Molina) Seigler & Ebinger	A. Pott	A. Pott 4409	S	E	Z	CO, S	
V. farnesiana (L.) Wright & Arn.	A. Pott	V.J. Pott 35	T	E	Z	CO, N, NE, S, SE	
Vatairea macrocarpa (Benth.) Ducke	A. Pott	A. Pott 7845	T	E	An	CO, N, NE, SE	
Vigna lasiocarpa (Mart. ex Benth.) Verdc.	V.J. Pott	V.J. Pott 10585	L	E	Au,Hy	CO, N, S	
V. longifolia (Benth.) Verdc.	R. Vanni	A. Pott 5731	L	E	Au,Hy	CO, N, S, SE	
V. luteola (Jacq.) Benth.	D.N.S. Machado	G. Martinelli 18610	L	E	Au	CO, N, NE, S, SE	
***V. unguiculata* (L.) Walp.			L	E	Au	Exotic	
Zapoteca formosa (Kunth) H.M.Hern.	A. Pott	A. Pott 12974	S	E	Au	CO	
Zornia cearensis Huber	J.F.M. Valls; R. Vanni; A. Sciamarelli	A. Prado 30.873	H	E	Au	CO, NE, SE	Brazil
Z. crinita (Mohlenbr.) Vanni	J.F.M. Valls; R. Vanni; A. Sciamarelli	A. Pott 4553	Ss	E	Au, Z	CO, N, S, SE	
Z. latifolia Sm.	R. Vanni	A. Pott 5470	Ss	E	Au	CO, N, NE, S, SE	
Z. reticulata Sm.	M. Brandão	A.C. Allem 1250	Ss	E	Au	CO, N, NE, S, SE	
Z. sericea Moric.	A.P. Fortuna-Perez	A.C. Allem 968	H	E	Au	CO, NE	

(continued)

Table 3.1 (continued)

Z. vichadana (Mohlenbr.) Fort.-Perez & A.M.G. Azevedo	A.P. Fortuna-Perez	U.M .Resende 453	Ss	E	Au	CO, N	
Zygia cataractae (Kunth) L. Rico	M.C.R. Silva	G. Guarim Neto 326	T	E	Au,Hy	CO, N, NE, SE	
Z. cauliflora (Willd.) Killip	A.L.B. Sartori	A.L.B. Sartori 353	T	E	Au,Hy	CO	
Z. latifolia (L.) Fawc. & Rendle	J.Y. Tamashiro	G.A. Damasceno Jr. 2618	T	E	Au,Hy	CO, N, NE, S, SE	
Z. inaequalis (Willd.) Pittier	L. Rico	A. Pott 5630	T	E	Au,Hy	CO, N	
Z. morongii Barneby & J.W.Grimes	R.C. Barneby	G. Hatschbach 60862	T	E	Au,Hy	CO	
Z. pithecoloboides (Kunth) Barneby & J.W. Grimes	J.W. Grimes	G. Hatschbach 38627	T	E	Au,Hy	CO	
Gentianaceae							
Chelonanthus alatus (Aubl.) Pulle	V.J. Pott	S.N. Moreira 947	H	E	Au	CO, N	
Coutoubea ramosa Aubl.	A. Pott	A. Pott 6590	H	E	Au	CO, N, NE, SE	
Curtia tenuifolia (Aubl.) Knobl.	E.F. Guimarães	A. Pott 4372	H	E	Au	CO, N, NE, S, SE	
Schultesia brachyptera Cham.	A. Jacobs-Brouwer	M. Schessl 2809	H	E	Au	CO, N, NE, SE	
S. guianensis (Aubl.) Malme	E.F. Guimarães	A. Pott 1536	H	E	Au	CO, N, NE, SE	
S. heterophylla Miq.	E.F. Guimarães	A. Pott 2918	H	E	Au	CO, N, NE, SE	
S. pohliana Progel	E.F. Guimarães	A. Pott 2762	H	E	Au	CO, N, NE, SE	

S. stenophylla Mart.	S. Tressens	A. Pott 1786	H	E, O	Au	CO	
Heliconiaceae							
Heliconia marginata (Griggs) Pittier	A. Pott	A. Pott 4722	H	E, O	Z	CO, N	
H. psittacorum L.f.	V.J. Pott	V.J. Pott 2070	H	E, O	Z	CO, N, NE, SE	
H. hirsuta L.f.	J.M.A. Braga	G. Martinelli 18734	H	E,O	Z	CO, N, S, SE	
Hernandiaceae							
Sparattanthelium borororum Mart.	S. Koehler	A. Pott 6295	L	E	Z	CO, N, NE, SE	
Hydrocharitaceae							
Apalanthe granatensis (Bonpl.) Planch.	C.D.K. Cook	V.J. Pott 3004	H	E	Hy	CO, N, NE, SE	
Egeria najas Planch.	C.D.K. Cook; R.R. Haynes; S. Koehler	V.J. Pott 3459	H	E	Hy	CO, NE, S, SE	
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine	C.D.K. Cook; R.R. Haynes	V.J. Pott 2767	H	E	Hy	CO, N, NE, S, SE	
Najas guadalupensis (Spreng.) Magnus	V.J. Pott; R.R. Haynes	V.J. Pott 570	H	Hy	Hy	CO, N, NE, S, SE	
N. microcarpa K.Schum.	R.R. Haynes	V.J. Pott 1507	H	Hy	Hy	CO, N, NE, SE	
Hydroleaceae (Hydrophyllaceae)							
Hydrolea elatior Schott	B.T. Walter	A.C. Allem 2517	Ss	E	Au	CO, N, S, SE	
H. spinosa L.	V.J. Pott; L.J. Davenport	V.J. Pott 1735	Ss	E	Au	CO, N, NE, S, SE	
Iridaceae							
Cipura paludosa Aubl.	A. Pott	A. Pott 4579	Hp	E	Au	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

Cypella exilis Ravenna (doubtful name)	A. Pott	A. Pott 4579	Hp	E	Au	CO	
Larentia linearis (Kunth) Klatt	J. Lovo	B.S.H. Ferreira 96	H	E	Z	CO	
Lamiaceae							
Aegiphila racemosa Vell.	F. França	A. Pott 4124	S	E	Z	CO, N, NE	
A. verticillata Vell.	F. França	A. Pott 1655	T	E	Z	CO, N, NE, S, SE	
A. vitelliniflora Walp.	F. França; G. Hatschbach	A. Pott 1897	S	E	Au	CO, N, NE, S, SE	
Cantinoa americana (Aubl.) Harley & J.B.F.Pastore	V.J. Pott	A. Pott 2693	Ss	E	Au	CO, N, NE, SE	
Cantinoa carpinifolia (Benth.) Harley & J.B.F.Pastore	V.J. Pott	S.N. Moreira 854	Ss	E	Au	CO, N, NE, SE	
C. mutabilis (Rich.) Harley & J.B.F.Pastore	F. França	A. Pott 5446	Ss	E	Au	CO, N, NE, S, SE	
**Eriope crassipes* Benth.	A. Pott	A. Pott 3923		E	Au	CO, N, NE, S, SE	
Gymneia interrupta (Pohl ex Benth.) Harley & J.F.B.Pastore	V.J. Pott	A. Pott 2276	H	E	Au	CO, N, SE	Brazil
Hyptis brevipes Poit.	V.J. Pott	V.J. Pott 1343	H	E	Au	CO, N, NE, S, SE	
H. campestris Harley & J.B.F.Pastore	A. Schinini; V.J. Pott	A. Pott 4300	H	E	Au	CO, N, NE, SE	

H. conferta Pohl ex Benth.	V.J. Pott	S.N. Moreira 814	S	E	Au	CO, N, NE, SE	
H. crenata Pohl ex Benth.	A. Pott	A. Pott 4304	Ss	E	Au	CO, N, NE, SE	
H. hirsuta Kunth	A. Pott	A. Pott 7706	Hp	E	Au	CO, N	
H. lappacea Benth.	A. Pott	V.J. Pott 2519	Hp	E	Au	CO	
H. lorentziana O.Hoffm.	V.J. Pott; R.M. Harley	V.J. PottP 2555	H	E	Au	CO, N, NE, S, SE	
H. lutescens Pohl ex Benth.	R.M. Harley	A.M. Giulietti 2480	Ss	E	Au	CO, N, NE, SE	
H. microphylla Pohl ex Benth.	A. Pott	A. Pott 5708	Ss	E	Au	CO, N, NE, SE	
H. recurvata Poit.	A. Pott	A. Pott 1900	H	E	Au	CO, N, NE, SE	
H. sinuata Pohl ex Benth.	A. Pott	A. Pott 2945	H, Ss	E	Au	CO, N, S, SE	
**Leonotis nepetifolia* (L.) R.Br.	A. Pott	A. Pott 5463	H	O, E	Au	CO, N, NE, S, SE	
**Leonurus japonicus* Houttl.	A. Pott	A. Pott 2805	H	E	Au	CO, N, NE, S, SE	
**Marsypianthes chamaedrys* (Vahl) Kuntze	A. Pott	A. Pott 1394	H	E	Au	CO, N, NE, S, SE	
***Mentha pulegium* L.			H	E		Exotic	
Mesosphaerum suaveolens (L.) Kuntze	R.M. Harley	A. Pott 8023	Ss	E	Au	CO, N, NE, S, SE	
***Paulownia tomentosa* (Thunb.) Steud.			T	E		Exotic	
***Plectranthus barbatus* Andr.			Ss	E	Au	Exotic	

(continued)

Table 3.1 (continued)

***Salvia splendens* Sellow ex Roem. & Schult.			H	E	Au	Exotic	
***Tectona grandis* L.f.			T	E, O		Exotic	
Vitex cymosa Bertero ex Spreng.	J.A. Ratter	A. Pott 3782	T	E	Z	CO, N, NE, S, SE	
Lauraceae							
Cassytha filiformis L.	A. Pott; F.M. Alves	A. Pott 3816	T	E	Z	CO, N, NE, S, SE	
***Cinnamomum verum* Presl.		A. Pott 5639	T	E	Z	Exotic	
***Laurus nobilis* L			T	E	Z	Exotic	
Mezilaurus vanderwerffii F.M.Alves & Baitello	F.M. Alves	A. Pott 2477	T	E	Z	CO	Brazil
Nectandra amazonum Nees	F.M. Alves	A. Pott 4678	T	E	Z	CO, N, NE	
N. angustifolia (Schrad.) Nees	F.M. Alves	A. Pott 4771	T	E	Z	CO, NE, S, SE	
N. gardneri Meisn.	F.M. Alves	S.N. Moreira 833	T	E	Z	CO, N, NE, SE	Brazil
N. pulverulenta Nees	M.A. Carniello	M.A. Carniello 6145	T	E	Z	CO, N	
N. warmingii Meisn.	J.B. Baitello	V.C. Souza 32326	T	E	Z	CO, N, NE, SE	Brazil
Ocotea cernua (Nees) Mez	J.A. Ratter; J.G. Rohwer	G. Hatschbach 60884	T	E	Z	CO, N, NE, SE	
O. diospyrifolia (Meisn.) Mez	J.A. Ratter; F.M. Alves	A. Pott 5079	T	E	Z	CO, N, S, SE	
Lecythidaceae							
Eschweilera nana (Berg) Miers	V.J. Pott	A. Pott 7731	H	E	Z	CO, N, NE	Brazil

Lentibulariaceae							
Genlisea repens Benj.	V.J. Pott	S.N. Moreira 1571	H	E	Hy	CO, N, NE, S, SE	
Utricularia amethystina Salzm. ex A.St.-Hil. & Girard	M.M. Arbo	A. Pott no n.	H	E	Hy	CO, N, NE, SE	
U. breviscapa C. Wright ex Griseb.	V.J. Pott	V.J. Pott 2780	H	E	Hy	CO, N, NE, SE	
U. erectiflora A.St.-Hil. & Girard	V.J. Pott	S.N. Moreira 1502	H	E	Hy	CO, N, S, SE	
U. fimbriata Kunth	V.J. Pott	A. Pott 2915	H	E	Hy	CO	
U. foliosa L.	V.J. Pott	V.J. Pott 2778	H	E	Hy	CO, N, NE, S, SE	
U. gibba L.	V.J. Pott	V.J. Pott 3139	H	E	Hy	CO, N, NE, S, SE	
U. hydrocarpa Vahl	M.M. Arbo	V.J. Pott 3041	H	E	Hy	CO, N, NE, S, SE	
U. lloydii Merl ex F. Lloyd	V.J. Pott	S.N. Moreira 1557	H	E	Hy	CO, N, NE	
U. myriocista A.St.-Hil. & Girard	V.J. Pott	V.J. Pott 3046	H	E	Hy	CO, N, NE, SE	
U. nana A.St.-Hil. & Girard	V.J. Pott	V.J. Pott 101331	H	E	Hy	CO, N, NE, S, SE	
U. *nigrescens* Sylvén	M.R.F. Cardoso	M.R.F. Cardoso 116	H	E	Hy	CO, N, S, SE	
U. poconensis Fromm	V.J. Pott	V.J. Pott 1483	H	E	Hy	CO, N, SE	Brazil
U. pusilla Vahl	V.J. Pott	V.J. Pott 2950	H	E	Hy	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

U. simulans Pilg.	V.J. Pott	A. Pott 2915	H	E	Au, Hy	CO, N, NE, SE	
U. subulata L.	V.J. Pott	S.N. Moreira 946	H	E	Au, Hy	CO, N, NE, S, SE	
U. trichophylla Spruce ex Oliv.	V.J. Pott	S.N. Moreira 1595	H	E	Hy	CO, N, NE, SE	
U. tricolor A.St.-Hil.	V.J. Pott	S.N. Moreira 1505	H	E	Hy	CO, N, NE, S, SE	Brazil
U. triloba Benj.	V.J. Pott	V.J. Pott 2950	H	E	Hy	CO, N, NE, S, SE	
U. warmingii Kamienski	V.J. Pott	V.J. Pott 3057	Hp	E	Hy	CO, SE	
Linderniaceae							
Lindernia crustacea L.F.Müll.	V.C. Souza	V.J. Pott 1112	H	E	Au	CO, N, NE, SE	
L. diffusa (L.) Wettst.	A.V. Scatigna	V.J. Pott 3669	H	E	Au	CO, N, NE, S, SE	
L. dubia (L.) Pennell	V.C. Souza	V.J. Pott 1532	H	E	Au	CO, N, S	
Micranthemum umbrosum (Walt. ex J.F.Gmel) S.F.Blake	V.C. Souza	A. Pott 4902	H	E	Au	CO, N, NE, S, SE	
Torenia thouarsii (Cham. & Schltdl.) Kuntze	V.C. Souza	V.J. Pott 2947	H	E	Au	CO, N, NE, S, SE	
Loasaceae							
Mentzelia aspera L.	A.M. Radovancich	A. Pott 4518	H	E	Z	CO, N, NE, SE	
Loganiaceae							
Strychnos mattogrossensis S.Moore	A.J.M. Leeuwenberg	W.W. Thomas 4613	L	E	Z	CO, N, NE	Brazil
S. pseudoquina A.St.-Hil.	A. Pott	A. Pott 1803	T	E	Z	CO, N, NE, SE	
Loranthaceae							

Passovia pedunculata (Jacq.) Kuijt	C.S. Caires; B.A. Dettke	V.J. Pott 2471	P	E	Z	CO, N, NE, SE	
Psittacanthus acinarius (Mart.) Mart.	B.A. Dettke	A. Pott 10939	P	Z	Z	CO, N, NE, SE	
P. cordatus (Hoffmanns.) G.Don	A.M. Radovancich; B.A. Dettke	A. Pott 2957	P	O	Z	CO, N, NE, SE	
P. robustus (Mart.) Mart.	C.R.H. Paula; B.A. Dettke	V.F. Kinupp 1100	P	O	Z	CO, N, NE, SE	
Struthanthus uraguensis (Hook. & Arn) G.Don	B.A. Dettke	E.P. Seleme 227	P	E	Z	CO, NE, S, SE	
Lythraceae (included Punicaceae)							
Adenaria floribunda Kunth	J.A. Ratter	A. Pott 5957	S	E	Au	CO, N, NE, SE	
Ammannia auriculata Willd.	T.B. Cavalcanti	A. Pott 1953	H	E	Au, Hy	CO, NE	
Cuphea carthagenensis (Jacq.) J.Macbr.	T.B. Cavalcanti	V.J. Pott 5786	H	E	Au	CO, N, NE, S, SE	
C. corisperma Koehne	T.B. Cavalcanti	A. Pott 5619	H	E	Au	CO	
C. ferruginea Pohl ex Koehne	T.B. Cavalcanti	A.C. Allem 199	Ss	E	Au	CO	Brazil
C. inaequalifolia Koehne	V.J. Pott	V.J. Pott 1012	Ss	E	Au	CO	
C. melvilla Lindl.	T.B. Cavalcanti	A. Pott 3410	Ss	O	Au	CO, N, NE, S, SE	
C. odonellii Lourteig	T.B. Cavalcanti	A. Pott 4392	Ss	E	Au	CO, N	
C. pterosperma Koehne	S.A. Graham	G. Hatschbach 74654	Ss	E	Au	CO, SE	

(continued)

Table 3.1 (continued)

C. repens Koehne	S.M. Ferrucci	A. Pott 2279	H	E	Au	CO, N, NE, SE	
C. retrorsicapilla Koehne	T.B. Cavalcanti	V.J. Pott 4121	Ss	E	Au	CO, N, SE	
C. sessiliflora A.St.-Hil.	T.B. Cavalcanti	V.J. Pott 6101	Ss	E	Au	CO, NE, SE	Brazil
Heimia salicifolia Link	T.B. Cavalcanti	A. Pott 12841	Ss	E	Au	CO, S, SE	
Lafoensia pacari A.St.-Hil.	J.A. Ratter	A. Pott 4328	T	E	Au	CO, N, NE, S, SE	
***Lagerstroemia indica* L.						Exotic	
Pleurophora saccocarpa Koehne	T.B. Cavalcanti	V.J. Pott 7825	H		Hy	CO	
***Punica granatum* L.	A. Pott	S.S. Moura 144	S	E	Z	Exotic	
Rotala mexicana Cham. & Schltdl.	C.D.K. Cook	V.J. Pott 1933	H		Au	CO, N. SE	
R. ramosior (L.) Koehne	C.D.K. Cook	V.J. Pott 7537	H	E	An	Not in Brazil?	
Malpighiaceae							
Aenigmatanthera lasiandra (A.Juss.) W.R.Anderson	M.C.H. Mamede	A. Pott 5055	L	E	An	CO, N, NE	
Alicia anisopetala (A.Juss.) W.R.Anderson	A. Francener	R.D. Delmão 42	L	E	An	CO, NE, S, SE	
Amorimia pubiflora (A.Juss.) W.R.Anderson	A. Francener	A. Pott 2688	L	E	An	CO, SE	Brazil
Aspicarpa pulchella (Griseb.) O'Donell& Lourteig	A. Francener	A. Pott 8855	Ss	E	An	CO, S, SE	
Banisteriopsis argyrophylla (A.Juss.) B.Gates	A. Francener	A. Pott 15584	L	E	An	CO, N, NE, SE	

B. muricata (Cav.) Cuatrec.	A. Francener	V.J. Pott 3106	L	E	An	CO, N, NE, S, SE	
B. oxyclada (A.Juss.) B.Gates	W.R. Anderson	G. Hatschbach 60758	L	E	An	CO, N, NE, SE	
B. stellaris (Griseb.) A.Gates	W.R. Anderson	A. Pott 2206	Ss	E	Z	CO, N, NE, SE	
***Bunchosia armeniaca* DC.			T	E	Z	Exotic	
B. pallescens Skottsb.	M.C.C. Mamede	A. Pott 5242	T	E	Z	CO, S, SE	
B. paraguariensis Nied.	J.A. Ratter	A. Pott 15869	T	E	Z	CO	
Byrsonima arthropoda A.Juss.	A. Francener	C.A. Conceição 2868	T	E	Z	CO, N	
B. coccolobifolia Kunth	J.A. Ratter	R.A. Mauro 87	T	E	Z	CO, N, NE, S, SE	
B. crassifolia (L.) Kunth	B. Gates	A. Pott 3809	T	E	Z	CO, N, NE, S, SE	
B. crispa A Juss.	B. Gates; A. Francener	A. Pott 2370	T	E	Z	CO, N, NE, SE	
B. cydoniifolia A.Juss.	B. Gates	A. Pott 5049	S	E	Z	CO, N, NE, SE	
B. intermedia A.Juss.	A. Francener	A. Pott 13597	S	E	Z	CO, N, NE, SE	Brazil
B. lancifolia (A. Juss.) A.Juss.	H.K. Keel	G. Schaller 44	T	E	Z	CO, N, NE, SE	
B. laxiflora Griseb.	A. Francener	A. Pott 3555	T	E	Z	CO, N, NE, SE	Brazil
B. verbascifolia (L.) DC.	A. Pott	A. Pott 2391	T	E	An	CO, N, NE, S, SE	
Callaeum psilophyllum (A.Juss.) D.M.Johnson	A. Francener	A. Pott 1855	L	E	An	CO, NE, S, SE	

(continued)

Table 3.1 (continued)

Camarea affinis A.St.-Hil.	A. Pott	A. Pott 2398	Ss	E	An	CO, NE, SE	
Dicella macroptera A.Juss.	M.C.H. Mamede	G.A. Damasceno Jr. 3130	L	E	An	CO, N, NE, SE	
Dicliptera squarrosa Nees	A. Pott	M.R. Sigrist 34	Ss	E	Na	CO, S, SE	
Diplopterys lutea (Griseb.) W.R.Anderson & C.C.Davies	A. Francener	A. Pott 3240	L	E	An	CO, N, NE, S, SE	
D. pubipetala (A.Juss.) W.R.Anderson & C.C.Davies	B. Gates; A. Francener	J.A. Ratter 5075	L	E	An	CO, N, NE, S, SE	
Galphimia australis Chodat	A. Francener	A. Pott 3838	Ss	E	An	CO, S, SE	
Heteropterys amplexicaulis Morong	A. Francener	C.A. Conceição 2702	S	E	An	CO	
H. byrsonimiifolia A.Juss.	M.C.H. Mamede	A. Pott 4383	S	E	An	CO, NE, S, SE	
H. cochlosperma A.Juss.	A. Francener	A. Pott 8052	L	E	An	CO, NE, S, SE	
H. dumetorum (Griseb.) Nied.	A. Francener	A. Pott 4415	S	E	An	CO, NE, S, SE	
H. glabra Hook. & Arn.	M.C.H. Mamede	A. Pott 4515	L	E	An	CO	
H. hypericifolia A.Juss.	A. Pott; A. Francener	A. Pott 1956	L	E	An	CO, S	
H. marginata W.R.Anderson	W.R. Anderson	M. Schessl 2226 (Syntype)	S	E	An	CO	Brazil
H. rhopalifolia A.Juss.	C. Pessoa	C.P. Calliari 29	S	E	An	CO, N, NE, SE	
H. tomentosa A.Juss.	A. Pott	A. Pott 3229	L	E	An	CO, SE	
Janusia guaranitica (A.St.-Hil.) A.Juss.	R. Sebastiani	A. Pott 12860	L	E	An	CO, S, SE	

J. janusioides (A.Juss.) W.R.Anderson	R. Sebastiani	A. Pott 7673	L	E	An	CO, N, NE, SE	
***Malpighia glabra* L.			T	E	Z	Exotic	
Mascagnia cordifolia (A.Juss.) Griseb.	A. Pott	A. Pott 4395	L	E	An	CO, N, NE, SE	
M. sepium (A.Juss.) Griseb.	M.C.H. Mamede	G.A. Damasceno Jr. 724	L	E	An	CO, N, NE, S, SE	
Niedenzuella stannea (Griseb.) W.R.Anderson	W.R. Anderson; A. Francener	A. Pott 3235	L	E	An	CO, N	
Peixotoa cordistipula A.Juss.	M.C.H. Mamede	A. Pott 4559	Ss	E	An	CO, N	
P. magnifica C.E.Anderson	C.E. Anderson	G. Schaller 89	Ss	E	An	CO	
Ptilochaeta densiflora Nied.	G.A. Damasceno Jr.	F.S. Carvalho 290	L	E		CO, NE, SE	
Stigmaphyllon calcaratum N.E.Br.	A.Pott	A. Pott 6225	L	E		CO, N	
S. macedoanum C.E.Anderson	A. Francener; R.F. Almeida	A. Pott 5617	L	E	An	CO, SE	Brazil
S. rotundifolium A.Juss.	M.C.H. Mamede	M. Sazima s/n	L	E	An	CO, NE, SE	Brazil
Tetrapterys hassleriana Nied.	A. Francener	A. Pott 7654	Ss	E	An	CO	
T. jussieana Nied.	M.C.H. Mamede	M. Gasparini 45	Ss	E	An	CO, N, NE, S, SE	
T. phlomoides (Spreng.) Nied.	M.C.H. Mamede; A. Francener	A. Pott 5494	L	E	An	CO, NE, S, SE	

(continued)

Table 3.1 (continued)

Thryallis laburnum S.Moore	A. Francener	A. Francener 941	L	E	An	CO	Brazil
Malvaceae (including Bombacaceae, Sterculiaceae, Tiliaceae)							
***Abelmoscus esculentus* L.			H	E	Z	Exotic	
Abutilon ramiflorum A.St.-Hil.	A. Krapovickas	A. Pott 3057	s	E	Au	CO, NE, SE	
Apeiba tibourbou Aubl.		T. Duarte 14	T	E	Au, Z	CO, N, NE, SE	
Ayenia odonellii Cristóbal	C.L. Cristóbal	A. Pott 4052	H	E	Au	CO	
A. tomentosa L.	C.L. Cristóbal	A.Pott 4707	Ss	E	Au	CO, NE, SE	
***Bombax ceiba* L.			T	E, Z	An	Exotic	
**Briquetiastrum spicatum* (Kunth in H.B.K.) Bovini	C. Takeuchi	A. Pott 5063	S	E	Au	CO, N, NE, SE	
Byttneria dentata Pohl	C.L. Cristóbal	A. Pott 4096	S	E	Au	CO, N, SE	
B. divaricata Benth.	C.L. Cristóbal	A. Pott 3561	S	E	A, Hy	CO, N	
B. filipes Mart. ex K. Schum.	C.L. Cristóbal	A. Pott 3022	S	E	A, Hy	CO, NE	
B. genistella Triana & Planch.	C.L. Cristóbal	A. Pott 5508	Ss	E	Au	CO, NE	
B. palustris Cristóbal	C.L. Cristóbal	A. Pott 3280	S	E	Au	CO, SE	Brazil
B. rhamnifolia Benth.	C.L. Cristóbal	A. Pott 5258	S	E	Au	CO, N	
B. scabra L.	C.L. Cristóbal	A. Pott 4492	S	E	Au	CO, N. NE, S, SE	
B. tucumanensis Cristóbal	C.L. Cristóbal	G. Hatschbach 60769	S	E	An	CO	

Ceiba pentandra (A.St.-Hil.) K.Schum.	E.R. Salviani & H. Lorenzi	E.R. Salviani & H. Lorenzi 52	T	Z	Na	CO, NE, SE	
C. samauma (Mart.) K. Schum.	A. Pott	A. Pott 5502	T	O	Au	CO, N, NE	
C. speciosa (A.St.-Hil.) Ravenna	G.A. Damasceno Jr.	D.R.C. Pdilha 30	T	Z	Na	CO, N. NE, S, SE	
Cienfuegosia affinis (Kunth) Hochr.	A. Krapovickas	V.J. Pott 1899	Ss	E	Au	CO, N, NE, SE	
C. drummondii (A.Gray) Lewton	A. Krapovickas; M.G. Bovini	A. Pott 6863	Ss	E	Au	CO, S	
Corchorus argutus Kunth	M.S. Ferrucci	A. Pott 3293	H	E	Au	CO, N. NE, S, SE	
C. hirtus L.	M.S. Ferrucci	A. Pott 1642	Ss	E	An	CO, N. NE, S, SE	
C. orinocensis Kunth	L.J. Dorr	G. Hatschbach 29592	Ss	E	Au	CO, N	
Eriotheca gracilipes (K.Schum.) A.Robyns	A.Pott & V.J. Pott	A. Pott 3227	T	E	An	CO, N, NE, SE	
Gaya bordasii Krapov.	A. Krapovickas; C. Takeuchi	A. Pott 6999	Ss	E	Au	CO	
G. meridionalis Hassl.	C. Takeuchi	A. Pott 2646	S	E	An	CO	
**Gossypium barbadense* L.	A. Krapovickas	A. Pott 3886	S	E	An	CO, N, NE	
Guazuma ulmifolia Lam.	J.A. Ratter	A. Pott 4276	S	E	Z	CO, N. NE, S, SE	
Helicteres corylifolia Nees & Mart.	C.L. Cristóbal	A. Pott 6282	S	O	Au	CO, N, NE, SE	Brazil

(continued)

Table 3.1 (continued)

H. gardneriana A.St.-Hil. & Naudin	C.L. Cristóbal	C.N. Cunha 10485	S	O	Au	CO, N, NE, SE	
H. guazumifolia Kunth	C.L. Cristóbal	A. Pott 3742	S	O	Au	CO, N, SE	
H. lhotzkyana (Schott & Endl.) K.Schum.	C.L. Cristóbal	A. Pott 3971	T	O	Au	CO, N, NE, SE	
H. sacarolha A.St.-Hil., Juss. & Cambess.	A. Krapovickas	A. Pott 1908	Ss	O	Au	CO, N, NE, SE	
Herissantia nemoralis (A.St.-Hil.) Brizicky	A. Krapovickas	A. Pott 4329	Ss	E	Au, Hy	CO, SE	Brazil
Hibiscus furcellatus Desr.	A. Krapovickas	A. Pott 5637	Ss	E	Au, Hy	CO, N. NE, S, SE	
***H. rosa-sinensis* L.	A. Pott	S.S. Moura 157	S	E		Exotic	
***H. sabdariffa* L.	M.A. Carniello	M.A. Carniello 4731	S	E		Exotic	
H. sororius L.		A. Pott 4664	Ss	E	Au, Hy	CO, N, S, SE	
***H. schizopetalus* Dyer.			S	E		Exotic	
H. striatus Cav.	A. Krapovickas	A. Pott 5611	Ss	E	Au	CO	
Luehea grandiflora Mart. & Zucc.	M.S. Ferrucci	A. Pott 6507	T	E	Au	CO, N. NE, S, SE	
L. paniculata Mart. & Zucc.	J.A. Ratter	A. Pott 3438	T	E	Au	CO, N. NE, S, SE	
Malachra radiata (L.) L.	A. Krapovickas	V.J. Pott 1208	Ss	E	Au	CO, NE, SE	
**Malvastrum americanum* (L.) Torr.	C.L. Cristóbal	A. Pott 2900	Ss	E	Au	CO, NE, S, SE	
**M coromandelianum* Garcke	C.L. Cristóbal	A. Pott 2899	Ss	E	Au	CO, N. NE, S, SE	
Melochia anomala Griseb.	C.L. Cristóbal	A. Pott 1732	Ss	E	Au	CO	

M. arenosa Benth.	C.L. Cristóbal	A. Pott 5777	Ss	E	Au	CO, N. NE, S, SE	
M. graminifolia A.St.-Hil.	A. Pott	S.V. Boff 117	Ss	E	Au	CO, N, SE	
M. parvifolia Kunth	C.L. Cristóbal	A. Pott 2999	Ss	E	Au	CO, N, SE	
M. pilosa (Mill.) Fawc. & Rendle	C.L. Cristóbal	A. Pott 7660	Ss	E	Au	CO, SE, S	
M. pyramidata L.	C.L. Cristóbal	A. Pott 5636	Ss	E	Au	CO, NE, S, SE	
M. simplex A.St.-Hil.	C.L. Cristóbal	A. Pott 5792	Ss	E	Au	CO, N, S, SE	
M. villosa (Mill.) Fawc. & Rendle	C.L. Cristóbal	A. Pott 1234	Ss	E	Au	CO, N. NE, S, SE	
M. werdermannii Golderg.	A. Pott & V.J. Pott	A. Pott 1721	Ss	E	Z	CO	
***Pachira aquatica* Aubl.			T	E, Q	Z	N, NE	
***P. insignis* (Sw.) Savigny			T	E, Q	Au	N	
Pavonia angustifolia Benth.	A. Krapovickas	A. Pott 3390	Ss	E	Au	CO, N, SE	
P. apiculata R.E.Fr.	A. Krapovickas	A. Pott 5484	Ss	E	Au	CO	
P. argentina Gürcke	A. Krapovickas	A. Pott 12896	Ss	E	Au	CO	
P. cancellata (L.) Cav.	G.L. Esteves	G.F. Arbocz 2305	H	E	Au	CO, N, NE, SE	
P. garckeana Gürke	A. Krapovickas	V.J. Pott 2069	Ss	E	Au	CO, NE, SE	
P. hieronymi Gürke	P.A. Fryxell	B. Dubs 172	Ss	E	Au	CO	
P. laetevirens R.E.Fr.	A. Krapovickas	A. Pott 5082	S	E	Au	CO	
P. opulifolia S.Moore	A. Krapovickas	A. Pott 3195	S	E	Au	CO, N, S, SE	
P. sidifolia Kunth	A. Krapovickas	A. Pott 4295	Ss	E	Au	CO, NE, SE	

(continued)

Table 3.1 (continued)

P. vitifolia Hochr. ex Chodat & Hassl.	T.S. Mendes	G. Martinelli 18621	Ss	E	Au	CO, N, S	
Peltaea riedelii (Gürke) Standl.	A. Krapovickas	A. Pott 5025	Ss	E	Au	CO, NE	
Pseudabutilon aristulosum (K.Schum.) Krapov.	C. Takeuchi	A. Pott 4302	Ss	E	Au	CO, NE, SE	
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	J.A. Ratter	A. Pott 4343	T	Q, E	An	CO, N. NE, S, SE	
P. marginatum (A. St.-Hil., Juss. & Cambess.) A.Robyns	J.A. Ratter	A. Pott 6972	T	Q, E	An	CO, N. NE, S, SE	
P. tomentosum (Mart.) A. Robyns	M.C. Duarte	S.R. Zaniolo s/n	T	E	An	CO, N, NE, SE	
Sida anomala A.St.-Hil.	A. Krapovickas	A. Pott 7899	Ss	E	Au	CO, S	
S. cerradoensis Krapov.	A. Krapovickas	A. Pott 4371	Ss	E	Au	CO, N. NE, S, SE	Brazil
S. ciliaris L.	A. Krapovickas	A. Pott 4447	H	E	Au	CO, NE	
**S. cordifolia* L.	A. Krapovickas	A. Pott 6876	Ss	E	Au	CO, N. NE, S, SE	
**S. glomerata* Cav.	A. Krapovickas	A.Pott 5681	Ss	E	Au	CO, N, NE, SE	
S. linearifolia A.St.-Hil.	E.F. Guimarães	G. Martinelli 18727	H	E	Au	CO	
S. linifolia Cav.	A. Pott	A. Pott 4321	H	E	Au	CO, N. NE, S, SE	
**S. planicaulis* L.f.	A. Krapovickas	A. Pott 7965	Ss	E	Au	CO, NE, S, SE	
**S. rhombifolia* L.	A. Krapovickas	A. Pott 5774	Ss	E	Au	CO, N. NE, S, SE	

S. rufescens A.St.-Hil.	A. Pott	A. Pott 6344	H	E	Au	CO, NE, SE	
S. rupicola Hassl.	C. Takeuchi	A. Pott 15556	Ss	E	Au	CO, NE, S	
S. santaremensis Mont.	A. Krapovickas	A. Pott 2515	Ss	E	Au	CO, N. NE, S, SE	
S. spinosa L.	A. Krapovickas	A. Pott 5682	Ss	E	Au	CO, NE, S, SE	
S. tuberculata R.E.Fr.	A. Krapovickas	A. Krapovickas 43124	Ss	E	Au	CO, NE, SE	
**S. viarum* A. St.-Hil.	A. Krapovickas	A. Pott 4474	Ss	E	Au	CO, NE, S, SE	Brazil
**Sidastrum multiflorum* (Jacq.) Fryxell	A. Pott	A. Pott 4844	Ss	E	Au	CO, NE, SE	
**S. paniculatum* (L.) Fryxell	A. Pott	A. Pott 2898	Ss	E	Au	CO, NE, SE	
Sterculia apetala (Jacq.) H.Karst.	C.L. Cristóbal	A. Pott 1923	T	E	Au, Z	CO, N	
S. striata A.St.-Hil. & Naudin	C.L. Cristóbal	A. Pott 13057	T	E	Au, Z	CO, N, NE, SE	Brazil
**Triumfetta rhomboidea* Jacq.	M.S. Ferrucci	V.J. Pott 3639	Ss	E	Z	CO, N, NE, S, SE	
**T. semitriloba* Jacq.	G.P. Nunes	D.K. Noguchi 10	Ss	E	Z	CO, N, NE, S, SE	
**Urena lobata* L.	A. Pott	A. Pott 1294	Ss	E	Z	CO, N, NE, S, SE	
Waltheria albicans Turcz.	S.G. Tressens	A. Pott 1082	Ss	E	Au	CO, N, NE, SE	
**W. indica* L.	C.L. Cristóbal	A. Pott 6222	Ss	E	Au	CO, N, NE, S, SE	
**W. viscosissima* A.St.-Hil.	C.L. Cristóbal	A. Pott 2945	Ss	E	Au	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

Wissadula amplissima (L.) R.E.Fr.	A. Krapovickas	A. Krapovickas 43104	Ss	E	Au	CO, N, NE, SE	Brazil
W. boliviana R.E.Fr.	M.G. Bovini	J.S. Silva 35	Ss	E	Au	CO	
W. decora S.Moore	P.A. Fryxell	B. Dubs 354	Ss	E	Au	CO	
**W. hernandioides* (L.Hér.) Garcke	A. Krapovickas; M.G. Bovini	A. Pott 6818	Ss	E	Au	CO, N, NE, S, SE	
**W. indivisa* R.E.Fr.	A. Krapovickas; P.A. Fryxell	G. Hatschbach 49238	S	E	Au	CO	
W. krapovickasiana Bovini	M.G. Bovini	G. Hatschbach 49213	Ss	E	Au	CO	
W. macrantha R.E.Fr.	A. Krapovickas	G. Hatschbach 60774	S	E	Au	CO	
W. paraguariensis Chodat	A. Krapovickas	A. Pott 2647		E	Au	CO, NE	
W. pauciflora (A.St.-Hil.) R.E.Fr.	A. Krapovickas; C. Takeuchi	A. Pott 1320	Ss	E	Au	CO, N. NE, S, SE	
Marantaceae							
Calathea trifasciata (Koch) Koernicke	J.M.A. Braga	A. Pott 5487	H	E	Z	CO	
Goeppertia flavescens (Lindl.) Borchs. & Suárez	S. Vieira	A. Pott 5467	H	E	Z	CO, SE, S	Brazil
Maranta amazonica L.Andersson	S. Vieira	G. Schaller 289	H	E	Z	CO	
M. arundinacea L.	S. Vieira	A.C. Cervi 3235	H	E	Z	CO	
M. pantanensis J.M.A.Braga	J.M.A. Braga	A. Pott 8025	H	E	Z	CO	
M. rugosa J.A.M.Braga & S.Vieira	J.M.A. Braga & S. Vieira	A. Pott 5536 (Typus)	E	E	Hy	CO	Brazil
Thalia densibracteata Petersen	J.M.A. Braga	V.J. Pott 2289	E	E	Hy	CO, N, NE, SE	

T. geniculata L.	J.M.A. Braga	V.J. Pott 3008	H	E	Hy	CO, N, NE, S, SE	
Martyniaceae							
Craniolaria integrifolia Cham.	M.M. Arbo	A. Pott 5486	H	E	Z	CO, SE	
Mayacaceae							
Mayaca fluviatilis Aubl.	V.J. Pott	V.J. Pott 3625	H	E	Hy	CO, N, NE, S, SE	
M. sellowiana Kunth	V.J. Pott	S.N. Moreira 1510	H	E	Hy	CO, N, NE, S, SE	
Melastomataceae							
Acisanthera alsinaefolia (Mart. & Schrank ex DC.) Triana	A. Martins	A. Pott 4583	H	E	Au	CO, SE, S	
A. paraguayensis (Hook.f.) Cogn.	R. Goldenberg	V.J. Pott 6258	H	E	Au	CO	
Chaetogastra clinopodifolia DC.	A. Pott	L.V.S. Campos 252	Ss	E	Au	CO, S, SE	
C. gracile (Bonpl.) DC.	V.J. Pott	V.J. Pott 7855	Ss	E	Au	CO, N, NE, S, SE	
Clidemia biserrata DC.	R. Romero	V.J. Pott 3674	Ss	E	Z	CO, N, NE, S, SE	
C. bullosa DC.	C.B.R. Munhoz	A. Pott 6279	S	E	Z	CO, N, NE, SE	
C. capitellata (Bonpl.) G.Don	V.J. Pott	V.J. Pott 8641	Ss	E	Z	CO, N, NE, S, SE	
C. hirta (L.) G.Don	S.S. Renner	A.A. Maciel 91	Ss	E	Z	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Desmoscelis villosa (Aubl.) Naudin	C. Munhoz	A.Pott 4911	Ss	E	Au	CO, N, NE, SE	
Macairea radula (Bonpl.) DC.	V.J. Pott	S.N. Moreira 1516	S	E	Au	CO, N, NE, SE	
Miconia albicans (Sw.) Triana	J.A. Ratter	A. Pott 4384	S	E	Z	CO, N, NE, S, SE	
M. nervosa (Sm.) Triana	V. Rocha	A. Pott 11809	S	E	Z	CO, N, NE, SE	
M. prasina (Sw.) DC.	A. Pott	A. Pott 5312	S	E	Z	CO, N, NE, S, SE	
M. stenostachya DC.	A.R. Rezende	A. Pott 2287	T	E	Z	CO, N, NE, S, SE	
Mouriri elliptica Mart.	J.A. Ratter	A. Pott 2220	T	E	Z	CO, N, NE, SE	Brazil
M. guianensis Aubl.	A. Pott	A. Pott 5077	T	E	Z	CO, N, NE, SE	Brazil
Noterophila limnobios (DC.) Mart.	R. Romero	A. Pott 5515	H	E	Au, Hy	CO, N, NE, SE	Brazil
Poteranthera pusilla Bong.	C. Mello-Silva	A.Pott 2224	H	E	Au	CO, S, SE	
Pterolepis trichotoma (Rottb.) Cogn.	V.J. Pott	S.N. Moreira 1514		E	Au, Hy	CO, N, NE, SE	Brazil
Rhynchanthera brachyrhyncha Cham.	S.S. Renner	G. Guarim Neto 275	Ss	E	Au	CO, S, SE	
R. grandiflora (Aubl.) DC.	V.J. Pott	V.J. Pott 8013	Ss	E	Au	CO, N, NE, SE	
R. hispida Naudin	E.F. Guimarães	G. Martinelli 18699	Ss	E	Au	CO, N, NE, SE	
R. novemnervia DC.	V.J. Pott	V.J. Pott 3705	Ss	E	Au, Hy	CO, N, NE, S, SE	
R. ursina Naudin	V.J. Pott	S.N. Moreira 1518	Ss	E	Au	CO, SE	Brazil

Siphanthera cordifolia (Benth.) Gleason	V.J. Pott	S.N. Moreira 1515	H	E	Au	CO, N	
Tibouchina barbigera (Naudin) Baill.	C. Munhoz; P.J.F. Guimarães	A. Pott 1846	Ss	E	Au	CO, N, NE, SE	
T. longistyla (Cogn.) Renner	F.S. Meyer	A. Pott 2562		E	Au	CO, SE	
T. parviflora Cogn.	A.L. Freitas	G. Hatschbach 21997	H	E	Au	CO	
T. pilosa Cogn.	V.J. Pott	S.N. Moreira 792	Ss	E	Au	CO, S	
Trembleya phlogiformis Mart. & Schrank ex DC.	V.J. Pott	S.N. Moreira 780	Ss	E	Z	CO, NE, S, SE	Brazil
Meliaceae							
***Azadirachta indica* A.Juss.	A. Pott	A. Pott 17933	T	E	Z	Exotic	
Cedrela fissilis Vell.	A. Pott	A. Pott 2058	T	E	An	CO, N, NE, S, SE	
Guarea guidonia (L.) Sleumer	H. Barreiros	A. Pott 5280	T	E	Z	CO, N, NE, S, SE	
G. macrophylla Vahl	A. Pott & V.J. Pott	A. Pott 2053	T	E	Z	CO, N, NE, S, SE	
***Melia azedarach* L.			T	E	Z	Exotic	
Swietenia macrophylla King	A. Pott	L.V.S. Campos 643	T	E	An	CO, N, NE	
Trichilia catigua A.Juss.	M.S. Ferrucci	A. Pott 5208	T	E	Z	CO, N, NE, S, SE	Brazil
T. claussenii C.DC.	J.A. Ratter	M.P. Silva 73	T	E	Z	CO, S, SE	Brazil

(continued)

Table 3.1 (continued)

T. elegans A. Juss.	J.A. Ratter; H. Barreiros	A. Pott 4473	T	E	Z	CO, N, NE, S, SE	Brazil
T. hirta L.	A. Pott	R.B. Rodrigues 14	T	E	Z	CO, N, NE, S, SE	Brazil
T. inaequilatera T.D.Penn.	T.D. Pennington	W.W. Thomas 4601	T	E	Z	CO, N, SE	
T. pallida Sw.	A. Pott	A. Pott 5075	T	E	Z	CO, N, NE, S, SE	
T. rubra C.DC.	J.R. Pirani	A. Pott 4017	T	E	Z	CO, N	
T. schomburgkii C.DC.	J.R. Pirani	V.J. Pott 471	T	E	Z	CO, N	
T. stellato-tomentosa Kuntze	H. Barreiros	A. Pott 4017	T	E	Z	CO	
Menispermaceae							
Abuta grandifolia (Mart.) Sandwith	A. Pott	A. Pott 7664	S	E	Z	CO, N, NE	
Cissampelos ovalifolia DC.	R.C. Barneby	A.C. Cervi 3276	L	E	Z	CO, N, NE, S, SE	
C. pareira L.	A.M. Radovancich	A. Pott 1309	L	E	Z	CO, N, NE, S, SE	
C. tropaeolifolia DC.	A. Schinini	A. Pott 5116	L	E	Z	CO, N, NE, S, SE	
Hyperbaena hassleri Diels	A. Schinini	A. Pott 4946	L	E	Z	CO, SE	
Odontocarya tamoides (DC.) Miers	A. Schinini	A. Pott 5173	L	E	Z	CO, N, NE, SE	
Menyanthaceae							
Nymphoides grayana (Griseb.) Kuntze	V.J. Pott	V.J. Pott 2725	H	E	Hy	CO, N, NE	

N. humboldtiana (Kunth) Kuntze	V.J. Pott	A. Pott 6868	H	E	Au	CO, N, NE, S, SE	
Metteniusaceae (Icacinaceae)							
Casimirella beckii (Fern. Casas) Breteler	J.A. Ratter	A. Pott 6513	T	E	Z	CO	
Emmotum nitens (Benth.) Miers	J.A. Ratter	A. Pott 4513	T	E	Z	CO, N, NE, SE	Brazil
Microteaceae (dismembered from Phytolaccaceae)							
Microtea celosioides Moq. ex Sennikov & Sukhor.	M.S. Marchioreto	A. Pott 5433	H	E	Au	CO, N, NE, SE	
Molluginaceae							
Glinus radiatus (Ruiz & Pav.) Rohrb.	T.M. Pedersen	A.Pott 5167	H	E	Au	CO, N, NE, S, SE	
Mollugo verticillata L.	A. Pott	A. Pott 3522	H	E	Z	CO, N, NE, S, SE	
Moraceae							
***Artocarpus heterophyllus* Lam.			T	E	Z	Exotic	
Brosimum gaudichaudii Trécul	A. Pott	A. Pott 4965	T	E	Z	CO, N, NE, S, SE	
B. lactescens (S. Moore) C.C.Berg	A.T. Oliveira F.	A. Pott 5137 (isolectotypus in E)	T	E	Z	CO, N, NE, S, SE	
Dorstenia brasiliensis Lam.	G. Hatschbach	A. Pott 4530	H	E	Z	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Ficus adhatodifolia Schott ex Spreng.	F. Kjellberg & R.A.S. Pereira	R.S. Arruda s/n	T	E	Z	CO, NE, S, SE	
***F. benjamina* L.			T			Exotic	
F. blepharophylla Vásq. Avila	C.C. Berg	W.W. Thomas 4589	T	E	Z	CO, N	
F. calyptroceras (Miq.) Miq.	G. Hatschbach	A. Pott 2743	T	E	Z	CO, NE, S, SE	
F. carautana L.J.Neves & Emygdio	F. Kjellberg & R.A.S. Pereira	A. Pott 10937	T	E	Z	CO	Brazil
F. citrifolia P.Miller	F. Kjellberg & R.A.S. Pereira	V.J. Pott 3497	T	E	Z	CO, N, NE, S, SE	
F. crocata (Miq.) Miq.	A. Pott	A. Pott 2316	T	E	Z	CO, N, NE, S, SE	
***F. elastica* Roxb.			T			Exotic	
F. enormis (Mart. ex Miq.) Mart.	G. Hatschbach; A.F.P. Machado	A.Pott 4522	T	E	Z	CO, N, S, SE	
F. gomelleira Kunth & C.D.Bouché	A.F.P. Machado	V.J. Pott 1754	T	E	Z	CO, N, NE, S, SE	
F. guaranitica Chodat	A.F.P. Machado	A. Pott 3445	T	E	Z	CO, S, SE	
F. hebetifolia Dugand	A.F.P. Machado	A. Pott 6516	T	E	Z	CO	
F. lagoensis C.C.Berg & Carauta	R.A.S. Pereira	R.A.S. Pereira 174	T	E	Z	CO, S, SE	Brazil
F. maxima Mill.	A.F.P. Machado	A. Pott 4577	T	E	Z	CO, N	
F. obtusifolia Kunth	F. Kjellberg & R.A.S. Pereira	A. Pott 2564	T	E	Z	CO, N, NE, S, SE	
F. pertusa L.f.	A. Pott	A. Pott 4524	T	E	Z	CO, N, NE, S, SE	
***F. pumila* L.			L			Exotic	

F. trigona L.f.	A. Pott	A. Pott 5645	T	E	Z	CO, N, NE, S, SE	
F. trigonata L.	S. Romaniuc-Neto	G.A. Damasceno Jr. 2311	T	E	Z	CO, N	
Maclura tinctoria (L.) D.Don ex Steud.	A. Pott	V.J. Pott 38	T	E	Z	CO, N, NE, S, SE	
Maquira coriacea (H.Karst.) C.C.Berg	C.C. Berg	W.W. Thomas 4626	T	E	Z	CO, N, NE	
***Morus nigra* L.		S.S. Moura 161	T		Z	Exotic	
Sorocea gilleminiana Gaudich.	J. Kuntz	C.P. Calliari 1055	T	E	Z	CO, NE, SE	Brazil
S. saxicola Hassl.	J.A. Ratter	A. Pott 3609	T	E	Z	CO	
Moringaceae							
***Moringa oleifera* Lam.	I.M. Bortolotto	I.M. Bortolotto 1511	T	E	Au, An	Exotic	
Muntingiaceae							
**Muntingia calabura* L.	F.M. Alves	I.H. Ishi 453	T	E	Z	Exotic	
Musaceae							
***Musa paradisiaca* L.			H	E	Z	Exotic	
Myoporaceae (included part of Scrophulariaceae)							
Capraria biflora L.	V.C. Souza	A. Pott 16766	Ss	E	Au	CO, N, NE, SE	
Myristicaceae							
Virola sebifera Aubl.	A. Pott	S.N. Moreira 786	T		Z	CO, N, NE, SE	
Myrtaceae							
Calyptranthes lucida Mart. ex DC.	M. Sobral; D. Villarroel	V.J. Pott 3607	T	E	Z	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Campomanesia adamantium (Cambess.) O.Berg	M. Sobral	A. Pott 6498	S	E	Z	CO, S, SE	
C. eugenioides (Cambess.) D.Legrand ex Landrum	J.R. Mattos; M. Sobral	A. Pott 5248	T	E	Z	CO, N, NE, S, SE	Brazil
C. linearifolia Ruiz & Pav.	C.E.B. Proença	V.J. Pott 740	T	E	Z	CO, N, SE	
C. sessiliflora (O.Berg) Mattos	J.R. Mattos	A. Pott 5689	Ss	E	Z	CO, NE, S, SE	
C. xanthocarpa (Mart.) O.Berg	C.E.B. Proença	A. Pott 6498	T	E	Z	CO, S, SE	
***Eucalyptus citriodora* Hook.	O.S. Ribas	G.B.S. Pinto 12-9-2003	T	E	Au	Exotic	
Eugenia angustissima O.Berg	M. Sobral	A. Pott 1172	SS	E	Z	CO, N, NE, SE	Brazil
E. anomala D.Legrand	M. Sobral	G. Hatschbach 76220	SS	E	Z	CO, S, SE	
E. aurata O.Berg	M. Sobral	A. Pott 4379	T	E	Z	CO, S, SE	Brazil
E. biflora (L.) DC.	C.E.B. Proença	A. Pott 6510	S	E	Z	CO, N, NE	
E. chiquitensis O.Berg	G.M. Barroso; M. Sobral	A. Pott 5634	T	E	Z	CO	
E. cristaensis O.Berg	G.M. Barroso; C. Proença	A. Pott 6566	T	E	Z	CO	Brazil
E. egensis DC.	M. Sobral	A. Pott 4927	S	E	Z	CO, N, NE, S, SE	
E. flavescens DC.	C.E.B. Proença	A. Pott 6518	Ss	E	Z	CO, N, NE, SE	
E. florida DC.	M. Sobral	A. Pott 3541	T	E	Z	CO, N, NE, S, SE	Brazil
E. hiemalis Cambess.	L.H. Soares e Silva	R.R.B. Negrelle 20/9/2002	S	E	Z	CO, S, SE	

E. inundata DC.	H.F. Leitão F.; L.H. Soares e Silva	A. Pott 5311	S	E	Z	CO, N, NE	
E. involucrata DC.	M. Sobral	A. Pott 12443	T	E	Z	CO, NE, S, SE	
E. lambertiana DC.	M. Sobral	V.J. Pott 8677	T	E	Z	CO, N, NE, SE	
E. limbosa O.Berg	M. Sobral	A. Pott 4770	T	E	Z	CO, N	
E. matogrossensis Sobral	T.S. Mendes	G. Martinelli 18718	T	E	Z	CO	Brazil
E. modesta O.Berg	C.M.D.E. Legrand	E. Pereira 202	S	E	Z	CO, NE, SE	Brazil
E. neoformosa Sobral	M. Sobral	A. Pott 11753	T	E	Z	CO, NE, SE	Brazil
E. neomattogrossensis Mazine	J.E.Q. Faria	C.A. Conceição 1716	Ss	E	Z	CO	Brazil
E. pantanalensis Faria & M. Sobral	M. Sobral	A.Pott 4379 (Typus)	T	E	Z	CO	Brazil
E. paracatuana O.Berg	M. Sobral; F.F. Mazine	G. Hatschbach 76221	S	E	Z	CO, S, SE	
E. pitanga (O.Berg) Nied.	M. Sobral	A. Pott 3826	S	E	Z	CO, NE, S, SE	
E. polystachya Rich.	M. Sobral	V.J. Pott 4770	S	E	Z	CO, N, NE	
E. punicifolia (Kunth) DC.	G.M. Barroso; C.E.B. Proença	A. Pott 6497	Ss, S	E	Z	CO, N, NE, S, SE	Brazil
E. pyriformis Cambess.	M. Sobral	A. Pott 4459	Ss	E	Z	CO, S, SE	
E. repanda O.Berg	M. Sobral	A. Pott 3457	S	E	Z	CO, S, SE	
E. sparsa S.Moore	M. Sobral	A. Pott 4379	T	E	Z	CO	Brazil
E. stictopetala Mart. ex DC.	M. Sobral	A. Pott 5634	T	E	Z	CO, N, NE, SE	
E. subterminalis DC.	M. Sobral	J. Couto 203	Ss	E	Z	CO, N, NE, S, SE	Brazil

(continued)

Table 3.1 (continued)

Myrcia amazonica DC.	B.K. Holst	G.T. Prance 26666	T	E	Z	CO, N, NE, S, SE	
M. bella Cambess.	M. Sobral	A. Pott 1659	T	E	Z	CO, N, NE, SE	
M. camapuanensis N.Silveira	C.E.B. Proença; M.Sobral	A. Pott 6496	T	E	Z	CO	Brazil
M. guianensis (Aubl.) DC.	C.E.B. Proença; M.Sobral	A. Pott 2226	T	E	Z	CO, N, NE, S, SE	
M. mollis (Kunth) DC.	M.L. Kawasaki	Damasceno Jr. 982	T	E	Z	CO, N, NE, SE	
M. palustris DC.	M. Sobral	A. Pott 5476	T	E	Z	CO, NE, S, SE	
M. selloi (Spreng.) N. Silveira	K.M.G. Bezerra & D. Villarroel	E.P. Seleme CGMS 24144	T	E	Z	CO, S, SE	
M. splendens (Sw.) DC.	M. Sobral	V.J. Pott 4771	T	E	Z	CO, N, NE, S, SE	Brazil
M. tomentosa (Aubl.) DC.	C.E.B. Proença	A. Pott 6548	T	E	Z	CO, N, NE, S, SE	
***Plinia cauliflora* (Mart.) Kausel	M. Sobral	I.M. Bortolotto 16-6-11998	T	E	Z	CO, NE, S, SE	Brazil
Psidium acutangulum DC.	R. Landrum	A. Pott 5248	T	E	Z	CO, N	
P. australe Cambess.	A. Pott	A. Pott 2384	T	E	Z	CO, NE, S, SE	
**P. guajava* L.	U.M. Resende	R.S. Arruda 303	S	E	Z	Exotic	
P. guineense Sw.	M. Sobral	A. Pott 3597	S	E	Z	CO, N, NE, S, SE	
P. kennedianum Morong	M. Sobral	A. Pott 3177	S	E	Z	CO, S	
P. nutans O.Berg	M. Sobral	A. Pott 1775	T	E	Z	CO, N, NE, SE	
P. ramboanum Mattos	J.R. Mattos	V.J. Pott 740	S	E	Z	CO	Brazil

P. sartorianum (O.Berg) Nied.	M. Sobral	V.C. Souza 32439	T	E	Z	CO, N, NE, S, SE	
P. striatulum Mart. ex DC.	D. Villarroel	U.M. Resende 520	S	E	Z	CO, N, NE, S	
***Syzygium cumini* (L.) Skeels			T	E	Z	Exotic	
***S. jambos* (L.) Alston		E. Barboza 1528	T	E	Z	Exotic	
Nyctaginaceae							
**Boerhavia coccinea* Mill.	G. Hatschbach	A.C. Cervi 4213	H	E	Z	CO, NE, S, SE	
**B. diffusa* L.	V.J. Pott	V.J. Pott 1559	H	E	Z	CO, N, NE, S, SE	
Bougainvillea berberidifolia Heimerl	Tao Chen	A. Pott 4920	T	E	Au	CO	
B. infesta Griseb.	A. Furlan	G.A. Damasceno Jr. 1929	T	E	Au	CO	
***B. spectabilis* Willd.			L	E	Au	CO, NE, S, SE	
**Mirabilis jalapa* L.	I.M. Bortolotto	I.M. Bortolotto 4-6-1998	S	E	Z	Exotic	
Neea hermaphrodita S.Moore	A.M. Radovancich	V.J. Pott 579	T	E	Z	CO, N, NE, SE	
Pisonia aculeata L.	A. Furlan	S.A. Rego 668	L	E	Z	CO, N, NE, S, SE	
P. zapallo Griseb.	A. Furlan	A. Pott 4919	T	E	Z	CO	
Reichenbachia paraguayensis (D.Parodi) Dugand & Daniel	G. Hatschbach	G. Hatschbach 49218	T	E	Z	CO	
Nymphaeaceae							

(continued)

Table 3.1 (continued)

Nymphaea amazonum Mart. & Zucc.	V.J. Pott	V.J. Pott 2957	H	E	Hy	CO, N, NE, S, SE	
N. belophylla Trickett	V.J. Pott	V.J. Pott 2049	H	E	Hy	CO, N	Brazil
N. gardneriana Planch.	V.J. Pott	V.J. Pott 2573	H	E	Hy	CO, N, NE, S, SE	
N. jamesoniana Planch.	V.J. Pott	V.J. Pott 2564	H	E	Hy	CO, NE, SE	
N. lingulata Wiersema	V.J. Pott	V.J. Pott 1557	H	E	Hy	CO, N, NE, SE	Brazil
N. oxypetala Planch.	V.J. Pott	V.J. Pott 1783	H	E	Hy	CO	
N. prolifera Wiersema	V.J. Pott	V.J. Pott 3109	H	E	Hy	CO, S	
Victoria amazonica (Poepp.) J.E.Sowerby	V.J. Pott	V.J. Pott 1999	H	E	Hy	CO, N	
Ochnaceae							
Ouratea castaneifolia (DC.) Engl.	A. Pott	A. Pott 3245	T	E	Z	CO, N, NE, SE	
O. claudei G.S.Salvador, E.P.Santos & A.C.Cervi	G.S. Salvador	A. Pott 5784	T	E	Z	CO, N, S	
O. hexasperma (A.St.-Hil.) Baill.	J.A. Ratter	A. Pott 3432	T	E	Z	CO, N, NE, SE	
Sauvagesia erecta L.	A. Schinini	A. Pott 3706	H	E	Au	CO, N, NE, S, SE	
S. racemosa A.St.-Hil.	V.J. Pott	S.N. Moreira 1520	H	E	Au	CO, N, NE, S, SE	
Olacaceae							
Dulacia egleri (Bastos) Sleumer	A. Schinini	A. Pott 4457	S	E	Z	CO, N	Brazil
Ximenia americana L.	J.A. Ratter	A. Pott 1456	T	E	Z	CO, N, NE, S, SE	

Oleaceae							
Priogymnanthus hasslerianus (Chodat) P.S.Green	J.A. Ratter	A. Pott 3201	T	E	Z	CO, N, NE	
Onagraceae							
Ludwigia affinis (DC.) H.Hara	V.J. Pott	V.J. Pott 4758	H	E	Au	CO, N, NE, SE	
L. bonariensis (Micheli) H.Hara	T.P. Ramamoorthy	J.M. Pires 17210	H	E	Au	CO, S	
L. decurrens Walter	V.J. Pott	V.J. Pott 1838	H	E	Au, Hy	CO, N, NE, S, SE	
L. densiflora (Micheli) H.Hara	A.O.S. Vieira	A. Pott 8081	S	E	Au	CO, N	
L. elegans (Cambess.) H.Hara	V.J. Pott; A.O.S. Vieira	V.J. Pott 4391	H	E	Au	CO, S, SE	
L. filiformis (Micheli) Ramamoorthy	V.J. Pott	V.J. Pott 3202	Ss	E	Au	CO, S, SE	Brazil
L. grandiflora (Michx.) Greuter & Burdet	V.J. Pott	V.J. Pott 6424	Ss	E	Au	CO, S	
L. helminthorrhiza (Mart.) H.Hara	V.J. Pott	V.J. Pott 4909	H	E	Hy	CO, N, NE, S, SE	
L. hexapetala (Hook. & Arn.) Zardini et al.	V.J. Pott	V.J. Pott 3202	H	E	Au	CO, S	
L. hyssopifolia (G.Don) Excell	A.O.S. Vieira	V.J. Pott 1909	Ss	E	Au, Hy	CO, N, NE, S, SE	
L. inclinata (L.f.) M. Gómez	V.J. Pott	V.J. Pott 3151	H	E	Hy	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

L. irwinii Ramamoorthy	V.J. Pott	V.J. Pott 3593	Ss	E	Au	CO, S, SE	
L. lagunae (Morong) H.Hara	V.J. Pott	V.J. Pott 4653	H	E	Au	CO, S, SE	
L. leptocarpa (Nutt.) H. Hara	V.J. Pott	V.J. Pott 4907	Ss	E	Au, Hy	CO, N, NE, S, SE	
L. longifolia (DC.) H. Hara	V.J. Pott	A. Pott 7684	Ss	E	Au	CO, N, NE, S, SE	
L. martii (Micheli) Ramamoorthy	A. Pott	S.S. Moura 176	Ss	E	Au	CO, S, SE	
L. myrtifolia Cambess.	V.J. Pott	C.D.K. Cook 524	Ss	E	Au	CO, S, SE	Brazil
L. neograndiflora (Munz) H.Hara	A.O.S. Vieira	G. Hatschbach 47154	Ss	E	Au, Hy	CO, S	
L. nervosa (Poir.) H.Hara	V.J. Pott	V.J. Pott 4409	S	E	Au	CO, N, NE, S, SE	
L. octovalvis (Jacq.) P.H.Raven	V.J. Pott	V.J. Pott 3127	H	E	Hy	CO, N, NE, S, SE	
L. peploides (Kunth) P.H.Raven	V.J. Pott	V.J. Pott 769	H	E	Hy	CO, S	
L. peruviana (L.) H.Hara	V.J. Pott	V.J. Pott 4971	S	E	Au, Hy	CO, N, S, SE	
L. rigida (Miq.) Sandwith	V.J. Pott	V.J. Pott 736	Ss	E	Hy	CO, N, NE	
L. sedoides (Humb. & Bonpl.) H.Hara	V.J. Pott	V.J. Pott 3114	H	E	Hy	CO, N, NE, SE	
L. tomentosa (Cambess.) H.Hara	V.J. Pott	V.J. Pott 5784	S	E	Au	CO, N, NE, SE	
Opiliaceae							
Agonandra brasiliensis Miers ex Benth. & Hook.f.	J.A. Ratter	A. Pott 4476	T	E	Z	CO, N, NE, SE	

Orchidaceae							
Aspidogyne bidentifera (Schltr.) Garay	F. Barros	V.J. Pott 3412	H	E	An	CO, S, SE	
A. debilis (Lindl.) Meneguzzo	J.A.N. Batista	A. Pott 4289	H	E	An	CO, N, NE, S, SE	
A. foliosa (Poepp. & Endl.) Garay	A. Pott	D. Gris 109	H	E	An	CO, N, NE, S, SE	
Campylocentrum neglectum (Rchb.f. & Warm.) Cogn.	F. Barros	A. Pott 2823	Ep	E	An	CO, NE, SE	
Catasetum fimbriatum (C.Morren) Lindl.	F. Barros	A. Pott 4622	Ep	E	An	CO, N, S, SE	
Cattleya nobilior Rchb.f.	C. Maury	A. Pott 6515	Ep	E	An	CO, N, NE	
C. walkeriana Gardner	V.J. Pott	L.V.S. Campos 306z	Ep	E	An	CO, N, NE, SE	
Cyrtopodium paludicolum Hoehne	V.J. Pott	S.N. Moreira 1553	H	E	An	CO, N, S, SE	
C. saintlegerianum Rchb.f.	M.L. Potzemheim	A. Pott 7109	Ep	E	An	CO, N, NE, SE	
C. virescens Rchb.f. & Warm.	L.B. Bianchetti; F. Barros	A. Pott 3442	H	E	An	CO, N, NE, SE	
Encyclia linerifolioides (Kraenzl.) Hoehne	T.E.C. Meneguzzo	R. Godinho no n.	Ep	E	An	CO, N, NE, S, SE	
Eulophia alta (L.) Fawc. & Rendle	L.B. Bianchetti; J.A.N. Batista	V.J. Pott 9118	Ep	E	An	CO, N, NE, S, SE	
Galeandra styllomisantha (Vell.) Hoehne	L.B. Bianchetti; J.A.N. Batista	A. Pott 7674	H	E	An	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Habenaria amambayensis Schltr.	J.A.N. Batista	A. Pott 7669	H	E	An	CO, N	
H. aricaensis Hoehne	J.A.N. Batista	A. Pott 7675	H	E	An	CO, N	
H. glazioveana Kraenzl.	P.J. Cribb	A. Pott 5591	H	E	An	CO, N, NE, SE	
H. nabucoi Ruschi	L.B. Bianchetti	V.J. Pott 5035	H	E	An	CO, N, NE, SE	
H. orchiocalcar Hoehne	L.B. Bianchetti; J.A.N. Batista	A. Pott 2531	H	E	An	CO, N, NE	
H. polycarpa Hoehne	F. Barros	A. Pott 4325	H	E	An	CO, N, NE	Brazil
H. pratensis (Salzm. ex Lindl.) Rchb.f.	F. Barros; J.A.N. Batista	A. Pott 7688	H	E	An	CO, N, NE, S	Brazil
H. repens Nutt.	J.A.N. Batista; F. Barros	V.J. Pott 1419	H	E	An	CO, N, NE, S, SE	
H. spathulifera Cogn.	A.K. Koch	A.L. Prado 5275	H	E	An	CO, N, S	
Ionopsis utricularioides (Sw.) Lindl.	E.A. Christenson	G. Schaller 323	Ep	E	An	CO, N, NE, S, SE	
Notylia lyrata S.Moore	A.M. Amaral	A.M. Amaral 132	Ep	E	An	CO, N, NE, S, SE	
(*?)*Oeceoclades maculata* (Lindl.) Lindl.	A. Pott	A. Pott 2056	H	E	An	CO, N, NE, S, SE	
Pelexia stenantha (Cogn.) Schltr.	G. Pabst	G. Hatschbach 22022	H	E	An	CO, SE	Brazil
Sacoila lanceolata (Aubl.) Garay	L.B. Bianchetti; J.A.N. Batista	A. Pott 3849	H	E	An	CO, N, NE, S, SE	
Trichocentrum cebolleta (Sw.) M.W. Chase & N.H. Williams	C.F. Hall	A.K.D. Salomão	Ep	E	An	CO	
T. cepula (Hoffmanns.) J.M.H.Shaw	T.E.C. Meneguzzo	C.P. Costa no n.	Ep	E	An	CO, N, NE, S, SE	

T. fuscum Lindl.	A. Petini-Benelle	A.M. Amaral 2	Ep	E	An	CO, N, NE, S, SE	
Vanilla palmarum (Salzm. ex Lindl.) Lindl.	E.A. Christenson	A. Pott 5045	L	E	An	CO, N, NE	
Orobanchaceae (dismembered from Scrophulariaceae)							
Agalinis glandulosa (G.M.Barroso) V.C.Souza	G.M. Barroso; V.C. Souza	A. Pott 4943	H	E	Au	CO, N	Brazil
Buchnera longifolia Kunth	V.C. Souza	A. Pott 4046	H	E	Au	CO, N, NE, S, SE	
B. palustris (Aubl.) Spreng.	V.C. Souza	A. Pott 8102	H	E	Au	CO, N, NE, SE	
Melasma melampyroides (Rich.) Pennell	V.C. Souza	A. Pott 4811	H	E	Au	CO, N, NE, S, SE	
M. stricta (Benth.) Hassl.	V.C. Souza	V.J. Pott 5681	H	E	Au	CO, N, SE	
Oxalidaceae							
***Averrhoa carambola* L.			T	E	Z	Exotic	
Oxalis barrelieri L.	V.J. Pott	A. Pott 16756	H	E	Au	CO, N, NE, S, SE	
O. erosa Knuth	A. Lourteig	G. Hatschbach 49231	Ss	E	Au	CO	
O. frutescens L.	M.C. Abreu	A. Pott 4138	Ss	E	Au	CO, N, NE, SE	
O. grisea A.St.-Hil. & Naudin	F.S. Cabral	G.A. Damasceno Jr. 3056	Ss		Au	CO, NE, SE	
O. physocalyx Zucc. ex Progel	G.M. Barroso	A. Pott 4558	H	E	Au	CO, N, NE, SE	Brazil

(continued)

Table 3.1 (continued)

O. triangularis A.St.-Hil.	A. Pott	L.V.S. Campos 387	H	E	Au	CO, N, NE, S, SE	
Papaveraceae							
**Argemone mexicana* L.	A. Pott	A. Pott 10250	H	E	Au	CO, NE, S, SE	
Passifloracaeae							
Passiflora amethystina J.C.Mikan	M.L. Milward de Azevedo	M.L. Milward de Azevedo 22	L	E	Z	CO, NE, S, SE	
P. chrysophylla Chodat	A.C. Cervi	A. Pott 1723	L	E	Z	CO	
P. cincinnata Mast.	A.C. Cervi	A. Pott 2753	L	E	Z	CO, N, NE, SE	
*,***P. edulis* Sims	A.C. Cervi	A.L. Sanches 71	L	E	Z	CO, N, NE, S, SE	
P. foetida L.	A.C. Cervi	A. Pott 4471	L	E	Z	CO, N, NE, S, SE	
P. gibertii N.E.Br.	A.C. Cervi	A. Pott 4698	L	E	Z	CO	
P. longilobis Hoehne	M.L. Milward de Azevedo	C. Nunes da Cunha 72	L	E	Z	CO, N, S, SE	Brazil
P. misera Kunth	M.L. Milward de Azevedo	A. Pott 7662	L	E	Z	CO, N, NE, S, SE	
P. morifolia Mast.	A.C. Cervi	S.R. Zaniolo 235	L	E	Z	CO, S, SE	
P. porophylla Vell.	A.C. Cervi	A. Pott 7750	L	E	Z	CO, NE, S, SE	Brazil
***P. quadrangularis* L.			L	E	Z	CO, N, NE, S, SE	
P. speciosa Gardner	A.C. Cervi	V.J. Pott 7528	L	E	Z	CO, SE	Brazil
P. transversalis M.L.Milward de Azevedo	C. Feuillet	G. Schaller 302	L	E	Z	CO, NE, S, SE	
P. tricuspis Mast.	A.C. Cervi	A. Pott 7756	L	E	Z	CO, N, NE, S, SE	

P. vitifolia Kunth	L.C. Bernacci	A. Pott 8716	L	E	Z	CO, N	
Phyllanthaceae (dismembered from Euphorbiaceae)							
Hyeronima alchorneoides Allemão	A. Pott	T.H. Stefanello 345	T	E	Z	CO, N, NE, S, SE	
Margaritaria nobilis L.f.	I. Cordeiro	M.G. Caxambu 2309	T	E	Au	CO, N, NE, S, SE	
Phyllanthus amarus Schumach.	L.J.M. Santiago	A. Pott 4504	H	E	Au	CO, N, NE, S, SE	
P. avicularis Müll.Arg.	I. Cordeiro; E.R. Martins	V.J. Pott 3050	H	E	Au	CO, N, SE	Brazil
P. chacoensis Morong	D.E. Prado	A. Pott 4350	T	E	Au	CO, NE	
P. fluitans Benth. ex Müll. Arg.	V.J. Pott	V.J. Pott 1768	H	E	Hy	CO, N, NE	
P. hyssopifolioloides Kunth	V.J. Pott	V.J. Pott 3050	H	E	Au	CO, N, S	
P. minutulus Müll. Arg.	E.R. Martins	A.L. Prado 30865	H	E	Au	CO, N, NE, S, SE	
**P. niruri* L.	I.M. Bortolotto	I.M. Bortolotto 15-4-1998	H	E	Au	CO, N, NE, S, SE	
P. orbiculatus Rich.	G.L. Webster	A. Pott 1919	H	E	Au	CO, N, NE, S, SE	
P. spartioides Pax & K.Hoffm.	G.L. Webster	L. Rossi s/n	H	E	Au	CO, NE, SE	
P. stipulatus (Raf.) G.L.Webster	G.L. Webster	V.J. Pott 3167	H	E	Au	CO, N, NE, S, SE	
Phytolaccaceae (including Petiveriaceae)							

(continued)

Table 3.1 (continued)

Gallesia integrifolia (Spreng.) Harms	C.N. Cunha	A. Pott 5073	T	E	Au	CO, N	
**Petiveria alliacea* L.	A. Pott	A. Pott 3901	H	E	Au	CO, N, S	
Richeria grandis Vahl	A. Schinini	A. Krapovickas 43114	T		Au	CO, N, NE, S, SE	
Rivina brasiliensis Nocca	W.A. Rodrigues	R.R.B. Negrelle 20	Ss	E	Z	CO	
**R. humilis* L.	J.A. Ratter	A. Pott 4770	H	E	Z	CO, N, NE, S, SE	
Seguieria aculeata Jacq.	J.A. Ratter	J.A. Ratter R6483	T	E	An	CO, N, NE, S, SE	
S. paraguayensis Morong	M.S. Marchioreto	A. Pott 4913	T	E	Z	CO	
Picramniaceae							
Picramnia sellowii Planch.	J.R. Pirani	M.A. Carniello 3094	T	E	Z	CO, N, NE, S, SE	
Piperaceae							
Peperomia circinnata Link	P.R.F. Amorim	A. Pott 12876			Z	CO, N, NE, S, SE	
P. pellucida (L.) Kunth	V.J. Pott	L.V.S. Campos no n.	H	E	Z	CO, N, NE, S, SE	
Piper aduncum L.	A. Pott	A. Pott 15634	H	E	Z	CO, N, NE, S, SE	
P. amalago L.	V.J. Pott	D. Gris 108	S	E	Z	CO, N, NE, S, SE	
P. arboreum L.	V.J. Pott	A. Pott 15604	S	E	Z	CO, N, NE, S, SE	
P. cuyabanum C.DC.	A. Pott	A. Pott 15605	S	E	Z	CO, N, NE, S, SE	
P. divaricatum G.Mey.	V.J. Pott	A. Pott 6557	S	E	Z	CO, N, NE, SE	

P. gaudichaudianum Kunth	E.F. Guimarães	A. Pott 6447	S	E	Z	CO, N, NE, S, SE	
P. hayneanum C.DC.	M. Carvalho-Silva	A.E. Ramos 1633	S	E	Z	CO, NE, SE	Brazil
P. hispidum Sw.	V.J. Pott	A. Pott 12445	S	E	Z	CO, N, NE, S, SE	
P. macedoi Yunck.	E.F. Guimarães	A. Pott 2775	S	E	Z	CO, NE, S, SE	Brazil
P. schottii (Miq.) C.DC.	E.F. Guimarães	A. Pott 4704	S	E	Z	CO, N, NE, SE	Brazil
P. tuberculatum Jacq.	A. Pott	A. Pott 7759	T	E	Z	CO, N, NE, S, SE	
Plantaginaceae (including part of Scrophulariaceae)							
Achetaria erecta (Spreng.) Wettst.	V.C. Souza	A. Pott no n.	H	E	Au	CO, NE	
Angelonia integerrima Spreng.	J. Cordeiro & E. Barboza	M.G. Caxambu 2337	H	E	Au	CO, S	
A. minor Fisch. & C.A.Mey.	V.C. Souza	A. Pott 4812	H	E	Au	CO, N	
A. salicarifolia Bonpl.	V.C. Souza	A. Pott 3840	H	E	Au	CO, NE	
Bacopa arenaria (Schmidt) Edwall	V.C. Souza	V.J. Pott 1236	H	E	Au	CO, N	
B. australis V.C.Souza	V.C. Souza	V.J. Pott 1312 (Paratype)	H	E	Au	CO, S	Brazil
B. dubia Chodat & Hassl.	V.C. Souza	V.J. Pott 331	H	E	Au	CO	
B. egensis (Poepp.) Pennell	V.C. Souza	V.J. Pott 6271	H	E	Au	CO, N	
B. gracilis (Benth.) Edwall	A.V. Scatigna	V.J. Pott 1920	H	E	Au, Hy	CO, N, NE	
B. monnierioides (Cham.) B.L.Rob.	C.D.K. Cook; V.C. Souza	V.J. Pott 3163	H	E	Hy	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

B. myriophylloides (Benth.) Wettst.	V.C. Souza	A. Pott 1237	H	E	Hy	CO, N, S, SE	
B. reflexa (Benth.) Edwall	V.C. Souza	V.J. Pott 2971	H	E	Hy	CO, N, NE	
B. reptans (Benth.) Wettst. ex Edwall	J.A. Kalunki	G. Schaller 125	H	E	Au	CO, N, SE	
B. rotundifolia (Michx.) Wettst.	V.C. Souza	V.J. Pott 760	H	E	Au	CO	
B. salzmannii (Benth.) Wettst. ex Edwall	V.C. Souza	V.J. Pott 1324	H	E	Au	CO, N, NE, S, SE	
B. scabra (Benth.) Descole & Borsini	V.C. Souza	A. Pott 3268	H	E	Au	CO, N, NE, S, SE	
B. stricta (Schrad.) Wettst. ex Edwall	V.C. Souza	A. Pott 4469	H	E	Au	CO, N, NE, S, SE	
Conobea scoparioides (Cham. & Schltdl.) Benth.	V.C. Souza	A. Pott 5124	H	E	Au	CO, N, NE, SE	
**Limnophila sessiliflora* (Vahl) Blume	A.V. Scatigna	V.J. Pott 1713	H	E	Au	Exotic	
Mecardonia procumbens (Mill.) Small	V.C. Souza	A. Pott 5124	H	E	Au	CO, N, NE, S, SE	
Monopera perennis (Chodat & Hassl.) Barringer	V.C. Souza	A. Pott 4741	H	E	Au	CO	
***Russelia equisetiformis* Schtldl. & Cham.		A. Pott 1112	Ss	E		Exotic	
Scoparia dulcis L.	V.J. Pott	A. Pott 1647	H	E	Au	CO, N, NE, S, SE	
S. montevidensis (Spreng.) R.E.Fr.	V.J. Pott	A. Pott 1391	H	E	Au	CO, N, S	

Stemodia durantifolia (L.) Sw.	V.C. Souza	V.J. Pott 4079	H	E	Au	CO, N, S, SE	
S. ericifolia K.Schum.	V.C. Souza	A. Pott 4624	H	E	Au	CO	
S. foliosa Benth.	A.V. Scatigna	V.J. Pott 341	H	E	Au	CO, NE, SE	
S. hassleriana Chodat	V.C. Souza; A.V. Scatigna	V.J. Pott 5990	H	E	Au	CO	
S. hyptoides Cham. & Schltdl.	V.C. Souza	A. Pott 3143	H	E	Au	CO, S, SE	
S. lanceolata Benth.	A.V. Scatigna	A. Pott 4079	H	E	Au	CO	
S. palustris A. St.-Hil.	A.V. Scatigna	G.A. Amador 97	H	E	Au	CO, S	
**Veronica persica* Poir.	A. Pott	A. Pott 8318	H	E	Au	CO, S, SE	
Plumbaginaceae							
Plumbago scandens L.	A. Pott	A. Pott 5084	H	H	Z	CO, N, NE, S, SE	
Poaceae							
Acroceras excavatum (Henrard) Zuloaga & Morrone	A. Guglieri-Caporal	B.E.M. Pinto 164	H	Na	Au	CO, N, NE, S, SE	
A. zizanioides (Kunth) Dandy	J.F.M. Valls	A. Pott 4107	H	An	An	CO, NE, S, SE	
Andropogon bicornis L.	A. Zanin	V.J. Pott 1545	H	An	An	CO, N, NE, S, SE	
**A. gayanus* Kunth		A.C. Allem 1008	H	An	An	Exotic	
A. hypogynus Hack.	J.F.M. Valls	V.J. Pott 4587	H	An	An	CO, N, SE	
A. lateralis subsp.*cryptopus* A.Zanin & Longhi-Wagner	A. Zanin	A. Pott no n.	H	An	An	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

A. leucostachyus Kunth	V.J. Pott	B.A. Coutinho 145	H	An	An	CO, N, NE, S, SE	
A. selloanus (Hack.) Hack.	A. Pott	A. Pott 2360	H	An	An	CO, N, NE, S, SE	
A. virgatus Desv.	J.F.M. Valls	A. Pott 2387	H	An	An	CO, N, NE, S, SE	
Anthaenantia lanata (Kunth) Benth.	J.F.M. Valls	A. Pott 1277	H	An	An	CO, N, NE, S, SE	
**Aristida adscencionis* L.	A. Guglieri	A. Guglieri 3117	H	An	An	CO, N, NE, SE	
Aristida capillacea Lam.	J.F.M. Valls	A.Pott 1124	H	An	An	CO, N, NE, SE	
A. glaziovii Hack. ex Henrard	H.M. Longhi-Wagner	A.C. Allem 1401	H	An	An	CO, N, SE	Brazil
A. longifolia Trin.	H.M. Longhi-Wagner	A.C. Allem 2267	H	An	An	CO, N, NE, SE	
A. megapotamica Spreng.	G. Davidse; J.F.M. Valls	A.C. Allem 1423	H	An	An	CO, N, NE, SE	
A. riparia Trin.	A. Guglieri	G.A. Damsceno Jr. 2322	H	An	An	CO, N, NE, S, SE	
A. setifolia Kunth	J.F.M. Valls; H.M. Longhi-Wagner	A.C. Allem 953	H	An	An	CO, N, NE, SE	
Arthropogon villosus Nees	J.F.M. Valls	J.F.M. Valls 9471	H	An	An	CO, N, NE, S, SE	
Arundinella hispida (Humb. & Bonpl. ex Willd.) Kuntze	T.S. Filgueiras & P.L. Viana	M. Macedo 2309	H	An	An	CO, N, NE, S, SE	
Axonopus affinis Chase	G. Davidse	A.C. Allem 1008	H	An	Au	CO, N, NE, S, SE	
A. argentinus Parodi	A. Guglieri	A. Pott 2951	H	An	Au	CO, S, SE	
A. aureus P.Beauv. (A. aureus)	A. Guglieri	J.A. Comastri Filho 76	H	An	Au	CO, N, NE, S, SE	

A. *brasiliensis* (Spreng.) Kuhlm.	J.F.M. Valls	A. Pott 1128	H	An	Au, An	CO, N, NE, S, SE	
A. *capillaris* (Lam.) Chase	J.F.M. Valls	A. Guglieri 2313	H	An	Au	CO, N, NE, S, SE	
A. *chrysoblepharis* (Lag.) Chase	J.F.M. Valls	L. Rebellato 219	H	An	Au	CO, N, NE, S, SE	
A. *complanatus* (Nees) Dedecca	J.F.M. Valls	J.F.M. Valls 9239	H	An	Au	CO, N, NE, SE	
A. *compressus* (Sw.) P.Beauv.	J.F.M. Valls	A. Pott 1152	H	An	Au	CO, N, NE, S, SE	
A. *fissifolius* (Raddi) Kuhlm.	J.F.M. Valls	A. Guglieri 1732	H	An	Au	CO, N, NE, S, SE	
A. *fusiformis* Valls & A.D. Silveira	J.F.M. Valls	J.F.M. Valls 9415	H	An	Au	CO	Pantanal
A. *leptostachyus* (Flüggé) Hitchc.	J.F.M. Valls	A. Pott 2951	H	An	Au, Hy	CO, N, S, SE	
A. *marginatus* (Trin.) Chase	J.F.M. Valls	A. Pott 1793	H	An	Au	CO, N, NE, S, SE	
A. *polydactylus* (Steud.) Deddecca	J.F.M. Valls	J.F.M.Valls 9477	H	An	Au	CO, N, NE, S, SE	
A. *pressus* (Nees ex Steud.) Parodi	J.F.M. Valls	A. Guglieri 2404	H	An	Au	CO, N, NE, S, SE	
A. *purpusii* (Mez) Chase	J.F.M. Valls	A. Pott 2102	H	An	Au, Hy	CO, N, NE, S, SE	
A. *siccus* (Nees) Kuhlm.	J.F.M. Valls	A. Pott 2510	H	An	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

A. suffultus (Mikan ex Trin.) Parodi	G. Davidse	A.C. Allem 2298	H	An	Au	CO, N, NE, S, SE	
,Bambusa vulgaris* L.						Exotic	
Bothriochloa barbinodis (Lag.) Herter	J.F.M. Valls	A. Pott 3979	H	An	An	CO, S	
B. eurylemma M.Marchi & Longhi-Wagner	J.F.M. Valls	J.F.M. Valls 8594	H	An	An	CO	
B. exaristata (Nash) Henrard	J.F.M. Valls	A.C. Allem 2153	H	An	An	CO, S, SE	
B. longipaniculata (Gould) Allred & Gould	J.F.M. Valls	A. Pott 4072	H	An	An	CO, S, SE	
B. saccharoides (Sw.) Rydb.	J.F.M. Valls	A. Pott 3317	H	An	An	CO, S	
**Cenchrus americanus* (L.) Morrone						Exotic	
**C. ciliaris* L.	A. Guglieri	A. Guglieri 2075	H	An	Z	CO, N, NE, S, SE	
**C. echinatus* L.	A. Pott	A. Pott 2569	H	An	Z	CO, N, NE, S, SE	
C. nervosus (Nees) Kuntze	J.F.M. Valls	A. Pott 4002	H	An	An	CO, NE, S, SE	Brazil
*,***C. purpureus* (Schumach.) Morrone			H	An		Exotic	
Chloris barbata Sw.	J.F.M. Valls	J.F.M. Valls 10326	H	An	Au, An	CO, NE, SE	
C. orthonoton Döll	J.F.M. Valls	A. Pott 4147	H	An	Au, An	CO, NE, S, SE	
C. pycnothrix Trin.	G. Davidse	T.S. Silva 117	H	An	Au, An	CO, NE, S, SE	
***Chrysopogon zizanioides* (L.) Roberty	T. Filgueiras	A. Pott 8908	H	An	Au	NE, SE	

Coleataenia prionitis (Nees) Soreng	J.F.M. Valls	J.F.M. Valls 10388	H	An	Au	CO, S	
C. stenodes (Griseb.) Soreng	J.F.M. Valls	A. Pott 1125	H	An	Au, Hy	CO, N	
Ctenium brevispicatum J.G.Sm.	A. Guglieri	A. Guglieri 3088	H	An	Au, An		
C. polystachion Balansa	A. Guglieri	B.E.M. Pinto 708	H	An	Au, An		
***Cymbopogon citratus* (DC.) Stapf			H	An		Exotic	
***C. martinii* (Roxb.) J.F.Watson			H	An		Exotic	
**Cynodon dactylon* (L.) Pers.	A. Guglieri	A. Guglieri 1724	H	An	Au, Z	CO, N, NE, S, SE	
C. maritimus Kunth	H.M. Longhi-Wagner	J. Alvarez no n.	H	An	Au, Z	CO, S, SE	
***C. nlemfuensis* Vand.			H	An	Au, Z	Exotic	
Cyphonanthus discrepans (Döll) Zuloaga & Morrone	J.F.M. Valls	A. Pott 1265	H	An	Au, Hy	CO, N, NE	Brazil
**Dactyloctenium aegyptium* (L.) Beauv.	A. Guglieri	A. Pott 1022	H	An	Au	Exotic	
Dichanthelium sciurotoides (Zuloaga & Morrone) Davidse	A. Guglieri	A. Pott 2406	H	An	Au	CO, N, S, SE	Brazil
Digitaria aequiglumis (Hack. & Arechav.) Parodi	T.S. Canto-Dorow	A. Guglieri 1744	H	An	Au	CO, N, NE, S	

(continued)

Table 3.1 (continued)

**D. bicornis* (Lam.) Roem. & Schult.	T.S. Canto-Dorow	A. Pott 1025	H	An	Au	CO, N, NE, S, SE	
**D. ciliaris* (Retz.) Koeler	T.S. Canto-Dorow	A. Pott 3696	H	An	Au	CO, N, NE, S, SE	
D. cuyabensis (Trin.) Parodi	A. Pott	V.J. Pott 8271	H	An	Au	CO, N, NE, S, SE	
D. cuyabensis ssp. *glabrescens* Dorow & Longui-Wagner	T.S. Canto-Dorow	A. Pott 3695 (Typus)	H	An	Au	CO	Brazil
,D. eriantha* ssp. *pentzii* (Stent) Kok			H	An		Exotic	
**D. fuscescens* (Presl.) Henrard	T.S. Canto-Dorow	A. Pott 1026A	H	An	Au	CO, N, NE, S, SE	
**D. horizontalis* Willd.	A. Pott	F. Bao 76	H	An	Au	CO, N, NE, S, SE	
**D. insularis* (L.) Fedde	T.S. Canto-Dorow	A.K.D. Salomão 385	H	An	An	CO, N, NE, S, SE	
D. laxa (Rchb.) Parodi	J.F.M. Valls; T.S. Canto-Dorow	A. Pott 1313	H	An	Au	CO, N, SE	
**D. nuda* Schumach.	T.S. Canto-Dorow	A.C. Allem 2160	H	An	Au	CO, N, NE, S, SE	
**D. queenslanica* Henrard	T.S. Canto-Dorow	A.C. Allem 2247	H	An	Au	CO, N, NE, S, SE	
Dinebra panicea (Retz.) P.M.Peterson & N. Snow	J.F.M. Valls	A. Pott 4049	H	An	Au	CO, NE	Brazil
D. panicoides (J.Presl) P.M. Peterson & N. Snow	J.F.M. Valls	J.F.M. Valls 9169	H	An	Au	CO, N, NE	

Diplachne fusca (L.) P.Beauv.	J.F.M. Valls	A. Pott 4146	H	An	Au	CO, NE, S, SE	Brazil
**Echinochloa colona* (L.) Link	A. Pott	A. Pott 1160	H	An	Au, Hy	CO, N, NE, S, SE	
**E. crusgalli* (L.) P. Beauv.	A. Pott	A. Pott 13574	H	An	Hy	CO, N, NE, S, SE	
**E. crus-pavonis* (Kunth) Schult.	J.F.M. Valls	J.F.M. Valls 8586	H	An	Hy	CO, N, NE, S, SE	
E. polystachya (Kunth) Hitchc.	V.J. Pott	V.J. Pott 3188	H	An	Hy	CO, N, NE, S, SE	
Echinolaena gracilis Swallen	J.F.M. Valls	A. Pott 1229	H	An	Au	CO, N	
**Eleusine indica* (L.) Gaertn.	J.F.M. Valls	A. Pott 3543	H	An	Au	Exotic	
**E. tristachya* (Lam.) Lam.	J.F.M. Valls	J.F.M. Valls 15773	H	An	An	Exotic	
Elionurus muticus (Spreng.) Kuntze	J.F.M. Valls	A. Pott 4029	H	An	An	CO, N, NE, S, SE	
E. tripsacoides Humb. & Bonpl. ex Willd.	G. Davidse	A.C. Allem 2274	H	An	An	CO, NE	
Eragrostis acutiflora (Kunth) Nees	S.C. Boechat	A.C. Allem 2582	H	An	Au	CO, N, NE, SE	
E. articulata (Schrank) Nees	J.F.M. Valls	A. Pott 1138	H	An	Au	CO, N, NE, S, SE	
E. bahiensis Schrad. ex Schult.	J.F.M. Valls; S.C. Boechat	A. Pott 1018	H	An	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

**E. ciliaris* (L.) R.Br.	S.C. Boechat	A. Pott 3904	H	An	Au	CO, N, NE, S, SE	
E. gloeodes Ekman	S.C. Boechat	J.F.M. Valls 13572	H	An	Au	CO	Brazil
E. hypnoides (Lam.) Britton, Sterns & Poggenb.	J.F.M. Valls; S.C. Boechat	A. Pott 2071	H	An	Au, Hy	CO, N, NE, S, SE	Brazil
**E. japonica* (Thunb.) Trin.	J.F.M. Valls	V.J. Pott 1541	H	An	Au	CO, N, NE, S, SE	
E. lugens Nees	A. Pott	A. Pott 3694	H	An	Au	CO, NE, S, SE	Brazil
**E. maypurensis* (Kunth) Steud.	H.M. Longhi-Wagner	T. Canto-Dorow 571a	H	An	Au	CO, N, NE, SE	
E. mexicana (Hornem.) Link	J.F.M. Valls	J.F.M. Valls 13586	H	An	Au	CO, N, NE, S, SE	
E. orthoclada Hack.	J.F.M. Valls	J.F.M. Valls 8657	H	An	Au	CO	
E. pastoensis (Kunth) Trin.	J.F.M. Valls	J.F.M. Valls 9381	H	An	Au	CO, N, SE	
**E. pilosa* (L.) P.Beauv.	S.C. Boechat	A. Pott 3409	H	An	Au	CO, N, NE, S, SE	
E. rojasii Hack.	S.C. Boechat	A. Pott 16874	H	An	Au	CO, S	
E. rufescens Schrad. ex Schult.	S.C. Boechat	A. Pott 1238	H	An	Au	CO, N, NE, SE	
**E. tenella* (L.) P. Beauv. ex Roem. & Schult.	S.C. Boechat	A.C. Allem 2364	H	An	Au	CO, N, NE, S, SE	
E. vallsiana Boechat & Longhi-Wagner	S.C. Boechat	A.C. Allem 1335 (Holotypus)	H	An	Au	CO, N, SE	
Eriochloa distachya Kunth	J.F.M. Valls	J.F.M. Valls 12582	H	An	Hy	CO, N, NE, S, SE	
***E. polystachya* Kunth	J.F.M. Valls	A.C. Allem 124	H	An	Au	Exotic	

E. punctata (L.) Desv. ex Ham.	J.F.M. Valls	A. Pott 2774	H	An	Au, Hy	CO, N, SE	
Eriochrysis warmingiana (Hack.) Kuhlm.	C.A.D. Welker	B. Tonic 406	H	An	An	CO, N, NE, S, SE	
Eustachys calvescens (Hack.) Caro & Sanchez	A. Guglieri-Caporal	A. Guglieri-Caporal 3045	H	Na	Au	CO, S, SE	
**E. distichophylla* (Lag.) Nees	A. Guglieri-Caporal	A. Guglieri-Caporal 3141	H	An	An	CO, NE, S, SE	
Gouinia brasiliensis (S.Moore) Swallen	J.F.M. Valls	A. Pott 1929	H	An	Au, Z	CO	
G. latifolia (Griseb.) Vasey	J.F.M. Valls	J.F.M. Valls 15763	H	An	Au, Z	CO, NE	
G. paraguayensis (Kuntze) Parodi	J.F.M. Valls	A. Pott 4050	H	An	Au, Z	CO	
Guadua chacoensis (Rojas) Londoño & P.M.Peterson		not collected	S	An	Au, Z	CO, S, SE	
G. paniculata Munro	J.F.M. Valls	A. Pott 13634	T	An	Au, Z	CO, N, NE, S, SE	
Gymnopogon fastigiatus Nees	J.F.M. Valls	A. Pott 2229	H	An	Au, An	CO, N, SE	
G. foliosus (Willd.) Nees	J.F.M. Valls	A. Pott 1984	H	An	Au, An	CO, N, NE, SE	
G. spicatus (Spreng.) Kuntze	J.F.M. Valls	A. Pott 1029	H	An	Au, An	CO, N, NE, S, SE	
Gynerium sagittatum (Willd.) P.Beauv.	A. Pott	A. Pott 3926	Ss	An	An, Hy	CO, N, NE, S, SE	
Hemarthria altissima (Poir.) Stapf & C.E.Hubb.	J.F.M. Valls	A. Pott 12850	H	An	Au	CO, N, S	

(continued)

Table 3.1 (continued)

Homolepis aturensis (Kunth) Chase	J.F.M. Valls	V.J. Pott 5159	H	An	Hy	CO, N, NE, SE	Brazil
Hymenachne amplexicaulis (Rudge) Nees	J.F.M. Valls	V.J. Pott 3146	H	An	Au,Hy, Z	CO, N, NE, S, SE	
H. donacifolia (Raddi) Chase	V.J. Pott; A. Guglieri	V.J. Pott 4616	H	An	Au, Z	CO, N, NE, S, SE	
H. grumosa (Nees) Zuloaga	A. Guglieri-Caporal	S.A. Rego 707	H	An	Au, Hy	CO, NE, S, SE	
H. pernambucensis (Spreng.) Zuloaga	J.F.M. Valls	V.J. Pott 1298	H	An	An	CO, N, NE, S, SE	
**Hyparrhenia rufa* (Nees) Stapf	A. Pott	S.N. Moreira 845	H	An	An	Exotic	
Imperata brasiliensis Trin.	J.F.M. Valls; C.A.D. Welker	A.C. Allem 2167	H	An	An	CO, N, NE, S, SE	
I. tenuis Hack.	J.F.M. Valls	V.J. Pott 3463	H	An	An	CO, S, SE	
Lasiacis divaricata (L.) Hitchc.	A. Guglieri	A.K.D. Salomão 438	Ss	An	Z	CO, N, NE, S, SE	
L. ligulata Hitchc. & Chase	A. Pott	F.S. Carvalho 74	Ss	An	Z	CO, N, NE, S, SE	
L. sorghoidea Desv. ex Ham.) Hitchc. & Chase	J.F.M. Valls	A. Pott 1197	Ss	An	Z	CO, N, NE, S, SE	
Leersia hexandra Sw.	J.F.M. Valls	V.J. Pott 3137	H	An	Hy	CO, N, NE, S, SE	
L. ligularis Trin.	A. Guglieri	A. Pott 15560	H	An	Au	CO, S, SE	
Leptochloa virgata (L.) P.Beauv.	J.F.M. Valls	A. Pott 2651	H	An	Au	CO, N, NE, S, SE	
Lithachne pauciflora (Sw.) P.Beauv.	J.F.M. Valls	J.F.M. Valls 9136	H	An	Au	CO, NE, S	

Loudetia flammida (Trin.) C.E.Hubb.	J.F.M. Valls	A. Pott 1254	H	An	An	CO, N, NE, SE	
Louisiella elephantipes (Nees ex Trin.) Zuloaga	J.F.M. Valls	V.J. Pott 2572	H	An	Hy	CO, N, NE, S, SE	
Luziola bahiensis (Steud.) Hitchc.	J.F.M. Valls	V.J. Pott 3393	H	An	Hy	CO, N, NE, S, SE	
L. fragilis Swallen	J.F.M. Valls	V.J. Pott 2724	H	An	Hy	CO, SE	
L. peruviana Juss. ex J.F.Gmel.	J.F.M. Valls	A. Pott 6845	H	An	Hy	CO, N, NE, S, SE	
L. spruceana Benth. ex Döll	J.F.M. Valls	A. Pott 4586	H	An	Hy	CO, N, S	
L. subintegra Swallen	J.F.M. Valls	VJP 3118	H	An	Hy	CO, N, NE	
**Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.I.Jacobs	A. Guglieri	A. Guglieri 2149	H	An	Au, Z	Exotic	
**Melinis minutiflora* P.Beauv.	A. Guglieri	W.M. Ramos 19	H	An	An	Exotic	
**M. repens* (Wild.) Zikka	A. Guglieri	A. Guglieri 2150	H	An	An	Exotic	
Mesosetum ansatum (Trin.) Kuhlm.	A. Pott	A. Pott 1176	H	An	Au	CO	Brazil
M. cayennense Steud.	A. Pott	A. Pott 2493	H	An	Au	CO, N, NE, SE	
M. chaseae Luces	A. Pott	A. Pott 2200	H	An	Au	CO, N, NE, SE	
M. loliiforme (Hochst.) Chase	A. Pott	A. Pott 1258	H	An	Au	CO, N, NE, SE	
M. sclerochloa (Trin.) Hitchc.	G.H. Rua	G.H. Rua 958	H	An	Au	CO	Brazil

(continued)

Table 3.1 (continued)

Microchloa indica (L.f.) P.Beauv.	A. Pott	A. Pott 1256	H	An	Au	CO, N, NE, S, SE	
Mnesithea aurita (Steud.) de Koning & Sosef	J.F.M. Valls	A. Pott 2245	H	An	Au	CO, N, NE, S, SE	
M. granularis (L.) de Koning & Sosef	J.F.M. Valls	A. Pott 7106	H	An	Au	CO, N, NE, SE	
M. subgibbosa (Winkl. ex Hack.) de Koning & Sosef	J.F.M. Valls	A. Pott 2015	H	An	Au	CO, N, NE, S, SE	
Ocellochloa stolonifera (Poir.) Zuloaga & Morrone	A. Guglieri	U.M. Resende 385	H	An	Au	CO, N, NE, S, SE	
Oedochloa procurrens (Nees ex Trin.) C. Silva & R.P. Oliveira	J.F.M. Valls; R.P. Oliveira	A. Pott 1195	H	An	Au	CO, N, NE, S, SE	
Olyra ciliatifolia Raddi	J.F.M. Valls	A. Pott 8042	H	An	Au	CO, N, NE, S, SE	
O. latifolia Desv.	J.F.M. Valls	V.J. Pott 1763	H	An	Au	CO, N, NE, S, SE	
Oplismenus hirtellus (L.) P.Beauv.	J.F.M. Valls	A. Pott 5401	H	An	Au	CO, N, NE, S, SE	
O. grandiglumis (Döll) Prod.	G. Davidse	A.C. Allem 1521	H	An	Hy	CO, N	
O. latifolia Desv.	J.F.M. Valls	V.J. Pott 1954	H	An	Hy	CO, N, NE, S	
**O. rufipogon* Griff.	I.I. Boldrini	S.R. Zaniolo 199	H	An	Hy	CO, N	
***O. sativa* L.			H	An	Au	Exotic	
Otachyrium piligerum Send. & Soderstr.	J.F.M. Valls	J.F.M. Valls 12580	H	An	Au	CO, SE	Brazil

O. versicolor (Döll) Henrard	L. Rebellato	L. Rebellato 210	H	An	Au	CO, N, NE, S, SE	
Panicum aquaticum Zuloaga & Morrone	G. Davidse	A.C. Allem 2171	H	An	Au	CO, N, NE, S, SE	
P. bergii Arechav.	F.O. Zuloaga	J.F.M. Valls 4919	H	An	Au, An	CO, N, NE, S, SE	
P. cayennense Lam.	J.F.M. Valls	A.C. Allem 1256	H	An	Au	CO, N, NE, S, SE	
P. dichotomiflorum Michx.	F.O. Zuloaga	A. Pott 3918	H	An	Au, Hy	CO, N, NE, S, SE	
P. exiguum Mez	F.O. Zuloaga	A. Pott 3862	H	An	Au	CO, N, NE, SE	
P. glabripes Döll	A. Guglieri	A.C. Allem 1194	H	An	Au	CO, N, NE, SE	
P. hirtum Lam.	A. Guglieri	A. Pott 1181	H	An	Au	CO, N, NE	
P. millegrana Poir.	A. Guglieri	A. Guglieri 1718	H	An	Au	CO, N, NE, S, SE	
P. pedersenii Zuloaga	A. Guglieri	A. Guglieri 1721	H	An	Au	CO, NE, S, SE	
P. peladoense Henrard	A. Guglieri	J.F.M. Valls 9118	H	An	Au	CO, N, NE, S, SE	
P. quadriglume (Döll) Hitchc.	A. Guglieri	A. Guglieri 2086	H	An	Au	CO, N, NE, SE	
**P. repens* L.	G. Davidse	A.C. Allem 2367	H	An	Au, Hy	CO, N, NE, S, SE	
P. rudgei Roem. & Schult.	J.F.M. Valls	A. Pott 1135	H	An	Au	CO, N, NE, S, SE	
P. stramineum Hitchc. & Chase	P.L. Viana	A.C. Allem 1237	H	An	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

P. trichanthum Nees	A. Guglieri	V.J. Pott 3659	H	An	Au	CO, N, NE, S, SE	
P. trichoides Sw.	A. Guglieri	A. Pott 2551	H	An	Au	CO, N, NE, S, SE	
P. tricholaenoides Steud.	J.F.M. Valls	A. Pott 4493	H	An	Au	CO, N, N, SE	
Pappophorum krapovickasii Roseng.	J.F.M. Valls	A. Pott 1032	H	An	An	CO	
P. mucronulatum Nees	A. Guglieri-Caporal	A. Guglieri-Caporal 3024	H	An	An	CO, N, SE	
P. pappiferum (Lam.) Kuntze	J.F.M. Valls	J.F.M. Valls 9488	H	An	An	CO, SE	
Paratheria prostrata Griseb.	J.F.M. Valls	A. Pott 1624	H	An	Au, Z	CO, N, SE	
Paspalidium geminatum (Forssk.) Stapf	J.F.M. Valls	A. Pott 2137	H	An	Au, Hy	CO, N, NE, S, SE	
Paspalum acuminatum Raddi	J.F.M. Valls	V.J. Pott 3178	H	An	Au, Hy	CO, S, SE	
P. almum Chase	J.F.M. Valls	A. Pott 1173	H	An	Au, Z	CO, S	
P. arundinellum Mez	O. Morrone	A.C. Allem 1497	H	An	Au	CO, NE, SE	
P. atratum Swallen	R.C. Oliveira	A. Guglieri 2121	H	An	Au	CO, N, NE, S, SE	
P. carinatum Humb. & Bonpl. ex Flüggé	J.F.M. Valls; R.C. Oliveira	A. Pott 2535	H	An	Au	CO, N, NE, S, SE	
P. chacoense Parodi	J.F.M. Valls	J.F.M. Valls 13558	H	An	Au	CO	
P. conjugatum P.J.Bergius	J.F.M. Valls	A.C. Allem 2151	H	An	Au	CO, N, NE, S, SE	
P. conspersum Schrad.	J.F.M. Valls	A. Guglieri 1747	H	An	Au	CO, N, NE, S, SE	

P. coryphaeum Trin.	G.H. Rua	A. Pott 3165	H	An	Au	CO, N, NE, SE	
P. denticulatum Trin.	J.F.M. Valls	J.F.M. Valls 13564	H	An	Au	CO, N, NE, S	
P. dilatatum Poir.	A. Guglieri	A. Guglieri 1733	H	An	Au	CO, S, SE	
P. distichum L.	A. Guglieri	A. Pott 2468	H	An	Au	CO, N, NE, S, SE	
P. eucomum Nees ex Trin.	G.H. Rua	M. Schessl 3096	H	An	Au	CO, S, SE	
P. fasciculatum Willd. ex Flüggé	J.F.M. Valls	V.J. Pott 2522	H	An	Au	CO, N, S	
P. foliiforme S.Denham	J.F.M. Valls; G.H. Rua	A. Pott 1522	H	An	Au	CO, N, NE, SE	
P. gardnerianum Nees	J.F.M. Valls	A. Pott 2386	H	An	Au	CO, N, NE, SE	
P. guenoarum Arechav.	J.F.M. Valls	A.C. Allem 2248	H	An	Au	CO, S, SE	
P. hartwegianum E.Fourn.	R.C. Oliveira	J.F.M. Valls 9503	H	An	Au	CO	
P. inaequivalve Raddi	J.F.M. Valls	A. Pott 5434	H	An	Au	CO	
P. intermedium Munro ex Morong & Britton	R.C. Oliveira	A. Pott 4101	H	An	Au	CO, NE, S, SE	
P. lenticulare Kunth	J.F.F.M. Valls	A. Pott 4126	H	An	Au	CO, N, NE, S, SE	
P. lineare Trin.	J.F.M. Valls	A. Pott 1127	H	An	Au	CO, N, NE, S, SE	
P. macranthecium Parodi	J.F.M. Valls	A. Pott 1147	H	An	Au	CO, N, NE, SE	
P. maculosum Trin.	G.H. Rua	S.N. Moreira 1535	H	An	Au	CO, N, NE, S, SE	
P. malacophyllum Trin.	G.H. Rua	A. Pott 2138	H	An	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

P. malmeanum Ekman	G.H. Rua	G.H. Rua 955	H	An	Au	CO	
P. maritimum Trin.	J.F.M. Valls	A. Pott 1858	H	An	Au	CO, N, NE, S, SE	
P. minus E. Fourn.	J.F.M. Valls	J.F.M. Valls 14010	H	An	Au	CO, N	
P. morichalense Davidse et al.	J.F.M. Valls	V.J. Pott 3395	H	An	Hy	CO, N, NE, SE	
P. multicaule Poir.	J.F.M. Valls	A. Pott 2174	H	An	Au	CO, N, NE, SE	
P. notatum Flüggé	A. Pott	A. Pott 2561	H	An	Au, Z	CO, N, NE, S, SE	
P. nudatum Luces	J.F.M. Valls	J.F.M. Valls 9022	H	An	Au	CO	
P. oteroi Swallen	G. Davidse	A.C. Allem 1332	H	An	Au	CO	Brazil
P. pallens Swallen	R.C. Oliveira	J.F.M. Valls 13784	H	An	Au	CO, SE	
P. palustre Mez	J.F.M. Valls	J.F.M. Valls 13565	H	An	Au	CO, N	
P. parviflorum Rhode ex Flüggé	J.F.M. Valls	J.F.M. Valls 12584	H	An	Au	CO, N, NE	
P. pictum Ekman	C.O. Moura	A. Pott 4792	H	An	Au	CO, N, SE	
P. pilosum Lam.	S.A. Renvoize	G. Hatschbach 49274	H	An	Au	CO, N, NE, S, SE	
P. plicatulum Mixch.	A. Pott	A. Pott 2109	H	An	Au	CO, N, NE, S, SE	
P. polyphyllum Nees	A.S. Silva	A.S. Silva 229	H	An	Au	CO, NE, S, SE	
P. pumilum **Nees**	A. Guglieri	A. Guglieri 2318	H	An	Au	CO, N, NE, S, SE	
P. repens P.J.Bergius	J.F.M. Valls	V.J. Pott 1740	H	An	Hy	CO, N, NE, S, SE	
P. rojasii Hack.	Valls; R.C. Oliveira	A. Pott 5883	H	An	Au	CO, N, S, SE	
P. simplex Morong	Valls; G.H. Rua	A. Pott 3913	H	An	Au	CO	

P. stellatum Humb. & Bonpl. ex Flüggé	R.C. Oliveira	A. Pott 1774	H	An	Au	CO, N, NE, S, SE	
P. subciliatum Chase	R.C. Oliveira	A. Pott 1521	H	An	Au	CO, N, SE	
P. unispicatum (Scribn. & Merr.) Nash	J.F.M. Valls	J.F.M. Valls 8610	H	An	Au	CO, N	
P. usterii Hack.	J.F.M. Valls; C.H. Rua	A. Pott 3977	H	An	Au	CO, SE	
P. vaginatum Sw.	J.F.M. Valls	V.J. Pott 247	H	An	Au	CO, N, NE, S, SE	
P. virgatum L.	J.F.M. Valls	A. Pott 2100	H	An	Au	CO, N, NE, S, SE	
P. wrightii Hitchc. & Chase	J.F.M. Valls	V.J. Pott 4585	H	An	Au	CO, N	
Raddia brasiliensis Bertol.	J.F.M. Valls	A. Pott 15564	H	An	Au	CO, NE, SE	Brazil
Reimarochloa acuta (Flüggé) Hitchc.	J.F.M. Valls	J.F.M. Valls 9217	H	An	Au	CO, N, NE, SE	
R. brasiliensis (Spreng.) Hitchc.	J.F.M. Valls; A. Guglieri	J.F.M. Valls 9322	H	An	Au	CO, N, NE	
**Rottboellia cochinchinensis* (Lourt.) Clayton	J.F.M. Valls	J.F.M. Valls 15477	H	An	Au	exot	
Rugoloa hylaeica (Mez) Zuloaga	J.F.M. Valls	A. Pott 2258	H	An	Au	CO, N, NE, S, SE	
R. pilosa (Sw.) Zuloaga	A. Guglieri	A. Pott 4896	H	An	Au	CO, N, NE, S, SE	
R. polygonata (Schrad.) Zuloaga	A. Guglieri	V.J. Pott 8893	H	An	Au, Hy	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Saccharum asperum (Nees) Steud.	V.J. Pott	V.J. Pott 8643	H	An	An	CO, S, SE	
***S. officinarum* L.			H	An	An	Exotic	
S. villosum Steud.	A. Pott	L.V.S. Campos 652	H	An	An	CO, N, NE, SE	
Sacciolepis angustissima (Hochst. ex Steud.) Kuhlm.	J.F.M. Valls	A. Pott 2211	H	An	Au	CO, N, NE, S, SE	
S. myuros (Lam.) Chase	J.F.M. Valls	A. Pott 2759	H	An	Au	CO, N, NE, SE	
S. vilvoides (Trin.) Chase	A. Pott	F.J. Kochanowski 504	H	An	Au	CO, N, NE, S, SE	
Schizachyrium condensatum (Kunth) Nees	A. Pott & V.J. Pott	S.N. Moreira 851	H	An	Au	CO, NE, S, SE	
S. microstachyum (Desv. ex Ham.) Roseng., B.R.Arril. & Izag.	J.F.M. Valls	A. Pott 1021	H	An	An	CO, N, NE, S, SE	
S. sulcatum (Ekman) S.T. Blake	J.F.M. Valls	A. Pott 1326	H	An	Au	CO, SE	
Setaria nicorae Pensiero	J.F.M. Valls	A.C. Allem 2208	H	An	Au	CO	
S. parviflora (Poir.) Kerguélen	A. Guglieri	A. Guglieri 1750	H	An	Au, Hy	CO, N, NE, S, SE	
S. scandens Schrad. ex Schult.	J.F.M. Valls	A. Pott 1142	H	An	Au	CO, NE, S, SE	
S. tenax (Rich.) Desv.	J.F.M. Valls	J.F.M. Valls 9420	H	An	Au	CO, N, NE, S, SE	
S. vulpiseta (Lam.) Roem. & Schult.	J.F.M. Valls	A. Pott 1033	H	An	Au	CO, N, NE, S, SE	
S. viridis (L.) P.Beauv.	A. Pott & G.A. Damasceno Jr.	F.S.Carvalho 80	H	An	Au	CO, NE, S, SE	

Sorghastrum setosum (Griseb.) Hitchc.	J.F.M. Valls	A. Pott 4119	H	An	Au, Z	CO, N, NE, S, SE	
**Sorghum bicolor* subsp. *arundinaceum* (Desv.) de Wet & J.R. Harlan	A. Pott	A. Pott 4109	H	An	Au	CO, N	
Sporobolus aeneus (Trin.) Kunth	J.F.M. Valls; S. Denham & S. Aliscione	A. Pott 1216	H	An	Au	CO, S, SE	
S. ciliatus J. Presl.	A. Guglieri	A. Guglieri 1762	H	An	Au	CO, NE, S, SE	
S. indicus (L.) R. Br.	A. Guglieri	A. Guglieri 1752	H	An	Au, Z	CO, N, NE, S, SE	
S. jacquemontii Kunth	A. Guglieri	A. Pott 1224	H	An	Au	CO, N, NE, S, SE	
S. monandrus Roseng., B.R.Arril. & Izag.	J.F.M. Valls	A. Guglieri 3015	H	An	Au, An	CO, NE, S	
S. pseudairoides Parodi	A. Guglieri-Caporal	A.K.D. Salomão 354	H	An	Au, An	CO, N, NE, S, NE	
S. pyramidatus (Lam.) Hitchc.	A. Pott	A. Pott 3449	H	An	Au	CO, N, NE, SE	
S. tenuissimus (Schrank) Kuntze	A. Guglieri-Caporal	A. Guglieri-Caporal 3096	H	An	Au	CO, N, NE, SE	
Stapfochloa canterae (Arechav.) P.M. Peterson	J.F.M. Valls	J.F.M. Valls 9509	H	An	An, Au	CO, S	
S. ciliata (Sw.) P.M. Peterson	J.F.M. Valls	J.F.M. Valls 9507	H	An	An, Au	CO, NE	
S. elata (Desv.) P.M. Peterson	A. Pott	A. Pott 3691	H	An	An, Au	CO, N, NE, S, SE	
Steinchisma decipiens (Nees ex Trin.) W.V.Br.	G. Davidse	G. Schaller 34	H	An	Au	CO, N, NE, S, NE	

(continued)

Table 3.1 (continued)

S. hians (Elliot) Nash	J.F.M. Valls	J.F.M. Valls 9457	H	An	Au	CO, N, NE, S, NE	
S. laxum (Sw.) Zuloaga	J.F.M. Valls	A. Pott 2660	H	An	Au, Hy	CO, N, NE, S, NE	
Stephostachys mertensii (Roth) Zuloaga & Morrone	J.F.M. Valls	V.J. Pott 5609	H	An	Au, Hy	CO, N, NE, S, NE	
Streptochaeta spicata Schrad. ex Nees	J.F.M. Valls	R.R.B. Negrelle 17	H	An	Z	CO, N, NE, S, NE	
Trachypogon spicatus (L.f.) Kuntze	I.I. Boldrini	A. Pott 1222	H	An	Au, Z	CO, N, NE, SE	
Tragus berteronianus Schult.	J.F.M. Valls	A. Pott 3895	H	An	Au	CO, NE, SE	
Tricanthecium parvifolium (Lam.) Zuloaga & Morrone	A. Guglieri	A. Guglieri 2390	H	An	Au, Hy	CO, N, NE, S, NE	
Tridens brasiliensis (Nees ex Steud.) Parodi	G. Davidse	A.C. Allem 1504	H	An	Au	CO, S	
T. flaccidus (Döll) Parodi	J.F.M. Valls	J.F.M. Valls 10359	H	An	Au	CO, N, NE	
Tripogon spicatus (Nees) Ekman	J.F.M. Valls	A. Pott 1257	H	An	Au	CO, NE, S, SE	
Tripsacum andersonii J.R.Gray	J.F.M. Valls	A. Pott 5586	H	An	Au, Z	CO, N, NE	
T. australe H.C. Cutler & E.S Anderson	J.F.M. Valls	J.F.M. Valls 13999	H	An	Au	CO, N	
**Urochloa adspersa* (Trin.) R.D.Webster	B.B.T. Walter	A. Pott 1876	H	An	Au	Exotic	
**U. arrecta* (Hack. ex Durand & Schinz) Morrone & Zuloaga		A. Pott 8633	H	An	Hy	Exotic	

*,***U. brizantha* (Hochst. ex A.Rich.) R.D.Webster	A. Guglieri	A. Guglieri 1737	H	An	Au, Z	Exotic	
*,***U. decumbens* (Stapf) R.D.Webster	A. Guglieri	A. Guglieri 1748	H	An	Au, Z	Exotic	
**U. distachyos* (L.) T.Q.Nguyen	A. Pott	A. Pott 2467	H	An	Au, Z	Exotic	
**U. fusca* (Sw.) B.F.Hansen & Wunderlin	J.F.M. Valls	A. Pott 13686	H	An	Au	Exotic	
*,***U. humidicola* (Rendle) Morrone & Zuloaga	J.F.M. Valls	A. Krapovickas 29.827	H	An	Au, Z	Exotic	
**U. lorentziana* (Mez) Morrone & Zuloaga	A. Guglieri	G.A. Damasceno Jr. 3137	H	An	Au	CO	
**U. mutica* (Forssk.) T.Q.Nguyen	G. Davidse	A.C Allem 2149	H	An	Au, Z	Exotic	
**U. paucispicata* (Morong) Morrone & Zuloaga	A. Pott	A. Pott 1141	H	An	Au	CO, NE	
**U. plantaginea* (Link) R.D. Webster	J.F.M. Valls	A. Pott 2685	H	An	Au	Exotic	
**U. platyphylla* Munro ex C.Wright) R.D.Webster	J.F.M. Valls	A. Pott 13856	H	An	Au	Exotic	
**U. reptans* (L.) Stapf	G. Davidse	A.C. Allem 2158	H	An	Au	Exotic	
***U. ruziziensis* (R.Germ. & Evrard) Crins			H	An	Au, Z	Exotic	
***Zea mays* L.	A. Guglieri	A. Guglieri 1427	H	An	Z	Exotic	

(continued)

Table 3.1 (continued)

***Zoysia matrella* (L.) Merr.	A. Pott	A. Pott 2304	H	An	Hy	Exotic	
Polygalaceae							
Acanthoclados dichromus (Steud.) J.F.B.Pastore	G.A. Damasceno Jr.	D.R.C. Padilha 61	S	E	Au	CO, NE, SE	
Asemeia extraaxillaris (Chodat) J.F.B.Pastore & J.R.Abbott	A. Pott & V.J. Pott	A. Pott 1203	H	E	Au	CO, S, SE	
A. rhodoptera (Mart. ex A.W.Benn.) J.F.B.Pastore & J.R.Abbott	A. Pott & V.J. Pott	A. Pott 1761	H	E	Au	CO, N, NE, S, NE	
A. violacea (Aubl.) J.F.B.Pastore & J.R.Abbott	A. Schinini	I.M. Bortolotto 1482	S	E	An	CO, N, NE, S, NE	
Bredemeyera floribunda Willd.	A. Pott	A. Pott 11817	H	E	Au	CO, N, NE, S, NE	
Polygala adenophylla A.St.-Hil. & Moq.	V.J. Pott	A. Pott 4968	H	E	Au	CO, S	
P. appendiculata Vell.	J.F.B. Pastore	V.J. Pott 3863	H	E	Au	CO, N, NE, S, NE	Brazil
P. asperuloides Kunth	A. Pott	A. Pott 9454	H	E	Au	CO, N, NE, SE	
P. brasiliensis L.	A. Pott	A. Pott 2524	H	E	Au	CO, S, SE	
P. celosioides Mart. ex A.W.Benn.	M.C. Marques	A. Pott 2171	H	E	Au	CO, N, NE, S, NE	Brazil
P. cuspidata DC.	A. Pott	A. Pott 1247	H	E	Au	CO, NE, SE	Brazil
P. gracilis Kunth	J.F.B. Pastore	A. Pott 3820	H	E	Au	CO, N, NE, SE	
P. grazielae Marques	R. Lüdtke	S.N. Moreira 787	L	E	An	CO	Brazil

P. longicaulis Kunth	M.C. Marques	J.F.M. Valls 9185	H	E	Au	CO, N, NE, S, NE	Brazil
P. molluginifolia A.St.-Hil. & Moq.	A. Pott	A. Pott 3553	H	E	Au	CO, N, NE, S, NE	Brazil
P. poaya Mart.	A. Pott	A. Pott 6577	H	E	Au	CO, S, SE	
P. subtilis Kunth	J.F.B. Pastore	V.J. Pott 3113	H	E	Au	CO, N, NE, SE	
P. tenuis DC.	A. Pott	A. Pott 3820	H	E	Au	CO, N, NE, S, NE	Brazil
P. timoutoides Chodat	A. Pott	A. Pott 4942	H	E	Au	CO, S, SE	
P. timoutou Aubl.	A. Pott	A. Pott 5273	H	E	Au	CO, N, NE, SE	
Securidaca ovalifolia A.St.-Hil. & Moq.	A. Pott	A. Pott 7976	T	E	Z	CO, N, NE, SE	Brazil
Polygonaceae							
***Antigonum leptotus* Hook. & Arn.		J.A. Ratter 5954	L	E	An	Exotic	
Coccoloba cujabensis Wedd.	E. Melo França	A. Pott 3263	T	E	Z	CO	
C. declinata (Vell.) Mart.	E. Melo França	J.A. Ratter 5107	S	E	Z	CO, NE, SE	
C. guaranitica Hassl.	E. Melo França	A. Pott 5290	T	E	Z	CO	
C. mollis Casar.	E. Melo França	A. Pott 6514	T	E	Z	CO, N, NE, SE	
C. obtusifolia Jacq.	E. Melo França	V.J. Pott 1917	T	E	Z	CO, N, NE	
C. ovata Benth.	E. Melo França	A. Pott 5623	T	E	Z	N, NE	
C. paraguariensis Lindau	E. Melo França	A. Pott 3416	T	E	Z	CO	
C. parimensis Benth. (*C. ochreolata*)	E. Melo França	A. Pott 4960	T	E	Z	CO, N, NE, SE	
C. rigida Meisn.	A. Pott	A. Pott 7976	T	E	Z	CO, SE	Brazil

(continued)

Table 3.1 (continued)

Polygonum acuminatum Kunth	E. Melo França	V.J. Pott 1746	H	E	Hy	CO, N, NE, S, NE	
P. ferrugineum Wedd.	E. Melo França	V.J. Pott 3192	H	E	Au, Hy	CO, N, NE, S, NE	
P. hispidum Kunth	E. Melo França	A. Pott 5034	H	E	Au	CO, N, NE, SE	
P. hydropiperoides Michx.	E. Melo França	N.C. Bueno 279	H	E	Au, Hy	CO, N, NE, S, NE	
P. punctatum Elliot	E. Melo França	V.J. Pott 4761	H	E	Au	CO, N, NE, S, NE	
P. meisnerianum Cham.	V.J. Pott	V.J. Pott 2960	H	E	Au, Hy	CO, NE, S, NE	
P. paraguayense Wedd.	E. Melo França	G. Hatschbach 21979	H	E	Au	CO, S	
P. stelligerum Cham.	E. Melo França	A. Pott 5770	T	E	An	CO, S, SE	
Ruprechtia brachysepala Meisn.	E. Melo França	A. Pott 4536	T	E	An	CO, N, NE	
R. exploratricis Sandwith	A. Pott	A. Pott 8887	T	E	An	CO	
R. tenuiflora Benth.		J.A. Ratter 5954	T	E	An	CO, N	
R. triflora Griseb.	D.E. Prado	A. Pott 4921	T	E	Au, Hy	CO	
Symmeria paniculata Benth.	R.A. Howard	W.W. Thomas 4603	T	E	An	CO, N, NE	
Triplaris caracasana Cham.	G. Hatschbach	G. Hatschbach 47693	E	E	An	CO	
T. americana L.	E. Melo França	A. Pott 4939	T	E	An	CO, N, NE, S	
T. gardneriana Wedd.	E. Melo França	A. Pott 3071	H	E	Hy	CO, N, NE, SE	
Pontederiaceae							
Eichhornia azurea (Sw.) Kunth	V.J. Pott	V.J. Pott 2151	H	E	Hy	CO, N, NE, S, NE	
E. crassipes (Mart.) Solm	V.J. Pott	V.J. Pott 2040	H	E	Hy	CO, N, NE, S, NE	
E. diversifolia (Vahl Urb.	V.J. Pott	V.J. Pott 4737	H	E	Au, Hy	CO, N, NE, SE	

E.meyeri A.G.Schulz	V.J. Pott	A. Pott 4738	H	E	Au, Hy	CO	
Heteranthera limosa (Sw.) Willd.	V.J. Pott; D.J.L. Sousa	A. Pott 4869	H	E	Au, Hy	CO, S	
H. multiflora (Griseb.) C.N.Horn	A. Pott & V.J. Pott	A. Pott 4866	H	E	Hy	CO, N, NE	
H. reniformis Ruiz & Pav.	V.J. Pott	N.C. Bueno 289	H	E	Hy	CO, N, NE, S	
Pontederia cordata L.	J. Velasquez	V.J. Pott 2533	H	E	Hy	CO, N, NE, S, NE	
P. parviflora Alexander	V.J. Pott	V.J. Pott 3193	H	E	Hy	CO, N, NE, SE	
P. rotundifolia L.f.	V.J. Pott	V.J. Pott 1785	H	E	Hy	CO, N, NE, S, NE	
P. subovata (Seub.) Lowden	V.J. Pott	V.J. Pott 1785	H	E	Hy	CO, N, NE, S, NE	
P. triflora (Seub.) G. Augustin et al.	V.J. Pott	A. Pott 4910	H	E	Hy	CO	
Portulacaceae							
Portulaca amilis Apeg.	A.O. Paes-Coelho	M. Schessl 2080	H	E	Au	CO, N, S, SE	
P. cryptopetala Speg.	A.O. Paes-Coelho	G.A. Damasceno Jr. 2370	H	E	Au	CO, S	
P. grandiflora Hook.	M.I.A. Rodrigues	G. Hatschbach 49254	H	E	Au	CO, NE, S, SE	
**P. oleracea* L.	A. Pott	A. Pott 3544	H	E	Au	CO, N, NE, S, SE	
P. pilosa L.	A. Furlan	Rossi s/n	H	E	Au	CO, N, SE	
P. umbraticola Kunth	A. Oliveira	G. Hatschbach 74.370	H	E	Au	CO, N, NE, S, SE	
Potamogetonaceae							

(continued)

Table 3.1 (continued)

Potamogeton pusillus L.	V.J. Pott	V.J. Pott 7907	H	Hy	Au	CO, NE, S, SE	
Primulaceae (include Myrsinaceae and Teophrastaceae)							
Clavija nutans (Vell.) B. Stahl	A. Schinini	A. Pott 4111	T	E	Z	CO, N, S, SE	
Lysimachia minima (L.) Manns & Anderb.	V.J. Pott	A. Pott 1981	T	E	Au	CO, NE, S, SE	
Myrsine umbellata Mart.	A. Pott	A. Pott 13210	T	E	Z	CO, N, NE, S, SE	
Proteaceae							
***Grevillea robusta* A.Cunn. ex R.Br.			T	E	Au	Exotic	
Roupala montana Aubl.	A. Pott	A. Pott 8878	T	E	Au	CO, N, NE, S, SE	
Ranunculaceae							
Clematis brasiliana DC.	I. Cordeiro	S.R. Zaniolo 239	L	E	An	CO, N, NE, S, SE	
C. campestris A.St.-Hil.	M.T. Strong	P. Acevedo-Rodriguez 116677				CO, NE, S, SE	
C. montevidensis Spr.	A. Schinini	A. Pott 7788	L	E	An	CO	
Rhamnaceae							
Colubrina retusa (Pittier) Cowan	R. Lima	M. Macedo 1567	T	E	Z	CO, N, S, SE	
Gouania latifolia Reissek	R. Lima	A. Pott 3084	L	E	Z	CO, NE, S, SE	
Rhamnidium elaeocarpum Reissek	J.A. Ratter	A. Pott 5062	T	E	Z	CO, N, NE, S, SE	
Sarcomphalus mistol (Griseb.) Hauenschild	D. Prado	A. Pott 4408	T	E	Z	CO	
Rosaceae							

***Eriobotrya japonica* (Thunb.) Lindl.			T	E	Z	Exotic	
Rubiaceae							
Alibertia edulis (Rich.) A.Rich.	A. Pott	A. Pott 4381	S	E	Z	CO, N, NE, SE	
Amaioua glomerulata (Lam. ex Poir.) Delprete & C.Persson	J.H. Kirkbride Jr.	B. Dubs 515	T	E	Z	CO, N, NE, SE	
A. guianensis Aubl.		C.P. Calliari 1217	T	E	Z	CO, N, NE, S, SE	
Borreria alata (Aubl.) DC.	A. Pott	A. Pott 2220	H	E	Au	CO, N, NE, S, SE	
B. brachystemonoides Cham. & Schltdl.	E.L. Cabral	A. Pott 1830	H	E	Au	CO, S, SE	
B. capitata (Ruiz & Pav.) DC.		B. Dubs 381	H	E	Au	CO, N, NE, S, SE	
B. cupularis DC.	L.M. Miguel	A. Pott 4090	H	E	Au	CO, N, NE, SE	
B. latifolia (Aubl.) K. Schum.	A. Pott	A. Pott 1538	H	E	Au	CO, N, NE, S, SE	
B. quadrifaria E.L.Cabral	E.L. Cabral	V.J. Pott 1472	H	E	Au	CO, S, SE	
B. tenella (Kunth) Cham. & Schltdl.	E.L. Cabral	A. Pott 2523	H	E	Au	CO, N, NE, S, SE	
B. verticillata (L.) G.Mey.	A. Pott	A. Pott 3212	H	E	Au	CO, N, NE, S, SE	
Calycophyllum multiflorum Griseb.	J.A. Ratter	A. Pott 1425	T	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Cephalanthus glabratus (Spreng.) K.Schum.	A. Pott	A. Pott 5406	T	E	Au	CO, S	
Chiochocca alba (L.) Hitchc.	H.F. Leitão F.	A. Pott 5464	SS	E	Z	CO, N, NE, S, SE	
Chomelia obtusa Cham. & Schltdl.	J.A. Ratter	N.C. Bueno 288	T	E	Z	CO, N, NE, S, SE	
C. pohliana Müll.Arg.	E.L. Cabral	A. Pott 5328	S	E	Z	CO, NE, SE	Brazil
Coccocypselum lanceolatum (Ruiz & Pav,) Pers.	V.J. Pott	S.N. Moreira 1556	H	E	Z	CO, N, NE, S, SE	
***Coffea robusta* L.			S	E	Z	Exotic	
Cordiera concolor (Cham.) Kuntze (Alibertia concolor)	S.L. Jung-Mendaçolli	J. Couto 196	SS	E	Z	CO, N, NE, S, SE	
C. sessilis (Vell.) K. Schum. (Alibertia sessilis)	J.A. Ratter; E.L. Cabral	A. Pott 5084	T	E	Z	CO, N, NE, SE	
Coussarea hydrangeifolia (Benth.) Müll.Arg.	G.A. Damasceno Jr.	T.H. Stefanello 286	S	E	Z	CO, N, NE, SE	
Coutarea hexandra (Jacq.) K. Schum.	A. Pott	A. Pott 13 620	T	E	Au	CO, N, NE, S, SE	
Declieuxia fruticosa (Willd. ex Roem. & Schult.) Kuntze	A. Pott	A. Pott 8012	H	E	Au	CO, N, NE, S, SE	
Diodia kuntzei K.Schum.	V.J. Pott; E.L. Cabral	V.J. Pott 1296	H	E	Au, Hy	CO, S, S	
D. macrophylla K.Schum.	E.L. Cabral	A. Pott 5520	H	E	Au	CO, N	Brazil
Duroia duckei Huber	D. Zappi	M.A. Carniello 6825	T	E	Z	CO, N	

D. micrantha (Ladbr.) Zarucchi	D. Zappi	A. Pott 5227	T	E	Z	CO, N	
Galianthe eupatorioides (Cham. & Schltdl.) E.L.Cabral	E.L. Cabral	V.J. Pott 1368	Ss	E	Au	CO, S, SE	
G. laxa paraguariensis (Chodat) E.L.Cabral	E.L. Cabral; J.E. Fiorentin	A. Pott 2797	Ss	E	Au	CO, S, SE	
Genipa americana L.	A. Pott	A. Pott 3850	T	E	Z	CO, N, NE, S, SE	
Geophila repens (L.) I.M.Johnst.	M.R. Barbosa	A. Pott 8053	H	E	Z	CO, N, NE, S, SE	
Guettarda uruguensis Cham. & Schltdl.	J.A. Ratter	J.A Ratter 6108	T	E	Z	CO, NE, S, SE	
G. viburnoides Cham. & Schltdl.	H.F. Leitão F.; E.L. Cabral	A. Pott 4546	T	E	Z	CO, N, NE, S, SE	
Hamelia patens Jacq.	D. Zappi	V.J. Pott 800	S	E	Au	CO, N, NE, S, SE	
**Hexasepala teres* (Walter) J.H Kirkbr.	E.L. Cabral	A. Pott 5573	H	E	Au	CO, N, NE, S, SE	
***Ixora coccinea* L.	M.A. Carniello	M.A. Carniello 4729	SE	E		Exotic	
Limnosipanea erythraeoides (Cham.) K.Schum.	D. Zappi	R.M. Harley 55369	H	E	Au	CO, NE, S, SE	
L. palustris (Seem.) Hook.f.	V.J. Pott	S.N. Moreira 1509	H	E	Au	CO, NE	
Machaonia acuminata Bonpl.	E.L. Cabral	A. Pott 5281	S	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Manettia cordifolia Mart.	P. Delpetre	G. Hatschbach 77223	S	E	Au	CO, N, NE, S, SE	
Mitracarpus hirtus (L.) DC.	A. Pott	A. Pott 13859	H	E	Au	CO, N, NE, S, SE	
**_Neolamarckia cadamba_ (Roxb.) Ross.	A. Pott	A. Pott 7732	T	E		Exotic	
Oldenlandia corymbosa L.	D. Zappi	A. Pott 13.880	H	E	Z	CO, N, NE, S, SE	
Palicourea crocea (Sw.) Roem. & Schult.	D. Zappi	A. Pott 5216	S	E	Z	CO, N, SE	
P. croceoides Ham.	C.M. Taylor	W.W. Thomas 4625	S	E	Z	CO, N, S, SE	
P. fastigiata Kunth	C.M. Taylor	P.G. Crawshaw 282	S	E	Z	CO, N	
Pentodon pentandrus (Schumach. & Thonn.) Vatke	D. Zappi	V.J. Pott 749	H	E	Au	CO, N, NE, S, SE	
Perama sp.	E.L. Cabral	V.J. Pott 749	S	E	Z		
Psychotria capitata Ruiz & Pav.	S.K.I. Castrillon	S.K.I. Castrillon no n.	S	E	Z	CO, N, NE, SE	
P. carthagenensis Jacq.	E.L. Cabral	A. Pott 4781	S	E	Z	CO, N, NE, S, SE	Brazil
P. leiocarpa Cham. & Schltdl.	M.C. Souza	S.R. Zaniolo 172	S	E	Z	CO, NE, S, SE	
Randia heteromera Judkevich & R.M. Salas	E.L. Cabral	A. Pott 5326	S	E	Z	CO, N, NE, S, SE	
Richardia brasiliensis Gomes	A. Pott	A. Pott 5341	H	E	Au	CO, N, NE, S, SE	
R. grandiflora (Cham. & Schltdl.) Steud.	A. Pott	A. Pott 5187	H	E	Au	CO, N, NE, S, SE	

R. scabra L.	S. Dessein	G. Schaller 72	H	E	Au, Hy	CO, N, NE, SE	
Rosenbergiodendron densiflorum (K.Schum.) Fagerl.	M. Gomes	G. Martinelli 18605	S	E	Z	CO, N	
Rudgea cornifolia (Kunth) Standl.	E.L. Cabral	A. Pott 8680	S	E	Z	CO, N, NE	
R. viburnoides (Cham.) Benth.	H.F. Leitão F.; E. Cabral	A. Pott 4546	T	E	Z	CO, N, NE, SE	
Sabicea aspera Aubl.	A. Pott	A. Pott 5503	L	E	Au	CO, N, SE	
S. mattogrossensis Wernham	D. Zappi	A. Pott 7699	L	E	Au	CO, N	
Simira corumbensis (Standl.) Steyerm.	E.L. Cabral	A. Pott 7933	T	E	Au	CO, N, S	Brazil
S. rubescens (Benth.) Bremek. ex Steyerm.	E.L. Cabral	A. Pott 5226	T	E	Au	CO, N, NE	
Sipanea biflora (L.) Cham. & Schltdl.	D. Zappi	A. Pott 3833	H	E	Au	CO, N, NE	
S. pratensis Aubl. (S. hispida)	V.J. Pott	V.J. Pott 12449	H	E	Au	CO, N, NE, SE	
S. veris S.Moore	S.F. Smith	G. Hatschbach 60916	H	E	Au	CO, N	
Spermacoce eryngioides (Cham. & Schltdl.) O. Kuntze	E.L. Cabral	A. Pott 4988	H	E	Au	CO, N, NE, S, SE	
S. glabra Michx.	E.L. Cabral	A. Pott 3289	H	E	Au	CO	
S. ocymoides Burm.f.	A. Pott	E.B. Souza 1314A	H	E	Au	CO	
S. prostrata Aubl.	L.M. Miguel	A. Pott 4088	H	E	Au	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

Sphinctanthus microphyllus K.Schum.	D. Zappi	Ratter 6098	S	E	Z	CO	
Staelia herzogii (S.Moore) R.M.Salas & E.L.Cabral	R.M. Salas	A. Pott 1537	H	E	Z	CO	
S. thymoides Cham. & Schltdl.	E.L. Cabral	V.J. Pott 1009	H	E	Au	CO, S	
Tocoyena brasiliensis Mart.	A. Pott	C.N. Cunha 2047	T	E	Z	CO, N, NE, SE	Brazil
T. formosa (Cham. & Schltdl.) K.Schum.	A. Pott	A. Pott 2405	T	E	Z	CO, N, NE, S, SE	
Uncaria guianensis (Aubl.) J.F.Gmel	M.A. Carniello	M.A. Carniello 3817	L	E	Z	CO, N, NE, SE	
Rutaceae							
**Citrus aurantifolia* Swingle	A. Pott	S.S. Moura 151	T	E	Z	Exotic	
***Citrus x aurantium* L.	A. Pott	E.P. Seleme 432	T	E	Z	Exotic	
***C. x limon* (L.) Osbeck			T	E	Z	Exotic	
***C. x paradisi* Macfad.	A. Pott	E.P. Seleme 441	T	E	Z	Exotic	
***C. reticulata* Blanco	A. Pott	E.P. Seleme 442	T	E	Z	Exotic	
***C. x sinensis* (L.) Osbeck			T	E	Z	Exotic	
***Citrus trifoliata* L.			S	E	Z	Exotic	
Ertela trifolia (L.) Kuntze		A. Pott 7975	Ss	E	Au	CO, N, NE	
Esenbeckia almavillia Kaastra	G.A. Damasceno Jr.	A. Pott 10917	S	E	Au	CO, N, NE, SE	
Helietta puberula R.E.Fr.		A. Pott 7968	T	E	An	CO	

***Murraya paniculata* L.	A. Pott	S.S. Moura 187	T	E	Au	Exotic	
***Ruta graveolens* L.			H	E	Au	Exotic	
Zanthoxylum acuminatum (Sw.) Sw.	J.R. Pirani	G.O. Romão 38	T	E	Au	CO, N, NE, SE	
Z. caribaeum Lam.	J.R. Pirani	J.A. Ratter 5101	T	E	Au	CO, N, NE, S, SE	
Z. fagara (L.) Sarg.	J.R. Pirani	A.Pott 5284	T	E	Au	CO, N, NE, S, SE	
Z. petiolare A.St.-Hil. & Tul.	J.A. Ratter; J.R. Pirani	C.N. Cunha 2093	T	E	Au	CO, NE, S, SE	
Z. rigidum Humb. & Bonpl. ex Willd.	J.R. Pirani	A. Pott 2956	T	E	Au	CO, SE	
Z. riedelianum Engl.	J.R. Pirani	A. Pott 1825	T	E	Au	CO, N, S, SE	
Z. sprucei Engl.	J.R. Pirani	M.R. Pace 576	T	E	Au	CO, N	
Salicaceae including Flacourtiaceae)							
Banara arguta Briq.	A. Pott	A. Pott 4519	T	E	Au	CO, N, NE	
Casearia aculeata Jacq.	A. Pott	A. Pott 2839	T	E	Au	CO, N, NE, S, SE	
C. decandra Jacq.	V.C. Souza	V.C. Souza 32277	T	E	An	CO, N, NE, S, SE	
C. gossypiosperma Briq.	J.Y. Tamashiro	A. Pott 1916	T	E	An	CO, N, NE, S, SE	
C. rupestris Eichler	J.A. Ratter	A. Pott 5520	T	E	Au	CO, N, SE	
C. sylvestris Sw.	J.A. Ratter	A. Pott 5062	T	E	Z	CO, N, NE, S, SE	
Laetia americana L.	J.A. Ratter	A. Pott 3629	T	E	An	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

Salix humboldtiana Willd	A. Pott	A. Pott 6239	T	E	An	CO, N, S, SE	
Xylosma venosa N.E.Br.	G. Hatschbach	A. Pott 3442	T	E	Z	CO, S, SE	
Santalaceae (including part of Loranthaceae)							
Acanthosyris falcata Griseb.	D.R.C. Padilha	D.R.C. Padilha 14	T	E	Z	CO	
Phoradendron bathyoryctum Eichler	G.A. Dettke	A. Pott 8868	P	E	Z	CO, N, NE, S, SE	
P. crassifolium (Pohl ex DC) Eichler	G. Hatschbach	A. Pott 4349	P	E	Z	CO, N, NE, S, SE	
P. mucronatum (DC.) Krug & Urb.	C.S. Caires	A. Pott 1974	P	E	Z	CO, N, NE, S, SE	
P. obtusissimum (Miq.) Eichler	J. Kuijt	A. Pott 4924	P	E	Z	CO, N, NE, S, SE	
P. piperoides (Kunth) Trel.	J. Kuijt	A. Pott 4974	P	E	Z	CO, N, NE, S, SE	
P. quadrangulare (Kunth) Griseb.	J. Kuijt; C.S. Caires; G.A. Dettke	A. Pott 10280	P	E	Z	CO, N, NE, SE	
Sapindaceae							
Allophylus pauciflorus Radlk.	J.A. Ratter	A. Pott 8060	S	E	Z	CO, S	
Cardiospermum corindum L.	M.S. Ferrucci	G. Martinelli 18690	L	E	Au	CO, NE, S, SE	
C. grandiflorum Sw.	E.F. Guimarães	A. Pott 4285	L	E	Au	CO, N, NE, S, SE	
C. halicacabum L.	M.S. Ferrucci	V.J. Pott 372	L	E	Au	CO, N, NE, S, SE	
Cupania castaneafolia Mart.	M.S. Ferrucci	A. Pott 5299	T	E	Z	CO, N	Brazil

C. cinerea Poepp. & Endl.	P. Acevedo-Rodríguez	C.A. Conceição 1436	T	E	Z	CO, N	
Dilodendron bipinnatum Radlk.	J.A. Ratter	A. Pott 1384	T	E	Z	CO, N, NE, SE	
Diplokeleba floribunda N.E.Br.	C.A. Conceição; J.A. Ratter	A. Pott 1926	T	E	Z	CO	
Magonia pubescens A. St.-Hil.	C.A. Joly	A. Pott 4398	T	E	An	CO, N, NE, SE	
Matayba guianensis Aubl	R.L.G. Coelho	C.N. Cunha 1112a	T	E	Z	CO, N, NE, S, SE	
Melicoccus lepidopetalus Radlk.	M.S. Ferrucci	A. Pott 2306	T	E	Z	CO, SE	
Paullinia clavigera Schltdl.	P. Acevedo-Rodríguez	M.R. Pace 209	L	E	Z	CO, N, NE	
P. elegans Cambess.	M.S. Ferrucci	A. Pott 4527	L	E	Z	CO, N, NE, S, SE	
P. pinnata L.	M.S. Ferrucci	A. Pott 2145	L	E	Z	CO	
P. spicata Benth.	M.S. Ferrucci	G. Hatschbach 62.395	L	E	Z	CO, N, NE, S, SE	
Sapindus saponaria L.	M.S. Ferrucci	A. Pott 3421	T	E	Z	CO, N, NE, S, SE	
Serjania adenophylla Ferrucci	M.S. Ferrucci	A.J. Ratter 5017	L	E	An	CO	
S. caracasana (Jacq.) Willd.	M.S. Ferrucci	A. Pott 3455	L	E	An	CO, N, NE, S, SE	
S. chaetocarpa Radlk.	M.S. Ferrucci	A. Pott 6712	L	E	An	CO	
S. confertiflora Radlk.	M.S. Ferrucci	J.E. Paula7544	L	E	An	CO, N, NE, SE	

(continued)

Table 3.1 (continued)

S. erecta Radlk.	M.S. Ferrucci	A. Pott 5474	L	E	An	CO, N, NE, S, SE	
S. fuscifolia Radlk.	P. Acevedo-Rodríguez	V.J. Pott 3485	L	E	An	CO, N, NE, S, SE	
S. glabrata Kunth	M.S. Ferrucci	J.M. Silva 4893	L	E	An	CO, N, NE, S, SE	
S. glutinosa Radlk.	M.S. Ferrucci	A. Pott 6444	L	E	An	CO, N, NE, S, SE	
S. hebecarpa Benth.	M.S. Ferrucci	B. Dubs 937	L	E	An	CO, NE, S, SE	
S. lethalis A.St.-Hil.	M.S. Ferrucci	A. Pott 6553	L	E	An	CO, N, NE, S, SE	
S. marginata Casar.	M.S. Ferrucci	A. Pott 4062	L	E	An	CO, N, NE, S, SE	
S. meridionalis Cambess.	M.S. Ferrucci	A. Pott 6346	L	E	An	CO, N, NE, S, SE	
S. minutiflora Radlk.	M.S. Ferrucci	G.A. Damasceno Jr. 3104	L	E	An	CO	
S. neei Acevedo-Rodriguez	P. Acevedo-Rodriguez	M.R. Pace 488	L	E	An	CO	
S. perulacea Radlk.	K.U. Kramer	G. Hatschbach 21967	L	E	An	CO, SE	
S. setigera Radlk.	M.S. Ferrucci	V.J. Pott 1271	L	E	An	CO	
Talisia esculenta (Cambess.) Radlk.	A. Pott	M.P. Silva 09	T	E	Z	CO, N, NE, SE	
Thinouia paraguayensis (Britton) Radlk.	M.S. Ferrucci	V.J. Pott 798	L	E	An	CO, NE, SE	
Urvillea filipes Radlk.	M.S. Ferrucci	A.C. Cervi 3303	L	E	An	CO	
U. laevis Radlk.	M.S. Ferrucci	A. Pott 10929	L	E	An	CO, NE, S, SE	
U. ulmacea Kunth	A. Pott	A. Pott 8048	L	E	An	CO, N, NE, S, SE	

Sapotaceae							
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	J.A. Ratter	A. Pott 3414	T	E	Z	CO, N, NE, SE	
C. gonocarpum (Mart. & Eihler ex Miq.) Engl.	T.R.F. Sinani	V.A. Assunção 788	T	E	Z	CO, N, NE, S, SE	
***Manilkara zapota* (L.) P.Royen	A. Pott	S.S. Moura 154	T	E	A	CO, N, NE, S, SE	
Pouteria gardneri (Mart. & Miq.) Baehni	J.Y.Tamashiro; A. Pott	A. Pott 2329	T	E	Z	CO, N, NE, S, SE	
P. glomerata (Miq.) Radlk.	C.N. Cunha	A. Pott 5436	T	E	Z	CO, N, NE, S, SE	
P. ramiflora (Mart.) Radlk.	A. Pott	A. Pott 5453	T	E	Z	CO, N, NE, SE	
P. torta (Mart.) Radlk.	V.J.Pott	V.J. Pott 3638	T	E	Z	CO, N, NE, SE	
Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	J.A. Ratter	A. Pott 4621	T	E	Z	CO, N, NE, S, SE	
Simaroubaceae							
Castela tweedii Planch.	J.R. Pirani	A. Pott 15674	T	E	Z	CO, S	
Homalolepis ferruginea (A.St.-Hil.) Devecchi & Pirani	M.F. Devecchi	A. Pott 13.026	S	E	Z	CO, N, NE, SE	
H. trichilioides (A.St.-Hil.) Devecchi & Pirani	J.R. Pirani	A. Pott 13010	T	E	Z	CO, N, NE, SE	
Simarouba versicolor A.St.-Hil.	A. Pott	A. Pott 3230	T	E	Z	CO, N, NE, SE	
Smilacaceae							

(continued)

Table 3.1 (continued)

Smilax brasiliensis Spreng.	R.H.P. Andreata	A. Pott 1689	L	E	Z	CO, SE	
S. fluminensis Steud.	R.H.P. Andreata	A. Pott 4018	L	E	Z	CO, N, NE, SE	
S. goyazana A.DC.	J. Cordeiro	A.R. Silva	L	E	Z	CO, NE, SE	
S. aff. *oblongifolia* Pohl ex Griseb.	R.H.P. Andreata	A. Pott 3985	L	E	Z	CO, NE, SE	
S. pilcomayensis Guaglianone & Gattuso	E.R. Guaglianone	A. Pott 4931	L	E	Z	CO	
S. polyantha Griseb.	R.H.P. Andreata	A. Pott 1388	S	E	Z	CO, NE, SE	
Solanaceae							
****Brugmansia suaveolens* (Willd.) Bercht. & J.Presl.			S	E		Exotic	
***Capsicum annuum* L.			H	E	Z	Exotic	
**C. baccatum* L.	A. Pott	G.A. Damasceno Jr. 4114	Ss	E	Z	CO, S, SE	
C. frutescens L.	L.B. Bianchetti	A. Pott 5562	Ss	E	Z	CO, N, NE	
Cestrum guaraniticum Chodat & Hassl.	A. Pott	A. Pott 7671	S	E	Z	CO	
C. obovatum Sendtn.	A. Pott	A. Pott 1799	S	E	Z	CO, NE, SE	
C. strigillatum Ruiz & Pav.	J.R. Stehmann	G.A. Damasceno Jr. 641	S	E	Z	CO, N, NE, S, SE	
**Datura stramonium* L.	A. Pott	A. Pott 14442	Ss	E	Au	CO, NE, S, SE	
Lycium boerhaaviifolium L.f.	J.R. Stehmann	A. Pott 16903	H	E	Z	CO, S	
**Nicotiana glauca* Graham	A.T. Hunziker	G. Hatschbach 30474	Ss	E	Au	CO, NE, S, SE	

**N. longiflora* Cav.	A. Pott	A. Pott 16903	H	E	Au	CO, S, SE	
**Physalis angulata* L.	A. Pott	A. Pott 2285	H	E	Z	CO, N, NE, S, SE	
P. pubescens L.	G. Hatschbach	A. Pott 5917	H	E	Z	CO, N, NE, S, SE	
P. viscosa L.	J.R. Stehmann	A. Pott 5490	H	E	Z	CO, S, SE	
Schwenckia americana Rooyen ex L.	J.R. Stehmann	A. Pott 7913	H	E	Au	CO, N, NE, S, SE	
S. angustifolia Benth.	A. Pott; A. Schinini	V.J. Pott 2967	H	E	Au	CO, N, NE	X
S. juncoides Chodat	J.R. Stehmann	S.N. Moreira 782	H	E	Au	CO, S	
Solanum americanum Mill.	A. Pott	A.Pott 3575	L	E	Z	CO, N, NE, S, SE	
S. amygdalifolium Steud.	A. Schinini	A.Pott 4725	Ss	E	Z	CO, S, SE	
S. atropurpureum Schrank	J.R. Stehmann	A. Pott 10887	Ss	E	Z	CO, N, S, SE	
***S. aethiopicum* L. (*S. gilo*)						Exotic	
S. glaucophyllum Desf.	J.R. Stehmann	A. Pott 2844	Ss	E	Z	CO, S	
S. jamaicense Mill.	A. Pott	V.J. Pott 3614	S	E	Z	CO, N, NE	
***S. lycopersicum* L.			H	E	Z	Exotic	
S. multispinum N.E. Br.	J.R. Stehmann	A. Pott 8864	H	E	Z	CO	
S. nigrescens M. Martens & Galeotti	A. Pott	A. Pott 1648	H	E	Z	CO	
S. olympicum Hassl.	L.L. Giacomini	J.S. Silva 194	H	E	Z	CO, NE	
S. palinacanthum Dunal	R.S. Silva	A. Pott 1527	S	E	Z	CO, N, NE, S, SE	

(continued)

Table 3.1 (continued)

S. paniculatum L.	G. Hatschbach	A. Pott 5420	S	E	Z	CO, N, NE, S, SE	
S. pilcomayense Morong	J.R. Stehmann	V.J. Pott 4382	Ss	E	Z	CO, S	
S. pseudoauriculatum Chodat & Hassl.	A. Pott; J.R. Stehmann	A. Pott 3516	S	E	Z	CO	
S. scuticum M.Nee	M.F. Agra	W.W. Thomas 4618	S	E	Z	CO, N, NE, S, SE	
**S. sisymbriifolium* Lam.	M.H. Nee	G. Hatschbach 49264	Ss	E	Z	CO, N, NE, S, SE	
S. turneroides Chodat	A. Pott	A. Pott 16138	Ss	E	Z	CO, SE	
**S. viarum* Dunal	U.M. Resende	A.C. Araújo	H		Z	CO, N, NE, S, SE	
Sphenocleaceae							
Sphenoclea zeylanica Gaertn.	V.J. Pott	V.J. Pott 1836	T	E	Hy	CO, N, NE, S, SE	
Styracaceae							
Styrax ferrugineus Nees & Mart.	A. Schinini	A. Pott 2085	S	E	Z	CO, N, S, SE	
Talinaceae (Portulacaceae)							
Talinum fruticosum (L.) Juss.	V.J. Pott	A. Pott 2696	H	E	Hy	CO, N, NE, S, SE	
**T. paniculatum* (Jacq.) Gaertn.	A.L.B. Sartori	F. Matos-Alves 408	H	E	Au	CO, N, NE, S, SE	
Trigoniaceae							

Trigonia boliviana Warm.	V.J. Pott	M.P. Silva 89	L	E	Au	CO, SE	
Turneraceae							
Piriqueta cistoides (L.) Griseb.	M.M. Arbo	A. Pott 3860	Ss	E	Au	CO, N, NE, S, SE	
P. corumbensis Moura	M.M. Arbo	A. Pott 1907	Ss	E	Au	CO	
Turnera concinna Arbo	M.M. Arbo	A. Pott 5550	Ss	E	Au	CO	
T. melochioides Cambess.	M.M. Arbo	A. Pott 4301	Ss	E	Au	CO, N, NE, SE	
T. morongii Rolfe	M.M. Arbo	G. Hatschbach 76401	Ss	E	Au	CO	
T. orientalis (Urb.) Arbo	M.M. Arbo	A. Pott 4502	Ss	E	Au	CO, N, NE, S, SE	
T. pumilea L.	M.M. Arbo	S.M. Salis 858	E	E	Au	CO, N, NE, SE	
T. subulata (Urb.) Arbo	M.M. Arbo	V.J. Pott 3271	Ss	E	Au	CO, N, NE, S, SE	
T. weddelliana Urb. & Rolfe	M.M. Arbo	A. Pott 16127	Ss	E	An	CO	
Typhaceae							
Typha domingensis Pers.	C.D.K. Cook	A. Pott 4915	H	An	An, Hy	CO, N, NE, S, SE	
Ulmaceae							
Phyllostylon rhamnoides Capan. ex Benth. & Hook.f.	Ratter	A. Pott 8061	T	E	An	CO, SE	
Urticaceae							
Cecropia pachystachya Trécul	J.A. Ratter	A. Pott 1924	T	E	Z	CO, SE	
Urera aurantiaca Wedd.	A. Pott	A. Pott 3563	S	E	Z	CO, N, S	

(continued)

Table 3.1 (continued)

U. caracasana (Jacq.) Griseb.	A.L. Gaglioti	G.A. Damasceno Jr. 23	T	E	Z	CO, N, NE, S, SE	
Verbenaceae							
Aloysia virgata (Ruiz & Pav.) Juss.	J.A. Ratter	A. Pott 4478	A	E	Au	CO, NE, S, SE	
Cytharexylon amabilis (Bocq.) Christenh. & Bing.	J.A. Ratter	A. Pott 2982	S	E	Au	CO	
Casselia chamaedryfolia Cham.	A. Schinini	A. Pott 6578	H	E	Au	CO, SE	
Glandularia aristigera (S.Moore) Tronc.	A. Pott	A. Pott 6816	H	E	Au	CO, S, SE	
G. nana (Moldenke) Tronc.	H.N. Moldenke	G. Hatschbach 29600	H	E	Au	CO, S	
G. phlogiflora (Cham.) Schnack & Covas	H.N. Moldenke	G. Schaller 311	H	E	Au	CO, S, SE	
***Duranta repens* L.			S	E	Z	Exotic	
Lantana achyranthifolia Fesf.	T.R.S. Silva; R. Liesner	V.J. Pott 2239	S	E	Z	CO, NE	
**L. camara* L.	U.M. Resende	A.C. Araújo 1265	S	E	Z	CO, N, NE, S, SE	
L. canescens Kunth	L. Sanders	A. Pott 4484	S	E	Au	CO, N, NE, S, SE	
L. fucata Lindl.	M.E. Múlgura	G. Hatschbach 30403	S	E	Z	CO, NE, S, SE	
L. trifolia L.	L. Sanders	A. Pott 5418	S	E	Z	CO, N, S, SE	

Lippia alba N.E.Br.	V.J. Pott	A. Pott 4358	Ss	E	Au	CO, N, NE, S, SE	
L. angustifolia L.f.	V.J. Pott	A .Pott 4597	Ss	E	Au	CO, S, SE	
L. aristata Schauer	F.R.G. Salimena	F.R.G. Salimena 3998	S	E	Z	CO, N, NE, S, SE	
L. asperrima Cham.	A. Pott	A. Pott 7613	Ss	E	Au	CO, S, SE	
L. lasiocalycina Cham.	N.S. Troncoso	G. Hatschbach 22.000	Ss	E	Au	CO, N, NE, S, SE	
L. lupulina Cham.	A. Pott	A. Pott 4374	Ss	E	Au	CO, N, NE, S, SE	
L. oxycnemis Schau.	N.S. Troncoso	G. Hatschbach 21895	H	E	Au	CO, SE	Brazil
Phyla betulifolia (Kunth) Greene	A. Schinini	A. Pott 5163	H	E	Au	CO, N, NE, SE	
P. nodiflora (L.) Greene	G. Hatschbach	A. Pott 5162	H	E	Au	CO, S	
**Priva lappulacea* (L.) Pers.	A. Pott	A. Pott 12758	H	E	Z	CO, N, NE, SE	
Stachytarpheta angustifolia (Mill.) Vahl	G. Hatschbach; F. França	A. Pott 4941	H	E	Au	CO, N, NE, SE	
**S. cayennensis* (Rich.) Vahl	G. Hatschbach; F. França	A. Pott 3828	H	E	Au	CO, N, NE, S, SE	
S. paraguariensis Moldenke	G. Hatschbach; F. França	A. Pott 4606	H	E	Au	CO, S	
S. polyura Schauer	S. Atkins	O.S. Ribas 2579		E	Au	CO, S, SE	
Violaceae							
Calyptrion pubescens (S.Moore) Paula-Souza	J.A. Ratter	J.A. Ratter 6097	L	E	Au	CO, N, NE	
Pombalia arenosa (Ule) Paula-Souza	B.M.T. Walter	A. Pott 13682	H	E	Au	CO, N, NE, SE	Brazil

(continued)

Table 3.1 (continued)

P. bigibbosa (A.St.-Hil.) Paula-Souza	J. Paula-Souza; B.M.T. Walter	A. Pott 11896	H	E	Au	CO, S, SE	
P. calceolaria (L.) Paula-Souza	G. Hatschbach; J. Paula-Souza	A. Pott 4320	H,Ss	E	Au	CO, N, NE, SE	
P. communis (A.St.-Hil.) Paula-Souza	J. Paula-Souza	V.J. Pott 3539	H	E	Au	CO, N, NE, S, SE	
P. oppositifolia (L.) Paula-Souza	J. Paula-Souza	A. Pott 9451	H	E	Z	CO, N, NE, SE	
Vitaceae							
Cissus campestris (Baker) Planch.	A. Dunaiski	A. Pott 2381	L	E	Z	CO, N, NE, SE	
C. erosa Rich.	A. Dunaiski	A. Pott 5277	L	E	Z	CO, N, NE, S, SE	Brazil
C. palmata Poir.	J. Lombardi	A. Pott 12842	L	E	Z	CO, N, NE, S, SE	
C. spinosa Cambess.	A. Dunaiski Jr.; J. Lombardi	A. Pott 4526	L	E	Z	CO, N, NE, S, SE	
C. verticillata (L.) Nicolson & C.E.Jarvis	A. Dunaiski	A. Pott 5410	L	E	Z	CO, N, NE, S, SE	
***Leea rubra* Blume			Ss			Exotic	
Vochysiaceae							
Callisthene fasciculata Mart.	C.N. Cunha	A. Pott 5308	T	E	An	CO, N, NE, SE	
Qualea grandiflora Mart.	A. Pott	A. Pott 2516	T	E	An	CO, N, NE, S, SE	
Q. multiflora Mart.	A. Pott	A. Pott 7667	T	E	An	CO, N, NE, S, SE	

Q. parviflora Mart.	A. Pott	A. Pott 2478	T	E	An	CO, N, NE, SE	
Salvertia convallariodora A.St.-Hil.	A. Pott	A. Pott 6508	T	E, O	An	CO, N, NE, SE	
Vochysia cinnamomea Pohl	P.E. Oliveira	A. Pott 2439	T	E, O	An	CO, N, SE	
V. divergens Pohl	A. Pott	A. Pott 1971	T	E, O	An, Hy	CO, N, SE	
V. haenkeana Mart.	J. Kalunki	G. Schaller 190	T	E, O	An	CO, N	
V. rufa Mart.	F. França	A. Pott 4386	T	E, O	An	CO, SE	
V. thyrsoidea Pohl	A. Pott	A. Pott 2233	T	E, O	An	CO, N, SE	Brazil
Xanthorrhoeaceae (Asphodelaceae)							
***Aloe vera* (L.) Burm.f.	M.A. Carniello	M.A. Carniello 1160	H	E		Exotic	
Xyridaceae							
Abolboda pulchella Humb. & Bonpl.	A. Schinini; G.O. Silva	A. Pott 2481	H	E	Au, Hy	CO, N, NE, SE	Brazil
Xyris jupicai Rich.	V.J. Pott	A. Pott 3818	H	E	Au, Hy	CO, N, NE, S, SE	
X. macrocephala Vahl	C.O. Silva	T.H. Stefanello 339	H	E	Au, Hy	CO, N, NE, S, SE	
X. savanensis Miq.	V.J. Pott	A. Pott 5272	H	E	Au, Hy	CO, N, NE, S, SE	
X. schizachne Mart.	V.J. Pott	S.N. Moreira 1544	H	E	Au, Hy	CO, N, NE, S, SE	Brazil

(continued)

Table 3.1 (continued)

Zingiberaceae							
***Alpinia zerumbet* (Pers.) B.L.Burtt & R.M.Sm.			H	O		Exotic	
***Curcuma zedoaria* Roscoe			H			Exotic	
**Hedychium coronarium* J.Koenig		M. Moraes 21	H	E	Hy	Exotic	
Zygophyllaceae							
Bulnesia sarmientoi Lorentz ex Griseb.	J.A. Ratter; J.H. Hunziker	V.J. Pott 2240	T	E	An	CO	

*naturalized, **cultivated; Habit; *T* tree, S shrub, *Ss* Subshrub, *H* herb, *L* liana, climber, scandent, *Ep* epiphyte, *P* parasite, *Polli.* pollination, *A* anemophilous, *E* entomophilous, *O* ornitophilous, *Z* zoophilous, *Dispers.* Dispersal, *An* anemochorous, *Au* autochorous, *Z* zoochorous, *Hy* hydrochorous, *Distr.* Distribution, Brazilian regions (*CO* Central West, *N* North, *NE* Northeast, *S* South, *SE* Southeast); Endem.-Endemic: Brazil endemic to Brazil, Pantanal endemic to Pantanal

Nevertheless, some species may be native to the adjacent hills, not present in the Pantanal, as might be the case of a few species that seem to occur exclusively on road embankments, probably from seeds brought with the gravel or dispersed by wind, animals, and vehicles. Also, a species can be native elsewhere in Brazil and adventitious in the Pantanal.

Nowadays, virtual herbaria are an amazingly helpful search tool to produce checklists. However, in the case of the Pantanal, care should be taken since many other wetlands have similar toponyms, e.g., *pantanalzinho*, Pantanal do Rio das Mortes, Pantanal do Araguaia, and others, and then they will also appear in a virtual search. Moreover, herbarium labels and records sometimes do not specify that the plant occurs in the Pantanal and then it was not retrieved. Another bias is related to labels of plants from the hills or uplands with location indications containing the word Pantanal, as often done as a broad indication in the upper basin. Selecting on municipalities is also not a good criterion because only part of their territory is located in the plain. Thus, our inclusion criterion was strictly the Pantanal sedimentary plain. Another criterion of inclusion we applied was a reliable identification by specialists and taxonomists. Some species listed for the Pantanal are yet missing in Flora do Brasil; most often they also occur in neighboring countries.

We consulted the website of Flora do Brasil (Flora do Brasil 2020) to check the validity of plant names since, of late; many name changes were accepted, also concerning species in the Brazilian regions of their occurrence. Indeed, some genera were split, as is the case of *Aeschynomene, Camptosema*, *Capparis*, *Cleome*, *Dioclea*, *Eupatorium*, *Panicum*, *Polygala*, and *Vernonia*, or several genera were lumped; e.g., *Cyperus* now encompasses the formerly segregated *Ascolepis*, *Kyllinga*, *Lipocarpha*, *Oxycaryum*, and *Pycreus*. Other genera names were replaced by another name considered to have priority, like *Euploca* for some *Heliotropium*, *Pombalia* for *Hybanthus*, *Varronia* for some *Cordia*, and *Passovia* for *Phthirusa*. Among the few families that have had rearrangements, a great change was the transfer of some genera traditionally included in Scrophulariaceae to other families such as Orobanchaceae and Plantaginaceae, and Bombacaceae, Sterculiaceae, and Tiliaceae were placed into Malvaceae; Phyllanthaceae was split from Euphorbiaceae. We followed Flora do Brasil (Flora do Brasil 2020) for families, thus disregarding some phylogenetic changes based on APG IV (Souza and Lorenzi 2019), e.g., Petiveriaceae and Rivinaceae are dismembered from Phytolaccaceae.

A few species may have been repeated due to the different naming by two specialists, and we were not able to check the specimens to decide. Moreover, perhaps few plant species may have been left out of the compilation because of the uncertainty of correct identification. Furthermore, some species we know and saw in the field are also lacking in the list because so far we could not collect fertile samples, though we included a few ones that have been recorded on photographs. Some ephemeral species may still not have been sampled in the Pantanal, as they appear or disappear over pluriannual periods. Also, there might occur a few more small and inconspicuous species, restricted to very particular habitats, e.g., terrestrial orchids.

3.2 Results

The checklist is presented in Table 3.1. It strictly considers the flora of the Pantanal sedimentary plain. This compilation includes records of 2567 species, of which 2272 are native, 166 naturalized and 130 cultivated, 13 being both cultivated and naturalized. In Poaceae alone, 40 species are naturalized, and generally are not spreading to flooded ground. We included cultivated plants, also listed in Flora do Brasil (2020,) because they are visited by insects and birds, or they can give some indication about the local climate, and some may escape from around the house and become weeds. A few native species planted around homesteads were not counted as cultivated. Only 244 species in Table 3.1 are endemic to Brazil, of which 13 belong to the genus *Arachis*, according to Flora do Brasil (2020). We explain such a low percentage of Brazilian endemics in the Pantanal to the fact that the majority of these species have wide distributions and or occur also in neighboring countries. Half of the species of the plain is wide-ranging (Pott and Silva 2015), as corroborated by our list.

The number of families is 149; those with most species being Fabaceae (344 species), Poaceae (302), Asteraceae (136), and Cyperaceae (117), adding up to 900 species, i.e., 29.4% or nearly 1/3 of the recorded flora. These families are followed by Euphorbiaceae (105), Malvaceae (105), Rubiaceae (74), Apocynaceae (62), Convolvulaceae (62), Myrtaceae (56), Malpighiaceae (52), Bignoniaceae (45), Sapindaceae (37), Solanaceae (35), and Orchidaceae (only 31), adding up to 662 species or *c.* 21%. Thus, these 15 families comprise half of the species. That fits the typical spectrum of Neotropical floras of open vegetation types. However, a striking feature about the Pantanal flora is the scarcity, on the sedimentary plain, of Lauraceae, a species-rich family in the Neotropics, as well as the absence of *Myrsine* (Primulaceae), always present in surrounding domains. Some species from the Caatinga and dry forest may seem strange to the Pantanal flora; but the Pantanal contains dry areas and the seasonal, annual rainfall is not high.

The species-richest families in the State of Mato Grosso do Sul are also Fabaceae (421 species) (Sartori and Pott 2018) and Poaceae (430) (Guglieri-Caporal et al. 2018). Thus, their numbers are relatively high in the Pantanal, considering that it covers only 38.4% of the state area. The total number of species of the Pantanal is also relatively high compared with *c.* 4000 so far recorded for Mato Grosso do Sul.

Regarding genera, the total number is 938. The species-richest genera are *Paspalum* (53), *Cyperus* (48), *Ipomoea* (32), *Mimosa* (32), *Croton* (28), *Eugenia* (28), *Ludwigia* (26), and *Arachis* (21), together attaining 268 species or *c.* 10% of the flora. Out of 66 species of *Arachis* in Brazil, 1/3 occur in the Pantanal, and many more in areas around the Pantanal.

Regarding endemic plants in the Pantanal, so far only nine species were recorded: *Arachis appressipila* (Fig. 3.1), *A. hoehnei* (Fig. 3.2), *A. linearifolia* (Fig. 3.3), *A. valida* (Fig. 3.4) (Krapovickas and Gregory 1994), *A. vallsii* (Valls and Simpson 2005) (Fig. 3.5), *Axonopus fusiformis* (Silveira and Valls 2016) (Fig. 3.6), *Euploca*

Fig. 3.1 *Arachis appressipila* Krapov. & W.C. Greg. (Photo: J.F.M. Valls)

Fig. 3.3 *Arachis linearifolia* Krapov. & W.C. Greg. (Photo: J.F.M. Valls)

Fig. 3.2 *Arachis hoehnei* Krapov. & W.C. Greg. (Photo: J.F.M. Valls)

Fig. 3.4 *Arachis valida* Krapov. & W.C. Greg. (Photo: J.F.M. Valls)

Fig. 3.5 *Arachis vallsii* Krapov. & W.C. Greg. (Photo: J.F.M. Valls)

pottii (Melo and Semir 1999) (Fig. 3.7), *Ipomoea pantanalensis* (Wood et al. 2016) (Fig. 3.8), and *Stilpnopappus pantanalensis* (Robinson 1995) (Fig. 3.9). Remarkably, five species belong to the genus *Arachis*. Such a high endemism of *Arachis* is explained by the species richness of the genus in Mato Grosso do Sul (Sartori and

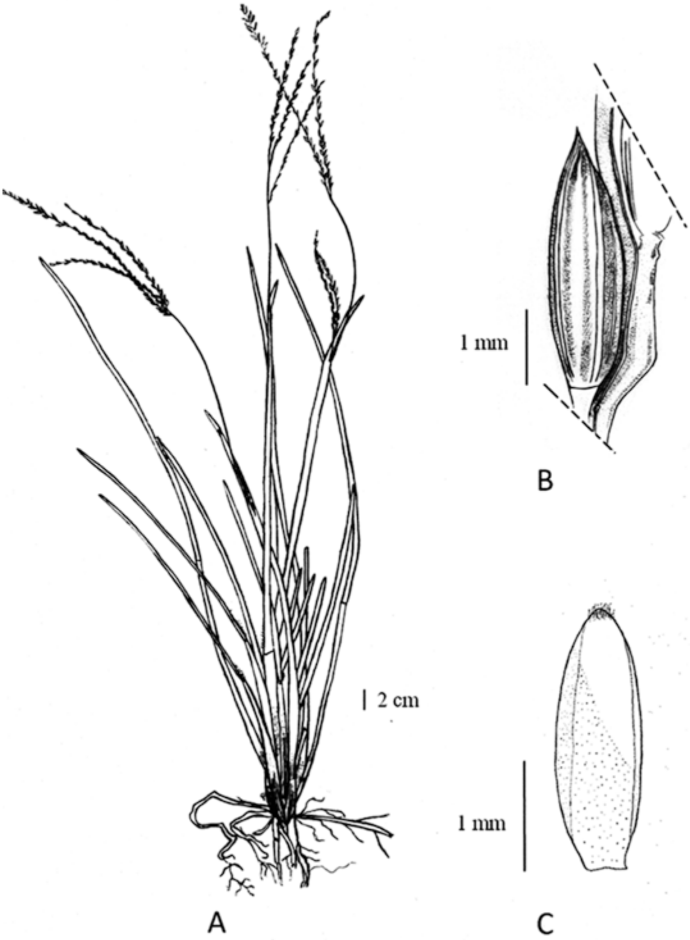


Fig. 3.6 *Axonopus fusiformis* Valls & A.D. Silveira (from Valls et al. number 9415, CEN – holotype). A. Habit. B. Segment of rachis showing spikelet in abaxial view. C. Fertile floret in abaxial view, showing THE back of the upper lemma with hairs at the tip. Drawn by A.D. Silveira. (Source: Silveira and Valls 2016)

Pott 2018), also in the middle of the center of origin (Krapovickas and Gregory 1994). The small herb *E. pottii* is only known from the type collection and has not been found again on that location. The recently described *Acrocomia corumbaensis* (Vianna 2017) is another endemic species, found very close to the wetland, and we believe that it occurs on the plain; therefore, it was included in the checklist, however, not as an endemic to the Pantanal. The scarce endemism is attributed to the geologically recent plain (Holocene), whereas the much older nearby hills have more endemics (Pott and Silva 2015). Sometimes a species was believed to be endemic because it has not been collected yet elsewhere, but then was found around

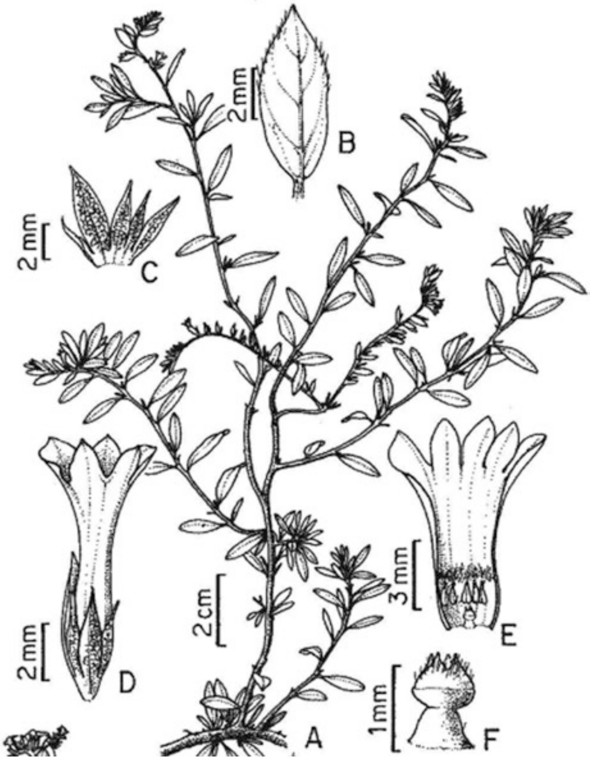


Fig. 3.7 *Euploca pottii* J.I.M. Melo & Semir (drawn from Pott 1397, UEC – holotype). A. Reproductive branch. B. Bract. C. Calyx. D. Flower. E. Opened corolla, showing stamens and pistil. F. Pistil. (Source: Melo and Semir 1999)

the Pantanal plain, such as *Zephyranthes pantanalensis*, and *Paspalum oteroi*, or in very few other farther places, such as *Eugenia pantanalensis*, *Maranta pantanalensis*, and *Xanthosoma pottii* (also in Bolivia, Gonçalves 1999). However, we maintained *Stilpnopappus pantanalensis* as endemic since the single record outside the Pantanal is from a herbal garden.

In Table 3.1, we marked the naturalized species with one asterisk *, following the information of Flora do Brasil (Flora do Brasil 2020), and the cultivated ones with two **; sometimes the same species has both marks. We mentioned who identified the species, voucher number, plant habit, pollination, and dispersal mechanisms. We also quoted the distribution in the Brazilian regions and endemism in Brazil, according to Flora do Brasil (Flora do Brasil 2020). Many species were not yet included in Flora do Brasil, or not yet cited there for Central West; however, some already appeared in the recently published checklists of families for Mato Grosso do Sul

Fig. 3.8 *Ipomoea pantanalensis* J.R.I. Wood & C. Urbanetz (Herbarium CGMS)

(e.g., Guglieri-Caporal et al. 2018). According to Flora do Brasil, *Rotala ramosior* does not occur in Brazil, but we kept it on the list because it was determined by C.D.K. Cook, who worked on this family, until further proper identification of such an abundant annual herb has been done. Also, in our view, *Oeceoclades maculata* does not seem to be naturalized, as it occurs in undisturbed woods.

Fig. 3.9 *Stilpnopappus pantanalensis* H. Rob. (Source: Pott and Pott 1994)

References

Allem AC, Valls JFM (1987) Recursos forrageiros nativos do Pantanal. Embrapa, Brasília (Documentos, 8)

Conceição AC, Paula JE (1986) Contribuição para o conhecimento da Flora do Pantanal Mato-Grossense e sua relação com a fauna e o homem. Simpósio sobre Recursos Naturais e Socio-econômicos do Pantanal, 1, Corumbá, 1994. Anais, pp 107–130. Brasília, Embrapa. http://ainfo.cnptia.embrapa.br/digital/bitstream/item/39154/1/anais1simposio.pdf

Dubs B (1998) Prodromus Florae Matogrossensis – Part I. Checklist of Angiosperms from Mato Grosso. Part II. Types from Mato Grosso. The Botany of Mato Grosso, Series B, n. 3. Betrona Verlag, Switzerland

Flora do Brasil (2020) Under construction. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/

GBIF. Global Biodiversity Information Facility (2017) Free and open access to data on biodiversity. https://www.gbif.org

Gonçalves EG (1999) A new pedate-leaved species of *Xanthosoma* Schott (Araceae: tribe Caladieae) with linear leaflets, from the Brazilian Pantanal. Aroideana 22:3–6

Guglieri-Caporal A, Pott A, Felismino MF, Caporal FJM, Valls JFM (2018) Check-list das Poaceae de Mato Grosso do Sul. Iheringia Série Botânica 73(Supl):313–328. https://doi.org/10.21826/2446-8231201873s313

Guarim Neto G (1981) Angiospermas do Estado de Mato Grosso - Pantanal. Acta Bot Bras 5(1):25–47

Hoehne FC (1923) Phytophysiomia do Estado de Matto Grosso e ligeiras notas a respeito da composição de sua flora: estudo preliminar. Editora Nacional, São Paulo. 103 p. il

Hoehne FC, Kuhlmann JB (1951) Índice bibliográfico e numérico das plantas colhidas pela Comissão Rondon. Secretaria da Agricultura, São Paulo, 400 p

Jabot. JBRJ – Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. Jabot – Banco de Dados da Flora Brasileira. http://jabot.jbrj.gov.br/

Krapovickas A, Gregory WC (1994) Taxonomy of the genus *Arachis* (Leguminosae). Bonplandia 8(1–4):1–186

Melo JIM, Semir J (1999) Two new Brazilian species and new combinations in *Euploca* (Heliotropiaceae) from Brazil. Kew Bull 64:285–289

Missouri Botanical Garden. http://www.tropicos.org

New York Botanical Garden. http://www.nybg.org

Pott VJ (1998) A família Nymphaeaceae no Pantanal, Mato Grosso e Mato Grosso do Sul. Acta Bot Bras 12(2):183–194

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa, Brasília

Pott A, Pott VJ (1999) Flora do Pantanal – listagem atual de Fanerógamas. In: Simpósio sobre Recursos Naturais e Socioeconômicos do Pantanal, 2. Corumbá. Anais, Embrapa Pantanal. pp 297–325

Pott VJ, Pott A (2000) Plantas aquáticas do Pantanal. Embrapa, Brasília

Pott A, Ratter JA (2011) Species diversity of terrestrial plants and human impact on the vegetation of the Pantanal. In: Jung WJ, Silva CJ, Cunha CN, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large Neotropical seasonal wetland. Sofia, Pensoft, pp 281–300

Pott A, Silva JSV (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal wetland in South America, The handbook of environmental chemistry, 37. Springer, Cham. https://doi.org/10.1007/609_2015_352

Pott A, Oliveira AKM, Damasceno GA Jr, Silva JSV (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71(1):265–273

Prance GT, Schaller GB (1982) Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. Brittonia 34(2):228–251

RBGE. Royal Botanic Garden Edinburgh. www.rbge.org

Robinson H (1995) *Stilpnopappus pantanalensis* H. Rob. Phytologia 78:398

Royal Botanic Gardens Kew. www.kew.org

Sampaio AJ (1916) A flora de Matto Grosso, memória em homenagem aos trabalhos da Comissão Rondon. Archivos do Museu Nacional do Rio de Janeiro, Rio de Janeiro, 125 p

Sartori ALB, Pott A (2018) Conhecimento florístico-taxonômico sobre a Flora Sul-Mato-Grossense: ontem e hoje. Iheringia Série Botânica 73(Supl):18–21. https://doi.org/10.21826/2446-8231201873s18

Sartori ALB, Lima LCP, Pott VJ, Valls JFM, Cristaldo ACM, Amaral CP, Costa L, Pott A, Fortuna-Perez AP, Silva GM, Vaz AMS, Torres RB, Pestana LT, Silva RR, Semidei E, Mansano VF, Sciamarelli A (2018a) Checklist das Leguminosae do Estado de Mato Grosso do Sul. Iheringia Série Botânica 73(Supl):239–254. https://doi.org/10.21826/2446-8231201873s239

Sartori ALB, Pott VJ, Pott A, Carvalho FS (2018b) Checklist das Angiospermas do Chaco de Mato Grosso do Sul. Iheringia Série Botânica 73(Supl):22–33. https://doi.org/10.21826/2446-8231201873s22

Schessl M (1997) Flora und Vegetation des nördlichen Pantanal von Mato Grosso, Brasilien: floristische Zuzammensetzung, Pflanzengesellschaften und Vegetationsdynamik saisonal und permanent überfluteter Standorte eines tropischen Sedimentationsbeckens. Martina Galunder-Verlag, Wiehl

Silva JSV, Abdon MM (1998) Delimitação do Pantanal Brasileiro e suas sub-regiões. Pesq Agrop Brasileira 33(n. especial):1703–1711

Silveira AD, Valls JFM (2016) A new species of *Axonopus* sect. *Axonopus* ser. *Axonopus* (Poaceae, Panicoideae) from the Brazilian Pantanal. Phytotaxa 26(3):263–266. https://doi.org/10.11646/phytotaxa.263.3.10

Souza VC, Lorenzi H (2019) Botânica Sistemática, 4th edn. Nova Odessa, Plantarum

Souza-Lima ES, Sinani TR, Pott A, Sartori ALB (2017) Mimosoideae (Leguminosae) in the Brazilian Chaco of Porto Murtinho, Mato Grosso do Sul. Rodriguésia 68(1):263–290. https://doi.org/10.1590/2175-7860201768131

Species Link. SpeciesLink Network. slink.cria.org.br

INCT – Instituto Nacional de Ciência e Tecnologia (2017) Herbário virtual da flora e d os fungos. Species Link SpeciesLink Network. http://inct.splink.org.br

Valls JFM, Simpson CE (2005) New species of Arachis (Leguminosae) from Brazil and Bolivia. Bonplandia 14:35–64

Vianna SL (2017) A new species of *Acrocomia* (Arecaceae) from Central Brazil. Phytotaxa 314(1):045–055. https://doi.org/10.11646/phytotaxa.314.1.2

Wood JRI, Muñoz-Rodriguez P, Williams BRM, Scotland RW (2020) A foundation monograph of *Ipomoea* (Convolvulaceae) in the New World. Phytokeys 143:1–823. https://doi.org/10.3897/phytokeys.143.322821

Chapter 4
Aquatic Plants

Vali Joana Pott and Arnildo Pott

4.1 Introduction

This chapter is an overview of the aquatic plants of the Pantanal wetland, compiling some of our field observations and prominent publications. It is divided into brief topics about taxonomy, flora (including endemism), phytogeography, ecology (traits), aquatic weeds, aquatic habitats (emphasis on floating meadows), life forms, effects of fire, dispersal, biology, collecting, current and potential usefulness, resilience, and conservation; and examples and curiosities are mentioned. We add an updated checklist of 534 species, including their life forms and habitats, based on herbarium records with reliable identification, mostly from our collections.

4.2 Taxonomy

The first reports including aquatic plants of the Pantanal were made by European botanists, e.g., Weddell, who discovered and described *Wolffia brasiliensis*. This species, together with *W. columbiana* (Fig. 4.1), are the world's smallest Angiosperms. The first book on Brazilian aquatic plants was written by Hoehne (1948), who collected as the botanist in the expeditions of General Rondon to build a telegraph line across the Pantanal. In 1986, we were strongly stimulated by a field course about aquatic plants in the Pantanal given by two experienced wetland

---

V. J. Pott (✉)
Herbário CGMS, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul,
Campo Grande, MS, Brazil

A. Pott
Laboratório de Ecologia Vegetal, Instituto de Biociências, Universidade Federal de Mato
Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_4

Fig. 4.1 *Wolffia columbiana* (duckweed), Araceae-Lemnoideae; this species and *L. brasiliensis* are the smallest Angiosperms, and they are rootless; most are mother-fronds and developing daughter-fronds (ruler in mm). (Photo: A. Spielmann)

Fig. 4.2 *Pontederia reflexa* (note the reflex bract on the inflorescence) showing morphological plasticity according to the habitat: on the left, at poor soil fertility and short flooding; on the right, at high soil fertility and prolonged flooding. (Photos: A. Pott, source Pott and Pott 2000)

botanists, Dr. Christopher D. K. Cook (Universität Zürich) and Prof. Dr. Bruno E. Irgang (UFRGS). A few taxonomic groups of Pantanal species had been surveyed and or revised, e.g., Poaceae (Allem and Valls 1987), Characeae (Bueno et al. 1996), Nymphaeaceae (Pott 1998) (Fig. 4.2), Lemnaceae (Pott and Cervi 1999), now Araceae-Lemnoideae (Fig. 4.1), and Pontederiaceae (Sanches et al. 2000). Also, an illustrated identification guide on aquatic plants of the Pantanal was published (Pott and Pott 2000).

Other families or orders were revised for the state of Mato Grosso do Sul, including species from the Pantanal: Cyperaceae (Araújo and Trevisan 2018), Nymphaeales

(Moreira and Pott 2018), Poaceae (Guglieri-Caporal et al. 2018), and Alismatales (Pott et al. 2018b). Other revised groups, including species from the Pantanal, were two genera of Fabaceae, *Aeschynomene* (joint vetches) (Lima et al. 2006) and *Arachis* (wild peanuts) (Krapovickas and Gregory 2007).

Some of the specimens of *Echinodorus* were sent to the specialist R.R. Haynes for identification (Pott and Pott 2000); they were examined and renamed by Lehtonen (2008) and Lehtonen and Myllys (2008), based on morphological and molecular analyses, whereby the earlier mentioned *E. macrophyllus* subsp. *scaber* was confirmed as its older name *E. scaber*; *E. grandiflorus* now has the valid name *E. longiscapus*; the valid name of *E. lanceolatus* now is *E. cylindricus*; *E. teretoscapus* turned into a synonym of *E. glaucus*; and the small species of the former subgenus *Helanthium,* which once already was recognized as a genus, were moved back to the genus *Helanthium* (*H. bolivianum*, *H. tenellum*). The previous Limnocharitaceae *Hydrocleys nymphoides*, *H. parviflora*, *Limnocharis flava*, and *L. laforestii* (Pott and Pott 2000) were placed into the Alismataceae, as also shown in the checklist of Alismatideae (Pott et al. 2018a, b). For *Polygonum* we still follow Flora do Brasil (2020), although the Brazilian species actually belong to the accepted genus *Persicaria* (Funez & Hassemer 2018).

The white-flowered *Pontederia* species, abundant throughout the Pantanal, used to be called *P. cordata* f. *ovalis.* Pott and Pott (2000) identified it as *P. parvifolia* and drew attention to its morphological plasticity according to the habitat in which it grows (Fig. 4.2). Recently it was described as the new species *P. reflexa* (Sousa et al. 2020).

4.3 Flora of Aquatic Plants

How many aquatic plant species are there in the Pantanal? That is a question we often receive. Pott and Pott (1997) reported that the total was 280 species. Pott and Pott (2000), in the book *Plantas do Pantanal*, mentioned 324 species. Now we updated that number to 533 species (Table 4.1), including many amphibious plants omitted before.

However, the concept of "aquatic plant species" is not a clear one. Thus, amphibious plant species may be included in or excluded from the concept of "aquatic species." And the Pantanal harbors many species that survive in short-flooded areas. As a consequence, there is no clear distinction between such species and several species that are usually considered "terrestrial." Many of those species grow in ecotones and thus are adapted to both habitats (Irgang and Gastal 1996). And this uncertainty also makes it difficult or questionable to compare the numbers of "aquatic species" for different areas. Thus, the concept of aquatics plants is varied and controversial. Some botanists define them as strictly aquatic, most prefer a broader spectrum, and others include even trees. Since it is difficult to define a limit between terrestrial and wetland species, as it is a continuum, the term "wetland plants" seems convenient, and it can also encompass woody species (Cronk and

Table 4.1 Updated list of aquatic macrophytes of the Pantanal wetland, of the groups Charophyta, Bryophyta, Polypodiopsida and Angiospermae, in alphabetic order of families, genera and especies, with their life forms and habitat. *naturalized, **cultivated; life form: **Am**=amphibious, **Eb**=embalsada (floating meadow), **Em**=emergent, **Ep**=epiphyte, **FF**=free-floating, **FS**=free-submerged, **RF**=rooted floating, **RS**=rooted submerged; Habitat: **AP**=alkaline pond, **FG**=flooded grassland, **FM**=floating meadow, **Fp**=floodplain, **L**=lake, **PP**=permanent pond, **TP**=temporary pond, **R**=river, **Rb**=River branch, **SS**=seasonal stream, **Sw**=swamp, **V**=vereda

Family, genus, apecies	Life form	Habitat
CHAROPHYTA (macroalgae)		
Characeae		
Chara fibrosa E.Agard *ex* Bruzelius emend. R.D.Wood	RS	AP
C. rusbyana M.Howe	RS	AP
Nitella acuminata A.Braun *ex* Wallman emend. R.D.Wood	RS	PP
N. cernua A.Braun	RS	PP
N. furcata (Roxb. *ex* Bruz.) E.Agardh	RS	R,Rb
N. gollmeriana A.Braun	RS	Fp
N. subglomerata A.Braun	RS	Fp,Rb
N. translucens (Pers.) A.Agradh emend. R.D.Wood	RS	Fp,AP
BRYOPHYTA		
Ricciaceae		
Ricciocarpus natans (L.) Corda	FF	R,Rb,L
POLYPODIOPSIDA		
Equisetaceae		
Equisetum giganteum L.	Em	FG,Sw
Isoetaceae		
Isoetes pedersenii H.P. Fuchs ex E.I.Meza & Macluf	Em,RS	FG,TP,SS
Marsileaceae		
Marsilea crotophora D.M. Johnston	RF	L,R,Rb
M. deflexa A. Braun	RF	TP
Ophioglossaceae		
Ophioglossum crotalophoroides Walter	Am	TP
Pteridaceae		
Acrostichum danaeifolium Langsd. & Fisch.	Am,Em	Sw,V
Ceratopteris pteridoides (Hook.) Hieron.	FF	R,L
C. thalictroides (L.) Brongn.	RS,RF,Em	Rb
Pityrogramma calomelanos (L.) Link	Em,Am	FM,PP,Sw
Salviniaceae		
Azolla caroliniana Willd.	FF	L,TP
A. filiculoides Lam.	FF	PP,TP
Salvinia auriculata Aubl.	FF	L,PP,Rb,TP
S. biloba Raddi emend. De La Sota (*S. herzogii*)	FF	L,PP,Rb
S. minima Bak.	FF	L,Rb

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
Thelypteraceae		
Cyclosorus interruptus (Willd.) H.Ito (*Thelypteris interrupta*)	Am	FM,Sw,V
ANGIOSPERMAE		
Acanthaceae		
Hygrophila costata Nees	Em,Am	Fp
Justicia comata (L.) Lam.	Am,Em	Fp,PP
J. laevilinguis (Nees) Lindau	Em,Am	Rb,Fp,TP,SS
J. lavandulifolia (Pohl ex Nees) Wassh.	Em	TP
Ruellia simplex C.Wright (*R. coerulea*, *R. tweediana*)	Em	FG
Alismataceae		
Echinodorus aschersonianus Graebn.	Em	TP
E. cordifolius (L.) Griseb.	Em	Sw
E. cylindricus Rataj	Em	FG,Fp,SS,TP
E. glaucus Rataj (*E. teretoscapus*)	Em	FG,FM,PP,SS,TP
E. longipetalus Micheli	Em	V
E. longiscapus Arechav.	Am,Em	FG,Fp,TP
E. paniculatus Micheli	Em,RS	FG,PP,TP,Rb
E. scaber Rataj (*E. macrophyllus* subsp. *scaber*)	Em	FG,SS,Sw
E. subalatus (Mart.) Griseb.	Em	Rb
Helanthium bolivianum (Rusby) Lehtonen & Myllys (*Echinodorus bolivianus*)	Em,RS	Fp
H. tenellum (Mart.) Britton (*Echinodorus tenellus*)	Em,RS, Am	FG,PP,TP,SS
Hydrocleys nymphoides (Willd.) Buchenau	RF	L,PP,TP
H. parviflora Seub.	RF	FG,SS,Sw
Limnocharis flava (L.) Buchenau	Em	FG,TP
L. laforesti Duchass. *ex* Griseb.	Em	FG
Sagittaria guayanensis Kunth	RF	FG,PP,TP
S. montevidensis Cham. & Schltdl.	Em	Fp,PP
S. planitiana G.Agostini	RF	V
S. rhombifolia Cham.	Em	PP,SS
Amaranthaceae		
Alternanthera aquatica (D.Parodi) Chodat	FF,RF	R,Rb,L
A. philoxeroides (Mart.) Griseb.	Am,Em	TP;PP
Gomphrena elegans Mart.	Em	Fp
Apocynaceae		
Funastrum clausum (Jacq.) Schltr.	Em	Fp,SS
Rhabdadenia madida (Vell.) Miers (*R. pohlii*)	Em	FG,Fp,PP
Tassadia berteroana (Spreng.) W.D.Stevens	Am	Fp,SS
***Araceae** (including Lemnaceae)*		
Lemna aequinoctialis Welw.	FF	Fp,PP,Rb,TP

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
L. minuta Kunth	FF	Fp,L,Rb
L. valdiviana Phil.	FF	PP,TP,R,Rb
Pistia stratiotes L.	FF	L,PP,Rb
Spirodela intermedia W.Koch	FF	Fp,PP,R,Rb
Urospatha sagittifolia (Rudge) Schott	Em	FM
Wolffia brasiliensis Wedd.	FF	PP,TP,Rb
W. columbiana Karst.	FF	PP,TP
Wolffiella lingulata (Hegelm.) Hegelm.	FF	Fp,R,Rb
W. oblonga (Phil.) Hegelm.	FF	PP,TP
W. welwitschii (Hegelm.) Monod	FF	Fp,TP
Xanthosoma aristeguietae (G.S.Bunting) Madison	Am	Fp
X. striatipes (Kunth & Bouché) Madison	Am,Em	FG
Araliaceae *(including part of Apiaceae)*		
Hydrocotyle ranunculoides L.f.	Em,FF,RF	Rb,L,Eb
H. verticillata Thunb.	Am,Em	SS
Asteraceae		
Acilepidopsis echitifolia (Mart. *ex* DC.) H. Rob.	Em	L,V
Aspilia latissima Malme	Em	Fp
Baccharis glutinosa Pers. (*B. medullosa*)	Am	FG
Barrosoa candolleana (Hook. & Arn.) R.M.King & H.Rob.	Am,Eb	FM
Clibadium armanii (Balb.) Sch. Bip. *ex* O.E.Schulz	Am	FG
Eclipta prostrata (L.) L.	Am	FG,FM,TP
E. palustris Gardner	Em	V
**Emilia sonchifolia* (L.) DC. *ex* Wight	Eb	FM
Enhydra anagallis Gardner	Em,RF	FM,R,Rb
Erechtites hieracifolius (L.) Raf. *ex* DC.	Eb	FM
Gymnocoronis spilanthoides (Hook. & Arn.) DC.	Em	Fp
Lagascea mollis Cav.	Am,Em	Fp
Lessingianthus rubricaulis (Humb. & Bonpl.) H. Rob.	Am	FG,V
Mikania cordifolia (L.f.) Willd.	Am	Fp
M. micrantha Kunth	Em	Fp
M. parodii Cabrera	Em	FG,TP
M. stenophylla W.C.Holmes	Em	TP
Pacourina edulis Aubl.	Em	FM,Fp
Pluchea sagittalis (Lam.) Cabrera	Am	FG
Begoniaceae		
Begonia cucculata Willd.	AM,Em	V,Eb
Bignoniaceae		
Tabebuia insignis (Miq.) Sandwith	Eb	FM
Cabombaceae		

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
Cabomba furcata Schult. & Schult.f.	RS	L,SS
C. haynesii Wiersema	RS	Fp,Rb,SS
Campanulaceae		
Centropogon cornutus (L.) Druce	Am	Sw,SS
Lobelia aquatica Cham.	Em	FG,FM,PP,SS
Cannaceae		
Canna glauca L.	Am,Em	Fp,SS,Sw,TP
Ceratophyllaceae		
Ceratophyllum demersum L.	FS	L,SS,Rb
C. submersum L. var. *echinatum* (A.Gray) Wilmot-Dear	FS	PP
Commelinaceae		
Commelina longicaulis Jacq. (*C. schomburgkiana*)	FF,Eb,Em	R,Rb,FM
Murdannia engelsii M.Pell. & Faden	Em	FG,SS
M. semifoliata (C.B.Clarke *ex* S.Moore) G.Brückn.	Am,Em	FG
Convolvulaceae		
Aniseia martinicensis (Jacq.) Choisy	Em	Fp
Camonea umbellata (L.) A.R.Simões & Staples (*Merremia umbellata*)	Em	FG,Fp
Ipomoea alba L.	Am	Fp
I. asarifolia (Desr.) Roem. & Schult.	Em	FG
I. carnea ssp. *fistulosa* (Mart. & Choisy) Austin	Em, Am	Fp,Sw
I. chiliantha Hall.	Em	FG,Fp
I. rubens Choisy	Em	Fp
I. subrevoluta Choisy	Am,Eb	FG,FM,Rb,SS
Cucurbitaceae		
Cayaponia podantha Cogn.	Em	Fp
Cyclanthera hystrix (Gill.) Arn.	RF,Eb	FM,Fp,R,Rb
Cyperaceae		
Bulbostylis capillaris (L.) C.B.Clarke	Am	FG,SS
B. hirtella (Schrad.) Urb.	Am	FG
B. paraensis (Schrad. & Nees) C.B.Clarke	Am	FG
B. scabra (J.Presl & C.Presl) C.B.Clarke	Am	FG
Calyptrocarya glomerulata (Brongn.) Urb.	Em	V
Cladium mariscus subsp. *jamaicense* (Crantz) Kük. (*C. jamaicense* Crantz)	Em	Sw
Cyperus articulatus L.	Em	FG,Fp,TP
C. blepharoleptos Steud. (*Oxycaryum cubense* (Poepp. & Kük.) Lye	Ep, Eb	FM,Fp,L,Rb,
C. brasiliensis (Kunth) Bauters (*Ascolepis brasiliensis*)	Em	FG
C. brevifolius (Rottb.) Endl. *ex* Hassk.	Em	FG
C. corymbosus Rottb.	Em	Fp

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
C. digitatus Roxb.	Am	FG,SS
C. esculentus L.	Am	FG
C. gardneri Nees	Eb,Ep	FM,Fp,PP,Sw
C. giganteus Vahl	Em	Fp,PP,TP,SS
C. haspan L.	Am	FG,TP
C. iria L.	Am	FG,Fp,TP
C. luzulae (L.) Retz.	Am	FG,Fp,R,Rb,Sw
C. ochraceus Vahl	Am	FG,Fp,Rb
C. odoratus L.	Am	FG,FM,Fp,Rb,TP
C. papyrus L.	Em	Fp,Sw
C. polystachyos Rottb.	Em	FG,Fp,SS,TP
C. prolixus Kunth	Am	FG
C. salzmannianus (Steud.) Bauters (*Lipocarpha salzmanniana*)	Am	FG
C. schomburgkianus Nees	Em	FG
C. sellowianus (Kunth) T.Koyama (*Lipocarpha humboldtiana*, *L. sellowiana*)	Am	FG
C. sesquiflorus (Torrey) Mattf. & Kük.	Am	FG
C. subsquarrosus (Muhl.) Bauters (*Hemicarpha micrantha*, *Lipocarpha micrantha*)	Em	FG
C. surinamensis Rottb.	Am	FG,TP,SS
C. virens Michx.	Em	FG,Fp
Eleocharis acutangula (Roxb.) Schult.	Em	FG,SS,TP
E. barrosii Svenson	Em	FG,Fp
E. contracta Vahl	Em	FG,Fp
E. elegans (Kunth) Roem. & Schult.	Em	FG,Sw,SS
E. filiculmis Kunth	Em	FG,PP
E. geniculata (L.) Roem. & Schult.	Am	AP
E. hatschbachii R.Trevis.	Am	Fp,PP
E. interstincta (Vahl) Roem. & Schult	Em	PP
E. jelskiana Boeckeler	Em	PP
E. maculosa (Vahl) Roem. & Schult.	Em	TP
E. minima Kunth	RS,Em,Am	FG,TP,SS,Sw
E. montana Kunth) Roem. & Schult.	Em	FG,Fp
E. mutata (L.) Roem. & Schult.	Am,Em	FG,FM,Fp
E. nana Kunth	Am	FG,Fp,R
E. nudipes (Kunth) Palla	Am,Em	FG,TP
E. plicarhachis (Griseb.) Svenson	Em,FF,Eb	FM,PP,Sw
E. viridans Kük. *ex* Osten	Em	Fp
Fimbristylis aestivalis Vahl	Em	FG
F. autumnalis (L.) Roem. & Schult.	Em	FG
F. complanata (Retz) Link	Em	FG,Fp,,L

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
F. dichotoma (L.) Vahl	Em	FG
F. littoralis Gaudich.	Em	FG,Sw
F. squarrosa Vahl	Em	Fp,R,Rb
Fuirena umbellata Rottb.	Am,Em	FG,SS,Sw
Rhynchospora armerioides J.Presl & C.Presl	Em	FG
R. asperula (Nees) Steud.	Eb,Em	FM,Rb
R. brevirostris Griseb.	Am,Em	FG
R. ciliata Kük.	Am	FG
R. corymbosa (L.) Britton	Am,Em	FG,SS,TP,V
R. emaciata (Nees) Boeckeler	Em	PP,TP,Rb,V
R. eximia (Nees) Boeckeler	Em	FG,TP
R. globosa (Kunth) Roem. & Schult.	Em	FG
R. hirta (Nees) Boeckeler	Em	FG
R. holoschoenoides (L.C.Rich.) Herter	Em	FG
R. nervosa (Vahl) Boeckeler	Em	FG
R. riparia (Nees) Boeckeler	Em	FG
R. rugosa (Vahl) Gale	Em	V
R. scutellata Griseb.	Em	Fp
R. tenerrima Nees *ex* Spreng.	Em	FG
R. tenuis Link	Em	PP
R. triflora Vahl	Em	FG,SS
R. trispicata (Nees) Schrad. *ex* Steud.	Em	FG,SS,TP
R. velutina (Kunth) Boeckeler	Am	FG,SS,TP
Schoenoplectiella supina (L.) Lye (*Scirpus supinus*)	Am,Em	FG
Scleria gaertneri Raddi (*S. melaleuca, S. pterota*)	Em	PP,SS,Sw
S. hirtella Sw.	Am,Em	FG
S. lacustris C.Wright	Em	Fp
S. latifolia Sw.	Em	FG
S. leptostachya Kunth	Em	FG
S. lithosperma (L.) Sw.	Em	FG
S. macrophylla J.Presl & C.Presl	Em	L
S. microcarpa Nees *ex* Kunth	Em	FG,Fp
S. pusilla Pilg. (*S. minima*)	Am	FG
S. reticularis Michx. *ex* Willd.	Em	FG
S. vaginata Steud.	Em	FG,Rb,SS
S. variegata (Nees) Steud.	Em	FG,SS
Droseraceae		
Drosera communis A.St.-Hil.	Em	FG
D. sessilifolia A.St.-Hil.	Em	V
Eriocaulaceae		
Syngonanthus caulescens (Poir.) Ruhland	Em	FG,V, Sw

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
S. cuyabensis (Poir.) Ruhland (*Philodice hoffmannseggii*)	Am	FG
Euphorbiaceae		
Caperonia castaneifolia (L.) A.St.-Hil.	Em	FG,FM,PP,TP,SS
C. palustris (L.) A.St.-Hil.	Am	FG
Fabaceae		
Aeschynomene americana L.	Am	FG,Fp
A. ciliata Vogel	Em	L,R,PP,SS
A. denticulata Rudd	Em	FG,SS
A. evenia C.Wright & Sauvalle	Em	Fp
A. fluminensis Vell.	Em	FG,PP,TP
A. magna Rudd	Em	FG,TP
A. montevidensis Vogel	Em	TP, Sw
A. rudis Benth.	Em	FG,R,Rb,SS
A. sensitiva Sw.	Em	FG,PP,Sw
Arachis diogoi Hoehne	Am	Fp
A. helodes Mart. *ex* Krapov. & Rigoni	Am	FG
A. hoehnei Krapov. & W.C.Gregory	Am	Fp
A. lignosa (Chodat & Hassl.) Krapov. & W.C.Gregory	Am	FG
A. linearifolia Valls et al.	Am	FG
A. lutescens Krapov. & W.C.Gregory	Am	FG
A. nitida Valls et al.	Am	Fp
A. valida Krapov. & W.C.Gregory	Am	FG
A. vallsii Krapov. & W.C.Gregory	Em	Fp
Clitoria falcata Lam.	Am	FG
Discolobium leptophyllum Benth.	Em	FG,SS
D. psoraliaefolium Benth.	Em	TP
D. pulchellum Benth.	Em	Fp,L,Rb,TP
Caetangil paraguariensis (Chodat & Hassl.) L. P. Queiroz (*Camptosema paraguariense*)	Am	FG
Mimosa pellita Humb. & Bonpl. *ex* Willd.	Am,Em	Fp
M. pigra L.	Am,Em	Fp, Rb
Neptunia oleracea Lourt.	FF,RF	FG,L,R,Rb
N. plena (L.) Benth.	Em,FF	L,Rb,Sw
Senna aculeata (Pohk *ex* Benth.) H.S.Irwin & Barneby	Am	PP,TP
S. pendula Humb. & Bonpl. *ex* (Willd.) H.S.Irwin & Barneby	Em	Fp
Sesbania emerus (Aubl.) Urb.	Em	Fp
S. exasperata Kunth	Em	FM,Fp,TP
S. sesban (L.) Merr.	Am	Fp
S. virgata (Cav.) Pers.	Am	Fp,TP,V

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
Vigna lasiocarpa (Mart. *ex* Benth.) Verdc.	Em	Fp,Rb,SS,Sw
V. longifolia (Benth.) Verdc.	Em	Fp
Gentianaceae		
Chelonanthus alatus (Aubl.) Pulle	Em	V
Coutoubea ramosa Aubl.	Em	FG
Curtia tenuifolia (Aubl.) Knobl.	Am,Em	FG
Heliconiaceae		
Heliconia marginata (Griggs) Pittier	Em	Fp
Hydrocharitaceae		
Apalanthe granatensis (Bonpl.) Planch.	RS	Rb,SS
Egeria najas Planch.	FS,RS	FG,PP,SS
Limnobium laevigatum (Humb. & Bonpl. *ex* Willd.) Heine	FF	PP,Rb,SS
Najas guadalupensis (Spreng.) Magnus	RS	AP
N. microcarpa K.Schum.	RS	Fp,PP,SS
Hydroleaceae		
Hydrolea elatior Schott	Em	FG
H. spinosa L.	Em	FG
Lamiaceae		
Hyptis brevipes Poit.	Am	FG,TP
H. lappacea Benth.	Am,Em	FG,SS
H. lorentziana O.Hoffm.	Am,Em	FG,Fp,SS,TP,PP
H. microphylla Pohl *ex* Benth.	Am,Em	TP,SS
Lentibulariaceae		
Genlisea repens Benj.	RS	V
Utricularia amethystina Salzm. *ex* A.St.-Hil. & Girard	RS	V
U. breviscapa C. Wright *ex* Griseb.	FS	FG,PP,SS
U. erectiflora A.St.-Hil. & Girard	FS	V
U. fimbriata Kunth	RS	FG
U. foliosa L.	FS	FG,PP,Rb,SS
U. gibba L.	FS	FG,PP,TP
U. hydrocarpa Vahl	FS	SS,Sw
U. lloydii Merl *ex* F.Lloyd	RS	FG
U. myriocista A.St.-Hil. & Girard	FS	FG
U. nana A.St.-Hil. & Girard	RS	V
U. nigrescens Sylvén	RS	V
U. poconensis Fromm	FS	FG,TP,PP
U. pusilla Vahl	RS	FG
U. simulans Pilg.	RS	FG
U. subulata L.	RS	FG,SS,V

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
U. trichophylla Spruce *ex* Oliv.	RS	FG
U. tricolor A.St.-Hil.	RS	FG
U. triloba Benj.	RS	TP,V
U. warmingii Kamienski	FS	FG,SS,Sw
Linderniaceae		
Lindernia crustacea L.F.Müll.	Am	FG,SS
L. diffusa (L.) Wettst.	Em	FG
L. dubia (L.) Pennell	Am	FG,Fp,PP
Torenia thouarsii (Cham. & Schltdl.) Kuntze (*Lindernia thouarsii*)	Em	FG
Lythraceae		
Ammannia auriculata Willd.	Em	FG,TP
Cuphea carthagenensis (Jacq.) J.Macbr.	Am	FG
C. corisperma Koehne	Am	FG,Fp
C. ferruginea Pohl *ex* Koehne	Am	FG
C. inaequalifolia Koehne	Am	FG
C. melvilla Lindl.	Am,Em	Fp
C. odonellii Lourteig	Am	FG,SS
C. pterosperma Koehne	Am	SS
C. repens Koehne	Am	FG,SS
C. retrorsicapilla Koehne	Am	FG
C. sessiliflora A.St.-Hil.	Am	Fp
Heimia salicifolia Link	Am	FG,Fp
Pleurophora saccocarpa Koehne	Em	FG
Rotala mexicana Cham. & Schltdl.	Em,RS	FG,SS
R. ramosior (L.) Koehne	Am	FG,TP
Malvaceae		
Byttneria genistella Triana & Planch.	Am	FG,SS,TP
B. palustris Cristóbal	Am,Em	FG
Hibiscus furcellatus Desr.	Am	Fp
H. sororius L.	Am,Em	FM,TP
H. striatus Cav.	Em	Fp
Malachra radiata (L.) L.	Am	FG,TP,SS
Melochia anomala Griseb.	Am	FG
M. arenosa Benth.	Am,Em	FG,Fp,SS
M. graminifolia A.St.-Hil.	Em	FG,TP
M. simplex A.St.-Hil.	Am,Em	FG,PP,TP
M. villosa (Mill.) Fawc. & Rendle	Am	FG,Fp,SS
Pavonia angustifolia Benth.	Am	FG
P. laetevirens R.E.Fr.	Am,Em	Fp,Rb,SS
Peltaea riedelii (Gürke) Standl.	Am	FG,TP

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
Marantaceae		
Thalia densibracteata Petersen	Em	TP,Sw
T. geniculata L.	Em,Am	FM,PP,TP,Sw, Fp
Mayacaceae		
Mayaca fluviatilis Aubl.	Em,RS	F,SS,TP
M. sellowiana Kunth	Em	V
Melastomataceae		
Clidemia biserrata DC.	Am,Em	SS
Macairea radula (Bonpl.) DC.	Am	V
Noterophila limnobios (DC.) Mart. (*Acisanthera limnobius*, *A. divaricata*)	Am,Em,RS	FG,SS
Poteranthera pusilla Bong.	Em	FG
Pterolepis trichotoma (Rottb.) Cogn.	Em	V
Rhynchanthera brachyrhyncha Cham.	Em	FG
R. grandiflora (Aubl.) DC.	Em	FG
R. hispida Naudin	Em	L
R. novemnervia DC.	Am, Eb	FM,Fp,SS
R. ursina Naudin	Am	Fp
Siphanthera cordifolia (Benth.) Gleason	Am,Em	V
Trembleya phlogiformis Mart. & Schrank *ex* DC.	Am	V
Menyanthaceae		
Nymphoides grayana (Griseb.) Kuntze	RF	PP,TP,SS
N. humboldtiana (Kunth) Kuntze (not =*N. indica*)	RF	TP,L
Nymphaeaceae		
Nymphaea amazonum Mart. & Zucc.	RF	PP
N. belophylla Trickett	RF	Fp,R
N. gardneriana Planch.	RF	FG,PP,TP
N. jamesoniana Planch.	RF	TP
N. lingulata Wiersema	RF	AP
N. oxypetala Planch.	RF,RS	Fp,Rb,SS
N. prolifera Wiersema	RF	FG,Fp,L
Victoria amazonica (Poepp.) J.E.Sowerby	RF	L,Rb,Fp
Ochnaceae		
Sauvagesia erecta L.	Am,Em	FG
S. racemosa A.St.-Hil.	Em	V
Onagraceae		
Ludwigia affinis (DC.) H.Hara	Em	SS
L. bonariensis (Micheli) H.Hara	Am	FG,Pp
L. decurrens Walter	Am,Em	Fp
L. densiflora (Micheli) H.Hara	Em	R
L. elegans (Cambess.) H.Hara	Em	Fp,R,SS

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
L. filiformis (Micheli) Ramamoorthy	Em	FG
L. grandiflora (Michx.) Greuter & Burdet	Em,RF	FG,TP,SS
L. helminthorrhiza (Mart.) H.Hara	FF	Fp,Rb,SS
L. hexapetala (Hook. & Arn.) Zardini et al.	Em	PP
L. hyssopifolia (G.Don) Excell	Em	FG,Fp
L. inclinata (L.f.) M.Gómez	RF	Fp,SS
L. irwinii Ramamoorthy	Am,Em	FG,SS
L. lagunae (Morong) H.Hara	Am,Em	FG,Fp,TP
L. leptocarpa (Nutt.) H.Hara	Am,Em	FG,FM,Fp,TP
L. longifolia (DC.) H.Hara	Am,Em	FG,TP,Sw
L. martii (Micheli) Ramamoorthy	Em	Fp
L. myrtifolia Cambess.	Em	FG
L. neograndiflora (Munz) H.Hara	Em	FG
L. nervosa (Poir.) H.Hara	Am,Em,Eb	FM,PP,SS
L. octovalvis (Jacq.) P.H.Raven	Am	FG,FM,Fp,TP
L. peploides (Kunth) P.H.Raven	RF,RS,Em,Am	PP,SS,Sw,L
L. peruviana (L.) H.Hara	Em	Fp,SS
L. rigida (Miq.) Sandwith	Am,Em	FG,PP
L. sedioides (Humb. & Bonpl.) H.Hara	RF	Fp,PP
L. tomentosa (Cambess.) H.Hara	Am,Em	FG
Orchidaceae		
Aspidogyne debilis (Lindl.) Meneguzzo (*Platythelys debilis*, *Erythrodes pumila*)	Am,Eb	FM
Cyrtopodium paludicolum Hoehne	Em	V
Eulophia alta (L.) Fawc. & Rendle	Eb	FM
Galeandra styllomisantha (Vell.) Hoehne	Am,Em	FG
Habenaria amambayensis Schltr.	Am	FG
H. aricaensis Hoehne	Em	TP,SS
H. glazioviana Kraenzl.	Am	FG
H. nabucoi Ruschi	Am,Eb,Em	FM,SS
H. orchiocalcar Hoehne	Am	FG
H. polycarpa Hoehne	Am	FG
H. pratensis (Salzm. *ex* Lindl.) Rchb.f.	Am	FG
H. repens Nutt.	Eb	FM
H. spathulifera Cogn.	Am	FG
Orobanchaceae		
Agalinis glandulosa (G.M.Barroso) V.C.Souza	Am	FG
Buchnera longifolia Kunth	Am	FG
B. palustris (Aubl.) Spreng.	Am,Em	Fp,SS
Melasma melampyroides (Rich.) Pennell	Eb,Em	FG,FM

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
M. stricta (Benth.) Hassl.	Am	FG
Passifloraceae		
Passiflora longilobis Hoehne	Em	Fp
P. misera Kunth	Em	FG,Fp,Rb,SS
Phyllanthaceae		
Phyllanthus amarus Schumach.	Em	FG,Fp
P. fluitans Benth. *ex* Müll. Arg.	FF	R,Rb,Pp
P. hyssopifolioloides Kunth	Em	Fp
P. stipulatus (Raf.) G.L.Webster	Em	FG,Fp,PP,TP
Plantaginaceae		
Bacopa arenaria (Schmidt) Edwall	Am,Em	FG,SS,TP
B. australis V.C.Souza	Em	FG,PP,SS,TP
B. dubia Chodat & Hassl.	Em	PP,Sw
B. egensis (Poepp.) Pennell	Em	Fp,TP
B. gracilis (Benth.) Edwall	Em	FG,TP
B. gratioloides (Cham.) Edwall	Em	FG
B. monnierioides (Cham.) B.L.Rob.	Em,RS	PP,TP
B. myriophylloides (Benth.) Wettst.	Am,Em,RS	FG,Fp,PP,SS
B. reflexa (Benth.) Edwall	Em,RS	Fp,SS
B. reptans (Benth.) Wettst. *ex* Edwall	Em	FG,Fp
B. rotundifolia (Michx.) Wettst.	Em,RF	Fp,SS
B. salzmannii (Benth.) Wettst. *ex* Edwall	Eb,Em	FM,Fp,SS,TP
B. scabra (Benth.) Descole & Borsini	Em	FG,SS
B. stricta (Schrad.) Wettst. *ex* Edwall	Em	FM,PP,SS,Sw
Conobea scoparioides (Cham. and Schltdl.) Benth.	Am,Em	FG,SS
Limnophila sessiliflora (Vahl) Blume	Em,RS	Fp,SS
Monopera perennis (Chodat & Hassl.) Barringer	Em	FG,L
Stemodia durantifolia (L.) Sw.	Am,Em	FG,Fp,TP
S. ericifolia K.Schum.	Em	FG
S. foliosa Benth.	Am	FG
S. hassleriana Chodat	Em	Sw
S. hyptoides Cham. & Schltdl.	Am,Em	FG,TP
S. lanceolata Benth.	Em	FG,Fp
S. palustris A.St.-Hil.	Em	FG
Poaceae		
Acroceras zizanioides (Kunth) Dandy	Am,Em	FG,Fp
Andropogon bicornis L.	Am, Eb	FG, FM
A. hypogynus Hack.	Am	FG,Fp,SS
A. lateralis subsp. *cryptopus* A.Zanin & Longhi-Wagner	Am	FG

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
A. virgatus Desv.	Am	FG
Axonopus leptostachyus (Flüggé) Hitchc.	Em	FG,SS
A. purpusii (Mez) Chase	Am	FG
A. siccus (Nees) Kuhlm.	Am	FG
Cenchrus nervosus (Nees) Kuntze (*Pennisetum nervosum*)	Am,Em	Fp,V
Coleataenia prionitis (Nees) Soreng (*Panicum prionitis*)	Em	FG
C. stenodes (Griseb.) Soreng (*Panicum stenodes*)	Am	FG
Cyphonanthus discrepans (Döll) Zuloaga & Morrone (*Panicum discrepans*)	Am	FG
**Echinochloa colona* (L.) Link	Am,Em	Fp
**E. crusgalli* (L.) P. Beauv.	Em	Fp,Rb
**E. crus-pavonis* (Kunth) Schult.	Em	Fp
E. polystachya (Kunth) Hitchc.	Am,Em,FF,RF	Fp,Rb,SS
Echinolaena gracilis Swallen	Am	FG
Eriochloa distachya Kunth	Em	Fp
***E. polystachya* Kunth	Em	Fp
E. punctata (L.) Desv. *ex* Ham.	Am	Fp
Eriochrysis warmingiana (Hack.) Kuhlm.	Em	V
Gynerium sagittatum (Willd.) P.Beauv.	Am	Fp
Hemarthria altissima (Poir.) Stapf & C.E.Hubb.	Am	FG,Fp
Hymenachne amplexicaulis (Rudge) Nees	Eb,Em,RF	FG,FM,Fp,L,PP,Rb,SS,TP
H. donacifolia (Raddi) Chase	Am	Fp
H. pernambucensis (Spreng.) Zuloaga (*Panicum pernambucense*)	Am,Em	FG,Fp,Rb
Imperata tenuis Hack.	Am, Eb	FG, FM
Leersia hexandra Sw.	Am,Em	FG,Fp,PP,SS,TP
Louisiella elephantipes (Nees *ex* Trin.) Zuloaga (*Panicum elephantipes*)	Em,RF	Fp,Rb,SS
Luziola bahiensis (Steud.) Hitchc.	Eb,RF	FG,FM,PP,SS
L. fragilis Swallen	RS	FG,TP,V
L. peruviana Juss. *ex* J.F.Gmel.	Am,Em	FG
L. spruceana Benth. *ex* Döll	Eb,FF,RF	FM,Fp,Rb
L. subintegra Swallen	Em,RF	Fp,L,PP,Rb,SS
Mnesithea aurita (Steud.) de Koning & Sosef	Am	FG
Oryza grandiglumis (Döll) Prod.	Em	Fp
O. latifolia Desv.	Em	FG,Fp
**O. rufipogon* Griff.	Em	Fp
***O. sativa* L.	Am	Fp

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
Panicum aquaticum Zuloaga & Morrone	Am	FG,TP
P. dichotomiflorum Michx.	Em	Fp,L,Rb
P. exiguum Mez	Em	V
P. pedersenii Zuloaga	Am	FG
**P. repens* L.	Am,Em	PP,TP,SS
P. tricholaenoides Steud.	Am	Fp,SS
Paratheria prostrata Griseb.	Am	FG
Paspalidium geminatum (Forssk.) Stapf (*P. paludivagum*)	Em	AP,FG,SS
Paspalum acuminatum Raddi	Em	PP,SS,Sw,TP
P. almum Chase	Am	FG
P. fasciculatum Willd. *ex* Flüggé	Am,Em	Fp
P. lenticulare Kunth	Em	Fp
P. morichalense Davidse et al.	Eb,Em	FG,FM,Sw,PP,TP
P. parviflorum Rhode *ex* Flüggé	Em	V
P. plicatulum Michx.	Am	FG,Fp
P. repens P.J.Bergius	RF	L,PP,R,Rb
P. vaginatum Sw.	Am	AP
P. virgatum L.	Am	FG
P. wrightii Hitchc. & Chase (*P. hydrophilum*)	Am,Em	FG,Fp,SS
Rugoloa hylaeica (Mez) Zuloaga (*Panicum hylaeicum*)	Am,Em	Fp
R. pilosa (Sw.) Zuloaga (*Panicum pilosum*)	Am,Em	Fp
R. polygonata (Schrad.) Zuloaga (*P. polygonatum*)	Am,Em	Fp
Saccharum asperum (Nees) Steud.	Em	V
S. villosum Steud.	Em	V
Sacciolepis angustissima (Hochst. *ex* Steud.) Kuhlm.	Em	SS
S. myuros (Lam.) Chase	Em	FG,TP,SS
S. vilvoides (Trin.) Chase	Em	FG
Schizachyrium condensatum (Kunth) Nees	Am	FG
S. sulcatum (Ekman) S.T. Blake	Am,Em	FG,SS
Setaria parviflora (Poir.) Kerguélen	Am,Em	FG,TP,SS
Sorghastrum setosum (Griseb.) Hitchc.	Am,Em	FG
Steinchisma decipiens (Nees *ex* Trin.) W.V.Br. (*Panicum decipiens*)	Am	FG
S. hians (Elliot) Nash (*Panicum hians*)	Am	FG
S. laxum (Sw.) Zuloaga (*Panicum laxum*)	Am,Em	FG,PP,TP,SS
Stephostachys mertensii (Roth) Zuloaga & Morrone (*Panicum mertensii*)	Am,Em	FG,Fp
**Urochloa arrecta* (Hack. *ex* Durand & Schinz) Morrone & Zuloaga (*Brachiaria arrecta*)	Am,Em,RF	Fp,Rb

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
***U. humidicola* (Rendle) Morrone & Zuloaga	Am	FG
Polygalaceae		
Polygala appendiculata A.St.-Hil. & Moq. (*P. leptocaulis*)	Em	FG
P. brasiliensis L.	Em	FG
P. longicaulis Kunth	Am,Em	FG
P. tenuis DC.	Em	FG
Polygonaceae		
Polygonum acuminatum Kunth	Am,Eb,Em	FG,FM,SS,Sw
P. ferrugineum Wedd.	Em,RF	Fp,R,Rb
P. hispidum Kunth	Em	Fp,SS
P. hydropiperoides Michx.	Am,Em	SS,Sw
P. meisnerianum Cham.	Am,Em	SS,Sw
P. paraguayense Wedd.	Em	Fp
P. punctatum Elliot	Am,Em	FG,Fp,Tp
P. stelligerum Cham.	Em	SS,Sw
Pontederiaceae		
Eichhornia azurea (Sw.) Kunth	RF	L,PP,R,Rb,SS
E. crassipes (Mart.) Solms	FF	Fp,R,Rb,L
E. diversifolia (Vahl Urb.	RF	Rb
E. meyeri A.G.Schulz	Em	FG
Heteranthera limosa (Sw.) Willd.	Em	FG,Fp,TP
H. multiflora (Griseb.) C.N.Horn	Em	TP
H. reniformis Ruiz & Pav.	RS,Em	Rb
Pontederia cordata L.	Em	FG,Fp,PP,SS,TP
P. reflexa D.J.L.Sousa (not *P. parviflora* Alexander)	Eb,Em	FG,FM,Fp,PP,SS,TP
P. rotundifolia L.f.	RF	Fp,R,Rb
P. subovata (Seub.) Lowden	RF	Fp,SS,TP
P. triflora (Seub.) G.Augustin et al.	Em,RF	SS
Potamogetonaceae		
Potamogeton pusillus L.	RS	AP
Rubiaceae		
Diodia kuntzei K.Schum.	Am	FG,PP,TP,SS
D. macrophylla K.Schum.	Am,Em	FG
Limnosipanea erythraeoides (Cham.) K.Schum.	Em	FG
L. palustris (Seem.) Hook.f.	Em	V
Pentodon pentandrus (Schumach. & Thonn.) Vatke	Am	TP
Sipanea biflora (L.) Cham. & Schltdl.	Am	SS
S. pratensis Aubl.	Am	V
S. veris S.Moore	Em	FG

(continued)

Table 4.1 (continued)

Family, genus, apecies	Life form	Habitat
Spermacocce glabra Michx.	Am	FG
Solanaceae		
Schwenckia angustifolia Benth.	Em	FG,SS
S. juncoides Chodat	Em	V
Solanum amygdalifolium Steud.	Am	Fp,Rb
Sphenocleaceae		
Sphenoclea zeylanica Gaertn.	Em	Fp,Rb,Sw
Typhaceae		
Typha domingensis Pers.	Em	PP,Sw
Urticaceae		
Cecropia pachystachya Trécul	Eb	FM
Urera aurantiaca Wedd.	Am	Fp
Verbenaceae		
Phyla betulifolia (Kunth) Greene	Am	Fp
P. nodiflora (L.) Greene	Am	FG
Stachytarpheta angustifolia (Mill.) Vahl	Em	FG,TP
Vitaceae		
Cissus spinosa Cambess.	Em	Fp,SS
Xyridaceae		
Abolboda pulchella Humb. & Bonpl.	Am	FG
Xyris jupicai Rich.	Am,Em	TP,SS,Sw
X. macrocephala Vahl	Em	FG
X. savanensis Miq.	Am	FG
X. schizachne Mart.	Em	FG
Zingiberaceae		
**Hedychium coronarium* J.Koenig	Em	Fp

Fennessi 2001). The expression wetland plants, widely used, seems more suitable for seasonally flooded savannas, such as the Pantanal. ‘Palustrine plants’ is another convenient term, also including shrubs and trees (Amaral et al. 2008).

Plant names were checked according to Flora do Brasil 2020 (2020). A few are not yet depicted in Flora do Brasil; in those cases, we consulted other databases, e.g., Jabot (Jabot. JBRJ – Instituto de Pesquisas Jardim Botânico do Rio de Janeiro), Mobot (that organizes The Plant List) (Mobot. Missouri Botanical Garden), JSTOR (Jstore 2020), SpeciesLink (INCT Instituto Nacional de Ciência e Tecnologia 2017), NYBG (NYBG New York Botanic Garden), and GBIF (GBIF Global Biodiversity Information Facility 2017).

From the 533 compiled species, 509 species were Angiosperms, comprising 76 families and 182 genera, nearly all native, only eight naturalized, and three cultivated. Macroalgae, liverwort, ferns, and allies add another 24 species (Table 4.1). In Table 4.1, we did not include voucher number, botanist(s) who identified the species, pollination type, dispersal syndrome, geographic distribution, and endemism in Brazil, already given in the Chap. 3 on Flora, to avoid repetition.

The species richness is far below that of *vereda* wetlands outside the Pantanal. For example, no species of *Sphagnum* has been found in the Pantanal; possibly, they are limited by the harsh regime of flood/drought and fire. The scarcity of Bryophyta in the Pantanal was also observed by Heckman (1998).

The species richest families are Cyperaceae (86 species), Poaceae (76), Fabaceae (35), and Plantaginaceae (24). The most numerous genera are *Ludwigia* (25 species), *Cyperus* (24), *Utricularia* (19), *Rhynchospora* (19), *Eleocharis* (17), *Bacopa* (14), *Scleria* (12), and *Echinodorus* (11) (see the Chap. 3 on Flora).

These families and genera are often the richest in most Neotropical wetlands, e.g., Poaceae and Cyperaceae in the Llanos del Orinoco (Rial 2009), Bolivia (Haase and Beck 1989; Ritter 2000; Beck and Asturizaga 2006; Martinez et al. 2020), Paraguay (Mereles et al. 2015), and the Paraná River floodplains of Esteros del Iberá in Argentina (Neiff et al. 2004, 2011, 2014; Neiff 2001, 2004) and in Brazil (Ferreira et al. 2011), in the North (Moura Júnior et al. 2015b) and the Northeast (Moura Júnior et al. 2015a).

What about **endemisms**? Although it is often said that there are no aquatic endemics in the Pantanal (Pott and Pott 2011), we now consider endemic the wild peanuts *Arachis hoehnei* and the quite recently described *A. linearifolia*, *A. valida*, and *A. vallsii*, all from floodplain grasslands of the Pantanal (Krapovickas and Gregory 2007). We observed that *Arachis vallsii* can send down the geocarpic fruit pegs into the flooded soil of a 60 cm deep lake edge. In contrast, in *vereda* wetlands of the upper basin there occur more endemic species than on the floodplain, such as *Cyperus valiae* Pereira-Silva, Hefler, and Trevis., found in Bonito by its sole collector Vali J. Pott (Pereira-Silva et al. 2018).

Recently two new species were described: *Murdannia engelsii*, already pointed out before as a new species (Pott and Pott 2000), and *Pontederia reflexa* (Sousa et al. 2020). New occurrences are likely to continue to be discovered since undetected species may occur in undersampled areas, or new incomers in disturbed habitats. We are not aware of species threatened by extinction, though a few possible naturally rare species can be considered diminished by selective overgrazing, such as *Discolobium leptophyllum* (Pott and Pott 2000).

A few species we hesitated to include, but we followed the criteria of a herbarium record and a reliable identification, e.g., *Cyperus papyrus*, the famous papyrus from the Nile, recorded as also native to Brazil (Flora do Brasil 2020). *Rotala ramosior* is reported as not occurring in Brazil (Flora do Brasil 2020), but it was identified by Dr. C.D.K. Cook and A. Schinini (Pott and Pott 2000), and occurs in Bolivia and Paraguay, so it could as well exist in the Pantanal.

The ideal would be to show a map of species richness per subbasin or subregion; however, the data available are far from enough because of the scarcity of plant collection in many areas, and deficient information about the location on herbarium labels before the existence of GPS.

4.4 Phytogeography

Like terrestrial species (see the Chap. 3 on Flora), the aquatic species can have various origins from other domains, such as the Cerrado, the Amazon Basin, the Atlantic Forest and the Chaco, besides many Neotropical widespread and some cosmopolitan species. Examples of cosmopolitan species are *Ceratophyllum demersum*, *Lemna aequinoctialis*, and *Pistia stratiotes* (Chambers et al. 2008). In general, aquatic species tend to be widespread, though there are exceptions. Murphy et al. (2019) tested the hitherto generally accepted hypothesis that most aquatic macrophytes have broad distributions and investigated the global distribution, diversity, and endemism patterns of 3457 species that occur in permanent, temporary, or ephemeral inland freshwater and brackish water bodies worldwide. They concluded that small-ranged species constitute most of Earth's species diversity. They found the highest diversity for Central Brazil, around Brasília (Murphy et al. 2019), in areas of headwaters and *veredas* (the *Cerrado* wetlands). For example, many species of *Utricularia* do not have wide distributions (Taylor 1989). An analysis of range-size versus latitudinal distribution of macrophytes showed significantly greater species range sizes at higher latitudes (Murphy et al. 2020). Indeed, many species of the Pantanal have a rather restricted occurrence in Central West Brazil (Pott and Pott 2000). Some have, so far, only been found in northern Pantanal subregions, others in the Chaco.

Floodplain vs. upper basin: many submerged plants in the crystalline waters of the karstic basin in the area of Bonito and the Bodoquena plateau (Pott 1999) contrast with fewer submerged species in the turbid rivers of the Pantanal, except in ponds and some branches of the lower delta of the Taquari, with *Cabomba*, *Echinodorus*, *Nitella* (Moreira et al. 2017b). The absence of Podostomaceae is notable because there are no rapids or waterfalls in the Pantanal and, so far, only *Tristicha trifaria* (Bory & Willd.) Spreng. and *Apinagia riedelii* (Wedd.) P. Royen were recorded in the Taquari upper basin, and *A. divaricata* (Tul.) Wedd. close to the northern limit of the plain.

Species of uncertain introduction into the Pantanal are *Sagittaria montevidensis*, so far only found in a ditch with eutrophicated water along the dyke around Porto Murtinho; *Sphenoclea zeylanica* occurs only in the Paraguay River, a sign that it was possibly brought in by ships from Asia (Pott and Pott 2000).

The Pantanal has floristic similarities with other large tropical and subtropical wetlands, mostly with the Paraná River floodplain (Ferreira et al. 2011) in Brazil and its continuation into Argentina, e.g., the Esteros del Iberá (12.000 km^2) (Neiff 2004; Neiff et al. 2011, 2014); all this area belongs to the La Plata River basin. However, the upper basin of rivers running south nearly connects with some headwaters of the Amazon domain. Thus, the Pantanal also shares species, mainly the most ubiquitous ones, with the Amazonian floodplains (Piedade et al. 2019) and wetlands of Araguaia (Bove 2001; Koehler & Bove 2004, Marimon et al. 2008), Guaporé (Souza and Nunes 2011), Roraima (Pinheiro and Jardim 2015), and Amapá in Brazil, as well as elsewhere in South America, such as the floodable savannas of

Beni (100,000 km^2) in Bolivia (Haase and Beck 1989; Beck and Asturizaga 2006), Argentina (Neiff 2001), Paraguay (Mereles et al. 2015), Peru (Kahn et al. 1993), and the Llanos in Colombia (Fernández et al. 2015, Madriñan et al. 2017) and Venezuela (Velasquez 1994; Rial 2009), etc. In Amapa, the wetland is under tidal influence through the Amazon River delta; i.e., water levels fluctuate up and down twice a day, and many species are the same as in the Pantanal, except some Amazonian species such as *Montrichardia* spp. Though not being coastal freshwater marshes, they are tidal (Mitsch and Gosselink 1993).

The Pantanal is an assembly of various floristic influences: the Cerrado, Amazonia, the Chaco, the Atlantic Forest (Adámoli 1982), the Seasonally Dry Forest, and many species have wide distributions (Prance & Schaller 1982, Pott and Ratter 2011; Pott and Silva 2015) (see the Chap. 2 on Vegetation Mapping). Thus, the Pantanal, with its many widespread aquatic species, fits the common phytogeographic pattern. Many of those species have Neotropical distributions. A few occur in two continents, such as *Cyperus haspan*, *Hemarthria altissima*, and *Steinchisma laxum*. Some even occur worldwide, pantropical, e.g., *Acroceras zizianoides*, *Cladium mariscus* subsp. *jamaicense*, *Ceratophyllum* spp., *Ceratopteris thalictroides*, *Cyclosorus interrupta*, *Cyperus digitatus*, *C. esculentus*, *C. haspan*, *C. odoratus*, *Echinochloa colona*, *E. crus-galli*, *Eclipta prostrata*, *Eleocharis acutangula*, *E. vaginata*, *Enydra radicans*, *Fimbristylis dichotoma*, *Fuirena umbellata*, *Hydrocotyle ranunculoides*, *Ipomoea asarifolia*, *Leersia hexandra*, *Lemna aequinoctialis*, *Ludwigia helminthorrhiza*, *L. leptocarpa*, *L. octovalvis*, *L. peploides*, *Neptunia prostrata*, *Nymphoides indica*, *Paspalum vaginatum*, *Pistia stratiotes*, *Pityrogramma calomelanos*, *Ricciocarpos natans*, *Rotala mexicana*, *Salvinia auriculata*, *Thalia geniculata*, *Typha domingensis*, *Utricularia foliosa*, *U. gibba*, and *Wolffiella welwitschii* (Chambers et al. 2008; Murphy et al. 2019). Most of them are weeds somewhere, also in irrigated crops and reservoirs in Brazil, but not in the Pantanal.

There are some species spread throughout the Pantanal, such as *Cyperus surinamensis*, *Echinodorus paniculatus*, *Eichhornia azurea*, *Sagittaria guayanensis*, and *Thalia geniculata* (Pott and Pott 2000), whereas others have a very limited distribution area. Also, some species have a disjunct distribution, e.g., *Nymphaea belophylla*, only recorded twice in the Pantanal, c. 500 km apart (Amador et al. 2013). Another species with a disjunct distribution is *Xanthosoma aristiguetae*, from Venezuela (Velasquez 1994), which, so far, we found only once near the Miranda river (Pott and Pott 2000). A few species are exclusive to the Northern Pantanal, e.g., *Apalanthe granatensis*, *Bacopa egensis*, *Ceratopteris thalictroides*, *Discolobium psoraleaefolium*, and *Eichhornia diversifolia* (Pott and Pott 2000). *Bacopa egensis* has recently been found near the northern border of Mato Grosso do Sul. With further sampling this may also be the case with other species so far believed exclusive from Mato Grosso, and vice-versa, also regarding eastern and western zones of the Pantanal. Likewise, others occur exclusively in the southern part, such as *Bacopa gratioloides* (previously identified as *B. cochlearia*, Pott and Pott 2000), *Cabomba haynesii*, *Ceratophyllum demersum*, *Eichhornia meyeri*, *Nymphoides indica*, *Sagittaria montevidensis*, and *Stemodia ericifolia* (Pott and

Pott 2000); some of these are among the 48 aquatic plants cited for the Brazilian Chaco (Sartori et al. 2018a, b). There is also a strong difference in soil types and flood level and flood duration reflected in species distribution between those from the eastern Pantanal, e.g., *Abolboda pulchella*, *Centropogon cornutus*, *Echinodorus longipetalus* (typical of *vereda*) (Pott and Pott 2000), and *Saccharum* spp. (typical *vereda* grasses), and those from the western areas (e.g., *Victoria amazonica*) of the floodplain. The giant water lily (*V. amazonica*) is restricted to the Cuiaba and Paraguay rivers but curiously does not occur downstream of Corumbá and Ladário, though reappearing further south in neighbouring Paraguay (Mereles et al. 2015). Numerous aquatic species of the upper basin, e.g., *Myriophyllum aquaticum*, *Potamogeton illinoensis*, and *P. gayi*, present in headwaters of the Miranda River in Bonito (Pott 1999), and also the introduced *Rorippa nasturtium-aquaticum* and *Vallisneria spiralis*, as well as many species from the *veredas*, are not found on the floodplain (Pott et al. 2011), e.g., *Miconia chamissois*, though their seeds are carried to the Pantanal. Surprisingly, *Nymphaea novogranatensis* is another species found in ponds upstream beyond the northern limit of the Pantanal (Silva and Carniello 2007); it is known from Venezuela but not yet recorded in Flora do Brasil 2020 (2020).

A few typical families of wetlands were not yet found in the Pantanal, though they occur in the upper basins: Juncaceae, Juncaginaceae, Ranunculaceae (except *Clematis*, terrestrial), and Rapateaceae. Podostemaceae are absent for lack of waterfalls.

It is important to point out that the geographical distribution of aquatic species in the Pantanal, as well as in other wetlands in South America (Neiff 2001), does not coincide with the phytogeographical regions of the terrestrial vegetation. That is because aquatic species have very broad niches that allow them to colonize very different habitats with highly variable hydroperiods. On the other hand, the lack of orographic barriers from Patagonia to the north of South America and the gradual nature of the climate gradient are favorable for the wider distribution range of the Pantanal aquatic plants.

For the past aquatic vegetation, see the Chap. 12 on Palynology.

4.5 Ecology

Ecology, biodiversity and conservation were addressed by Neiff (2004), Nunes da Cunha et al. 2010, Junk et al. 2011, Junk and Nunes da Cunha (2016), Many reports on the vegetation of the Pantanal are not exclusively on aquatic species and involve some aspect of ecology (Da Silva 1989; Pott et al. 1999; Schessl 1999; Junk and Nunes da Cunha 2016, Catian et al. 2018), while others focus on aquatic species (Pott and Pott 2011; Catian et al. 2019; Delatorre et al. 2019). Diversity and species richness are higher in the wet phase in floodable grasslands (Rebellato and Cunha 2005). Floodable herbaceous communities in the Pantanal have a high beta-diversity (Rebellato et al. 2012). In the Pantanal National Park, the richness of different habitats varied between 11 and 45 species and the diversity index of Shannon-Wiener was higher in the flooded phase (Pott and Pott 2011).

There are various reports on the structure or phytosociology of aquatic vegetation (e.g., Catian et al. 2012; Cunha et al. 2012; Lehn et al. 2012; Rebellato and Cunha 2005; Pivari et al. 2008; Rebellato et al. 2012; Rocha et al. 2015; Gomes & Aoki 2016, Moreira et al. 2017a).

There also are a number of papers on the biomass productivity of individual species, such as *Pontederia lanceolata* (now *P. reflexa*) (Penha et al. 1999), floating mats (*camalotes*) such as *Eichhornia azurea* (Lima et al. 1999, Oliveira et al. 2005), and oxbow lakes (Kufner et al. 2011). For example, in five ponds in the Nhecolândia subregion, *Cyperus blepharoleptos* (=*Oxycaryum cubense*) presented the greatest aerial biomass (194 g.m^{-2} dry weight) on floating meadows (Pott and Pott 2011). The dynamics of aquatic vegetation have been described by various researchers, such as Pott et al. (1999), Rebellato and Cunha (2005), Rebellato et al. (2012), and Coutinho et al. (2017).

Grasslands and swamps may not look beautiful after drawdown because of rotten leaves and organic debris. Debris can hamper the regrowth and seedling emergence, mainly in low areas, such as seasonal ponds (Bao et al. 2018). That dry plant material feeds periodical wildfires, even in temporarily deep-flooded areas (see the Chap. 18 on Fire).

Functional traits recently receive attention (Catian et al. 2018; Delatorre et al. 2019). We consider the following traits as particular to aquatic species (see more details in the Chap. 16 of Morpho-anatomical Adaptations):

- Adventitious roots are found on most aquatic species. In dicots, they are more profuse in *Aeschynomene* spp., *Aspilia latissima*, *Discolobium* spp., *Hibiscus sororius*, *Ipomoea carnea*, *Ludwigia* spp., *Pavonia angustifolia*, *P. laetevirens*, *Polygonum* spp., *Sesbania exasperata*, *Vigna lasiocarpa*. Also, many aquatic grasses also emit roots on aerial nodes (e.g., *Leersia hexandra*). It is adaptive at sites where water rises fast, and also eases rooting when the flood recedes, e.g., *Oryza*. *Ludwigia* spp. produce white adventitious aerenchymatous roots for gas exchange.
- Hollow stems, leaf petioles, and roots are very common in true hydrophytes (*Victoria amazonica*), facilitating upward growth and flotation and providing oxygen to the roots; thick leaves with aerenchyma (*Limnobium laevigatum*) and inflated flower pedicels (*Limnocharis flava*) have similar functions. Spongy stems (not always aerenchyma)play the same role (*Aeschynomene* spp., *Alternanthera aquatica*, *Discolobium* spp., *Schwenckia angustifolia*). Leaf-like fistulous stems with membranous cross partitions, when grazed or injured, reduce the entrance of water and pathogenes, e.g., in *Eleocharis interstincta* (Pott and Pott 2000).
- Hydrophobous leaves, with waxy cuticles on the upper surface (*Nymphaea* spp., *Nymphoides grayana*, *Spirodela intermedia*) or hydrophobous trichomes (*Pistia stratiotes*, *Salvinia* spp.), are nearly unwettable (Kaul 1976). Hydrophobous flowers also repel water, e.g., in *Limnobium laevigatum*, either the female or the

male flowers close when pulled below the water surface or hit by a wave, as well as hairy flowers of *Nymphoides* spp. Stomatodes function as drains for rainwater in *Victoria amazonica* (Kaul 1976), and it has a drainage slot on one side of the lifted leaf rim (Fig. 4.12).

It seems paradoxical that in aquatic habitats, whitout water shortage, some species have almost leafless green branches, such as *Byttneria genistella*, or narrow leaves as *Discolobium leptophyllum*, *D. psoraleaefolium* and *Schwenckia angustifolia*. Perhaps this might reduce herbivory, at least in the case of *Discolobium* spp., relished by cattle and deer. The presence of latex also seems strange, e.g., in Alismataceae.

4.6 Aquatic Weeds

Aquatic weed is perhaps not a nice designation for aquatic plants, but many species cause problems and require expensive control. However, in the Pantanal, where in balance with their predators, from fungi to animals, they are not as weedy as where they have been introduced. One of the great predators and consumers of aquatic plants in the Pantanal is the mollusc *Pomacea* (Cruz et al. 2015), as well as capybaras, fish, insects, and even ants. That snail becomes a pest in cultivation tanks when its larvae come with the plants from the wild, far from the snail kite that feeds on it. Many other associations with fauna were not referred to here.

Sometimes, aquatic macrophytes can become a nuisance even in the Pantanal; they can hinder navigation, e.g., as floating meadows and floating mats displaced by floods, going downstream (Fig. 4.3). For example, massive water hyacinth mats and floating meadows often chock waterways used by riverine people to access their houses or fishing areas, generally at flood. Some other species can form dense floating mats at flood, e.g., *Hymenachne amplexicaulis* and *Luziola subintegra* (Kissmann and Groth 1997; Beck and Asturizaga 2006). Floating mats of *E. crassipes* may block the Tamengo channel between Brazil and Bolivia. Once a large floating meadow pushed over the pillars of a wooden bridge (Pott and Silva 2015).

In other countries, by far the worst and most famous aquatic weed is the water hyacinth *Eichhornia crassipes*. *Eichhornia* and other Pontederiaceae contain calcium oxalate crystals (Prychid and Rudall 1999), probably a defense mechanism against herbivory, and it may explain the invasivesness of this species outside its natural habitat. But capybaras can feed on it (Heckman 1998). In fact, researchers have looked for natural enemies of *E. crassipes* in the Pantanal, to be used for biological control, and one is the grasshopper *Cornops aquaticum* that feeds exclusively on Pontederiacee (Llano et al. 2005).

Besides *E. crassipes*, many other invasive species occur in artificial lakes and reservoirs in Brazil, including submerged species, such as *Egeria densa* and *E. najas*. Some other less troublesome weeds in impoundments are *Alternanthera philoxeroides*, *Eclipta prostrata*, *Hydrocotyle ranunculoides*, *Hymenachne*

Fig. 4.3 Floating mats and floating meadows of aquatic plants, displaced by flooding, many disrupted, drifting downstream to Paraguay and Argentina, Paraguay River, near Porto Murtinho, the southernmost portion of Pantanal wetland. (Photo: A. Pott)

amplexicaulis, *Ipomoea carnea*, *Limnocharis flava, Phyllanthus fluitans*, *Pistia stratiotes*, *Salvinia biloba*, and *Typha domingensis*. We have seen *Cyperus blepharoleptos* invading reservoirs, as one in the Sucuriu River, where the floating meadows are being retained by steel cables to stop them from chocking the hydroelectric power turbines. In other reservoirs such problems have been caused mainly by submerged plants (Marcondes et al. 2003), while only later the sedge invaded.

Several exotic aquatic weeds of continental waters have been found in Brazil (Ferreira et al. 2016b). And though exotic weeds certainly can be a nuisance in many wetlands around the world, the Pantanal has not yet been affected. That is related to the flat geomorphology and the alternation of flood and dry phases. So far, no woody invaders such as *Melaleuca* or *Schinus* have entered the Pantanal (Pott and Pott 2000). The worst exotic aquatic weed and by far the most severe threat in the Pantanal is the African tanner grass *Urochloa arrecta* (earliear misidentified as *U. subquadripara*), that spreads in clayey habitats (Pitelli et al. 2000), even into undisturbed systems such as the aquatic vegetation in the Parque Nacional do Pantanal (Pott and Pott 2003; Pott and Pott 2011). However, the vigorous *Louisiella elephantipes* (*Panicum elephantipes*) competes quite well with it (Pott et al. 2011); both are C_4 grasses (Fig. 4.4). Other species of *Urochloa* are less invasive, such as the widely cultivated *U. humidicola*, that is controlled by native aquatic plants during the floods (Bao et al. 2019), and the smaller spontaneous *U. distachyos*, which also mixes quite well with the native species.

Another weedy species is the Australian *Panicum repens* (torpedo-grass) (Pott and Pott 2003), very tolerant of grazing. Introduced as a forage plant for floodable

Fig. 4.4 Underwater garden with *Ludwigia inclinata* (red leaves) and some submerged juveniles of *Eichhornia azurea* (green), in crystalline water filtered by aquatic vegetation, in a branch of the lower Taquari River. (Photo: A. Pott)

areas, it quickly spreads around ponds and seasonal streams, outcompeting native species.

Luckily, so far, no invasive, exclusively aquatic plant species has appeared in the Pantanal. But it might be just a matter of time, for the feared, submerged *Hydrilla verticillata* to arrive in the Paraguay River, a tributary of the Paraná River, where the species already infests hydroelectric power reservoirs. Any seed or vegetative piece can propagate and spread this species, stuck on fishing gear or boats, or perhaps even with migrating fish. Another species that might soon enter the plain is *Limnophila sessiliflora* (Asian marshweed), an aquarium plant, already present on shores of reservoirs close to the Pantanal watershed. The Asian *Hedychium coronarium* is abundant around the floodplain but, so far, has spread only a little across the border.

4.7 Aquatic Habitats

In Table 4.1 we mention the predominant habitat for each species. However, we simplified the habitats into a few broad types since to split them into the macrohabitat (see the Chap. 7 on Macrohabitats) described by Nunes da Cunha et al. (2014) would be too long and repetitive, as many species can occupy various habitats. Apart from the macrohabitat, there are countless suitable microhabitats.

Species differ in preference for lotic or lentic water, but some occur in both. Often a habitat can switch between lotic and lentic, depending on the flood height and duration of flood and drought phase. The predomantly lotic habitats of the Pantanal are rivers, branches (*corixos*), old riverbeds, and seasonal streams (*vazantes*). The predominantly lentic water bodies are shallow lakes, oxbow lakes (except at flood), freshwater ponds, temporary ponds, brackish ponds, swamps, borrow pits, and floodable grasslands (Pott and Pott 2000).

Some habitats that can be either lotic or lentic (Catian et al. 2012), i.e., lentic at low waters and lotic at floods, such as paleocanals and anabranches. The water in the connection channels of these habitats with the river may flow in or out, according to the river's pulse. All these water bodies are more or less equivalent to the macrohabitats classified in a hierarchical system by Nunes da Cunha et al. (2014) (see the Chap. 7 on Macrohabitats).

Another habitat characteristic is the origin of the flood waters: whether it is pluvial, as most of the Pantanal with waterlogging areas, or fluvial (flooded), and often it can be both (Pott and Pott 2000). The *salina*, alkaline pond, is a closed system fully fed by rain and runoff and percolation from the enclosing sandy ridge.

The geomorphology and thereby the type of water bodies varies between subregions: so, the eastern part of the subregions of Nhecolândia and Aquidauana have closed drainage systems (lentic), with many ponds fed by rainfall, with little or no connection to rivers, whereas ponds of Abobral are more subjected to river overflow. In other subregions, such as Miranda, Paiaguás, Poconé, Barão de Melgaço and Cáceres, instead of ponds, the drainage is open (Pott and Pott 2011). The Paraguay subregion covers the almost permanently, deep-flooded parts of the river floodplain, like backswamps, oxbow lakes, and other lakes. These are the usually shown Pantanal images, where tourism and sightseeing is concentrated, but rivers and lakes are rather scarce in most of the plain.

We describe briefly the main habitats of aquatic plants (see the Chap. 7 on Macrohabitats):

River It seems so obvious what a river is, but navigating in the Pantanal can give another impression, mainly when the unaware takes a wrong diversion that seems to be the main bed. Besides the present riverbed, there is an associated anastomosed or meandric system of channels, oxbow lakes and shallow lakes in its floodplain, typical of floodplain rivers. There usually is a zonation of oligo-dominant aquatic species, e.g., of the genera *Aspilia*, *Oryza*, *Eichhornia*, *Polygonum*, *Thalia*, etc.

The water bodies of the Paraguay River floodplain can have a diverse aquatic vegetation, with many species with high dominance (Souza et al. 2013). Near Porto do Amolar, species richness was around 65 species (Aoki et al. 2017). The water velocity can have a limiting effect on some aquatic plant species: some occur near the convex margin, and not or less at the opposite, concave side where the flow in the channel is faster. The calm side, generally shallower, is a habitat of tall emergent (e.g., *Polygonum* spp. and several grasses) and floating plants, that are anchored (e.g., *Eichhornia azurea*, *Pontederia rotundifolia*), sheltering small free-floating species (e.g., *Azolla filiculoides*, *Phyllanthus fluitans*, *Salvinia auriculata*) from being carried by the current.

River Branches, Paleocanals, and Anabranches They are regionally called *corichos*, from Bolivian Spanish *curiche* (Beck and Asturizaga 2006), or floodplain streams. Anabranches or river branches are regionally called rivers (e.g., Bracinho, Nabileque, Negrinho, Paraguai Mirim, Paraguaizinho, Verde), but they are false rivers because they lack an own upper watershed. Paleocanals are ancient riverbeds, such as the Areião, Cassange, Corixão, Mutum, Pixaim, Saran; some are also called rivers (e.g., Abobral and Vermelho). They can be new channels, such as the Taquari River delta defluents, e.g., the new Taquari River, originating from a crevasse of the old bed. Most running waters in the Pantanal are turbid. Thus, transparent waters only occur in ponds or after being filtered by aquatic vegetation. For example, in a branch of the lower Taquari River, 21 species were recorded in an underwater garden (Moreira et al. 2017a); such waters became diving and spear-fishing spots. Some of the rooted submerged species in clear waters are *Echinodorus paniculatus*, the juvenile form of *Eichhornia azurea*, *Eleocharis minima*, and *Ludwigia inclinata* (Fig. 4.4) (Moreira et al. 2017a). The branches and canals can become clogged by local and incoming floating meadows, e.g., the Paraguay River branch Mirim was choked for 20 years, and that histosol dried in 2020 and turned into a colossal wildfire (see the Chap. 18 on Fire). Dense, anchored mats of *Louisiella elephantipes* are frequent (Fig. 4.5).

Oxbow Lake They are lentic most time of the year and sometimes lotic, when they are connected to the river, at flood. Oxbow lakes are the main habitat of *Victoria amazonica*, generally associated with *Paspalum repens*. There are other types of riverine lakes of similar origin; they developed from abandoned riverbed sections and are isolated, though coalescent at high waters (Nunes da Cunha et al. 2014).

Fig. 4.5 Dense, anchored floating mats of *Louisiella elephantipes* (elephant panicgrass), Paraguay River branch, at high water. (Photo: A. Pott, July 9, 2013)

Seasonal Stream (*vazante*) They are lotic, intermittent shallow courses, mostly without a well-defined channel. They distribute and collect water to and from the floodable grasslands in the wet-and-dry regime. The largest streams have parts with a deeper channel (where stagnant pools can remain over the entire dry season), gallery forest (with *Leptobalanus parvifolius* as the main tree, see the Capt. on Monodominants), nesting colonies of wading birds where fish concentrate. In the nearly transparent, slow-flowing water-rooted submerged plants grow, such as *Bacopa myriophylloides*, *B. reflexa*, *Ludwigia inclinata*, and *Nitella cernua* (Pott and Pott 2000). Some streams in Nhecolândia have a name, e.g., Aguassuzal, Capivari, Corixinha, Mangabal, and Riozinho. In the Paiaguás subregion there are more seasonal streams, such as the Arrozal and Formoso, that also are probably ancient overflow streams diverted from the Taquari River bed, whose flood is discharged in these defluents.

Pond They can exhibit various shapes and sizes. There is not a sharp distinction between "lake" and "pond," "permanent" and "temporary pond," and "temporary pond" and "flooded grassland"; they rather form a continuum. But only very few "permanent" ponds remain in dry years, when some are deepened to water cattle, which creates an extra habitat diversity. The ponds generally have a high cover of aquatic vegetation, detectable from satellite images (Abdon et al. 1998) and drones, nowadays with enough resolution to identify species. Many ponds are sinuously lined up, more or less parallel to paleolevees, which is attributed to their origin in alluvial fans, as they are old meander scrolls. Those in a same drainage line become interconnected at flood time, and this affects dispersal of seeds and propagules (Catian et al. 2018). Pond vegetation is generally arranged in a concentric zonation (Fig. 4.6) according to water depth (Pott et al. 1989) and the composition varies much seasonally and plurianually according to rainfall and river fluctuations (Pott and Pott 2000; Da Silva et al. 2001; Pott and Silva 2015; Ximenes et al. 2017; Catian et al. 2018).

Floodplain This is a widely occurring low-lying landscape, seasonally flooded by rivers as well as by local rain, located in between long-lasting water bodies and flood-free ground. It is also a most variable habitat, showing a continuum of flood depths and durations, lotic to lentic water, and various sediment types. An abundant landform is the backswamp, often with monodominant species such as *Eichhornia* spp. and grasses, where histosol accumulates and someday burns when it dries. In a broad sense, floodplain includes most habitat types of the Pantanal. Riparian forests, when flooded, shelter a few aquatics, mainly the shade-tolerant as *Lemna*.

Lake Most large lakes in the Pantanal – Cáceres, Castelo, Gaíva, Mandioré, Negra, Uberaba, and Vermelha (see map in the Chap. 2 on Vegetation mapping) – are located near the Serra do Amolar range, where they remained as such probably because they stayed out of the main sediment flux of the Paraguay River. Though connected with the river, the lakes receive water at times of flood or discharge water that arrived through tributaries from the hills. Many are partially in Bolivian terri-

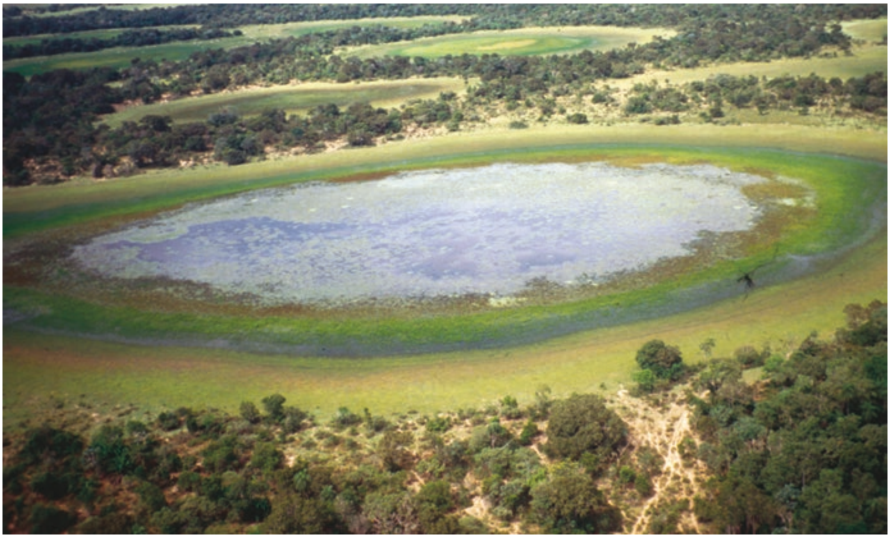


Fig. 4.6 Concentric zonation of aquatic vegetation in a pond. (Photo: A. Pott, October 30, 1993)

tory. A few lakes are further inside the plain, on the Cuiabá River floodplain, such as Chacororé and Sinhá Mariana. The lakes hold predominantly open and turbid waters and tend to have aquatic plants only in zones that are more protected from high waves, or at shallower places where emergent species, that are somehow wave-tolerant, can grow (e.g., *Discolobium pulchellum*, *Oryza latifolia, Polygonum* spp., *Thalia geniculata*), often behind a wave-breaking barrier of anchored floating mats of *Eichhornia azurea*. The aquatic plant cover has increased over the last decades (Lo et al. 2016). The habitat is lentic at low waters and slightly lotic at flood time (Catian et al. 2012). The aquatic vegetation of the lake system is composed of around 67 species in the Cáceres lake (Frey 1995), in the Mandioré 59 species (Catian et al. 2012), and in the Castelo 57 species (Cunha et al. 2012). Nonetheless, the Jacadigo lake has a high cover of aquatic vegetation, including floating mats of *Typha domingensis*, perhaps because it is smaller and in dry years it nearly dries out, allowing marshy plants to grow, such as *Cyperus giganteus*. Marsh size influences species zonation (Mitsch and Gosselink 1993). The Jacadigo lake receives a creek polluted by iron and manganese mining activities. In dry years, even floating mats of *C. giganteus* can burn (Rocha et al. 2015). In the drought of 2020, the Jacadigo lake dried out, just as other shallow lakes, and wildfires swept through the dry vegetation and accumulated histosol. The buoyancy of *Typha* floating mats is caused by gases trapped beneath them (Mitsch and Gosselink 1993).

Alkaline Pond (*salina*) They are isolated from surface freshwater by a surrounding ridge (paleodike) and are endorheic, but are different from the truly salty *salinas* in the semiarid Argentinian Chaco and arid Bolivia; instead of sodium chloride, the predominant salts are carbonates of sodium (319 ppm) and potassium (290 ppm) (Pott et al. 1987), though the southwesternmost *salinas* near the junction of the roads MS-184 and MS-228 are saltier. The water is blue or green, containing mostly algae, including macroalgae (*Chara*, *Nitella*), and very few macrophytes, such as the submerged *Ceratophyllum demersum* and *Najas guadalupensis*, or none at all where the pH is up to 10, and just a few halophytes occur on the shore, e.g., *Eleocharis vaginata*, *Eragrostis pyramidatus*, and *Paspalum vaginatum*.

Floating Meadows They are floating marshes, with a substrate composed of a thick organic mat, entwined with living roots; they occur in tropical wetlands worldwide (Mitsch and Gosselink 1993), also in the Amazon (Junk 1970). They are also called sudd (Heckman 1998), that is a similar type in South Sudan (Mefit-Babtie 1983). The floating marsh is a curious case of succession since it seems to be an endpoint in development and to support a stable community (Mitsch and Gosselink 1993). Plant succession in water bodies starts from *Cyperus blepharoleptos* (formerly *Oxycaryum cubense*) growing on top of floating mats of *Salvinia* spp. and other free-floating plants, forming a floating meadow with its entangled rhizomes filled with air, and accumulating debris (Fig. 4.7), followed by the build-up of a floating histosoil and further colonization by hydrophylous species (Pott and Pott 2003; Pivari et al. 2008; Coutinho et al. 2017).

Fig. 4.7 A floating mat of *Cyperus blepharoleptos* (formerly *Oxycaryum cubense*) growing as an epiphyte on top of *Salvinia auriculata*, beginning to form a floating meadow of entangled rhizomes and debris, the start of a floating soil (histosol). (Photo: A. Pott)

The subshrub *Rhynchanthera novemnervia* (Fig. 4.8) and the shrub *Ludwigia nervosa* colonize the floating meadow. Later on, follow terrestrial herbs (e.g., *Erechtites hieracifolius*) and even treelets, such as *Cecropia pachystachya* and *Tabebuia insignis* (Pott and Pott 2003; Pivari et al. 2008; Coutinho et al. 2017). These plants expand their roots in the form of a dish in the top 20 cm of the soil, occupying more area than their crown, to increase the support of the treelets (Neiff 2004). In Bolivian wetlands also occur floating islets of *T. insignis* (Beck and Asturizaga 2006). The floating meadow seems to function as a hydroponic system since the roots grow in floating, waterlogged, organic soil with water underneath, but the aerial part stays safe from submersion because the floating substrate keeps up with the rise in water level; thus, even non-aquatic plants can grow on it. It probably is an important seed bank, but that would need research. Diaspores can come in via wind (*Andropogon bicornis*, *Barrosoa*, *Erechtites*, *Imperata*, *Tabebuia insignis*, the ferns *Pityrogramma calomelanos*, and *Cyclosorus interrupta*), via water [*Ipomoea carnea*, *Luziola* spp., *Polygonum* spp. (Catian et al. 2017), Pontederiaceae], via birds and bats (*Cecropia pachystachya*), and mammals and fish (some grasses). Even caymans and capybaras disperse plants on their back. Caymans also nest on top of floating islets.

Some species growing on such floating meadows were included into the epiphytic life form by Tur (1972), and this was taken over by other wetland botanists (Irgang and Gastal 1996; Pott and Pott 2000). But Pivari et al. (2008) restricted the term “epiphyte” to the species of the initial succession phase, mainly *C. blepharoleptos*, growing on top of *Salvinia* spp., *Limnobium laevigatum*, *Utricularia gibba*. In contrast, Pivari et al. (2008) called those later-stage plant species rooted on the histosol *embalsadas*, meaning “on a barge or ferry boat.” It is almost the same term *embalsados* in Spanish, used in Argentina (Neiff 2004). In the Uberaba lagoon, the *embalsadas* can form a 40 cm thick, floating, organic soil (Fybric Histosol), on which can occur more than 20 species in a 20×20 m plot (J.J. Neiff, Pers. Comm. 2020). The histosol thickness is an indication of the water residence time. After a few years, the histosol can reach a thickness of 1 m or more, on which people can walk (Fig. 4.9). Should the woody species be considered aquatic? Well, it is a floating habitat, a floating island. The *Cecropia* is mostly terrestrial; and *T. insignis*, despite its wind-blown seeds, is not found anywhere else in the Pantanal, only in wetlands (*veredas*) in the upper watershed. In atypically dry years, when the histosol dries up, as happened in 2020, it is fuel for massive wildfires that are hard to control, and that can spread below the surface and last for weeks.

Floodable Grasslands They occur in between longer-lasting water bodies and flood-free ground; the sites where they occur are very variable as regards flood gradient and soil type. There are many reports on the floristics of this wet-and-dry zone (Allem and Valls 1987; Prado et al. 1994; Heckman 1998; Schessl 1999; Rebelatto and Cunha 2005; Pott and Pott 2011; Rebelatto et al. 2012; Bao et al. 2014, 2017). It is by far the main landscape in the Pantanal: it is seasonally shallowly flooded or waterlogged, usually only by local rains, with a wet phase when the aquatic plants appear; some are perennials arising from dormant rhizomes (e.g., *Echinodorus*

Fig. 4.8 Floating meadow with *Ludwigia nervosa*, one of the shrubs that colonizes the floating histosol. (Photo: A. Pott)

Fig. 4.9 A floating meadow with 1 m deep histosol (9 persons walking on it, including the photographer, at a Field Course on Aquatic Macrophytes); *Polygonum acuminatum* in the foreground, the red plant is *Rhynchanthera novemnervia*, and riparian forest is seen in the back, in lake Baía Vermelha, near the Paraguay River, Pantanal wetland, Brazil. (Photo: A. Pott, June 2, 2009)

paniculatus and *Eleocharis acutangula*), but most annuals emerge from the soil seed bank (e.g., *Bacopa arenaria*, *Helanthium tenellum*, and *Sacciolepis myuros*). After the flood, the leaves of rooted floating life form plants dry up and the aerial parts stop growing, but some species can produce new, smaller leaves and still flower (e.g., *Nymphaea gardneriana* and *Sagittaria guayanensis*). Many natural grasslands have been invaded by trees, mainly *Curatella americana* and *Vochysia divergens* (see the Chap. 11 on Encroachment), and consequently herbaceous vegetation diminished, including the seasonal cover of aquatic species. There are many types of natural grasslands, on soils with different texture and fertility levels, under various flood depths and residence time, resulting in various dominant species. The main natural grassland types as regards the dominants and their companion species are as follows:

(a) *Paspalum lineare*/*P. carinatum* (*fura-bucho*) grassland occur mainly in the eastern zone of Paiaguás and Nhecolândia, on very nutrient-poor sands, with *Abolboda pulchella*, *Coleataenia stenodes*, *Drosera communis*;
(b) *Elionurus muticus* (*caronal*) is a nearly flood-free grassland, but during the rainy season a few short-lived hygrophytes can show up, e.g., *Hyptis brevipes*, *Ludwigia octovalvis*, and *Schoenoplectiella supina*;
(c) *Axonopus purpusii* carpets contain *Cyperus* spp. and the ephemeral *Curtia tenuifolia*, *Helanthium tenellum*;
(d) *Andropogon hypogynus*/*Reimarochloa* spp. grassland has intermingled aquatic species, e.g., *Hymenachne amplexicaulis*, *Leersia hexandra*, *Murdannia engelsii*, *Steinchisma laxum*;
(e) *Paspalum wrightii* dominates the herbaceous stratum between earthmounds of the *Tabebuia aurea* savanna, with *Andropogon hypogynus*, *Echinodorus longiscapus*, *Paspalum plicatulum*, *Sorghastrum setosum*;
(f) *Paspalum fasciculatum* forms riverside grassland with interspersed *Cyperus ochraceus*, *Echinodorus glaucus*, *Melochia arenosa*, shrubs and vines;
(g) *Vereda*: This permanently wet habitat was rather recently mentioned for the Pantanal. Silva et al. (2000) mapped *Mauritia flexuosa* in the Pantanal, and Moreira et al. (2017b) showed that some of those areas are true *veredas*, with typical associated species, while others are *buritizais* with companion species shared with aquatic and floodable habitats of the Pantanal (Fig. 4.10).

Artificial Water Bodies They are burrow pits (a civil engineer term) along the few roads, some clay pits for brick factories, and water holes for cattle, excavated to

Fig. 4.10 *Buritizal* of the palm *Mauritia flexuosa*. The herbaceous stratum is composed of aquatic species of the Pantanal (e.g., *Cyperus giganteus* and *Pontederia reflexa*), not of *vereda* species. The picture is taken in the wet season, in the State Park of Rio Negro, Pantanal. (Photo: A. Pott, April 25, 2007)

access the groundwater in ranches without natural ponds. Burrow pits along roads are relevant because of their length and their availability as a refuge for species in the dry season. At cattle ranches, landfills were made for aeroplane strips and houses, also leaving burrow pits. These human-made water bodies become colonized by aquatic plants, that can also undergo succession to floating meadows. Another type of seasonally water bodies, also linear, are vehicle tracks; the deepest are those left by tractors, the usual vehicle; they are colonized mainly by *Eleocharis minima*, *Pontederia reflexa*, and *Sagittaria guayanensis*.

4.8 Life Forms

The classification of life forms in relation to the water surface proposed by Irgang and Gastal (1996), followed by Pott and Pott (2000), and modified by Pivari et al. (2018), is very practical. The Raunkiaer's system, considering the position of the survival buds (phanerophytes, chamaephytes, hemicryptophytes, geophytes, and therophytes), is not suitable for aquatic plant species, as it applies to plants in general. Approximately 70% of the aquatic plant species in the Pantanal are emergent and amphibious (Pott and Pott 2011). The low occurrence of submerged species is attributed to dense covers of *Salvinia* (Heckman 1998) and turbidity.

Neiff (1979, 1990) described the plasticity of some of the species occurring in the Pantanal. The presence of different ecophenes in each phase (waterlogged/dry) is frequent (Neiff 1979). As known, some plants (*Ludwigia* spp., *Nymphoides* spp., *Victoria amazonica*) can accelerate their growth rate by up to five times when covered by flood water, without modifying their bioform, as Neiff (1990) commented. Also, as mentioned before (Irgang and Gastal 1996; Pott and Pott 2011), many species can show more than one life form, i.e., two or more combined life forms during the life cycle. For example, *Helanthium tenellum* changes from rooted submerged to emergent, to terrestrial, i.e., amphibious; the filamentous and viviparous submerged *Eleocharis minima* is quite distinct from the terrestrial fertile form; *Neptunia plena* can be a free-floating herb or an erect terrestrial subshrub, as well as *Leersia hexandra* (Pott and Pott 2000). Some plants do not have a readily definable life form, e.g., a few species of *Genlisea* and *Utricularia* that have no leaves but phyllodes growing submerged in the mud instead of in water, only the inflorescence is emergent; they were included in the rooted submerged life form. See more details about phenotypical plasticity in the Chap. 16 on Morpho-anatomical Adaptations.

Not often mentioned, and a variant of the emergent life form, are vines that are able to develop adventitious roots in the water: *Cissus spinosa*, *Camonea umbellata*, *Cyclanthera hystrix*, *Funastrum clausum*, *Ipomoea* spp., *Mikania* spp., *Rhabdadenia madida*, *Tassadia berteroana*, *Vigna* spp. (Fig. 4.11). In fact, the Pantanal has many climbing plants in flooded areas, where they can be rooted in a favorable spot and display their foliage over other plants. Their adventitious roots hold sediments.

Fig. 4.11 Aquatic plants (*Paspalum repens* and water hyacinths) and vines (with submerged adventitious roots) on woody species along rivers and branches, at rising waters. (Photo: A. Pott, June 3, 2009)

The zonation of aquatic vegetation according to water depth and related to life forms and succession has been described by Pott and Pott (2000); for example, *Pontederia reflexa* grows in 5–60 cm deep water, often forming a belt near the shores of a pond or it can be dominant in temporary ponds. Freshwater marshes have their typical plant species and vegetation structure at various depth zones (Mitsch and Gosselink 1993). Such zonation can be seen everywhere in the Pantanal, especially along water courses and in ponds (Fig. 4.6). Zonation fluctuates with the seasonal flood pulse and the decadal climate oscillations. But the vegetation can also largely differ between nearby ponds, and this offers an intriguing question for long-term studies on plant succession.

4.9 Effects of Fire

Influences of fire on diversity in wetlands were reported by Neiff (2001). In years of a prolonged dry season, wildfire can reach the aquatic vegetation where the flood has completely receded. Many aquatic plant species are fire-sensitive, mainly the floating species; that is why flamethrowers can control them. However, most emergent and amphibious plants regrow well from rhizomes after a fire, e.g., *Cyperus giganteus*, and the associated species richness is not much affected (Rocha et al. 2015). Others resprouting after a fire are *Canna glauca*, *Cyperus esculentus*, *C. haspan*, *Ipomoea carnea*, and *Pontederia reflexa* (Pott and Pott 2000). Floodable grasslands are quite fire-prone compared with deep-flooded habitats and contain various aquatic macrophytes which resprout from underground organs after top-kill, e.g., *Echinodorus longiscapus* (Pott and Pott 2000). Other species come back from the seed bank, such as *Oryza latifolia* (Bertazzoni and Damasceno-Junior 2011). Many legumes have their hard-seededness broken by fire, e.g., *Aeschynomene sensitiva* (Pott and Pott 2000). Few publications dealt with the seed bank in relation to fire and flood (Tirintan et al. 2018). The floating meadows that took over the permanently flooded delta of the silted lower Taquari River, and the accumulated histosol dried in 2020 caught fire for months. When the floating meadow histosol dries up and is reached by a wildfire, probably a rich seed bank is lost, but this needs further research (see the chapters on Fire (Chap. 18) and Seed bank (Chap. 15)).

4.10 Dispersal

Dispersal syndromes of the aquatic plant species include autochory, hydrochory (Araceae-Lemnoideae, *Cyclanthera hystrix*, Pontederiaceae, *Egeria najas*, *Ipomoea carnea*), anemochory (*Funastrum clausum*, *Erechtites hieracifolius*, *Mikania* spp.), and zoochory. Hydrochory is facilitated by corky pods (*Aeschynomene fluminensis*, *A. sensitiva*, *Sesbania virgata*), hairy seeds (*Ipomoea carnea*) (Pott and Pott 2000), or, in most cases, simple buoyancy. At fructification, the inflorescences of many hydrophytes grow downward into the water, probably an adaptation for hydrochory, such as Pontederiaceae, *Alternanthera aquatica*, *Limnobium laevigatum*, *Limnocharis flava*, and *Nymphaea* spp. (Pott and Pott 2000). Submerged fruits of Nymphaeaceae and Pontederiaceae release the seeds into the water, and later they reach the bottom or a shore. Hydrochoric diaspores have various degrees of buoyancy; for example, *Lemna* and *Wollffia* seeds float for a few hours and then sink (Cronk and Fennessi 2001), but often they set seed straight on the mud, as they flower at drawdown (Pott and Pott 2000). Ants carry fruits of *Discolobium pulchellum* (Pott and Pott 2000). Migratory birds play a role in the distribution of some ubiquitous aquatic plant species; for example, *Lemna* and *Wollffia* adhere to their feathers and feet (Landoldt 1987). Exozoochoric dispersal by fish was observed in *Oryza latifolia* (Bertazzoni and Damasceno-Junior 2011) and some endozoochorous small-seeded grasses (Silveira and Weiss 2014). The seed morphology and physiology of a few species were studied, such as *Victoria amazonica* (Tozin et al. 2016).

4.11 Biology

Most aquatic plant species have bisexual flowers, but *Egeria najas* is monoecius; thus a specific pond may have only male or female plants, depending mostly on vegetative propagation. A few submerged plant species flower, are pollinated (hydrophily), and fructify under water, e.g., *Ceratophyllum* spp., *Najas* spp., but most have aerial flowers, such as *Apalanthe*, *Cabomba*, *Egeria*, and *Ludwigia inclinata*.

Most aquatic plants with conspicuous flowers are pollinated or at least visited by bees such as the feral *Apis mellifera* and other small native stingless bees. *Thalia geniculata* has explosive pollination (Davis 1987). Other large flowers such as *Discolobium* and *Rhynchanthera* are visited by bumblebees, and *Nymphaea* and *Victoria* by the beetle *Cyclocephala* (Pott and Pott 2000).

Opening a flower a day seems a strategy to spread seed set over a prolonged time and escape unfavorable days, e.g., as shown in species of *Discolobium*, *Hyptis*, *Hydrocleys*, *Ipomoea*, *Justicia*, *Ludwigia*, *Rhynchanthera*, and *Utricularia*. In contrast, opening the whole inflorescence at once and lasting just a single day seems a waste of resources, as in *Eichhornia crassipes*, but it can have its advantages of concentrating pollination opportunities for tristylic species. Tristyly was recorded in *Eichhornia* spp. (Cunha et al. 2014). Some plants, like *Victoria amazonica*, have nycthemeral rhythms in their flowering: they open their flowers at dusk and close them at dawn and are visited by nocturnal pollinators (Gessner 1960, Prance & Arias 1975). At the first night, the flower of *V. amazonica* is white, opening pink in the second night, after beetle pollination (Fig. 4.12). The species of *Nymphaea*, all of the subgenus *Hydrocallis*, behave the same way in the Pantanal, opening for two consecutive nights (Pott 1998). For phenology, see the Chap. 13 on Plant Phenology.

Life cycle: Some species have a short life cycle of few weeks: the mud ephemeral species (Keddy 2000), e.g., *Noterophila limnobios*, *Anagallis minima*,

Fig. 4.12 *Victoria amazonica* (Victoria lily, giant water lily), Nymphaeaceae, the world's largest aquatic plant and the second largest flower; flowers opening the first night are white; western edge of the Pantanal wetland, Serra do Amolar range in the back (Photo: V.J. Pott); at the second night of anthesis, after beetle pollination, the flowers turn pink; note the drainage slot on one side of the lifted leaf rim. (Photo: A. Pott)

Burmannia spp., *Curtia tenuifolia*, *Euploca filiformis*, *Helanthium tenellum*, *Ludwigia octovalvis*, *Poteranthera pusilla*, *Rotala ramosior*, *Schoenoplectiella supina*, *Syngonanthus gracilis,* etc. Some floating species can survive for a few days on the wet mud after the water receded, e.g., *Salvinia* spp., even producing sporocarps (Pott et al. 1989), and duckweeds may fructify (Pott and Cervi 1999).

Seed: Annual species or therophytes tend to produce great numbers of seeds, but some perennials also do (Pott and Pott 2000). Many are stored in soil seed banks (Bao et al. 2014; Souza et al. 2016; Catian et al. 2018) and seedlings emerge from flooded soil (Bao et al. 2017).

Seed bank: This has been surveyed in a few areas (Bao et al. 2014, 2017; Souza et al. 2016; Lima et al. 2018a, Tirintan et al. 2018) (see the Chap. 15 on Soil seed bank). Seed identification manuals are scarce and include only the main species (Catian et al. 2021). Seeds of *E. crassipes* can survive for 20 years in the seed bank (EPPO 2008). Species of *Nymphaea* can colonize an entire pond just from the seed bank (Ferreira et al. 2016a), as well as *Pistia* and *Salvinia* spp., although both genera also show fast vegetative propagation. Nonetheless, most seeds require moist but not flooded conditions for germination (Mitsch and Gosselink 1993); thus, most aquatic species do not germinate underwater, although some do, e.g., *Typha domingensis* (Pott and Pott 2000) and *E. crassipes*.

Vegetative propagation: This is a strategy for fast growth where flood waters rise within few days, such as areas inundated by rivers close to the uplands, e.g., Aquidauana and Miranda, also, for persistence in prolonged-flooded areas.

- Stolons: These are produced mainly in monocots, such as *Commelina longicaulis*, *Egeria najas*, *Limnobium laevigatum*, *Murdannia engelsii*, and many Poaceae, but also in some dicots, e.g., *Hydrocotyle ranunculoides*, and fern-allies as *Marsilea* spp.
- Rhizomes: These or other underground organs are present on most monocots, e.g., Alismataceae, Cyperaceae, Poaceae, *Abolboda puchella*, *Canna glauca*, *Nymphaea* spp., *Nymphoides* spp*.*, *Rhabdadenia madida*, *Thalia geniculata*, and *Typha domingensis*. The rhizome of *Paspalum wrightii* has such a strong tip that it perforates tough plastic bags; this probably is an adaptation to grow in heavy expandable clays or vertisols of the floodable *Tabebuia aurea* savanna. The rhizomes of *Cyperus blepharoleptos* are long and entangled under its dense floating mats in the early succession of the floating meadows (described in the topic on habitats).
- Tubers: *Eleocharis acutangula* has tubers of 1 mm in diameter, 15 cm deep (not yet reported as far as we know), and also rhizomes near the surface. *Hyptis brevipes* also has 15–20 cm deep tubers, 1–2 cm thick (not reported before either). *Fuirena umbellata* has tubers like rosary beads (Pott and Pott 2000).

Some aquatic plant species have reserves in subterranean organs; e.g., *Echinodorus paniculatus* stores starch in its roots, in the form of nodules, enabling it to regrow soon after the dry season (Scremin-Dias and Morretes 1999). It may be difficult to tell stolon and rhizome apart in floating plants (e.g., *Eichhornia azurea*) since in this case the rhizome is not buried as in terrestrial species; this is the reason why often we find contrasting descriptions for a particular macrophyte.

An interesting case is *Nymphaea prolifera*, which produces aerial bulbils and plantlets on the floating, sterile inflorescences, besides fertile single flowers (Pott and Pott 2000) (Fig. 4.13). That is a strategy of persistence in seasonally flooded savannas, producing offspring in the short flooding time, apart from propagation by seed.

Vegetative propagation gives great competitive advantage, whereby many species tend to form monodominant stands (see the Chap. 8 on Monodominants), e.g., *Cyperus giganteus*, *Enhydra radicans*, *Hymenachne pernambucensis*, *Paspalum wrightii* (earlier identified as *P. hydrophilum*), *Polygonum acuminatum*, *P. ferrugineum*, *Thalia geniculata* (Fig. 4.14), and *Typha domingensis* (Pott and Pott 2000).

A noteworthy strategy of competition is the steel-tower-like venation architecture of the expanding *Victoria amazonica* leaves pushing other plants aside, as can be seen on the leaf underside (Fig. 4.15). Also, as *V. amazonica* becomes crowded, its leaf rim grows higher, still leaving a sort of drainage channel.

The small *Salvinia* spp. rely on a massive number of spores and fast vegetative propagation to cover the water surface. We observed a more discrete strategy in *Hydrocleys nymphoides* emitting a spear-like new leaf through a dense cover of *Salvinia*. *Wollffiella* spp. occupy tiny microhabitats almost near the water surface, among the roots of other plants.

Ecological anatomy demonstrates the frequent adaptative strategies to flood, as exhibited in differences in leaf shapes and size plasticity between submerged and

Fig. 4.13 *Nymphaea prolifera* (water lily), with aerial bulbils and plantlets on the floating sterile inflorescence and a flower bud (left), and an open fertile flower (right). (Photos: A. Pott)

Fig. 4.14 Monodominant stand of *Thalia geniculata* (fireflag or *caeté*), Paraguay River floodplain, Pantanal wetland. (Photo: A. Pott, June 3, 2009)

Fig. 4.15 Steel-tower-like venation architecture of the leaf of *Victoria amazonica* (Victoria lily, giant water lily) that, when expanding, pushes other plants aside. (Photo: A. Pott)

aerial plants (Scremin-Dias 2009; Scremin-Dias et al. 2011) (see the Chap. 16 on Morpho-anatomical Adaptations). Examples are *Nymphaea* (Adamowicz and Scremin-Dias 2007; Catian and Scremin-Dias 2013, 2015), *Ludwigia* (Rodrigues et al. 2007), *Aeschynomene* (Leme and Scremin-Dias 2014), *Polygonum* (Catian et al. 2018), *Bacopa myriophylloides*, *Helanthium* spp., *Limnocharis laforestii*, *Ludwigia helminthorrhiza*, *Sagittaria* spp., *Thalia geniculata* (Pott and Pott 2000). The small *Eleocharis minima* varies from an aquatic filamentous, viviparous form to a small, terrestrial, flowering tussock. Sometimes this can be misleading; e.g., a plant previously depicted as a more vigourous *Sagittaria rhombifolia* (Pott and Pott 2000) is actually the very similar *S. planitiana*, common in upper basin streams. Some species vary so much in plant size and leaf width depending on water depth that the small and the tall individuals seem distinct species, e.g., *Caperonia castaneifolia* and *Justicia laevilinguis*.

4.12 Collecting Aquatic Plants for the Herbarium

Aquatic plants require some special care to prepare good-quality herbarium specimens. In general, the plants wilt very fast; some should be preferably collected in the early morning since the fragile petals easily drop and all fall by late afternoon, e.g., *Hydrocleys*, *Ipomoea*, *Justicia*, *Ludwigia*, *Utricularia*, and Melastomataceae. Yet, *Nymphaea* spp. in the Pantanal have to be gathered at night, for their nocturnal anthesis, or we can cheat their physiology by keeping them in the dark during the day, to open the flowers.

Apart from the external water on the roots and leaves, most aquatic plants are spongy, full of aerenchyma, or crass, with a high moisture content. First, we have to gently wash the mud off and shake off the surplus of that free water, and remove debris and the excess of roots. Care should be taken to not overlap various leaves or stems and arrange them as good as possible since after pressing it will be difficult to correct the mess.

Before putting the plants straight into the press, specimens will turn out better if pre-pressed in an old book, such as telephone directories, or change the newspaper before they go to the drying press and again before going to the drying oven. We use a bound matrix printer paper (A2, 18 × 24″), the same size as a standard press and very practical to handle in wetlands. In the evening, the specimens have to be definitely pressed between two corrugated cardboards and corrugated aluminum to dry in an electric, air-circulating oven at around 50° C. During expeditions, a portable, gas-heated drier can be used instead, but at low fire, otherwise the delicate specimens can become dark (baked). An alternative is to moisten the newspaper and pressed plants with alcohol, in sealed plastic bags; with this treatment they will not rot for 2–3 weeks, although the colors fade. Submerged and tiny species, e.g., Lemnoideae, *Cabomba*, *Egeria*, *Najas*, *Nitella*, and *Utricularia*, are best placed in a tray with water and then carefully captured with a sheet of A4 paper from underneath, so that the fragile plants spread out over on the paper (Fidalgo and Bononi

Fig. 4.16 Collecting submerged plants, spreading them on a sheet of paper in the water, in a tray (source: Fidalgo and Bononi 1984) or in the field. (Photo: A. Pott)

1984, Fig. 4.16), as they become stuck; next, the material has to be covered with non-woven tissue or a non-adherent paper, and then put into the press; the exsiccatae are later mounted with that A4 paper. It can also be improvised in the field (Fig. 4.16) and then pressed. After drying, little is left of the original turgid plant. Since they are essential for identification, utricles of *Utricularia* must be collected. After washing off the mud of the utricles, some should also be kept in liquid (used at Kew: water 37%, ethanol 53%, formaldehyde 5%, glycerol 5%), preferably already in the field, while the specimens to be dried should be put directly into a mini field press (Taylor 1989). Dissolved $CuSO_4$ (10g/L) can be added to partially preserve the colors of Lemnoideae and submerged plants, handling it with care as it is poisonous.

Large plants such as *Canna*, *Cyperus giganteus*, *Stephostachys*, *Thalia*, and *Typha* should be measured and a portion that fits the herbarium cardboard should be selected, or more than one part to be mounted can be displayed on separate sheets, naming the specimens A, B, C after the same collecting number. Choosing small individuals may mislead the perception of the average size. Botanizing the Victoria lilly (*Victoria amazonica*) takes a while, as every organ is big and thick, even the flower, and also spiny, and thus to be handled with gloves. Drying is facilitated when the thick plant parts are split and then pressed with layers of porous cardboard pieces around the plant material to balance the volume.

Data on fading plant features (colors, latex, smell, stickyness), habitat, and life form should be recorded in order to be mentioned on the herbarium label and in the data bank, including the geographical coordinates. Photographs of the samples are desired to complement the information and for publication and presentation. Aquatic plants are not that easy to photograph as they are fragile to handle and wilt very quickly. Pictures taken in the habitat generally include more than the aimed species. Night-flowering plants, as the abovementioned *Nymphaea* spp., can be left in the dark during the day, so their flowers open.

When plants are sterile in the field, they might be taken for cultivation until flowering. In fact, growing aquatic plants is a great way to observe them closely and find out more about them. Actually, tanks with aquatic plants give excellent opportunities for observations, e.g., on their competition: for example, after cultivating and examining duckweeds for 28 years, only now we noted that, kept in still water, *Lemna valdiviana* tends to form 4 fronds, though we did not observe that in the wild.

4.13 Current and Potential Uses

Aquatic plants may have various actual and potential uses: they may be edible, produce pollen and nectar, provide forage, are used to produce medicines and fibers, may be used as biofuel and for remediation and restoration, etc.

Bee Plants Various families and genera, e.g., Alismataceae, Asteraceae, Fabaceae, Plantaginaceae (*Bacopa*), Polygonaceae (*Polygonum*), Pontederiaceae, Rubiaceae, *Hydrocleys* spp., *Hydrolea spinosa*, *Hyptis* spp., *Ludwigia* spp., *Melochia* spp. attract bees (Pott and Pott 2000).

Edible Species An aquatic plant species grown as a vegetable is watercress (*Nasturtium officinale*), and another common one in Brazil is *jambu* (*Acmella oleracea*). But the most important aquatic food plant of the Pantanal is the wild rice species *Oryza latifolia*. Presently, it is harvested and sold as a gourmet food with a high nutritive value (see the Chap. 19 on Food plants). The whole plant of *Pacourina edulis* is edible (Redwood 1818), especially its flower head receptacle, like an artichoke. *Neptunia prostrata* (symnonym *N. oleracea*) is being harvested and even cultivated for its edible shoots and green pods, in Thailand and Vietnam (National Academy of Sciences 1976). *Victoria amazonica* is sometimes consumed (see the Chap. 19 on Wild Food Plants). The cooked rhizomes of *Nymphaea amazonum* are eaten by indigenous people, and those of *Sagittaria montevidensis* are consumed in some Asian countries (Amaral et al. 2008). The legendary lotus (*Nelumbo nucifera*) (*Nymphaeaceae*) is cultivated for their rhizomes (also sold in Brazil), as well as Chinese water chestnut (*Eleocharis dulcis*), taro (*Colocasia esculenta*), and arrowhead (*Sagittaria trifolia*) (National Academy of Sciences 1976). Rhizomes of *Typha domingensis*, rich in starch, are edible, as well as its young shoots, inflorescence, pollen, and seed oil. Rhizomes of *Thalia geniculata* are also rich in starch (Lorenzi 1992; Amaral et al. 2008). Many others are eaten; e.g., *Ceratopteris thalictroides*, water spinach (*Ipomoea aquatica*), *Limnocharis flava*, and duckweeds (*Lemna*, *Landoltia*, *Spirodela*) have a high protein content (14–25%) and are a potential human food (Velasquez 1994). In Brazil, duckweeds are not eaten, but they are consumed in Asia and certainly will become a more widely used food source. *Landoltia punctata* reaches 35% crude protein (Mohedano et al. 2012). However, not all attractive-looking leaves are edible; e.g., water hyacinths (*Eichhornia*, *Pontederia*) have high levels of oxalates, as well as the poisonous *Pistia stratiotes*, despite its misleading common name of water lettuce. Several species provide valuable germoplasm, i.e., gene sources for plant breeding in agriculture, e.g., *Arachis* and *Oryza*.

Forage plants Aquatic plant parts such as leaves, fruits, and seeds are eaten by domestic and wild animals, mainly horses, capybaras, marsh deer, duck, fish, insects such as ants, and moluscs. Flowers are also eaten by birds, insects, and fish; e.g., the fallen flowers of *Discolobium pulchellum* are ingested by fish (Pott and Pott 2000).

Most aquatic grasses have good forage value, e.g., *Hemarthria altissima*, *Hymenachne amplexicaulis*, *Leersia hexandra*, *Luziola subintegra*, *Paspalidium geminatum*, *Paspalum acuminatum*, *P. almum*, *P. fasciculatum*, *P. repens*, and *Steinchisma laxum* (Allem and Valls 1987; Pott and Pott 2000).

As regards aquatic legumes, the following species are recommended as good native forage plants: *Aeschynomene americana* and *A. fluminensis* eaten by domestic and native herbivores; *A. americana* (joint-vetch) is cultivated on wet soils in Florida (USA), but it originated from the Pantanal (Pott & Pott 2000). The wild peanuts have good protein levels and outstanding other features; e.g., *Arachis diogoi* withstands 4 m deep floods. *Discolobium pulchellum* has the impressive crude protein content of 28% (Pott and Pott 1987), no wonder cabybaras and *pacu* snapper fish chew even their stems (Pott and Pott 2000). Many aquatic plants are consumed by fish, such as *Azolla* and duckweeds (*Lemna*, *Landoltia*, *Spirodela*, *Wollfia*, *Wolffiella*).

Phytoremediation Various aquatic plants respond to eutrophication, reason why they become weedy in reservoirs receiving sewage or other types of nutrients, e.g., *Eichhornia crassipes*, *Egeria* spp., *Typha dominguensis*, and *Urochloa arrecta* (Thomaz et al. 2003). Many such macrophytic species can be utilized for wastewater treatment, but small free-floating plants are easier to manage. A preliminary trial using *Landoltia punctata*, non-native to the Pantanal, was tested to polish decanted wastewater from a slaughterhouse: three small sequential ponds cleaned the dark water enough for fish survival (Pott and Pott 2002). At the start of the treatment, the effluent has to be diluted as otherwise it can cause some death of *L. punctata* and algae boom of *Chlorococcales* (Bortolini et al. 2010). The system needs a few days to get into balance for a continuous flow. That duckweed *L. punctata* was tested for piggery farm waste water treatment in polishing ponds, with outstanding results: removal of 98% nitrogen and 99% phosphorous, dissolved oxygen level rises from 0 to 3 mg/L, and a production of 60t/ha/year of biomass, with 35% crude protein; this shows the transformation of a pollution problem into a valuable resource (Mohedano et al. 2012).

Azolla caroliniana and *Salvinia auriculata* are useful to treat fish farm effluent (Toledo and Penha 2011). *Azolla* can remove heavy metals (Joyce 1990), as well as *Salvinia* (Dhir & Srivastava 2011), that accumulated them in a Brazilian wetland (Lima et al. 2018b). Few such studies were reported on natural wetlands in Brazil, e.g., one on biotransformation potential for xenobiotics and biocides of 13 aquatic macrophytes and two halophytes in subtropical coastal wetlands (Santos et al. 2021). Dry *Salvinia* can be used to absorb oil spills, and the microstructures of their superhydrophobic leaves inspire cleanup materials (Zeiger et al. 2016). Dry mass of *T. domingensis* can be used as biosorbent for heavy metals in wastewater (Abdel-Ghani et al. 2009).

Biofuel Biofuel or bio-oil production from aquatic plants has a high potential use, e.g., duckweeds (Landoldt 1987; Duarte 2018). Harvesting in hydroelectric power reservoirs is a promising economic and environmentally friendly way of invasive weed control and management, as it is a good raw matter of biofuel and other products. An innovative project is converting biomass of weedy aquatic plants into bio-oil using thermal pyrolysis, with a yield of 27% from *Egeria najas* in large reservoirs in the Paraná River (Cardoso et al. 2020). Other species being tested have also shown a promising high potential for pyrolytic bio-oil, such as *Eichhornia crassipes*, *Nymphoides indica*, and *Typha domingensis*; it is an initiative leading to a sustainable productive system that brings new jobs to local people (Ferreira et al. 2020). Thus, the conversion of weedy aquatic plants into a renewable energy source is a notable new solution for an old problem. In Argentina, downriver drift floating mats are used to produce biogas. The symbiont *Anabaena azollae* of *Azolla* can release hydrogen from water, a promising biological method of producing fuel (National Academy of Sciences 1976).

Restoration *Pacourina edulis* can be used to vegetate river sediments (according to the Pantanal rancher Armando Lacerda, Corumbá, MS) (see Pott and Pott 2000), as well as *Canna glauca* and tall grasses such as *Paspalum fasciculatum.* The latter species is more long-lasting as it is perennial and rhizomatous. Aquatic macrophytes are harvested from reservoirs and composted to produce organic fertilizer and substrate for nurseries and gardens, and for soil amelioration in forestry and degraded areas. Usually floating and submerged aquatic plants will not continue to grow on non-flooded soil, except in frequently watered nurseries pots. A local tradition is the use of pond bed organic soil in old canoes to cultivate scallion and herbs.

Nitrogen Fixation Noteworthy are the stem nodules of *Discolobium pulchelum.* They are capable of fixing N, even when submerged, and to photosynthesize because they are green (Loureiro et al. 1994). Other aquatic legumes, such as *Aeschynomene* spp., *Sesbania exasperata* and *Vigna lasiocarpa,* also have functional N-fixing nodules on submerged roots (James et al. 2001). *Azolla* spp. are valuable N-fixing plants by the symbiotic blue-green alga diazotrophic cyanobacterium *Anabaena azollae*, and are as such acting as a fertilizer in rice fields (National Academy of Sciences 1976; Talley et al. 1977) and in integrated fish-rice farming systems.

Medicinal Duckweeds have been known as medicinal plants for centuries, but there is not much information on their pharmaceutical substances. However, Lemnoideae can be used to produce enzymes (Landolt 1987). Several species are used in folk medicine, e.g., *Pluchea sagittalis* (Pott and Pott 1994); *Echinodorus scaber*, *Polygonum* spp. (Pott and Pott 2000), *Eclipta prostrata*, and *Typha domingensis* (Amaral et al. 2008). Various compounds with biolological activities were discovered in aquatic plants, e.g., antiprotozoal in *Thalia geniculata* (Lagnika et al. 2008), antifungal in *Nymphaea gardneriana* (Adamowicz 2012), and antimicrobial in *Aspilia latissima* (Souza et al. 2015). Triterpenoids and steroids were detected in *Eleocharis acutangula* and *E. sellowiana*, and two new substances were discovered in *E. sellowiana* (Amaral et al. 2004). Little studied in local aquatic plants, endophytic fungi were found in association with *Aeschynomene fluminensis* and *Polygonum acuminatum* (Pietro-Souza et al. 2017). Several species produce aromatic substances, e.g., *Bacopa gratioloides*, *B. monnierioides*, *Gymnocoronis spilanthoides*, *Hyptis* spp., and *Stemodia hyptoides* (Pott and Pott 2000) and *Pluchea sagittalis*. The water hyacinth (*E. crassipes*) is being utilized for cosmetics (Atualidade Cosmética 2014).

Ornamental Some species are already used as aquarium plants, e.g., *Cabomba* spp., *Ceratophyllum demersum*. Others can be grown in aquatic gardens: *Canna glauca*, *Cyperus giganteus*, *Hydrocleys nymphoides*, *Ipomoea carnea*, *Limnocharis flava, Ludwigia sedioides*, *Nymphaea* spp., *Nymphoides grayana*, *Rhabdadenia madida*, and *Rhynchanthera novemnervia*. With the current concern with disease-vector mosquitoes, it is worthy to mention that *Chara* inhibits their larvae, since tanks in which we grew these macroalgae were mosquito-free. The Pantanal Aquarium, in Campo Grande, shall exhibit *Victoria amazonica*, much photographed at sightseeing, and some other aquatic plants of the Pantanal in its thematic garden pools.

Bait Habitat Riverside people sieve floating mats to catch associated crabs and *tuvira* fish (*Gymnotus carapo*) as bait sold to the sport fishing tourists.

Handicrafts Various aquatic plant species have fibers (*Cyperus giganteus*, *Eichhornia*, *Typha*) to produce mats and objects, can be used as dry flowers (*Cladium*, *Nymphaea*, *Rhynchospora*, *Typha*), and other handicrafts.

4.14 Impacts and Conservation Status

Concerning impacts, besides the most severe from outside (Pott & Pott 2004), some are caused inside the Pantanal. One of the natural causes of disturbance are the high population densities of fauna (Pott and Pott 2000). Aquatic birds do intense trampling in the last pools at the end of the flooding period (Pott and Pott 2000). Caymans and capybaras disrupt aquatic plants, overturn them, and increase turbidity (Pott and

Pott 2000). Feral pig digging after rhizomes and cattle trampling disturb mainly the littoral zone of ponds, seasonal streams, and low-lying grasslands, creating microrelief and favoring annual and pioneer plants (Pott and Pott 2000). Some annual or short-perennial plant species colonize disturbed soil, e.g., *Cyperus brevifolius* and *Setaria parviflora* (Beck and Asturizaga 2006). Eutrophication by cattle is very localized since stocking is rather light. Some plants grow well in nutrient-enriched water, such as *Paspalum acuminatum* (Beck and Asturizaga 2006), *Ceratophyllum echinatum*, *Lemna aequinoctialis*, *Ludwigia helminthorrhiza*, *Pistia stratiotes*, *Pontederia subovata* and *Wolffia brasiliensis*, and also *Limnocharis flava* in pools near gates (Pott and Pott 2000). Also, duckweeds are frequent in pools eutrophicated by cattle dung. Cattle tend to overgraze near homesteads, however, overgrazing is worse in ranches with sheep, that are kept near the houses because of pumas and jaguars. Horses have some preference to graze in ponds, though they are in low numbers. We observed that buffaloes have a highly negative impact on aquatic plants of ponds, mainly in low-water years, reducing species richness to a high cover of *Pistia stratiotes*; after removal of the buffaloes these sites recover, at high floods (Pott et al. 1999). We also observed a seasonal pond taken over by *Senna aculeata* under many years of grazing by buffaloes.

Nowadays, the Pantanal ranchers do not raise buffaloes because they cross fences and go wild, becoming aggressive. Some feral groups remain near the Taquari River, however. In wetland areas of Amapá, we noticed that overgrazing by buffaloes caused a dramatic change of floodable grasslands into monodominant stands of *Ipomoea carnea*. In Guaporé wetlands, feral buffalo tracks function as drainage canals and have interfered with the hydrology. However, the Pantanal still is considered a pristine (Heckman 1998), natural wetland (Junk et al. 2011), despite over 200 years of cattle ranching, and probably precisely for that low-impact activity on the vegetation. Quite different from African savannas, the Pantanal did not have large herds of native grazers; thus, the cattle fit in a nearly empty niche with a great surplus of forage grasses, that otherwise would become fuel and turn into wildfires.

The most severe impacts occurred on the lower Taquari River, by far the most dramatic ecological change in the Pantanal, caused by heavy siltation from erosion in the sandy upper basin (Pott and Pott 2005). Other rivers already show increased sand banks. Aquatic habitats of the upper basin are being degraded (Wantzen et al. 2005). A hydropower dam on the Manso River, in the upper basin of the Cuiabá River, changed its flood regime downstream. However, the aquatic vegetation rapidly adjusts to changes.

4.15 Resilience

In contrast with woody vegetation (see the Chap. 20 on Restoration), the floodable vegetation of the Pantanal seems to have quite a good resilience, as it tends to be renewed by the floods and can recover from disturbance. For example, in the 1960–1970s, irrigated rice was cultivated on the Cuiabá riverside. That was abandoned in 1974 when the heavy floods came back after 14 years without flood, and nowadays hardly any sign of that disturbance can be seen. Until 1980, small slash-and-burn shifting cultivation was common along the rivers at low waters, but the traces of that is no longer perceived by those whom are not acquainted with changes in that riparian vegetation. In the decade of 1980, *U. arrecta* x *mutica* was planted on the São Lourenço River floodplain; it did not spread from there and it did not persist. Being abandoned, the natural swamp recovered.

Inside the Pantanal, not much interference has been done with the hydrology, such as constructing drains or dikes Pott & Pott 2004). However, often some short canals are opened to access backwaters for residents and fishing boats. The dynamic balance exists because the Pantanal still is largely a pristine (Heckman 1998), natural wetland (Junk et al. 2011). Nevertheless, the changes caused by heavy silting of the Taquari River were much more severe and are long-lasting, killing most trees, although having increased the area of marsh vegetation (Pott and Pott 2005). Nevertheless, lately (2008–2020) a slow recovery of original landscapes occurs in some delta lobes. But other rivers are also being silted, such as the Paraguay River. Shore sediments contain and retain seeds and become colonized by early succession stages.

4.16 Final Remarks

The aquatic plant species are the components of the Pantanal vegetation that respond most rapidly to seasonal hydrological changes and also to pluriannual oscillations, either favorable to them or not. They persist over dry periods in the soil seed bank and or as dormant vegetative propagules and can recolonize habitats with both mechanisms.

Concerning research gaps about aquatic plants, we mention the need for studies on seed banks *vs* fire in floating meadows, accumulated organic material of deep-flooded areas, and water body sediments; seed physiology *vs* flood and fire; plant demography; aquatic flora of the eastern parts of the Pantanal; identification manuals of seeds, seedlings, and pollen; genetic variability; and management of food plants such as wild rice.

References

Abdel-Ghani NT, Hegazy AK, El-Chaghaby GA, Lima EC (2009) Factorial experimental design for biosorption of iron and zinc using *Typha domingensis* phytomass. Desalination 249:343–347

Abdon MM, Pott VJ, Silva JSV (1998) Avaliação da cobertura por plantas aquáticas em lagoas da sub-região da Nhecolândia no Pantanal por meio de dados Landsat e SPOT. Pesq Agropec Bras 33(no. esp):1675–1681

Adámoli J (1982) O Pantanal e suas relações fitogeográficas com os cerrados. Discussão sobre o conceito "complexo do Pantanal". In: Congresso Nacional de Botânica, 32. Teresina, 1981. Anais. Teresina, Sociedade Botânica do Brasil, pp 109–119

Adamowicz, RAG (2012) Estudo fitoquímico e testes biológicos de um espécime de *Nymphaea amazonum* (Nymphaeaceae) ocorrente no Pantanal/MS, Brasil. Dissertation, Universidade Federal de Mato Grosso do Sul. livros01.livrosgratis.com.br/cp097990.pdf

Adamowicz RAG, Scremin-Dias E (2007) Aspectos estruturais e ontogenéticos dos diafragmas das raízes de *Nymphaea amazonum* L. (Nymphaeaceae). Rev Bras Bioci 5:198–200

Allem AC, Valls JFM (1987) Recursos forrageiros nativos do Pantanal Mato-Grossense. Embrapa, Brasília

Amador GA, Damasceno-Junior GA, Silva RH, Pott A, Pott VJ (2013) Nymphaeaceae, *Nymphaea belophylla* Trickett: new state record. Check List (Online) 9:440–442. https://biotaxa.org/cl/article/view/9.2.440/11818

Amaral MCE, Faria AD, Magalhães AF, Magalhães EG, Ruiz ALTG (2004) Steroids and triterpenoids from Eleocharis acutangula and E. sellowiana (Cyperaceae). Phytoch Anal 15:125–129

Amaral MCE, Bittrich V, Faria AD, Anderson O, Aona LYS (2008) Guia de campo para plantas aquáticas e palustres do Estado de São Paulo. Holos, São Paulo

Aoki C, Teixeira-Gamarra MC, Gamarra RM, Medeiros SCH, Pott VJ, Damasceno-Junior GA, Pott A, Scremin-Dias E (2017) Abiotic factors drive the structure of aquatic plant assemblages in riverine habitats of the Brazilian Pantanal. Braz J Bot (Printed) 4:01–11

Araújo AC, Trevisan R (2018) Cyperaceae da flora sul-matogrossense: composição florística. Iheringia Sér Bot 73(supl):190–200. https://doi.org/10.21826/2446-8231201873s190

Atualidade Cosmética (2014) LOccitane au Brésil lança produtos inspirados na flor do Aguapé. http://cosmeticanews.com.br

Bao F, Pott A, Ferreira FA, Arruda R (2014) Soil seed bank of floodable native and cultivated grassland in the Pantanal wetland: effects of flood gradient, season and species invasion. Braz J Bot (Printed) 37:239–250

Bao F, Elsey-Quirk T, Assis MA, Pott A (2017) Seed bank of seasonally flooded grasslands: experimental simulation of flood and post-flood. Aquat Ecol 52(1):93–105. https://doi.org/10.1007/s10452-017-9647-y

Bao F, Elsey-Quirk T, Assis MA, Arruda R, Pott A (2018) Seasonal flooding, topography, and organic debris interact to influence the emergence and distribution of seedlings in a tropical grassland. Biotropica 1:1

Bao F, Elsey-Quirk T, Assis MA, Souza EB, Pott A (2019) Do aquatic macrophytes limit the invasion of exotic species in Pantanal grasslands? Wetlands 40:135–142. https://doi.org/10.1007/s13157-019-01168-5

Beck SG, Asturizaga AS (2006) Guía ilustrada de los pastos nativos de la sabana húmeda del Beni. Herbário Nacional de Bolivia, La Paz

Bertazzoni EC, Damasceno-Junior GA (2011) Aspectos da biologia e fenologia de *Oryza latifolia* Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Bot Bras 25(2):476–786. https://doi.org/10.1590/S0102-33062011000200023

Bortolini JC, Biolos S, Bueno NC, Godinho LR, Pott VJ (2010) *Chlorococcales sensu lato* (Chlorophyceae) em tanques de depuração de efluente de origem bovina no Mato Grosso do Sul, Brasil. Iheringia Ser Bot 65(1):63–74

Bove CP (2001) Araguaia, o paraíso das plantas aquáticas (Araguaia, the paradise of aquatic plants). Aquarium 4(26):34–37. www.unirio.br/ccbs/ibio/herbariohuni/pdfs/araguaia-o-paraiso-das-plantas-aquaticas

Bueno NC, Bicudo SEM, Piccelli-Vicentim I, Ishii IH (1996) Characeae (Charophyta) do Pantanal do Mato Grosso do Sul, Brasil. Hoehnea 23(2):21–31

Cardoso DEV, Okamura LA, Ferreira FA, Gomes WP, Santos JM, Tanimoto ST, Camargo JS, Assis HM, Barros R (2020) Produção de biocombustível a partir de macrófita aquática. In: Nobre CP, Oliveira ACS (org.) Estudos Ambientais e Agronômicos: resultados para o Brasil. São Luiz, Editora Pascal. V. 01, Chap 24:281–291. https://editorapascal.com.br/wp-content/uploads/2020/04/ESTUDOS-AMBIENTAIS-E-AGRON%C3%94MICOS-1.pdf. DOI: 10.29327/514614

Catian G, Scremin-Dias E (2013) Compared leaf anatomy of *Nymphaea* (Nymphaeaceae) species from Brazilian flood plain. Braz J Biol 73:809–817

Catian G, Scremin-Dias E (2015) Phenotypic variations in leaf anatomy of *Nymphaea gardneriana* (Nymphaeaceae) demonstrate its adaptive plasticity. J Torrey Bot Soc 142:18–26

Catian G, Leme FM, Francener A, Carvalho FS, Pott A, Pott VJ, Scremin-Dias E, Damasceno-Júnior GA (2012) Macrophyte structure in lotic-lentic habitats from Brazilian Pantanal. Oecol Aust 16(4):782–796

Catian G, Pott A, Scremin-Dias E (2017) Reproductive phenology of *Polygonum hispidum* Kunth and *P. punctatum* Elliott (Polygonaceae), in response to the flooding cycle in the Pantanal, Brazil. Bol Mus Para Emílio Goeldi Ciênc Nat 12:197–207

Catian G, Silva DM, Suárez YR, Scremin-Dias E (2018) Effects of flood pulse dynamics on functional diversity of macrophyte communities in the Pantanal wetland. Wetlands 38:975–991. https://doi.org/10.1007/s13157018-1050-5

Catian G, Scremin-Dias E, Pott A (2019) Reproductive phenology of macrophyte community in response to wetland flooding cycle. Oecologia Australis 23(04):856–873

Catian G, Lima GT, Fabiano VS, Gonçalves VM, Scremin-Dias E (2021) A guide to the identification of diaspores of the main macrophytes in the Pantanal. Phytotaxa 487(3):2015–2232

Chambers P, Lacoul P, Murphy KJ, Thomas SM (2008) Global diversity of aquatic macrophytes in frewhwater. Hidrobiol 595:9–26. https://doi.org/10.1007/s10750-007-9154-6

Coutinho BA, Pott VJ, Arrua BA, Aoki C, Pott A (2017) Ecological succession of aquatic macrophytes on floating meadows in the Pantanal wetland. Braz J Bot (Printed) 41:65–75

Cronk JK, Fennessi MS (2001) Wetland plants: biology and ecology. Lewis Publishers, Boca Raton

Cruz C, Silva AF, Venturini AF, Garlich N, Pitelli RLCM, Pitelli RA (2015) Food preference and consumption of aquatic macrophytes submerged by snail *Pomacea canaliculata*. Planta Daninha 33:433–439

Cunha NL, Delatorre M, Rodrigues RB, Vidotto C, Gonçalves F, Scremin-Dias E, Damasceno-Junior GA, Pott VJ, Pott A (2012) Structure of aquatic vegetation of a large lake, western border of the Brazilian Pantanal. Braz J Biol 72:519–531

Cunha NL, Fischer E, Lorenz-Lemke AP, Barrett SCH (2014) Floral variation and environmental heterogeneity in a tristylous clonal aquatic of the Pantanal wetlands of Brazil. Annals Bot (Print) 114:1–13

Da Silva CJ (1989) Macrófitas aquáticas e as condições físicas e químicas dos alagados, corixos e rios, ao longo da Rod. Transpantaneira-Pantanal Matogrossense (Poconé-MT). Rev Bras Biol 49(3):691–697

Da Silva CJ, Wantzen KM, Nunes da Cunha C, Machado FA (2001) Biodiversity in the Pantanal Wetland, Brazil. In: Gopal B, Junk WJ, Davis JA (org.). Biodiversity in Wetlands: assessment, function and conservation. Backwell Science, Leiden 2:187–217

Davis MA (1987) The role of flower visitors in the explosive pollination of *Thalia geniculata* (Marantaceae), a Costa Rican marsh plant. Bull Torrey Bot Club 114:134–138

Delatorre M, Cunha NL, Rodrigues RB, Damasceno-Junior GA, Ferreira VL (2019) Trait-environment relationship of aquatic vegetation in a tropical pond complex system. Wetlands. https://doi.org/10.1007/s13157-019-01189-0

Dhir B, Srivastava S (2011) Heavy metal removal from a multi-metal solution and wastewater by *Salvinia natans*. Ecol Eng 37(6):893–896. https://doi.org/10.1016/j.ecoleng.2011.01.007

Duarte LFC (2018) *Pirólise* de *macrófitas lemnáceas* para obtenção de *bio-óleo*. Dissertation, Universidade Tecnológica do Paraná, Londrina. http://repositorio.roca.utfpr.edu.br/jspui/handle/1/10303

EPPO (2008) EPPO Bull 38:441–449

Fernández M, Bedoya AM, Madriñán S (2015) Plants acuáticas de las planícies inundables de la Orinoquia colombiana. Biota Colomb 16(1):96–105

Ferreira FA, Mormul RP, Thomaz SM, Pott A, Pott VJ (2011) Macrophytes in the upper Paraná river floodplain: checklist and comparison with other large South American wetlands. Rev Biol Trop 59:541–556

Ferreira FA, Catian G, Pott A (2016a) Diaspore bank of aquatic macrophytes maintaining species diversity in a Neotropical pond. Acta Scient. Biol Sci (Online) 38:419–427

Ferreira FA, Pott A, Pott VJ, Latini RO, Resende DC (2016b) Espécies exóticas invasoras de Águas Continentais. Cap. 11. In: Latini RO, Resende DC, Pombo VB, Coradin, L (Org) Macrófitas aquáticas, Ministério do Meio Ambiente, Brasília 1:657–726. http://mma.gov.br/publicacoes/biodoversidade/especiesexoticas.invasoras.pdf

Ferreira FA, Okamura LA, Santos JM, Cardoso DEV, Tanimoto ST, Camargo JS, Oliveira FA, Barros R (2020) Do resíduo ao biocombustível: manejando as macrófitas aquáticas visando o estabelecimento de uma cadeia produtiva sustentável. In: IX Seminário Brasileiro de Meio Ambiente e responsabilidade social do setor elétrico, Rio de Janeiro

Fidalgo O, Bononi VLR (1984) Técnicas de coleta, preservação e herborização de material botânico. Instituto de Botânica, São Paulo

Flora do Brasil (2020) Under construction. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/

Frey R (1995) Flora and vegetation of "Las Piedritas" and the margin of Laguna Cáceres, Puerto Suárez, Bolivian Pantanal. Bull Torrey Bot Club 122:314–319. https://doi.org/10.2307/2996324

Funez LA, Hassemer G (2018) Novelties in the genus *Persicaria* (Polygonaceae) in Brazil: A new species, a new combination, and a diagnostic key to all species. Nordic J Bot 2018:e011631. https://doi.org/10.1111/njb.01631

GBIF – Global Biodiversity Information Facility (2017) Free and open access to data on biodiversity. https://www.gbif.org

Gessner F (1960) Die Blütenöffnung derVictoria regia in ihrer Beziehung zum Licht. Planta 54 (5):453–465

Gomes AC, Aoki C (2016) Efeito da sazonalidade hídrica sobre a fitossociologia de macrófitas aquáticas em uma lagoa no Pantanal, Brasil. (Effect of hydro seasonality on the phytosociology of aquatic macrophytes in a lake in the Pantanal, Brazil). Rev Biol Neotrop/J Neotrop Biol 12(1):1–7. https://doi.org/10.5216/rbn.v1i1.33966

Guglieri-Caporal A, Valls JFM, Pott A, Felismino MF, Caporal FJM (2018) Checklist das Poaceae do Estado de Mato Grosso do Sul, Brasil. Iheringia Sé Bot 73(1 Supl):312–328. https://doi.org/10.21826/2446-8231201873s313

Haase R, Beck SG (1989) Structure and composition of savanna vegetation in Northern Bolivia: a preliminary report. Brittonia 41(1):80–100

Heckman CW (1998) The Pantanal of Poconé: biota and ecology in the northern section of the World's largest pristine wetland. Kluwer Academic Publishers, Dordrecht

Hoehne FC (1948) Plantas aquáticas. Instituto de Botânica, São Paulo

INCT – Instituto Nacional de Ciência e Tecnologia (2017) Herbário virtual da flora e d os fungos. Species Link SpeciesLink Network. http://inct.splink.org.br

Irgang BE, Gastal CVS (1996) Macrófitas aquáticas da Planície Costeira do RS. Porto Alegre, authors edition

Jabot. JBRJ – Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. Jabot – Banco de Dados da Flora Brasileira. http://jabot.jbrj.gov.br/.

James EK, Loureiro MF, Pott A, Pott VJ, Martins C, Franco AA, Sprent JI (2001) Flooding-tolerant legume symbiosis from the Brazilian Pantanal. The New Phytol 150:723–738

Joyce JC (1990) Practical uses of aquatic weeds. In: Pieterse AH, Murphy KJ (eds) Aquatic weeds: the ecology and management of nuisance aquatic vegetation. Oxford University Press, Oxford, pp 274–291

Jstore (2020) www.jstore.org.

Junk WJ (1970) Investigations on the ecology and production biology of the "floating meadows" (Paspalo-Echinochloetum) on the middle Amazon. 1. The floating vegetation and its ecology. Amazonia: Limnologia et Oecologia Regionalis Systematis Fluminis Amazonas 2(4):449–495

Junk WJ, Nunes da Cunha C (2016) The pantanal: a brief review of its ecology, biodiversity, and protection status, The wetland book. Springer, Dordrecht, pp 1–15

Junk WJ, Nunes da Cunha C, da Silva CJ, Wantzen KM (2011) The Pantanal: a large South American wetland and its position in limnological theory. In: JungWJ SCJ, Nunes da Cunha C, Wantzen KM (eds) The pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia, pp 23–44

Kahn F, Léon B, Young KR (eds) (1993) Plantas vasculares en las aguas continentals del Peru. IFEA, Lima

Kaul RB (1976) Anatomical observations on floating leaves. Aquat Bot 2:215–234

Keddy PA (2000) Wetland ecology: principles and conservation. Cambridge University Press, Cambridge

Kissmann KG, Groth D (1997) Plantas infestantes e nocivas, Tomo I. BASF, São Paulo

Koehler S, Bove CP (2004) Alismatales from the upper and middle Araguaia river basin (Brazil). Rev Bras Bot [online] 27(3):439–452. https://doi.org/10.1590/S0100-84042004000300005

Krapovickas A, Gregory WC (2007) Taxonomy of the genus *Arachis* (Leguminosae). Bonplandia 16(Supl):1–205

Kufner DCL, Scremin-Dias E, Guglieri A (2011) Composição florística e variação sazonal da biomassa de macrófitas aquáticas em lagoa de meandro do Pantanal (Floristic composition and seasonal variation of aquatic macrophyte biomass in oxbow lake of the Pantanal). Rodrig 62:803–812

Lagnika L, Attioua B, Weniger B, Kaiser M, Sanni A, Vonthron-Senecheau C (2008) Phytochemical study and antiprotozoal activity of compounds isolated from *Thalia geniculata*. Pharm Biol 46:162–165

Landoldt E (1987) The family of Lemnaceae – a monographic study. Veröff Geobot Inst ETH Stiftung Rübel, Zürich, 7:1–247, 1980; 71:1–556, 1986; 95:1–638, 1987 (published as a book)

Lehn CR, Bueno ML, Kufner DCL, Scremin-Dias E, Pott VJ, Damasceno Junior GA (2012) Fitossociologia de macrófitas aquáticas associadas ao Rio Miranda, Pantanal, MS, Brasil. Rev Biol Neotr/J Neotr Biol 8(2):23–31. https://doi.org/10.5216/rbn.v8i2.12004

Lehtonen S (2008) An integrative approach to species delimitation in *Echinodorus* (Alismataceae) and the description of two species. Kew Bull 63:525–563

Lehtonen S, Myllys L (2008) Cladistic analysis of *Echinodorus* (Alismataceae): simultaneous analysis of molecular and morphological data. Cladistics 24:218–239. https://doi.org/10.1111/j.1096-0031.2007.00177.x

Leme FM, Scremin-Dias E (2014) Ecological interpretations of the leaf anatomy of amphibious species of *Aeschynomene* L. (Leguminosae – Papilionoideae). Braz J Biol 74:41–51

Lima ZM, Paula AM, Sérgio EC, Soares CR, Macedo M (1999) Aspectos ecológicos da dispersão em "camalotes" de macrófitas aquáticas na Baía Piuvial, Pantanal de Poconé - MT. In: Anais do II Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, Manejo e Conservação. Embrapa-DDT, Corumbá, pp 381–385

Lima LCP, Sartori ALB, Pott VJ (2006) *Aeschynomene* (Leguminosae, Papilionoideae, Aeschynomeneae) no Estado de Mato Grosso do Sul, Brasil. Hoehnea 33(4):419–453

Lima GT, Catian G, Luz GP, Manvailer S-DE (2018a) Plântulas e sementes de macrófitas aquáticas de lagoas do Pantanal Sul-Mato-Grossense. Iheringia Sér Bot 73:69–87. https://doi.org/10.21826/2446-8231201873201

Lima ACP, França F, Jesus TB (2018b) Avaliação dos níveis de metais pesados no pantanal dos Marimbus, Bahia, Brasil. Eng Sanit Amb 23(3):591–598. https://doi.org/10.1590/S1413-41522018164218

Llano MG, Adis J, Marques MI, Battirola LD (2005) *Cornops aquaticum* (Orthoptera, Acrididae, Leptysminae): aceitação de plantas alimentares por ninfas vivendo em *Eichhornia azurea* (Pontederiaceae) no Pantanal Norte, Brasil. Amazon 18(3/4):397–404

Lo EL, Silva A, McGlue MM, Silva BLP, Silva APS, Pereira LE, Macedo HÁ, Assine ML, Silva ERS (2016) Papel das macrófitas aquáticas na sucessão ecológica em sistemas fluvio-lacustres do Pantanal: Lago Uberaba. Anais 6º Simpósio de Geotecnologias no Pantanal, Cuiabá, MT, 22 a 26 de outubro 2016 Embrapa Informática Agropecuária/INPE, pp 224–233

Lorenzi H (1992) Plantas daninhas do Brasil. Plantarum, Nova Odessa

Loureiro MF, Faria SM, Pott A, Franco AA (1994) Nitrogen-fixing stem nodules of the legume *Discolobium pulchellum* Benth. New Phytol 128:283–295

Madriñán S, Rial A, Bedoya AM, Fernández-Lucero M (2017) Plantas Acuáticas de la Orinoquia Colombiana. Universidad de los Andes, Ed. Uniandes, Bogotá. http://ipt.sibcolombia.net/sib/resource.do?r=plantas_acuaticas_orinoquia. https://doi.org/10.15472/tlqst

Marcondes DAS, Mustafá AL, Tanaka RH (2003) Estudos para manejo integrado de plantas aquáticas no reservatório de Jupiá. In: Thomas SM, Bini LM (eds) Ecologia e manejo de macrófitas aquáticas. EDUEM, Maringá, pp 299–317

Marimon BS, Marimon Junior BH, Lime HS, Jancowski HS, Mews HA, Franczak DD, Moresco MC (2008) Pantanal do Araguaia – Ambiente e Povo: guia de ecoturismo (Pantanal of Araguaia – Environment and People: ecoturism guide). Editora Unemat, Cáceres

Martinez MT, Ledezma R, Miranda V (2020) Forrajeras nativas del Pantanal ANMI San Matias. Fundación Noel Kempff Mercado, La Paz

Mefit-Babtie S (1983) Development studies of the Jonglei Canal Area, Range Ecology Survey, Final Report, vol 2, Background. Khartoum, Sudan: USAID PCE-I-00-96-00002-00

Mereles F., De Egea-Elsam J, Céspedes G, Peña-Chocarro MC, Degen de Arrúa R (eds.) (2015) Plantas acuáticas y palustres del Paraguay. Vol. 1: Bryophyta, Pteridophyta y Angiospermae Monocotyledoneae. Rojasiana Serie Especial 2(1):1–236

Mitsch WJ, Gosselink JG (1993) Wetlands, 2nd edn. Van Nostrand Reinold, New York

Mobot. Missouri Botanical Garden. www.tropicos.org

Mohedano RA, Costa RHR, Tavares FA, Belli Filho P (2012) High nutrient removal rate from swine wastes and protein biomass production by full-scale duckweed ponds. Bioresour Technol 112:98–104. https://doi.org/10.1016/j.biortech.2012.02.083

Moreira SN, Pott VJ (2018) Lista das *Nymphaeales* de Mato Grosso do Sul, Brasil. Iheringia Sé Bot 73(1 Supl):283–286. https://doi.org/10.21826/2446-8231201873s283

Moreira SN, Assunção VA, Bueno B, Rodrigues LS, Silva RH, Pott VJ, Pott A, Damasceno-Junior GA, Scremin-Dias E (2017a) Aquatic macrophytes in Paraguay River branches in the Brazilian Pantanal, Mato Grosso do Sul, Brazil. Bol Museu Paraense Emilio Goeldi, Ci Nat 12:177–185

Moreira SN, Pott VJ, Souza EB, Pott A (2017b) Are *Mauritia flexuosa* L.f. palm swamps in Brazilian Pantanal true *veredas*? A floristic appraisal. Bol Museu Paraense Emilio Goeldi, Ci Nat 12:221–238

Moura Júnior EG, Lima LF, Silva SSL, Paiva RMS, Ferreira FA, Zickel CS, Pott A (2015a) Aquatic macrophytes of Northeastern Brazil: Checklist, richness, distribution and life forms [with erratum]. Check List (Online) 9:298

Moura Júnior EG, Paiva RMS, Ferreira AC, Pacopahyba LD, Tavares AS, Ferreira FA, Pott A (2015b) Updated checklist of aquatic macrophytes from Northern Brazil. Acta Amaz 45:111–132

Murphy K, Efremov A, Davidson T, Molina-Navarro E, Fidanza K, Betiol TCC, Chambers P, Grimaldo JT, Martins SV, Springuel I, Kennedy M, Mormul RP, Dibble E, Balázs AL, Gebler D, Baastruo-Spohr L, Urrutia J (2019) World distribution, diversity and endemism of aquatic macrophytes. Aquat Bot 158. https://doi.org/10.1016/j.aquabot.2019.06.006

Murphy K, Carvalho P, Efremov A, Grimaldo JT, Molina-Navarro E, Davidson TA, Thomaz SM (2020) Latitudinal variation in global range-size of aquatic macrophyte species shows evidence for a Rapoport effect. Freshw Biol 65. https://doi.org/10.1111/fwb.13528

National Academy of Sciences (1976) Making aquatic weeds useful: some perspectives for developing countries. National Academy of Sciences, Washington

Neiff JJ (2001) Diversity in some tropical wetland systems of South America. In: Gopal B, Junk WJ, Davies JA. Biodiversity in wetlands: assessment, function and conservation. Vol 2. Backhuys, Leiden. pp 157–186

Neiff JJ (1979) Fluctuaciones de la vegetación acuática em lagunas del río Paraná en la transección Paraná-Santa Fé entre 1970 y 1977. Physis 38(95):41–53

Neiff JJ (1990) Ideas para la intepretación ecológica del Paraná. Interciencia 15(6):424–441

Neiff JJ (2004) El Iberá...en peligro? Ed. Fundación Vida Silvestre de Argentina

Neiff JJ, Casco SL, Cózar A, Poi de Neiff ASG, Ubeda B (2011) Vegetation diversity in a large Neotropical wetland during two different climate scenarios. Biodivers Conserv 20(9):2005–2020. https://doi.org/10.1007/s10531-011-0071-7

Neiff JJ, Casco SL, Mari EK, Di Rienzo JA, Poi A (2014) Do aquatic plant assemblages in the Paraná River change along the river's length? Aquat Bot 114:50–57

Nunes da Cunha C, Rebellato L, Costa CP (2010) Vegetação e flora: experiência pantaneira no sistema de grade. In: Fernandes IM, Signor CA, Penha J (org.) Biodiversidade no Pantanal de Poconé. Centro de Pesquisa do Pantanal, Cuiabá

Nunes da Cunha C, Piedade MTF, Junk WJ (2014) Classificação e delineamento das Áreas Úmidas Brasileiras e de seus macrohabitats. EdUFMT, Cuiabá

NYBG. New York Botanical Garden. www.nybg.org

Oliveira AKM, Favero S, Costacurta MB (2005) Variação temporal da biomassa de *Eichhornia azurea* (Sw.) Kunth (Pontederiaceae) e macrófitas aquáticas associadas em uma lagoa do Rio Negro, pantanal do RioNegro, Mato Grosso do Sul. Natureza online 3(1):7–12. [online] http://www.naturezaonline.com.br

Penha JMF, da Silva CJ, Bianchini-Júnior I (1999) Productivity of the aquatic macrophyte *Pontederia lanceolata* Nutt. (Pontederiaceae) on floodplains of the Pantanal Mato-grossense, Brazil. Wetl Ecol Manage 7(3):155–163

Pereira-Silva L, Hefler SM, Trevisan R (2018) *Cyperus longiculmis* and *C. valiae* (Cyperaceae), two new species from Brazil. System Bot 43(3):741–746. https://doi.org/10.1600/036364418X697454

Piedade MTF, Lopes A, Dalmarchi LO, Junk WJ, Wittmann F, Schöngart J, Cruz J (2019) Guia de campo de herbáceas aquáticas da várzea amazônica. Ed INPA, Manaus

Pietro-Souza W, Mello IS, Vendruscullo SJ, Silva GF, Cunha CN, White JF, Soares MA (2017) Endophytic fungal communities of *Polygonum acuminatum* and *Aeschynomene fluminensis* are influenced by soil mercury contamination. PLoS One 12:e0182017

Pinheiro MNM, Jardim MAG (2015) Composição florística e formas biológicas de macrófitas aquáticas em lagos da Amazônia Ocidental, Roraima, Brasil. Biota Amaz 5:1–6

Pitelli RA, Pitelli RLCM, Marcondes DAS (2000) Controle biológico de macrófitas aquáticas. In: Workshop Ecologia e Manejo de Macrófitas Aquáticas, 2000, Maringá, PR. Resumos, pp 23–23

Pivari MOD, Pott VJ, Pott A (2008) Macrófitas aquáticas das ilhas flutuantes (baceiros) nas sub-regiões do Abobral e Miranda, Pantanal, MS, Brasil. Acta Bot Bras 22(2):563–571

Pivari MOD, Melo PHA, Souza FS, Stehmann JR, Moura Júnior EG, Moreira SN, Pott VJ, Pott A, Lopes A, Moço MCC, Oliveira LS, Lins ALA, Arruda R, Morais IL, Silva S, Ferreira RM (2018) New initiatives for Brazilian aquatic plant data management. Acta Bot Bras 32: Epub Nov 29, 20

Pott VJ (1998) A família Nymphaeaceae no Pantanal. Acta Bot Bras 12(2):183–194

Pott VJ (1999) Riqueza verde em meio azul. In: Scremin-Dias E, Pott VJ, Hora R, Souza PR. Nos jardins submersos da Bodoquena: guia para identificação das plantas aquáticas de Bonito e região. UFMS, Campo Grande. pp 59–93. https://ecoa.org.org/wp – content/uploads/2016/12/Nos – Jardins – Submersos – da – Bodoquena.pdf

Pott VJ, Cervi AC (1999) A família Lemnaceae Gray no Pantanal (Mato Grosso e Mato Grosso do Sul), Brasil. Rev Bras Bot 22:153–174

Pott EB, Pott A (1987) Níveis de nutrientes de plantas não–gramíneas pastejadas por bovinos na sub-região dos Paiaguás, do Pantanal Mato-grossense. Pesq Agropec Bras 22(11/12):1293–1299

Pott A, Pott VJ (1997) Checklist das macrófitas aquáticas do Pantanal, Brasil. Acta Bot Bras 11(2):215–227

Pott VJ, Pott A (2000) Plantas Aquáticas do Pantanal. Embrapa, Brasília

Pott VJ, Pott A (2002) Potencial de uso de plantas aquáticas na despoluição da água. Sér Doc Embrapa 133:1–10. Embrapa, Campo Grande. https://core.ac.uk/download/pdf/33884086.pdf

Pott VJ, Pott A (2003) Dinâmica da vegetação aquática do Pantanal. In: Thomaz SM, Bini MB (eds) Ecologia e manejo de macrófitas aquáticas. Eduem, Maringá, pp 143–162. www.eduem.uem.br/livros/ebook/ebook_eemdma.pdf

Pott A, Pott VJ (2004) Features and conservation of the Brazilian Pantanal. Wetl Ecol Manage 12(6):547–552

Pott A, Pott VJ (2005) Alterações florísticas na planície do Baixo Rio Taquari. In: Galdino S, Vieira LM, Pellegrin LA (eds) Impactos e ambientais e sócio-econômicos na Bacia do Rio Taquari, Pantanal. Embrapa Pantanal, Corumbá. https//:ainfo.cnptia.embrapa.br/digital/bitstream/item/38652/1/Livro025.pdf

Pott VJ, Pott A (2011) Species diversity, distribution, and biomass of aquatic macrophytes of the Pantanal. In: Junk WJ, Da Silva CJ, Nunes da Cunha CN, Wantzen KM (eds) The pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia, pp 257–279

Pott A, Ratter JA (2011) Species diversity of terrestrial plants and human impacts on the vegetation of the Pantanal. In: Junk WJ, Da Silva CJ, Nunes da Cunha CN, Wantzen KM (eds) The pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia, pp 281–300

Pott VJ, Pott A, Lima LCP, Moreira SN, Oliveira AKM (2011) Aquatic macrophyte diversity of the Pantanal wetland and upper basin. Braz J Biol 71(1 Suppl):255–263

Pott A, Silva JSV (2015) Terrestrial and Aquatic Vegetation Diversity of the Pantanal Wetland. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal wetland in South America, The Handbook of Environmental Chemistry, 37:111–132. Springer, Switzerland. https://doi.org/10.1007/698_2015_352

Pott EB, Brum PAR, Almeida IL, Comastri Filho JA, Dynia JF (1987) Nutrição mineral de bovinos de corte no Pantanal Mato-GrossenseL 1. Levantamento de macronutrientes na Nhecolândia (parte central). Pesq Agropec Bras 22(9):1093–1109

Pott VJ, Bueno NC, Pereira RAC, Vieira NL, Salis S (1989) Distribuição de macrófitas aquáticas numa lagoa na Fazenda Nhumirim, Nhecolândia, Pantanal, MS. Acta Bot Bras 3(supl):153–168

Pott VJ, Cervi AC, Bueno NC, Pott A (1999) Dinâmica da vegetação aquática de uma lagoa permanente da Fazenda Nhumirim, Pantanal da Nhecolândia, MS. In: Simpósio sobre Recursos Naturais e Socio-Econômicos do Pantanal; Manejo e Conservação. Corumbá, 1996. Anais: 227–235. Embrapa, Corumbá

Pott A, Valls JFM, Coradin L, Costa NMS (2018a) Espécies forrageiras – Fabaceae. In: Vieira RF, Camilo J, Coradin N (eds) Centro-Oeste. Espécies nativas da Flora Brasileira de valor econômico atual ou potencial: plantas para o futuro: região Centro-Oeste, vol 1. MMA, Brasília, pp 434–589. http://ainfo.cnptia.embrapa.br/digital/bitstream/item/162165/1/regio-centro-oeste-26-07-20171.pdf

Pott VJ, Moreira SN, Arantes ACV (2018b) Lista de Alismatales do estado de Mato Grosso do Sul, Brasil. Iheringia 73(1Suppl):117–122. https://doi.org/10.21826/2446-8231201873s117

Prado AL, Heckman CW, Martins FM (1994) The seasonal succession of biotic communities of wetlands in the tropical wet-and-dry climatic zone. II. The aquatic macrophyte vegetation in the Pantanal of Mato Grosso, Brazil. Int Rev Ges Hydrobiol 79(40):569–589

Prance GT, Arias JR (1975) A study of the floral biology of *Victoria amazonica* (Poepp.) Sowerby (Nymphaeaceae). Acta Amaz 5(2):109–139

Prance GT, Schaller GB (1982) Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. Brittonia 34(2):228–251

Prychid CJ, Rudall PJ (1999) Calcium oxalate crystals in Monocotyledons: a review of their structure and systematics. Annals Bot 84:725–739

Rebellato L, Cunha CN (2005) Efeito do “fluxo sazonal mínimo da inundação” sobre a composição e estrutura de um campo inundável no Pantanal de Poconé, MT, Brasil. Acta Bot Bras [online] 19(4):789–799. https://doi.org/10.1590/S0102-33062005000400015

Rebellato L, Cunha CN, Figueira JEC (2012) Respostas da comunidade herbácea ao pulso de inundação no Pantanal de Poconé, Mato Grosso. Oecol Austral 16:797–818

Redwood T (1818) Gray's Supplement to the Pharmacopoea: being a concise but comprehensive dispensatory and Manual of facts and formulae for the chemist and druggist and medical practicioner, 2nd edn. Longman, London

Rial A (2009) Plantas acuáticas de los llanos inundables del Orinoco, Venezuela. Orinoco y Amazonas editores, Caracas

Ritter N (2000) Biodiversity and Phytogeography of Bolivia's wetland flora. Dissertation, University of New Hampshire

Rocha M, Santos Júnior CC, Damasceno-Junior GA, Pott VJ, Pott A (2015) Effect of fire on a monodominant floating mat of *Cyperus giganteus* Vahl in a Neotropical wetland. Braz J Biol (Printed) 75:114–124

Rodrigues S, Scremin-Dias E, Medeiros SCH, Souza MC (2007) Alterações estruturais do caule e da folha de *Ludwigia inclinata* (L.f.) M. Goméz, desenvolvidos emersos e submersos no Pantanal Sul-Mato-Grossense. Rev Bras Bioci 5:174–176

Sanches AL, Cervi AC, Pott VJ (2000) Levantamento taxonômico de Pontederiaceae Kunth do Pantanal nos estados de Mato Grosso e Mato Grosso do Sul. In: III Simpósio sobre Recursos Naturais e Socio-econômicos do Pantanal. Embrapa Pantanal, Corumbá. 29 p. (CD-ROM)

Santos RN, Machado BR, Hefler SM, Zanette J (2021) Glutathione *S*-transferase activity in aquatic macrophytes and halophytes and biotransformation potential for biocides. J Plant Res. https://doi.org/10.1007/s10265-021-01266-8

Sartori ALB, Pott A, Pott VJ, Carvalho FS (2018a) Checklist das Angiospermas do Chaco de Mato Grosso do Sul. Iheringia Sér Bot 73(1, Supl):22–33. https://doi.org/10.21826/2446-8231201873s22

Sartori ALB, Lima LCP, Pott VJ, Valls JFM, Cristaldo ACM, Amaral CP, Costa LC, Pott A, Fortuna-Perez AP, Vaz AMSF, Silva GM, Bortoluzzi RLC, Pestana LT, Silva RR, Semidei E, Mansano VF, Sciamarelli A (2018b) Checklist das Leguminosae do Estado de Mato Grosso do Sul. Iheringia Sér Bot 73(1, Supl):239–254. https://doi.org/10.21826/2446-8231201873s239

Schessl M (1999) Floristic composition and structure of floodplain vegetation in the Northern Pantanal of Mato Grosso, Brazil. Phyton 39(2):303–336

Scremin-Dias E (2009) Tropical aquatic plants – Morphoanatomical adaptations. In: Del Claro K, Oliveira PS, Rico-Gray V (Org) Encyclopedia of tropical biology and conservation management. EOLSS. Tropical biology and natural resources. UNESCO/EOLSS, Paris. pp 84-132

Scremin-Dias E, Morretes BL (1999) Raizes laterais armazenadoras de amido em *Echinodorus paniculatus* Micheli (Alismataceae): uma característica de adaptação à sazonalidade do Pantanal. In: 50° Congresso Nacional de Botânica, 1999, Blumenau, SC. Anais do 50° Congresso Nacional de Botânica. p 3

Scremin-Dias E, Lorentz-Lemke AP, Oliveira AKM (2011) The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress. Braz J Biol 71:275–282

Silva RMM, Carniello MA (2007) Ocorrência de macrófitas em lagoas intermitentes e permanentes em Porto Limão Cáceres-MT. Rev Bras Bioci 5(2):519–521

Silva MP, Mauro RA, Mourão G, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Rev Bras Bot 23(2):143–152

Silveira RML, Weiss B (2014) Evidence for herbaceous seed dispersal by small-bodied fishes in a Pantanal seasonal wetland. Braz J Biol 74(3):588–596. https://doi.org/10.1590/bjb.2014.0089

Sousa DJL, Siqueira GB, Giulietti AM (2020) Two new species of *Pontederia* L. (Pontederiaceae Kunth) to South America. Phytotaxa 432(3). https://doi.org/10.11646/phytotaxa.432.3.2

Souza LS, Nunes O (2011) Levantamento de macrófitas aquáticas no rio Méquens. Rev Facimed 3:211–223

Souza CS, Barros MF, Freitas TG, Pott VJ, Pott A, Scremin-Dias E, Damasceno-Junior GA (2013) Assembléias de macrófitas aquáticas em diferentes áreas no Rio Paraguai. In: 6° SIMPAN – Simpósio do Pantanal, 2013, Corumbá, MS. Anais do 6° SIMPAN

Souza JME, Chang MR, Brito DZ, Farias KS, Damasceno-Junior GA, Turatti ICC, Lopes NP, Santos EA, Carollo CA, Souza JME, Chang MR, Brito DZ, Farias KS, Damasceno-Junior GA, Turatti ICC, Lopes NP, Santos EA, Carollo CA (2015) Antimicrobial activity of *Aspilia latissima* (Asteraceae). Braz J Microbiol 46:1103–1110

Souza EB, Ferreira FA, Pott A (2016) Effects of flooding and its temporal variation on seedling recruitment from the soil seed bank of a Neotropical floodplain. Acta Bot Bras 30:560–568

Talley SN, Talley BJ, Rains DW (1977) Nitrogen fixation by *Azolla* in rice fields. In: Hollaender A et al (eds) Genetic engineering for nitrogen fixation, Basic life sciences, 9. Springer, Boston

Taylor P (1989) The genus *Utricularia*, a taxonomic monograph. Royal Botanic Garden Kew, London

Thomaz SM, Souza DC, Bini LM (2003) Species richness and beta diversity of aquatic macrophytes in a large subtropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. Hydrobiologia 505(1):119–128. https://doi.org/10.1023/B:HYDR.0000007300.78143.e1

Tirintan G, Catian G, Luz GP, Gonçalves VM, Scremin-Dias E (2018) Plântulas e sementes de macrófitas aquáticas de lagoas do Pantanal Sul-Mato-Grossense. Iheringia Sér Bot 73(2):69–87. https://doi.org/10.21826/2446-8231201873201

Toledo JJ, Penha J (2011) Performance of *Azolla caroliniana* Willd. and *Salvinia auriculata* Aubl. on fish farming effluent. Braz J Biol (printed) 71:37–45. https://doi.org/10.1590/S1519-69842011000100007

Tozin LRS, Lima LB, Scremin-Dias E (2016) Fruit and seed biometry and germination of *Victoria amazonica* (Poepp.) J.C. Sowerby (Nymphaeaceae) from the Pantanal floodplain. Acta Scient. Biol Sci (online) 38:221–227

Tur NM (1972) Un caso de epifitismo acuático. Bol Soc Arg Bot 10(4):323–327

Velasquez J (1994) Plantas acuáticas vasculares de Venezuela. Universidad Nacional de Venezuela, Caracas

Wantzen KM, Drago E, Silva CJ (2005) Aquatic habitats of the Upper Paraguai River Floodplain system and parts of the Pantanal (Brazil). Ecohydrol Hydrobiol 6(2):107–126

Ximenes LSV, Pott VJ, Aoki C (2017) Plantas aquáticas do Parque Municipal Lagoa Comprida, Aquidauana, Mato Grosso do Sul, Brasil. Bol Museu Paraense Emilio Goeldi Ci Nat 12:187–195

Zeiger C, Silva ICR, Mail M, Kavalenka MN, Barthlot W, Hölsner H (2016) Microstructures of superhydrophobic plant leaves – Inspiration for efficient oil spill cleanup materials. Bioinspir Biomim 11(5):056003. https://doi.org/10.1088/1748-3190/11/5/056003

Chapter 5
Leguminosae in the Pantanal

Ângela Lúcia Bagnatori Sartori, Giovani Carlos Andrella, Luan Hernandes Pinho Nogueira, Vivian Almeida Assunção, and Thomaz Ricardo Favreto Sinani

5.1 Introduction

The third largest family of angiosperms, Leguminosae Juss. (Fabaceae Lindl.), comprises 770 genera and 19,500 species (APG IV 2016; Lewis et al. 2005). A recent phylogenetic study proposes six subfamilies for Leguminosae – Caesalpinioideae DC., including the Mimosoid clade, Cercidoideae LPWG, Detarioideae Burmeist., Handb. Naturgesch., Dialioideae LPWG, Duparquetioideae LPWG, and Papilionoideae DC. (LPWG 2017).

With cosmopolitan distribution, Leguminosae are encountered in the main terrestrial biomes. Members of this family are ecologically important constituents of tropical and subtropical forests and savannas. They also occur in desertic and temperate regions (Schrire et al. 2005). The morphological diversity is reflected in their growth habits, which vary from trees, woody vines, and shrubs to ephemeral herbs (Lewis et al. 2005). Legumes represent one of the most important sources of plant proteins either as food or temperate and tropical fodder crops (Yahara et al. 2013).

The family Leguminosae is well represented in the Neotropics, in Africa, and in Oceania, but relatively less in Asia (Klitgaard and Lewis 2010). The species of the subfamily Caesalpinioideae including the Mimosoid clade are mainly tropically and subtropically distributed, while the members of Papilionoideae are primarily found in temperate regions, although some genera are restricted to the Tropics (Klitgaard and Lewis 2010). Other subfamilies, such as Cercidoideae, Detarioideae, and Dialioideae, are represented in the Tropics. The high ecological plasticity of the family is a distinctive feature that significantly influences its great diversity in Neotropical vegetational formations (de Queiroz 2009), which comprise seasonally

---

Â. L. B. Sartori (✉) · G. C. Andrella · L. H. P. Nogueira · V. A. Assunção · T. R. F. Sinani
Laboratório de Sistemática Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_5

dry tropical forests (SDTFs), Cerrado, and Chaco (Prado and Gibbs 1993; Pennington et al. 2000).

Arboreal representatives of the family Leguminosae compose the South American seasonally dry forests, distributed in discontinuous vegetation stripes (Pennington et al. 2006) that often penetrate Pantanal areas. Thus, it is worth mentioning the occurrence of some genera such as *Amburana* Schwacke & Taub., *Andira* Lam.*, Acosmium* Schott*, Ateleia* (DC.) Benth., *Bowdichia* Kunth*, Dalbergia* L.f.*, Geoffroea* Jacq.*, Machaerium* Pers., *Platypodium* Vogel, *Pterodon* Vogel, and *Vatairea* Aubl. In recent phylogenetic studies, many genera emerge in the early-branching clades of Papilionoideae (Cardoso et al. 2012). It is thus important to obtain more accurate knowledge on the biology of species such as *Acosmium, Amburana*, *Andira, Ateleia*, *Bowdichia, Dalbergia, Geoffroea, Machaerium, Platypodium*, *Pterodon*, and *Vatairea*, which are found in the Pantanal (Pott and Pott 1999).

Pantanal is a recent formation in geological terms. It presents low rates of plant endemism and shelters wide-ranging species. Among the 1277 reported species of angiosperms, 54 are endemic (Flora do Brasil 2020, under construction). Nevertheless, the high biodiversity of the world's largest floodable plain is still little known by the scientific community in terms of associated flora and biological aspects of its species.

Taxonomic studies related to Leguminosae in the Pantanal, which is considered the third richest family in this region (Flora do Brasil 2020, under construction), are still at their early stage. Data on its richness, which varies between 165 and 240 species (BFG 2015; Flora do Brasil 2020, under construction, Pott and Pott 1999), are thus inaccurate. In fact, Flora do Brasil 2020 (under construction) only mentions 165 species of Leguminosae in the whole Pantanal, which may be an underestimation if we consider that Pott and Pott (1999) reported 240 species for this family, including exotics. This number has risen to 320 species.

The Pantanal is floristically influenced by the Cerrado to the East, the Atlantic forest to the South, the Chaco to the West, and the Amazon rainforest to the North. In addition, due to flood pulses, a heterogeneous set of legume species able to survive flooding stress may influence the richness and taxonomic distinctness of this family.

To assess the plant community structure many indices can be used. Among them is the taxonomic distinctness, which involves the phylogenetic distance between the species occurring in a given area (Webb 2000, Gurevitch et al. 2009). According to Warwick and Clarke (2001), taxonomic distinctness shows properties of an assemblage and measures features of its overall taxonomic spread. Comparisons are made of one assemblage with another, with the primary motivation of environmental assessment and monitoring of biodiversity change, usually over wide space and time scales.

Among the abiotic variables, waterlogging is an important factor in the selection of the plant species that grow in the Pantanal. According to Pott and Silva (2015), species diversity is found within subregions and there are several categories regarding flood intensity (low, medium, and high Pantanal), rivers (Pantanal of Taquari, Pantanal of Rio Negro, and Pantanal of Taboco), and others. Waterlogging intensity may vary according to local rainfall and to water flowing from the uplands to the plain (Pott and Silva 2015).

In this chapter, we investigate the richness of Leguminosae in the Pantanal and calculate the taxonomic distinctness of the whole family and growth habits.

5.2 Databank on Leguminosae in the Pantanal: Procurement, Standardization, and Analyses

Data were obtained consulting the GBIF.org databank (2018). Our search was customized through a rectangular polygon including the whole Pantanal found in Olson's (2001) Terrestrial Ecoregions of the World. We used the terms "Leguminosae" and "Fabaceae" as filters and only considered data with geographical coordinates without geospatial problems; this yielded 14,060 occurrences. Then, QGIS 2.18.2 (2018) helped us to obtain the accurate contours of the collection points within the vector map of the Pantanal. Since this floodplain reaches its maximum extension at around 300 meters above sea level, we excluded all the collection points located above this altitude to avoid reports on hills that are usually areas of transitional vegetation. We then reduced our occurrences to 3496.

Data on the growth habits were supplied by the exsiccata labels prepared by collectors and complemented by consultations to taxonomic revisions and floristic-taxonomic studies. Habits were grouped into three categories: (1) trees-shrubs; (2) herbaceous-subshrubs; and (3) climbers.

Data on rainfall were obtained through the bioclimatic variable BIO12: Annual Precipitation, with a spatial resolution at 30 seconds; this supplied the average annual rainfall for the years 1970–2000, available on WorldClim version 2.0 (Fick and Hijmans 2017). Records between 946 and 1141 mm, 1142 and 1337 mm, and 1338 and 1532 mm were considered as low, medium, and high rainfall, respectively.

Botanical names were updated according to information provided by the sites of Flora do Brasil 2020 under construction, IPNI (2018), The Plant List (2018), and Tropicos.org (2018). We disregarded duplicates present in more than one site, taxa with the same geographical coordinates, and names of species considered naturalized and exotic. The classification system for Leguminosae follows the most recent proposal for this group (LPWG 2017).

Species richness was recorded and the number of individuals collected for each species was considered to calculate abundance (Gurevitch et al. 2009). The abundance considered was related to the occurrence found for each species in the database. Taxonomic distinctness (Δ^*) was calculated using the Program PAST (Hammer et al. 2001). The main premise is that taxonomic distinctness (Δ^*) is greater in communities with the higher number of taxa. Data were categorized into taxonomic levels: species, genus, and subfamily.

Data on rainfall were attributed to each occurrence and later used in the analyses on the QGIS software, which then drew the map.

5.3 Richness and Taxonomic Distinctness

The data on the richness of Leguminosae in the Pantanal come from 2621 plant collections (Fig. 5.1). This family encompasses 411 taxa (Table 5.1), distributed into five subfamilies, 105 genera, 377 species, and 37 infraspecific categories (Figs. 5.2, 5.3, 5.4, 5.5 and 5.6). The most representative subfamily is Papilionoideae (62 genera, 219 species, 10 of which are subspecies or varieties, Figs. 5.2 and 5.3), followed by Caesalpinioideae (33 genera, 129 species, 25 of which are subspecies or varieties, Figs. 5.4 and 5.5), Cercidoideae (3 genera, 18 species, Fig. 5.6d), Detarioideae (5 genera, 9 species, 2 of which are subspecies or varieties, Fig. 5.6a, b and e), and Dialioideae (2 genera, 2 species, Fig. 5.6c). Among the richest genera are *Mimosa*

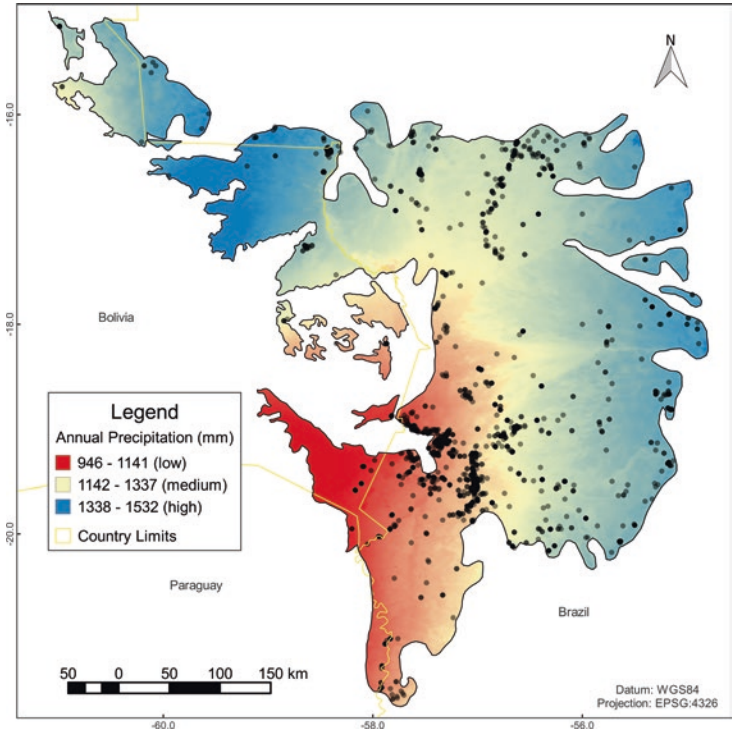


Fig. 5.1 Map of annual rainfall, from 1970 to 2000, for the Pantanal. Collection records are plotted in semi-transparent black circles. A higher intensity of black means a higher concentration of taxa

Table 5.1 List of Leguminosae taxa occurring in the Pantanal with growth habits and rainfall

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
Caesalpinioideae		
Albizia		**LMH**
A. edwallii (Hoehne) Barneby & J.W.Grimes	AS	
A. inundata (Mart.) Barneby & J.W.Grimes	AS	
A. multiflora (Kunth) Barneby & J.W.Grimes	AS	
A. niopoides (Spruce ex Benth.) Burkart	AS	
A. polycephala (Benth.) Killip ex Record	AS	
Anadenanthera		**LMH**
A. colubrina (Vell.) Brenan	AS	
A. colubrina var. *cebil* (Griseb.) Altschul	AS	
A. peregrina (L.) Speg.	AS	
A. peregrina var. *falcata* (Benth.) Altschul	AS	
Calliandra		**LMH**
C. harrisii (Lindl.) Benth.	AS	
C. longipes Benth.	HS	
C. parviflora Benth.	AS	
Cassia		**LMH**
C. grandis L.f.	AS	
Cenostigma		**LMH**
C. macrophyllum Tul.	AS	
C. pluviosum (DC.) Gagnon & G.P.Lewis	AS	
Chamaecrista		**LMH**
C. campestris H.S.Irwin & Barneby	HS	
C. desvauxii (Collad.) Killip	HS	
C. desvauxii var. *brevipes* (Benth.) H.S.Irwin & Barneby	HS	
C. desvauxii var. *latistipula* (Benth.) G.P.Lewis	HS	
C. diphylla (L.) Greene	HS	
C. flexuosa (L.) Greene	HS	
C. kunthiana (Schltdl. & Cham.) H.S.Irwin & Barneby	HS	
C. nictitans (L.) Moench	HS	
C. nictitans subsp. *brachypoda* (Benth.) H.S.Irwin & Barneby	HS	
C. nictitans subsp. *disadena* (Steud.) H.S.Irwin & Barneby	HS	
C. nictitans subsp. *patellaria* (DC. ex Collad.) H.S.Irwin & Barneby	HS	
C. repens (Vogel) H.S.Irwin & Barneby	HS	
C. rotundifolia (Pers.) Greene	HS	
C. rotundifolia var. *grandiflora* (Benth.) H.S.Irwin & Barneby	HS	
C. serpens (L.) Greene	HS	
Chloroleucon		**LM**
C. foliolosum (Benth.) G.P.Lewis	AS	
C. tenuiflorum (Benth.) Barneby & J.W.Grimes	AS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
C. tortum (Mart.) Pittier	AS	
Desmanthus		**LM**
D. leptophyllus Kunth	HS	
D. virgatus (L.) Willd.	HS	
Dimorphandra		**MH**
D. mollis Benth.	AS	
Diptychandra		**LMH**
D. aurantiaca Tul.	AS	
Entada		**L**
E. polystachya (L.) DC.	C	
Enterolobium		**LMH**
E. contortisiliquum (Vell.) Morong	AS	
E. timbouva Mart.	AS	
Hydrochorea		**M**
H. corymbosa (Rich.) Barneby & J.W.Grimes	AS	
Inga		**LMH**
I. cylindrica (Vell.) Mart.	AS	
I. disticha Benth.	AS	
I. edulis Mart.	AS	
I. laurina (Sw.) Willd.	AS	
I. marginata Willd.	AS	
I. nobilis Willd.	AS	
I. stenopoda Pittier	AS	
I. vera Willd.	AS	
I. vera subsp. *affinis* (DC.) T.D.Penn.	AS	
Libidibia		**LM**
L. paraguariensis (D. Parodi) G.P. Lewis	AS	
Microlobius		**LM**
M. foetidus (Jacq.) M.Sousa & G.Andrade	AS	
M. foetidus subsp. *paraguensis* (Benth.)M . Sousa & G. Andrade	AS	
Mimosa		**LMH**
M. adenocarpa Benth.	AS	
M. apodocarpa Benth.	AS	
M. balansae Micheli	HS	
M. bimucronata (DC.) Kuntze	AS	
M. candollei R.Grether	HS	
M. chaetosphaera Barneby	AS	
M. craspedisetosa Fortunato & Palese	AS	
M. debilis Humb. & Bonpl. ex Willd.	HS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
M. debilis var. *vestita* (Benth.) Barneby	HS	
M. diplotricha C.Wright ex Sauvalle	HS	
M. exalbescens Barneby	AS	
M. filipes Mart.	HS	
M. glutinosa Malme	AS	
M. hexandra Micheli	AS	
M. hirsutissima Mart.	HS	
M. invisa Mart. ex Colla	HS	
M. laticifera Rizzini & A.Mattos	AS	
M. ourobrancoensis Burkart	AS	
M. pellita Humb. & Bonpl. ex Willd.	AS	
M. pigra L.	AS	
M. pigra var. *dehiscens* (Barneby) Glazier & Mackinder	AS	
M. polycarpa Kunth	HS	
M. polycarpa var. *spegazzinii* (Pirotta ex Hook.f.) Burkart	HS	
M. pudica L.	HS	
M. quadrivalvis var. *tetragona* (Poir.) Barneby	HS	
M. sensibilis Griseb.	AS	
M. sensibilis var. *urucumensis* Barneby	AS	
M. sensitiva L.	HS	
M. setosa Benth.	HS	
M. setosa var. *paludosa* (Benth.) Barneby	HS	
M. somnians Humb. & Bonpl. ex Willd.	HS	
M. somnians var. *leptocaulis* (Benth.) Barneby	HS	
M. strigillosa Torr. & A.Gray	HS	
M. tweedieana Barneby ex Glazier & Mackinder	HS	
M. velloziana Mart.	HS	
M. weddelliana Benth.	AS	
M. xanthocentra Mart.	HS	
M. xanthocentra var. *subsericea* (Benth.) Barneby	HS	
M. xavantinae Barneby	AS	
Neptunia		**LMH**
N. oleracea Lour.	HS	
N. plena (L.) Benth.	HS	
N. pubescens Benth.	HS	
Parapiptadenia		**L**
P. rigida (Benth.) Brenan	AS	
Parkinsonia		**L**
P. aculeata L.	AS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
Peltophorum		**LM**
P. dubium (Spreng.) Taub.	AS	
Piptadenia		**LM**
P. gonoacantha (Mart.) J.F.Macbr.	AS	
P. stipulacea (Benth.) Ducke	AS	
P. viridiflora (Kunth) Benth.	AS	
Plathymenia		**LMH**
P. reticulata Benth.	AS	
Prosopis		**LM**
P. fiebrigii Harms	AS	
P. hassleri Harms	AS	
P. rubriflora Hassler	AS	
P. ruscifolia Griseb.	AS	
Pterogyne		**LMH**
P. nitens Tul.	AS	
Samanea		**LMH**
S. tubulosa (Benth.) Barneby & J.W.Grimes	AS	
Senegalia		**LMH**
S. langsdorffii (Benth.) Seigler & Ebinger	AS	
S. lewisii (Bocage & Miotto) L.P.Queiroz	AS	
S. loretensis (J.F.Macbr.) Seigler & Ebinger	AS	
S. martii (Benth.) Seigler & Ebinger	AS	
S. nitidifolia (Speg.) Seigler & Ebinger	AS	
S. polyphylla (DC.) Britton & Rose	AS	
S. praecox (Griseb.) Seigler & Ebinger	AS	
S. recurva (Benth.) Seigler & Ebinger	AS	
S. tenuifolia (L.) Britton & Rose	AS	
Senna		**LMH**
S. aculeata (Pohl ex Benth.) H.S.Irwin & Barneby	HS	
S. alata (L.) Roxb.	AS	
S. corymbosa (Lam.) H.S.Irwin & Barneby	AS	
S. hirsuta (L.) H.S.Irwin & Barneby	HS	
S. hirsuta var. *puberula* H.S.Irwin & Barneby	HS	
S. morongii (Britton) H.S.Irwin & Barneby	HS	
S. mucronifera (Mart. ex Benth.) H.S.Irwin & Barneby	HS	
S. obtusifolia (L.) H.S.Irwin & Barneby	HS	
S. occidentalis (L.) Link	HS	
S. paraensis (Ducke) H.S.Irwin & Barneby	HS	
S. pendula (Humb.& Bonpl.ex Willd.) H.S.Irwin & Barneby	C	
S. pendula var. *paludicola* H.S.Irwin & Barneby	C	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
S. pendula var. *tenuifolia* (Benth.) H.S.Irwin & Barneby	C	
S. pilifera (Vogel) H.S.Irwin & Barneby	C	
S. pilifera var. *subglabra* (S.Moore) H.S.Irwin & Barneby	C	
S. pistaciifolia (Kunth) H.S.Irwin & Barneby	AS	
S. reticulata (Willd.) H.S.Irwin & Barneby	AS	
S. scabriuscula (Vogel) H.S.Irwin & Barneby	HS	
S. silvestris (Vell.) H.S.Irwin & Barneby	AS	
S. silvestris subsp. *bifaria* H.S.Irwin & Barneby	AS	
S. silvestris var. *unifaria* H.S. Irwin & Barneby	AS	
S. spectabilis (DC.) H.S.Irwin & Barneby	AS	
S. splendida (Vogel) H.S.Irwin & Barneby	C	
S. tora (L.) Roxb.	HS	
S. velutina (Vogel) H.S.Irwin & Barneby	AS	
Stryphnodendron		**LMH**
S. rotundifolium Mart.	AS	
Tachigali		**LMH**
T. aurea Tul.	AS	
T. subvelutina (Benth.) Oliveira-Filho	AS	
T. vulgaris L.G.Silva & H.C.Lima	AS	
Vachellia		**LM**
V. caven (Molina) Seigler & Ebinger	AS	
V. farnesiana (L.) Wight & Arn.	AS	
Zapoteca		**L**
Z. formosa (Kunth) H.M.Hern.	AS	
Zygia		**LM**
Z. cauliflora (Willd.) Killip ex Record	AS	
Z. inaequalis (Willd.) Pittier	AS	
Z. latifolia (L.) Fawc. & Rendle	AS	
Z. latifolia var. *communis* Barneby & J.W.Grimes	AS	
Cercidoideae		
Bauhinia		**LMH**
B. aculeata L.	AS	
B. anomala Hassl.	AS	
B. bauhinioides (Mart.) J.F.Macbr.	AS	
B. brevipes Vogel	AS	
B. cheilantha (Bong.) Steud.	AS	
B. conwayi Rusby	AS	
B. corniculata Benth.	AS	
B. curvula Benth.	AS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
B. forficata Link	AS	
B. leptantha Malme	AS	
B. marginata (Bong.) Steud.	AS	
B. mollis (Bong.) D.Dietr.	AS	
B. pentandra (Bong.) D.Dietr.	AS	
B. pulchella Benth.	AS	
B. rufa (Bong.) Steud.	AS	
B. ungulata L.	AS	
Phanera		**LMH**
P. glabra (Jacq.) Vaz	C	
Schnella		**H**
S. outimouta (Aubl.) Wundelin	C	
Detarioideae		
Copaifera		**LM**
C. langsdorffii Desf.	AS	
C. langsdorffii var. *grandifolia* Benth.	AS	
C. malmei Harms	AS	
C. martii Hayne	AS	
Cynometra		**L**
C. bauhiniaefolia Benth.	AS	
Guibourtia		**LM**
G. chodatiana Hassl.	AS	
Hymenaea		**LMH**
H. courbaril L.	AS	
H. martiana Hayne	AS	
H. stigonocarpa Mart. ex Hayne	AS	
H. stigonocarpa var. *brevipetiolata* N.Mattos	AS	
Peltogyne		**M**
P. confertiflora (Mart. ex Hayne) Benth.	AS	
Dialioideae		
Apuleia		**H**
A. leiocarpa (Vogel) J.F.Macbr.	AS	
Poeppigia		**M**
P. procera C.Presl	AS	
Papilionoideae		
Acosmium		**LM**
A. cardenasii H.S.Irwin & Arroyo	AS	
Aeschynomene		**LMH**
A. americana L.	HS	
A. ciliata Vogel	HS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
A. denticulata Rudd	HS	
A. evenia C.Wright & Sauvalle	HS	
A. fluminensis Vell.	HS	
A. fluminensis var. *tuberculata* (Griseb.) Rudd	HS	
A. rudis Benth.	HS	
A. sensitiva Sw.	HS	
Amburana		**L**
A. cearensis (Allemão) A.C.Sm.	AS	
Ancistrotropis		**LM**
A. firmula (Mart. ex Benth.) A. Delgado	C	
A. peduncularis (Kunth) A. Delgado	C	
Andira		**LMH**
A. cujabensis Benth.	AS	
A. humilis Mart. ex Benth.	AS	
A. inermis (W.Wright) DC.	AS	
A. vermifuga (Mart.) Benth.	AS	
Arachis		**LMH**
A. appressipila Krapov. & W.C.Greg.	HS	
A. archeri Krapov. & W.C.Greg.	HS	
A. benthamii Handro	HS	
A. cardenasii Krapov. & W.C. Greg.	HS	
A. cryptopotamica Krapov. & W.C.Greg.	HS	
A. diogoi Hoehne	HS	
A. glabrata Benth.	HS	
A. glandulifera Stalker	HS	
A. gregoryi C.E. Simpson, Krapov. & Valls	HS	
A. helodes Mart. ex Krapov. & Rigoni	HS	
A. hoehnei Krapov. & W.C.Greg.	HS	
A. kretschmeri Krapov. & W.C.Greg.	HS	
A. kuhlmannii Krapov. & W.C.Greg.	HS	
A. lignosa (Chodat & Hassl.) Krapov. & W.C	HS	
A. lutescens Krapov. & Rigoni	HS	
A. magna Krapov., W.C. Greg. & C.E. Simpson	HS	
A. major Krapov. & W.C.Greg.	HS	
A. marginata Gardner	HS	
A. matiensis Krapov. & W.C. Greg.	HS	
A. oteroi Krapov. & W.C.Greg.	HS	
A. paraguariensis Chodat & Hassl.	HS	
A. simpsonii Krapov. & W.C.Greg.	HS	
A. subcoriacea Krapov. & W.C.Greg.	HS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
A. valida Krapov. & W.C.Greg.	HS	
A. vallsii Krapov. & W.C.Greg.	HS	
Ateleia		**LMH**
A. guaraya Herzog	AS	
Betencourtia		**LM**
B. scarlatina (Mart. ex Benth,) L.P. Queiroz	C	
Bowdichia		**LMH**
B. virgilioides Kunth	AS	
Caetangil		**LM**
C. paraguariensis (Chodat & Hassl.) L.P. Queiroz	C	
Calopogonium		**LM**
C. caeruleum (Benth.) C.Wright	C	
C. mucunoides Desv.	C	
C. velutinum (Benth.) Amshoff	C	
Camptosema		**LM**
C. rubicundum Hook. & Arn.	C	
Canavalia		**LMH**
C. brasiliensis Mart. ex Benth.	C	
C. mattogrossensis (Barb.Rodr.) Malme	C	
Centrosema		**LMH**
C. acutifolium Benth.	C	
C. angustifolium (Kunth) Benth.	C	
C. arenarium Benth.	C	
C. brachypodum Benth.	C	
C. brasilianum (L.) Benth.	C	
C. macranthum Hoehne	C	
C. macrocarpum Benth.	C	
C. pascuorum Mart. ex Benth.	C	
C. plumieri (Turpin ex Pers.) Benth.	C	
C. pubescens Benth.	C	
C. sagittatum (Humb. & Bonpl. ex Willd.) Brandegee	C	
C. schottii (Millsp.) K.Schum.	C	
C. vexillatum Benth.	C	
C. virginianum (L.) Benth.	C	
Cerradicola		**LM**
C. boavista (Vell.) L.P. Queiroz	HS	
C. elliptica (Desv.) L.P. Queiroz	C	
C. longifolia (Benth.) L.P. Queiroz	HS	
Chaetocalyx		**M**
C. brasiliensis (Vogel) Benth.	C	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
Clitoria		**LMH**
C. falcata Lam.	C	
C. guianensis (Aubl.) Benth.	HS	
C. stipularis Benth.	C	
Cochliasanthus		**L**
C. caracalla (L.) Trew	C	
Coursetia		**LM**
C. hassleri Chodat	HS	
Cratylia		**MH**
C. argentea (Desv.) Kuntze	C	
Crotalaria		**LMH**
C. incana L.	HS	
C. juncea L.	AS	
C. lanceolata E.Mey.	HS	
C. maypurensis Kunth	HS	
C. micans Link	AS	
C. pallida Aiton	HS	
C. pilosa Mill.	HS	
C. stipularia Desv.	HS	
Ctenodon		**LMH**
C. falcatus (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. gracilis (Vogel) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. histrix (Poir.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. histrix var. *densiflorus* (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. histrix var. *incanus* (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. oroboides (Benth.) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. paniculatus (Willd. ex Vogel) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima	HS	
C. racemosus (Vogel) D.B.O.S.Cardoso, Filardi & H.C.Lima	HS	
C. viscidulus (Michx.) D.B.O.S.Cardoso & A.Delgado	HS	
Dahlstedtia		**M**
D. araripensis (Benth.) M.J. Silva & A.M.G. Azevedo	AS	
D. muehlbergiana (Hassl.) M.J.Silva & A.M.G.Azevedo	AS	
Dalbergia		**LM**
D. acuta Benth.	AS	
D. cuiabensis Benth.	AS	
D. riedelii (Benth.) Sandwith	C	
Desmodium		**LMH**

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
D. affine Schltdl.	HS	
D. album (Schindl.) J.F. Macbr.	AS	
D. axillare (Sw.) DC.	HS	
D. barbatum (L.) Benth.	HS	
D. cajanifolium (Kunth) DC.	AS	
D. cuneatum Hook. & Arn.	AS	
D. distortum (Aubl.) J.F.Macbr.	HS	
D. glabrum (Mill.) DC.	HS	
D. incanum (Sw.) DC.	HS	
D. leiocarpum (Spreng.) G.Don	AS	
D. procumbens (Mill.) Hitchc.	HS	
D. sclerophyllum Benth.	HS	
D. scorpiurus (Sw.) Desv.	HS	
D. subsecundum Vogel	HS	
D. tortuosum (Sw.) DC.	HS	
D. triflorum (L.) DC.	HS	
Dioclea		**LMH**
D. burkartii R.H.Maxwell	C	
D. guianensis Benth.	C	
D. virgata (Rich.) Amshoff	C	
Dipteryx		**LMH**
D. alata Vogel	AS	
Discolobium		**LMH**
D. leptophyllum Benth.	HS	
D. psoraleaefolium Benth.	HS	
D. pulchellum Benth.	HS	
Dolichopsis		**LM**
D. paraguariensis (Benth.) Hassl.	C	
Eriosema		**LMH**
E. brachyrhachis Harms	HS	
E. crinitum (Kunth) G.Don	HS	
E. crinitum var. *pulchellum* Benth.	HS	
E. heterophyllum Benth.	HS	
E. longifolium Benth.	HS	
E. platycarpon Micheli	HS	
E. simplicifolium (Kunth) G.Don	HS	
Erythrina		**LM**
E. dominguezii Hassl.	AS	
E. fusca Lour.	AS	
E. similis Krukoff	AS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
E. verna Vell.	AS	
Galactia		**LMH**
G. dubia DC.	C	
G. glaucescens Kunth	HS	
G. latisiliqua Desv.	C	
G. striata (Jacq.) Urb.	C	
G. striata var. *crassirachis* Burkart	C	
G. striata var. *villosa* (Wight & Arn.) Verdc.	C	
Geoffroea		**L**
G. spinosa Jacq.	AS	
Holocalyx		**M**
H. balansae Micheli	AS	
Indigofera		**LMH**
I. asperifolia Bong. ex Benth.	HS	
I. campestris Bong. ex Benth.	HS	
I. guaranitica Hassl.	HS	
I. hirsuta L.	HS	
I. lespedezioides Kunth	HS	
I. microcarpa Desv.	HS	
I. pascuorum Benth.	HS	
I. sabulicola Benth.	HS	
I. suffruticosa Mill.	HS	
I. truxillensis Kunth	HS	
Leptolobium		**LMH**
L. dasycarpum Vogel	AS	
L. elegans Vogel	AS	
Leptospron		**LM**
L. adenanthum (G. Mey.) A. Delgado	C	
Lonchocarpus		**LM**
L. pluvialis Rusby	AS	
L. sericeus (Poir.) Kunth ex DC.	AS	
Luetzelburgia		**M**
L. sotoi D.B.O.S. Cardoso, L.P. Queiroz & H.C. Lima	AS	
Machaerium		**LMH**
M. aculeatum Raddi	C	
M. acutifolium Vogel	C	
M. amplum Benth.	AS	
M. brasiliense Vogel	C	
M. eriocarpum Benth.	AS	
M. hirtum (Vell.) Stellfeld	AS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
M. isadelphum (E.Mey.) Amshoff	C	
M. lanceolatum (Vell.) J.F.Macbr.	C	
M. latifolium Rusby	C	
M. paraguariense Hassl.	AS	
M. villosum Vogel	AS	
Macropsychanthus		**LM**
M. glabrus (Benth.) L.P. Queiroz & Snak	C	
M. violaceus (Mart. ex Benth.) L.P. Queiroz & Snak	C	
Macroptilium		**LMH**
M. bracteatum (Nees & Mart.) Maréchal & Baudet	C	
M. gracile (Poepp. ex Benth.) Urb.	C	
M. lathyroides (L.) Urb.	C	
M. martii (Benth.) Maréchal & Baudet	C	
M. sabaraense (Hoehne) V.P.Barbosa	C	
Muellera		**LM**
M. filipes (Benth.) M.J. Silva & A.M.G. Azevedo	AS	
M. fluvialis (Lindm.) Burkart	AS	
M. nudiflora (Burkart) M.J.Silva & A.M.G.Azevedo	AS	
M. sericea (Micheli) M.J. Silva & A.M.G. Azevedo	AS	
M. variabilis (RR.Silva & AMG.Azevedo) MJ.Silva & AMG. Azevedo	AS	
Nanogalactia		**L**
N. pretiosa var. *trifoliolata* (Hassl.) L.P. Queiroz	HS	
Nissolia		**M**
N. fruticosa Jacq.	C	
Periandra		**H**
P. heterophylla Benth.	HS	
Phaseolus		**M**
P. lunatus L.	C	
Platymiscium		**MH**
P. floribundum Vogel	AS	
P. floribundum var. *nitens* (Vogel) Klitg.	AS	
P. pubescens Micheli	AS	
Platypodium		**LMH**
P. elegans Vogel	AS	
Pterocarpus		**LMH**
P. rohrii Vahl	AS	
P. santalinoides L'Hér. ex DC.	AS	
Pterodon		**LMH**
P. emarginatus Vogel	AS	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
P. pubescens (Benth.) Benth.	AS	
Rhynchosia		**LM**
R. balansae Micheli	HS	
R. balansae var. *psilantha* Fortunato	HS	
R. corylifolia Mart. ex Benth.	HS	
R. edulis Griseb.	C	
R. melanocarpa Grear	C	
R. minima (L.) DC.	C	
R. senna var. *texana* (Torr. & A.Gray) M.C.Johnst.	C	
Riedeliella		**LMH**
R. graciliflora Harms	AS	
Sesbania		**LMH**
S. emerus (Aubl.) Urb.	AS	
S. exasperata Kunth	AS	
S. oligosperma Taub.	AS	
S. virgata (Cav.) Pers.	AS	
Stylosanthes		**LMH**
S. capitata Vogel	HS	
S. gracilis Kunth	HS	
S. guianensis (Aubl.) Sw.	HS	
S. hamata (L.) Taub.	HS	
S. humilis Kunth	HS	
S. montevidensis Vogel	HS	
S. scabra Vogel	HS	
Swartzia		**MH**
S. jorori Harms	AS	
Sweetia		**L**
S. fruticosa Spreng.	AS	
Tephrosia		**LMH**
T. adunca Benth.	HS	
T. cinerea (L.) Pers.	HS	
T. domingensis (Willd.) Pers.	HS	
T. sessiliflora (Poir.) Hassl.	HS	
Teramnus		**LM**
T. uncinatus (L.) Sw.	C	
T. volubilis Sw.	C	
Vatairea		**MH**
V. macrocarpa (Benth.) Ducke	AS	
Vigna		**LMH**
V. lasiocarpa (Mart.ex Benth.) Verdc.	C	

(continued)

Table 5.1 (continued)

Subfamily *Genus* *Species* (infraspecific category)	Habit	APC
V. longifolia (Benth.) Verdc.	C	
V. luteola (Jacq.) Benth.	C	
V. unguiculata (L.) Walp.	C	
Zornia		**LMH**
Z. crinita (Mohlenbr.) Vanni	HS	
Z. latifolia Sm.	HS	
Z. pardina Mohlenbr.	HS	
Z. reticulata Sm.	HS	

Fig. 5.2 Representatives of Papilionoideae in the Pantanal. (**a**) – *Pterocarpus rohrii* Vahl. (**b**) – *Aeschynomene fluminensis* Vell. (**c**) – *Ctenodon paniculatus* (Willd. ex Vogel) D.B.O.S.Cardoso, P.L.R.Moraes & H.C.Lima (**d**) – *Amburana cearensis* (Allemão) A. C. Sm. (**e**) – *Stylosanthes hamata* (L.) Taub. (Photographs A – C, E courtesy of P.R.de Souza, D courtesy of E.P.Seleme)

Fig. 5.3 Representatives of Papilionoideae in the Pantanal. (**a**) – *Discolobium pulchellum* Benth. (**b**) – *Dipteryx alata* Vogel. (**c**) – *Galactia striata* (Jacq.) Urb. (**d**) – *Coursetia hassleri* Chodat. (**e**) – *Dolichopsis paraguariensis* (Benth.) Hassl. (**f**) – *Machaerium eriocarpum* Benth. (Photographs courtesy of P.R.de Souza, except (**c**) by T.R.F. Sinani)

L. (39 taxa, 32 species, 8 varieties, Fig. 5.4d and e), *Senna* Mill. (25 taxa, 5 varieties, 1 subspecies, Fig. 5.5c, d) and *Arachis* L. (25 species).

Papilionoideae is the only subfamily with more collections in areas with medium and high rainfall levels (Fig. 5.7a), followed by Caesalpinioideae (Fig. 5.7b), Cercidoideae (Fig. 5.7c), Detarioideae (Fig. 5.7d), and Dialioideae (Fig. 5.7e). Caesalpinioideae presents more collections in areas with low rainfall level followed by Papilionoideae, Cercidoideae, and Detarioideae. Dialioideae does not present collections in areas with low rainfall level (Fig. 5.7e). Forty-nine genera occur in areas under different rainfall levels, from low to high (Table 5.1), twenty-four genera in low and medium rainfall areas, and only five in medium and high rainfall areas. Among the genera reported only in areas with low rainfall (946 to 1141 mm) are *Amburana* (Fig. 5.2d), *Cochliasanthus* Trew, *Cynometra* L., *Entada* Adans., *Geoffroea*, *Parapiptadenia* Brenan (Fig. 5.4f), *Parkinsonia* L. (Fig. 5.5b), *Sweetia* Spreng., and *Zapoteca* H.M.Hern. On the other hand, some genera such as *Apuleia* Mart. and *Periandra* Mart. *ex* Benth. were only collected in areas with high rainfall level. The third category includes genera in medium rainfall areas, such as *Chaetocalyx* DC., *Holocalyx* Micheli, *Luetzelburgia* Harms, *Peltogyne* Vogel, *Phaseolus* L., and *Poeppigia* C. Presl. (Fig. 5.6c).

Fig. 5.4 Representatives of Caesalpinioideae (Mimosoide clade) in the Pantanal. (**A**) – *Neptunia pubescens* Benth. (**b**) – *Vachellia caven* (Molina) Seigler & Ebinger. (**c**) – *Anadenanthera colubrina* (Vell.). Brenan (**d**) – *Mimosa hexandra* Micheli. (**e**) – *Mimosa polycarpa* Kunth. (**f**) – *Parapiptadenia rigida* (Benth.) Brenan. (Photographs courtesy of P.R.de Souza)

As for the growth habits, trees and shrubs were recorded in 178 taxa (166 species) (Table 5.1), being preponderant, followed by herbs and subshrubs in 158 taxa (140 species), and climbers in 75 taxa (70 species). As for legumes as a whole, we found 1297 trees and shrubs, 909 herbs and subshrubs, and 415 climbers, respectively, 49.5%, 34.7%, and 15.8% of the habits sampled for Leguminosae.

The taxonomic distinctness of the community of legumes in the Pantanal is Δ* 3.55. With regard to growth habits, it is Δ* 3.58, Δ* 3.35, and Δ* 3.27 for trees and shrubs, herbs and subshrubs, and climbers, respectively.

5.4 Knowledge Gaps and Perspectives for Studies on Leguminosae in the Pantanal

Most collections of Leguminosae took place in the Southwest and the North of the Pantanal and only a small number occur in its Eastern and Central parts. Among the Brazilian phytogeographic domains, the highest species richness for Leguminosae is found in the Cerrado, with 1261 species, followed by the Amazon forest with 1145 species, the Atlantic forest with 1004 species, and the Caatinga with 612

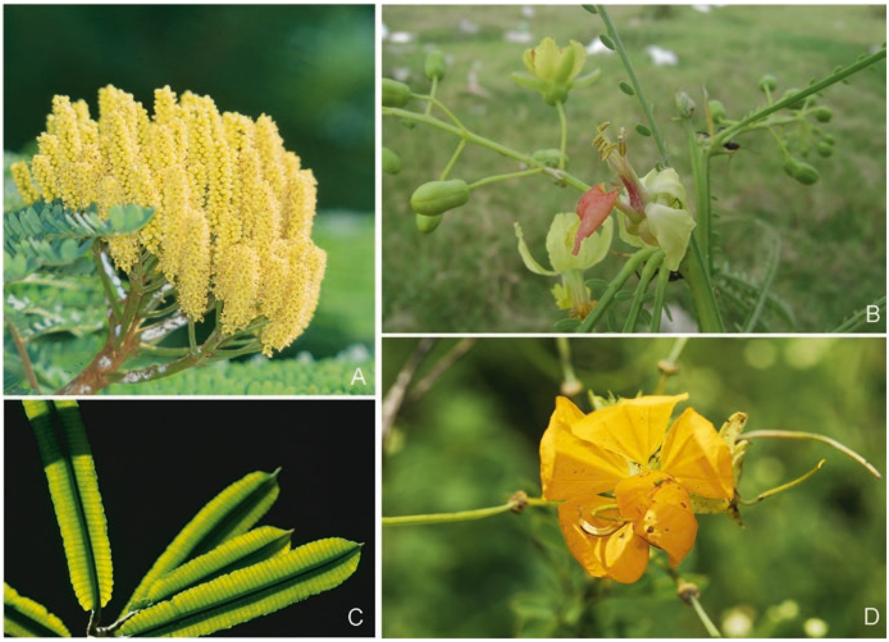


Fig. 5.5 Representatives of Caesalpinioideae in the Pantanal. (**a**) – *Dimorphandra mollis* Benth. (**b**) – *Parkinsonia aculeata* L. (**c**) – *Senna alata* (L.) Roxb. (**d**) – *Senna splendida* (Vogel) H.S.Irwin & Barneby. (Photographs A, C, D courtesy of P.R.de Souza, B courtesy of F.M.Alves)

species, according to Flora do Brasil 2020 (under construction). The richness of Leguminosae in the Pantanal varies between 165 (Flora do Brasil 2020, under construction) and 240 species (Pott and Silva 2015), which does not agree with the data recorded in our study. The delimitation of the Pantanal area considered here, encompassing reduced extensions of Bolivia and Paraguay, may have contributed to this increase in richness. In addition, specimens deposited in the collections of the states of Mato Grosso and Mato Grosso do Sul were possibly not analyzed by specialists of certain genera of Leguminosae, therefore yet missing in Flora do Brasil 2020 (under construction).

The genera that occur in the areas of the Pantanal with low rainfall level are usually found in seasonally dry forests and sometimes in the Cerrado and Caatinga. They are neotropically distributed and exclusive to South America, except for *Cynometra* L. which is found in Africa, Asia, and Madagascar (Mackinder 2005) and *Entada* Adans. with occurrence in these continents and Australasia (Luckow 2015). It is worth mentioning that in this group, *Cynometra* and *Entada* are considered Amazonian and *Geoffroea,* Chaquean. *Entada* occurs in the Paraguay River valley (see Chap. 3). Tolerant of the here considered high rainfall of the Pantanal, *Dimorphandra* (Fig. 5.5a), *Apuleia* Mart., and *Periandra* are exclusive to South America (Lewis 2005; Schire 2005) and widely distributed since they are found in floodable (*Dimorphandra* and *Apuleia*) or tropical wet forests and Cerrado

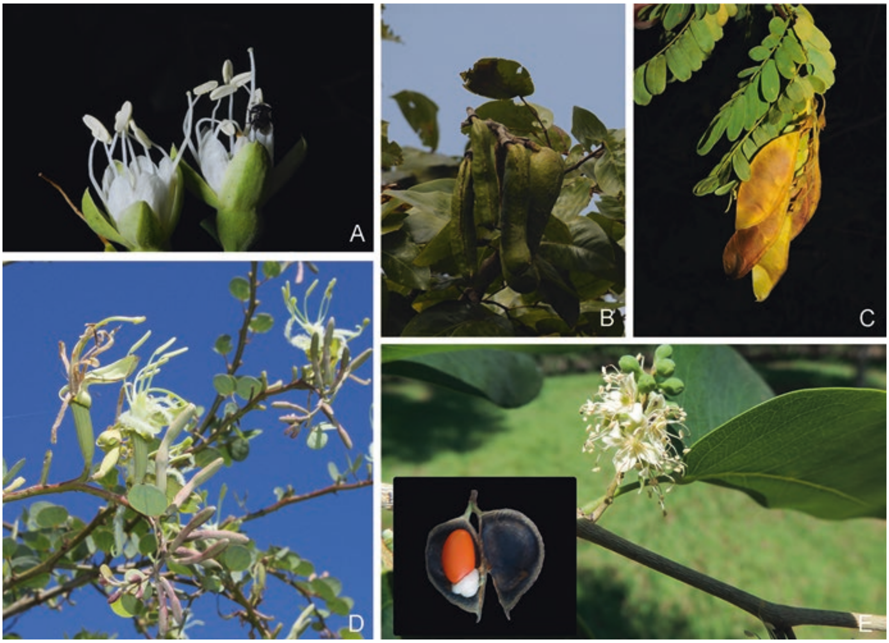


Fig. 5.6 Representatives of Cercidoideae, Detarioideae, and Dialioideae in the Pantanal. (**a**) – *Hymenaea martiana* Hayne. (**b**) – *Hymenaea stigonocarpa* Mart. ex Hayne (Detarioideae). (**c**) – *Poeppigia procera* Presl (Dialioideae). (**d**) – *Bauhinia bauhinioides* (Mart.) J.F.Macbr. (Cercidoideae). (**e**) – *Guibourtia chodatiana* Hassl. (Detarioideae). (Photographs A – B, D courtesy of P.R.de Souza, C courtesy of R. T. Queiroz, E courtesy of F.J. Kochanovski)

(*Periandra*). *Chaetocalyx*, *Holocalyx*, *Luetzelburgia*, *Peltogyne*, *Phaseolus*, and *Poeppigia* are tolerant of medium rainfalls. They are usually Neotropical genera, except *Phaseolus*. They commonly occur in seasonally dry forests (Ireland 2005; Pennington et al. 2005), warm temperate forests (Klitgaard and Lavin 2005), subtropical forests (Ireland 2005), and less commonly in the caatinga (*Poeppigia* – Lewis 2005), an aspect that may favor their presence in the areas of Pantanal with medium rainfall (1142–1337 mm).

Species-rich (*Mimosa*, Fig. 5.4d and e, *Senna*, Fig. 5.5c and d) or widely distributed (*Machaerium,* Fig. 5.3f) genera can comprise species adapted to more or less moist areas, under distinct rainfall levels, what hinders the detection of patterns. In this regard, additional studies are needed before anything can be asserted on patterns at the species level. *Aeschynomene* and *Ctenodon* Baill. (Fig. 5.2b and c, respectively), for example, comprises a group of species adapted to floodable areas and another group less tolerant of waterlogging (Leme and Scremin-Dias 2014).

The results of taxonomic distinctness reported for the Chaco (Δ* 3.47), seasonal forests (Δ* 3.54), and thorny woodlands (Δ* 3.50), which are considered dry South American areas (Lima et al. 2015), as well as for Brazilian Savannas (Δ* 3.54), are smaller than those obtained for the Pantanal. Features such as microphylly,

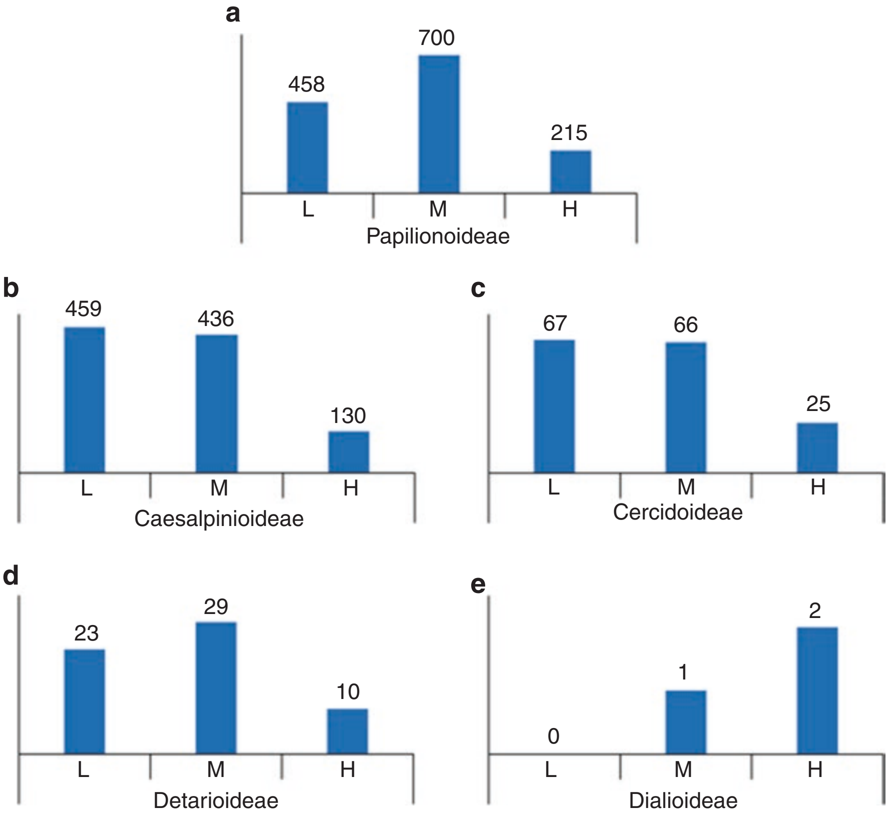


Fig. 5.7 Graphical representations of the quantities of collection records per subfamily of Leguminosae in three categories of Annual Rainfall (1970–2000): low (L), medium (M), and high (H)

spinescence, and hard seed testae may contribute to the family richness in drier environments. In given areas of the Pantanal subjected to flood during part of the year, water plays an important role in species selection, and this may contribute to higher taxonomic distinctness. This aspect is evidenced, for example, when comparing the taxonomic distinctness index of hyperseasonal (Δ * 4.06) and non-floodable (Δ * 4.10) Cerrados, since that of the former is lower (Silva and Batalha 2006). It is worth mentioning that Lima et al. (2015) considered three subfamilies in their classification of Leguminosae: Papilionoideae, Caesalpinioideae, and Mimosoideae and tribes, while our study considers Cercidoideae, Detarioideae, and Dialioideae in addition to the first two.

Neotropical seasonally dry forests hold variable data of richness and floristic affinity. In Central Brazil, for example, there is a higher species richness and a lower percentage of exclusive species, which results in a greater number of species shared with adjacent floristic groups (DRYFLOR 2016). The floristic heterogeneity found in the Neotropical seasonally dry forests occurs also in the Pantanal. However, this one shows lower taxonomic distinction. The periodic floods of the Pantanal contribute to the selection of species from different South American domains, and this gives it a unique character. It is important to assess the specificities of the Pantanal with respect to those plant species characteristics that contribute to the understanding of their distribution patterns, and this will be useful for the initiatives aimed at conservation.

5.5 Final Considerations

Further information on the occurrence of Leguminosae in the Brazilian states where the largest floodable plain is located, above all in Mato Grosso do Sul, is still needed since the limited access to certain areas during part of the year, when they are flooded, results in knowledge gaps on this family. In this regard, collection efforts should be directed toward the Eastern zone of the Pantanal, closer to the upland Cerrado, for a more satisfactory sampling of Leguminosae.

Phytogeographic domains such as the Chaco, the Cerrado, the Atlantic and Amazonian forests influence the floristic composition of the Pantanal, as proven by the presence of legume species with different diversification histories. Since it is one of the families with the highest richness in this domain, whose floristic composition is heterogeneous, additional studies to detect patterns at the species level are still required in order to elucidate relevant biogeographic issues.

References

Angiosperm Phylogeny Group (2016) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181(1):1–20

Brazilian Flora Group (2015) Growing knowledge: an overview of seed plant diversity in Brazil. Rodriguésia 66(4):1085–1113

Cardoso D, de Queiroz LP, Pennington RT et al (2012) Revisiting the phylogeny of papilionoid legumes: new insights from comprehensively sampled early-branching lineages. Am J Bot 99:1991–2013

de Queiroz LP (2009) Leguminosas da caatinga. Universidade Estadual de Feira de Santana, Feira de Santana

DRYFLOR (2016) Plant diversity patterns in neotropical dry forests and their conservation implications. Science 353:1383–1387

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315

Flora do Brasil 2020 em construção (2018) Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br. Accessed 12 Jun 2018

GBIF.org (2018) GBIF occurrence download. https://doi.org/10.15468/dl.rlx9q0. Accessed 21 May 2018

Gurevitch J, Scheiner SM, Fox GA (2009) Ecologia Vegetal. 2ª Edição. Artmed, Porto Alegre

Hammer O, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9

International Plant Names Index (2018) The royal botanic gardens, Kew, Harvard University Grassaria & Libraries and Australian National Botanic Gardens. http://www.ipni.org. Accessed 12 June 2018

Ireland HE (2005) Tribe Swartzieae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Richmond, pp 215–226

Klitgaard BB, Lavin L (2005) Tribe Dalbergieae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Ricchmond, pp 307–335

Klitgaard BB, Lewis GP (2010) Neotropical Leguminosae. In: Milliken W, Klitgård B, Baracat A (eds) Neotropikey – interactive key and information resources for flowering plants of the Neotropics. Available via DIALOG. http://www.kew.org/science/tropamerica/neotropikey/families/Leguminosae_(Papilionoideae).htm. Accessed 14 Feb 2014

Legume Phylogeny Working Group (2017) A new subfamily classification of the Leguminosae based on taxonomically comprehensive phylogeny. Taxon 66(1):44–77

Leme FM, Scremin-dias E (2014) Ecological interpretations of the leaf anatomy of amphibious species of Aeschynomene L. (Leguminosae – Papilionoideae). Braz J Biol 74:41–51

Lewis GP (2005) Tribe Cassieae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Richmond, pp 111–126

Lewis GP, Schrire B, Mackinder B, Lock M (eds) (2005) Legumes of the world. Royal Botanic Gardens, Kew, Richmond

Lima JR, Tozzi AMGA, Mansano VF (2015) A checklist of woody Leguminosae in the south American corridor of dry vegetation. Phytotaxa: A Rapid International Journal for Accelerating the Publication of Botanical Taxonomy 207:1–38

Luckow M (2015) Tribe Detarieae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Richmond, pp 163–183

Mackinder B (2005) Tribe Detarieae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Richmond, pp 69–110

Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51(11):933–938

Pennington RT, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and quaternary vegetation changes. J Biogeogr 27(2):261–273

Pennington CH, Stirton CH, Schrire BD (2005) Tribe Sophoreae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Richmond, pp 227–249

Pennington RT, Lewis GP, Ratter JA (2006) An overview of the plant diversity, biogeography and conservation of Neotropical Savanas and seasonally dry forests. In: Taylor & Francis Group (ed) Neotropical savannas and seasonally dry forests. Plant diversity, biogeography, and conservation, vol 69. CRC Press, London, pp 01–29

Pott A, da Silva JSV (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I, Assine M (eds) Dynamics of the Pantanal Wetland in South America. The handbook of environmental chemistry, vol 37. Springer, Cham, pp 111–131

Pott A, Pott VJ (1999) Flora do Pantanal, listagem atual de Fanerógamas. In: Anais II Simpósio sobre Recursos Ambientais e Socio-econômicos do Pantanal, manejo e conservação. Embrapa, Brasília, pp 297–325

Prado DE, Gibbs PE (1993) Patterns of species distribution in the dry seasonal forest of South America. In: Annals of the Missouri Botanical Garden, vol 80. Missouri Botanical Garden, St. Louis, pp 902–927

QGIS Development Team (2018) QGIS Geographic Information System v. 2.18.2. Open Source Geospatial Foundation Project. https://qgis.org/. Accessed May 2018

Schrire BD, Lavin M, Lewis GP (2005) Global distribution patterns of the Leguminosae: Insights from recent phylogenies. In: Friis I, Balslev H. (eds.) Plant diversity and complexity patterns: local, regional and global dimensions. Copenhagen, Biologiske Skrifter. p 375–422

Schire BD (2005) Tribe Phaseoleae. In: Lewis G, Schire B, Mackinder B, Lock M (eds) Legumes of the world. Royal Botanic Gardens, Kew, Richmond, pp 393–431

Silva IA, Batalha MA (2006) Taxonomic distinctness and diversity of a hyperseasonal savanna in Central Brazil. Divers Distrib 12:725–730

The Plant List (2018) Version 1.1. http://www.theplantlist.org/. Accessed 12 June 2018

Tropicos.org (2018) Missouri Botanical Garden. http://www.tropicos.org Accessed 12 June 2018

Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. Oceanogr Mar Biol Annu Rev 39:207–231

Webb CO (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. Am Nat 156:145–155

Yahara T, Javadi F, Onoda Y, Queiroz LP, Faith DP, Prado DE, Akasaka M, Kadoya T, Ishihama F, Davies SJW, Ferry Slik FJW, Yi T, Ma K, Bin C, Darnaedi D, Pennington RT, Tuda M, Shimada M, Ito M, Egan AN, Buerki S, Raes N, Kajita T, Vatanparast M, Mimura M, Tachida H, Iwasa Y, Smith FG, Janine E, Victor JE, Nkonki T (2013) Global legume diversity assessment: concepts, key indicators, and strategies. Taxon 62(2):249–266

Chapter 6
Lichenized *Ascomycota* from the Pantanal in Mato Grosso do Sul state, Brazil

Luciana da Silva Canêz, Natália Mossmann Koch, Thiago Dias Barbosa, Marcos Junji Kitaura, Adriano Afonso Spielmann, Neli Kika Honda, Patrícia Jungbluth, Alice Gerlach, Robert Lücking, and André Aptroot

6.1 Introduction

The Pantanal is an area of savanna that is seasonally partly flooded, located in the upper Paraguay River depression, and which extends between the Central Brazilian Shield and the foothills of the Andes (Junk and Nunes da Cunha 2016). In Brazil, the Pantanal is included in the Cerrado domain, a large phytogeographic region with high vegetation heterogeneity (Bueno et al. 2018) and comprises many woody species (around 750) as well as a great number of herbaceous plants (around 1,150), including 250 aquatic and/or palustrine species (Junk et al. 2014).

L. da Silva Canêz (✉) · N. M. Koch · T. D. Barbosa · A. A. Spielmann · A. Aptroot
Universidade Federal de Mato Grosso do Sul, Instituto de Biociências, Laboratório de Botânica/Liquenologia, Av. Costa e Silva s/n, Bairro Universitário,
Campo Grande, MS, Brazil
luciana.canez@ufms.br

M. J. Kitaura
Universidade Federal de Mato Grosso do Sul, campus de Aquidauana,
Aquidauana, MS, Brazil

N. K. Honda
Universidade Federal de Mato Grosso do Sul, Instituto de Química,
Campo Grande, MS, Brazil

P. Jungbluth
Universidade Federal de Santa Maria, Campus de Palmeira das Missões – RS, Departamento de Zootecnia e Ciências Biológicas, Palmeira das Missões, RS, Brazil

A. Gerlach
Conservatoire et Jardin botaniques de la Ville de Genève, Chambésy/GE, Switzerland

R. Lücking
Botanischer Garten und Botanisches, Museum, Berlin, Germany

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_6

Lichens are a symbiotic association of at least two partners: a fungus (the mycobiont) and an alga and/or a cyanobacterium (the photobiont) that together results in a thallus with varying morphologies (Purvis 2000, Marcelli 2006). Lichens are good indicators of environmental changes (Giordani et al. 2002, Aptroot and van Herk 2006, Koch et al. 2013, Matos et al. 2019), so documenting their diversity is an important tool for monitoring and conservation efforts.

Gustav Malme visited the state of Mato Grosso do Sul during the First and the Second Regnellian Expedition, from 1892 to 1894 and from 1901 to 1902, respectively. It was during the first expedition that he paid close attention to lichens (Baptista 1996). Malme specifically visited the municipality of Corumbá, which belonged to Mato Grosso state at that time. He studied the major part of his collections (e.g. Malme 1897, 1902, 1923, 1924a, b, 1927), but many of his materials were also studied by other lichen taxonomists (e.g., Lynge 1914, 1924; Motyka 1936, 1938; Redinger 1933a, b, 1935, 1936, 1940). For a complete list of Malme publications and those based on his collections, see Marcelli (1998).

Unfortunately, no complete compilation of the findings based on Malme's collections is available, but Spielmann and Canêz (2012) presented a small list of new species discovered by him. Besides Malme, other researchers also contributed to the knowledge of lichen biodiversity in the state, e.g., Klaus Kalb, Marcelo Marcelli, Mariana Fleig, and Neli Honda (Spielmann and Canêz 2012).

Klaus Kalb had the opportunity to collect in Brazil; his findings, including those made in Mato Grosso do Sul, were mostly treated in his exsiccate series, *Lichens Neotropici* I to XIII (Kalb 1982a, b, c, d, 1983a, b, 1984, 1986, 1988, 1990, 1991, 2001a, b).

Fleig and Riquelme (1991) studied specimens from the municipality of Piraputanga and found 72 species, including 23 new records to the State. Osorio (1992) studied macrolichens from the municipality of Ponta Porã, reporting 42 taxa including 16 new records. On a smaller scale other lichenologists had access to Mato Grosso do Sul specimens, e.g., Lynge (1924), Redinger (1936, 1940), Marcelli (1993), Staiger (2002), and Kitaura et al. (2019). Despite these important contributions, it is not yet possible to reliably assess the diversity of lichenized fungi in the state because in part there is no compiled information. Furthermore, one has to be careful when searching the literature for taxa reported from this area because before 1977 Mato Grosso do Sul was a territorial part of the now neighboring Mato Grosso State.

Based on the above considerations, the objectives of the present work were to compile bibliographic data and to update and improve data available in several papers that reported lichens from the Pantanal. We also report new collections made by us in 2010 (Fig. 6.1), mainly from Morraria do Urucum, an area of hills situated along the Paraguay River. It is important to note that not all the collected material is described here. Further taxa that need more studies will be published elsewhere.

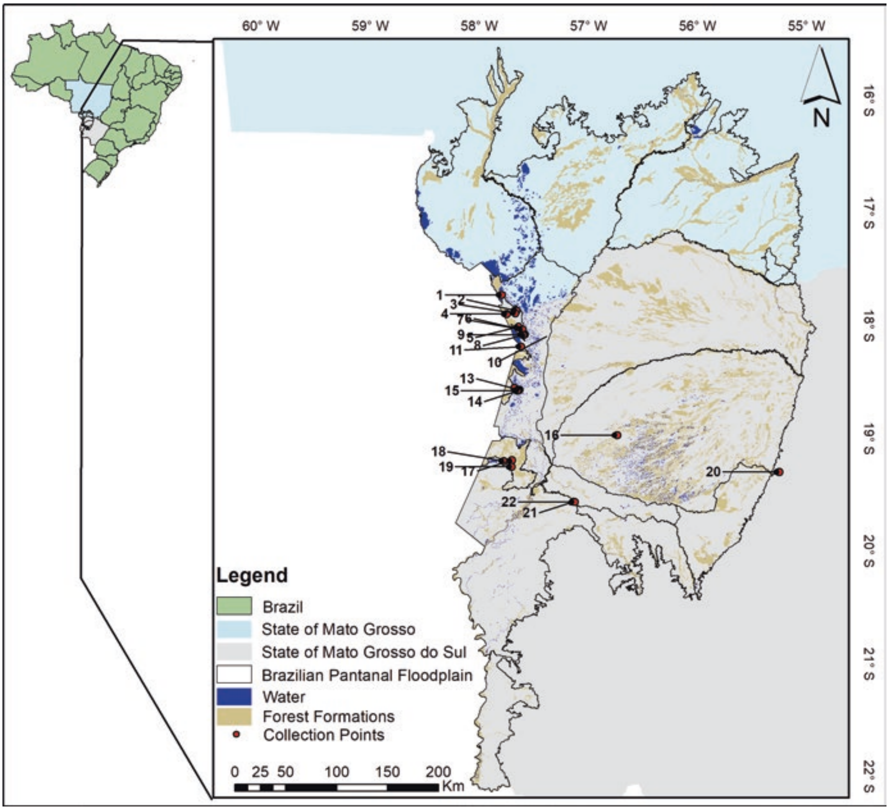


Fig. 6.1 Sample areas treated in this chapter. 1 = *RPPN Rumo ao Oeste, Ecotropica*; 2 = *RPPN Acurizal*; 3 = *Reserva Acurizal, Córrego Fundão*; 4 = *Fazenda Gaíva, Jaguaribe*; 5, 8, 9, and 10 = *RPPN Eliezer Batista, Novos Dourados*; 6 = *Baía do Taquaral*; 7 = *Morro do Amolar,* margin of *Baía do Taquara*; 11 = *Baía do Mandioré*; 12, 13, 14 and 15 = *Baía do Castelo*; 16 = *Fazenda Nhumirim, Salinado 8, Reserva*; 17 = *Morro do Urucum*; 18 = *Morro Tromba dos Macacos*; 19 = *Morro São Domingos – Mineração Corumbaense*; 20 = Margin of the road *MS-419*, between *Rio Negro* and *Rio Verde de Mato Grosso* municipalities; 21 = *Passo do Lontra, Base de Estudos do Pantanal – UFMS*; 22 = *Passo do Lontra, Base de Estudos do Pantanal – UFMS, Baía da Medalha*. All these points are in Corumbá municipality, except point 20 that is in Rio Negro municipality.

6.2 Taxa Previously Reported from the Pantanal

Based on published records, we previously found 129 reported names (97 species, 32 infraspecific taxa). After taxonomic and nomenclatural revision, we had 115 species and four infraspecies adding up to the compiled list 119 taxa of lichen fungi from the Pantanal in Mato Grosso do Sul state (Table 6.1). Most of these records are from the Corumbá region, including many species that were described based on specimens from the southern Pantanal region. *Arctomia leptospora* (Malme) Otálora & Wedin, *Biatora kalbii* (Brako) S. Y. Kondr., *Pertusaria platystoma* Malme, *Porina*

Table 6.1 List of taxa already reported in the literature relevant to Pantanal areas from Mato Grosso do Sul state, the basionym and the current name for each taxon, and references

Recorded name	Current name	References
Anomomorpha sordida Staiger	*Anomomorpha sordida* Staiger	Staiger (2002)
Anthracothecium duplicans (Nyl.) Müll. Arg.	*Pyrenula duplicans* (Nyl.) Aptroot	Malme (1929a) and Aptroot et al. (2008)
Anthracothecium leucostomum (Ach.) Malme	*Pyrenula leucostoma* Ach.	Malme (1929a)
Anthracothecium papilliferum (Nyl.) Müll. Arg.	*Pyrenula papillifera* (Nyl.) Aptroot	Malme (1929a) and Aptroot (2012)
Anthracothecium paraguayense Malme	*Pyrenula globifera* (Eschw.) Aptroot	Malme (1929a) and Aptroot et al. (2008)
Bacidia chorisiae Malme	*Bacidia russeola* (Kremp.) Zahlbr.	Malme (1935)
Bacidia medialis (Tuck.) Zahlbr.	*Bacidina medialis* (Tuck.) Kistenich, Timdal, Bendiksby & S. Ekman	Malme (1935) and Kistenich et al. (2018)
Bacidia russeola (Kremp.) Zahlbr.	*Bacidia russeola* (Kremp.) Zahlbr.	Malme (1935)
Bacidia russeola var. *lamprocheila* Malme	*Bacidia russeola* (Kremp.) Zahlbr.	Malme (1935)
Bacidia vulgata Malme	*Fellhanera vulgata* (Malme) Lücking comb. nov.	Malme (1935)
Buellia modesta (Kremp.) Müll. Arg.	*Cratiria americana* (Fée) Kalb & Marbach	Malme (1927) and Marbach (2000)
Buellia myriocarpa (DC.) Mudd	*Amandinea extenuata* (Müll. Arg.) Marbach	Malme (1927) and Marbach (2000)
Buellia subareolata Müll. Arg.	*Buellia subareolata* Müll. Arg.	Malme (1927)
Calicium hyperelloides Nyl.	*Calicium hyperelloides* Nyl.	Tibell (1996)
Calicium salicinum Persoon	*Calicium salicinum* Pers.	Tibell (1996)
Callopisma subvitellinum Müll. Arg.	*Caloplaca subvitellina* (Müll. Arg.) Zahlbr.	Malme (1926)
Catillaria americana Malme	*Catillaria americana* Malme	Malme (1923)
Coccocarpia pellita var. *isidiophylla*	*Coccocarpia palmicola* (Spreng.) Arv. & D.J. Galloway	Malme (1925) and Arvidsson and Galloway (1979)
Collema leptosporum Malme	*Arctomia leptospora* (Malme) Otálora & Wedin	Malme (1924a) and Otálora et al. (2014)
Collema paraguayense Malme	*Collema pustulatum* Ach.	Malme (1924a) and Degelius (1974)
Collema pycnocarpum f. *crassiusculum* Malme	*Enchylium conglomeratum* (Hoffm.) Otálora, P.M. Jørg. & Wedin	Malme (1924a) and Otálora et al. (2014)
Dermatocarpon australe Malme	*Dermatocarpon australe* Malme	Malme (1928)
Dimerella myriocarpa Malme	*Coenogonium pusillum* (Mont.) Lücking, Aptroot & Sipman	Malme (1934) and Rivas Plata et al. (2006)

(continued)

Table 6.1 (continued)

Recorded name	Current name	References
Dimerella subdiluta Malme	*Coenogonium subdilutum* (Malme) Lücking, Aptroot & Sipman	Malme (1934) and Rivas Plata et al. (2006)
Dirinaria aegialita (Afzel. ex Ach.) Moore	*Dirinaria aegialita* (Afzel. ex Ach.) B.J. Moore	Barbosa (2019)
Dirinaria africana (Müll.Arg.) D.D. Awasthi	*Dirinaria africana* (Müll.Arg.) D.D. Awasthi	Barbosa (2019)
Dirinaria confluens (Fr.) D.D. Awasthi	*Dirinaria confluens* (Fr.) D.D. Awasthi	Barbosa (2019)
Dirinaria consimilis (Stirt.) D.D. Awasthi	*Dirinaria consimilis* (Stirt.) D.D. Awasthi	Kalb et al. (2009)
Dirinaria papillulifera (Nyl.) D.D. Awasthi	*Dirinaria papillulifera* (Nyl.) D.D. Awasthi	Barbosa (2019)
Dirinaria picta (Sw.) Clem. & Shear	*Dirinaria picta* (Sw.) Clem. & Shear	Barbosa (2019)
Dirinaria pruinosa Kalb	*Dirinaria pruinosa* Kalb	Barbosa (2019)
Dirinaria purpurascens (Vain.) B.J. Moore	*Dirinaria purpurascens* (Vain.) B.J. Moore	Barbosa (2019)
Endocarpon adscendens Malme	*Endocarpon malmeanum* Zahlb.	Malme (1928) and Zahlbruckner (1931)
Glyphis cicatricosa Ach.	*Glyphis cicatricosa* Ach.	Staiger (2002)
Glyphis favulosa var. *intermedia* Müll. Arg.	*Glyphis cicatricosa* Ach.	Redinger (1933a)
Graphina bipartita f. *corumbensis* Redinger	*Graphis bipartita* (Müll. Arg.) Lücking	Redinger (1933b) and Lücking et al. (2008)
Graphina puiggarii var. *corumbensis* Redinger	*Graphis puiggarii* (Müll. Arg.) Lücking	Redinger (1933b) and Lücking et al. (2008)
Graphina virginea (Eschw.) Müll.Arg.	*Diorygma poitaei* (Fée) Kalb, Staiger & Elix	Redinger (1935) and Kalb et al. (2004)
Graphis assimilis Nyl.	*Graphis assimilis* Nyl.	Redinger (1935)
Graphis furfuracea Leight.	*Fissurina furfuracea* (Leight.) A.W. Archer	Kalb (1986) and Archer (2007)
Graphis hyphosa Staiger	*Graphis hyphosa* Staiger	Staiger (2002)
Graphis immersa Fink	*Graphis aurita* Eschw.	Redinger (1935)
Graphis lineola var. *comma* (Ach.) Redinger	*Allographa comma* (Ach.) Lücking & Kalb	Redinger (1935) and Lücking and Kalb (2018)
Graphis noumeana Müll. Arg.	*Allographa calcea* (Fée) Lücking & Kalb	Redinger (1935) and Lücking and Kalb (2018)
Gyalectina nana (Tuck.) Vězda	*Gyalecta nana* Tuck.	Kalb (1983a) and Lücking et al. (2019)
Haematomma puniceum var. *subinnatum* Malme	*Haematomma subinnatum* (Malme) Kalb & Staiger	Malme (1937) and Staiger and Kalb (1995)
Lecanactis insignior var. *fusca* (Müll.Arg.) Zahlbr.	*Cresponea leprieurii* (Mont.) Egea & Torrente	Malme (1926) and Egea and Torrente (1993)

(continued)

Table 6.1 (continued)

Recorded name	Current name	References
Lecanora granifera Ach.	*Malmidea granifera* (Ach.) Kalb, Rivas Plata & Lumbsch	Malme (1936a) and Kalb et al. (2011)
Lecanora intrusa Nyl.	*Rinodina intrusa* (Nyl.) Malme	Malme (1902)
Lecidea compaginata (Müll. Arg.) Zahlbr.	*Phyllopsora thaleriza* (Stirt.) Swinscow & Krog	Malme (1936a), Brako (1989), and Kistenich et al. (2019)
Lecidea gyalectoides Malme	*Malmidea gyalectoides* (Vain.) Kalb & Lücking	Malme (1936a) and Kalb et al. (2011)
Lecidea scyphulifera Ach.	*Glyphis scyphulifera* (Ach.) Staiger	Staiger (2002)
Leptogium brebissonii Mont.	*Leptogium brebissonii* Mont.	Malme (1924a)
Leptogium chloromelum (Sw.) Nyl.	*Leptogium chloromelum* (Sw.) Nyl.	Malme (1924a)
Leptogium cochleatum (Dicks.) Jørg. & James	*Leptogium cochleatum* (Dicks.) Jørg. & James	Kitaura et al. (2019)
Leptogium cyanescens (Rabenh.) Körb.	*Leptogium cyanescens* (Rabenh.) Körb.	Kitaura et al. (2019)
Leptogium diaphanum (Sw.) Mont.	*Leptogium diaphanum* (Sw.) Mont.	Kitaura et al. (2019)
Leptogium fusisporum (Tuck.) C.W. Dodge	*Leptogium fusisporum* (Tuck.) C.W. Dodge	Kitaura et al. (2019)
Leptogium phyllocarpum (Pers.) Nyl.	*Leptogium phyllocarpum* (Pers.) Nyl.	Malme (1924a)
Leptotrema wightiii (Tayl.) Müll. Arg.	*Sanguinotrema wightii* (Taylor) Lücking	Redinger (1936) and Lücking et al. (2015)
Melanotheca anomala (Ach.) Malme	*Pyrenula anomala* (Ach.) Vain.	Malme (1923) and Aptroot (2012)
Melanotheca arthonioides var. *lueheae* Malme	*Pyrenula anomala* (Ach.) Vain.	Malme (1924b) and Aptroot (2012)
Opegrapha alborimosa f. *brevicarpa* Redinger	*Opegrapha astraea* Tuck.	Redinger (1940) and Ertz (2009)
Opegrapha alborimosa var. *globulifica* Redinger	*Opegrapha astraea* Tuck.	Redinger (1940) and Ertz (2009)
Opegrapha alborimosa var. *reticulata* Redinger	*Opegrapha astraea* Tuck.	Redinger (1940) and Ertz (2009)
Opegrapha alborimosa var. *senescens* Redinger	*Opegrapha astraea* Tuck.	Redinger (1940) and Ertz (2009)
Opegrapha aperiens f. *crustosa* Redinger	*Opegrapha aperiens* f. *crustosa* Redinger	Redinger (1940)
Opegrapha aperiens Vain.	*Opegrapha aperiens* Vain.	Redinger (1940)
Opegrapha bonplandi var. *condrochracea* Redinger	*Zwackhia bonplandii* (Fée) Ertz	Redinger (1940) and Diederich et al. (2012)
Opegrapha chionoplaca Redinger	*Opegrapha chionoplaca* Redinger	Redinger (1940)

(continued)

Table 6.1 (continued)

Recorded name	Current name	References
Opegrapha corumbensis Redinger	*Opegrapha corumbensis* Redinger	Redinger (1940)
Opegrapha cylindrica Raddi	*Opegrapha cylindrica* Raddi	Kalb (1986)
Opegrapha lichenoides Pers.	*Opegrapha lichenoides* Pers.	Redinger (1940)
Opegrapha lichenoides var. *subchondrina* Redinger	*Opegrapha lichenoides* var. *subchondrina* Redinger	Redinger (1940)
Opegrapha multiseptata var. *brevicarpa* Redinger	*Opegrapha multiseptata* var. *brevicarpa* Redinger	Redinger (1940)
Opegrapha ochroplaca Redinger	*Opegrapha ochroplaca* Redinger	Redinger (1940)
Opegrapha prolificans Redinger	*Opegrapha prolificans* Redinger	Redinger (1940)
Opegrapha pulicaris f. *minuta* (Chevall.) H. Olivier.	*Alyxoria varia* (Ach.) Ertz & Tehler	Redinger (1940) and Ertz and Tehler (2011)
Parathelium crassiusculum Malme	*Pyrenula crassiuscula* (Malme) Aptroot	Malme (1923) and Aptroot (2012)
Parathelium dilutum Malme	*Pyrenula adacta* Fée	Malme (1923) and Aptroot (2012)
Parathelium fusisporum Malme	*Pyrenula fusispora* (Malme) Aptroot	Malme (1923) and Aptroot (2012)
Parathelium subferrugineum f. *expallescens* Malme	*Pyrenula circumfiniens* Vain.	Malme (1923) and Aptroot (2012)
Parathelium subferrugineum Malme	*Pyrenula subferruginea* (Malme) R.C. Harris	Malme (1923) and Aptroot (2012)
Parmelia argentina Kremp.	*Parmotrema argentinum* (Kremp.) Hale	Hale (1965)
Parmelia melanochaeta Kurok.	*Parmotrema melanochaetum* (Kurok.) O. Blanco, et al.	Hale and Kurokawa (1964)
Parmelia valenzueliana Mont.	*Ramonia valenzueliana* (Mont.) Stitzenb.	Malme (1934)
Patellaria domingensis Pers.	*Letrouitia domingensis* (Pers.) Haf. & Bellem.	Malme (1923)
Pertusaria platystoma Malme	*Pertusaria platystoma* Malme	Malme (1936b)
Phaeographina chapadana Redinger	*Pallidogramme chapadana* (Redinger) Staiger, Kalb & Lücking	Staiger (2002) and Lücking et al. (2008)
Phaeographis neotricosa f. *dissipata* Redinger	*Phaeographis neotricosa* Redinger	Redinger (1935)
Phyllopsora corallina var. *santensis* (Tuck.) Brako	*Phyllopsora santensis* (Tuck.) Swinscow & Krog	Brako (1991) and Swinscow and Krog (1981)
Phyllopsora kalbii Brako	*Biatora kalbii* (Brako) S. Y. Kondr.	Brako (1991) and Kondratyuk et al. (2019)
Physcia aegialita f. *coccinea* Lynge	*Dirinaria rhodocladonica* Kalb, Schumm & Elix	Lynge (1924) and Kalb et al. (2020)
Physcia alba var. *linearis* Lynge	*Physcia kalbii* Moberg	Lynge (1924) and Moberg (1990)

(continued)

Table 6.1 (continued)

Recorded name	Current name	References
Physcia alba var. *obsessa* (Mont.) Lynge	*Physcia integrata* Nyl.? See comment in Jungbluth (2010)	Lynge (1924)
Physcia integrata var. *sorediosa* Vain.	*Physcia sorediosa* (Vain.) Lynge	Lynge (1924)
Physcia melanocarpa Müll. Arg.	*Dirinaria melanocarpa* (Müll. Arg.) Dodge	Awasthi (1975)
Physcia syncolla f. *convexa* Lynge	*Hyperphyscia syncolla* (Tuck. ex Nyl.) Kalb	Lynge (1924) and Kalb (1983a)
Physcia syncolla Tuck.	*Hyperphyscia syncolla* (Tuck. ex Nyl.) Kalb	Lynge (1924) and Kalb (1983a)
Pleurothelium inclinatum Müll. Arg.	*Pyrenula ravenelii* (Tuck.) R.C. Harris	Malme (1924b) and Aptroot (2012)
Porina cryptostoma Malme	*Porina cryptostomoides* Lücking, Aptroot & Spielmann nom. nov.	Malme (1929b)
Porina melanops Malme	*Porina melanops* Malme	Malme (1929b)
Porina subcarpinea Malme	*Porina subcarpinea* Malme	Malme (1929b)
Pyrenastrum depauperatum Malme	*Pyrenula cryptothelia* (Müll. Arg.) Aptroot & Etayo	Malme (1924b) and Aptroot (2012)
Pyrenastrum fulvum Malme	*Pyrenula subgregantula* Müll. Arg.	Malme (1923) and Aptroot (2012)
Pyrenula emersa Malme	*Pyrenula quassiaecola* Fée	Malme (1929a) and Aptroot (2012)
Pyrenula fulvescens Malme	*Pyrenula quassiaecola* Fée	Malme (1929a) and Aptroot (2012)
Pyrenula plumbea Malme	*Pyrenula quassiaecola* Fée	Malme (1929a) and Aptroot (2012)
Pyxine cocoes var. *eschweileri* Tuck.	*Pyxine eschweileri* (Tuck.) Vain.	Malme (1897) and Vainio (1890)
Pyxine meissneri var. *convexula Malme*	*Pyxine petricola* var. *convexula* (Malme) Kalb	Malme (1897) and Kalb (1987)
Pyxine meissneri var. *genuina* Malme	*Pyxine petricola* Nyl.	Malme (1897)
Pyxine meissneri var. *physciaeformis* Malme	*Pyxine berteriana* (Feé) Imshaug	Malme (1897)
Rinodina conspersa Müll. Arg.	*Rinodina conspersa* Müll. Arg.	Malme (1902)
Toninia isidiata Malme	*Phyllopsora cinchonarum* (Fée) Timdal	Malme (1937) and Brako (1989)
Rinodina dispersa Malme	*Rinodina dispersa* Malme	Malme (1902)
Sarcographa actinobola (Nyl.) Müll. Arg. var. *latruncularia* Redinger	*Sarcographa labyrinthica* (Ach.) Müll. Arg.	Redinger (1933a)
Sarcographa actinobola (Nyl.) Müll. Arg. var. *perradiata* Redinger	*Sarcographa cinchonarum* Fée	Redinger (1933a)
Thelenella nitidula Malme	*Thelenella brasiliensis* (Müll. Arg.) Vain.	Malme (1928) and Mayrhofer (1987)

(continued)

Table 6.1 (continued)

Recorded name	Current name	References
Thelotrema cavatum Ach.	*Ocellularia cavata* (Ach.) Müll. Arg.	Redinger (1936)
Trachylia leucampyx Tuck.	*Heterocyphelium leucampyx* (Tuck.) Vain.	Tibell (1996)
Trypethelium eluteriae Spreng.	*Trypethelium eluteriae* Spreng.	Malme (1924b)
Trypethelium ochroleucum (Eschw.) Nyl.	*Astrothelium porosum* (Ach.) Aptroot & Lücking	Malme (1924b) and Aptroot and Lücking (2016)
Trypethelium ornatum Müll. Arg.	*Trypethelium ornatum* Müll. Arg.	Malme (1924b)
Tylophoron moderatum Nyl.	*Tylophoron moderatum* Nyl.	Tibell (1996)
Urceolaria compuncta Ach.	*Leucodecton occultum* (Eschw.) Frisch	Redinger (1936) and Frisch et al. (2006)
Ustalia junghuhnii Mont. & Bosch	*Diorygma junghuhnii* (Mont. & Bosch) Kalb, Staiger & Elix	Kalb et al. (2004)
Verrucaria brunneola Malme	*Verrucaria brunneola* Malme	Malme (1937)
Verrucaria myriocarpella Malme	*Verrucaria myriocarpella* Malme	Malme (1937)
Verrucaria tropica Ach.	*Nigrovothelium tropicum* (Ach.) Lücking, M.P. Nelsen & Aptroot	Malme (1924b) and Aptroot and Lücking (2016)

melanops Malme, *Pyrenula cryptothelia* (Müll. Arg.) Aptroot & Etayo, and *Rinodina dispersa* Malme are examples of species that had their types collected in Corumbá.

6.3 Species Diversity and Taxonomic Treatment

In this chapter, the taxonomic organization follows the idea of morphological groups that do not necessarily reflect natural taxa. In this way, all genera with crustose, microfoliose, or squamulose thallus are treated in the section "Microlichens," while those with cyanobacteria as photobionts are grouped in the "Cyanolichens" section. Families with a greater diversity, as *Caliciaceae*, *Physciaceae*, and *Parmeliaceae,* are treated separately.

We are providing short descriptions and comments to the 72 taxa of lichenized fungi that were recently collected and identified by us from Pantanal areas in the state of Mato Grosso do Sul. These taxa represent 30 genera and 18 families.

The most diverse was the group of microlichens with 22 taxa distributed in several families, being 18 new records to the Pantanal. Regarding the other groups, the increase in diversity of known *Parmeliaceae* species was of 16 new records, since only two species were previously cited in the literature to the Pantanal region. Foliose *Caliciaceae* and *Physciaceae* were represented by 21 taxa including 7 new records. The cyanolichens were represented here by 11 species including three new records to the study area.

As shown above (Table 6.1), 119 taxa were previously reported in the literature as occurring in the Pantanal. These previous data combined with the species reported by us sum up to a total of 165 taxa including four infraspecific taxa; thus, 46 new taxa were added to the list of lichen fungi known from the Pantanal. The previously reported taxa are not explicitly treated below, except the new combination *Fellhanera vulgata* and the new replacement name *Porina cryptostomoides*.

Opegrapha rissoensis Redinger is a new record for Brazil, *Agonimia* Zahlbr., *Crypthonia* Frisch & G. Thor, *Marcelaria* Aptroot, M.P. Nelsen & Parnmen and *Neoprotoparmelia* Garima Singh, Lumbsch & I. Schmitt are genera newly reported for Mato Grosso do Sul state (●), and 12 species are reported to occur in Mato Grosso do Sul for the first time (*). These include *Parmotrema confusum* Hale, reported before only from Mato Grosso state, *P. soredioaliphaticum* Estrabou & Adler, cited only for Rio Grande do Sul state, and *Peltula auriculata*, which was previously reported to Roraima state (Schultz and Aptroot 2008). The new reports to the Pantanal region are represented by (°).

The species list with their respective families is presented below.

List of Lichenized *Ascomycota* identified in newly collected material from the Pantanal and treated below:

Class *Arthoniomycetes*
Order *Arthoniales*
Family *Arthoniaceae*

● *Crypthonia albida* (Fée) Frisch & G. Thor

Family *Chrysothricaceae*

°*Chrysothrix xanthina* (Vain.) Kalb

Family *Lecanographaceae*

Alyxoria varia (Pers.) Ertz & Tehler

Family *Opegraphaceae*

Opegrapha astraea Tuck.
°*Opegrapha rissoensis* Redinger

Class *Dothideomycetes*
Order *Trypetheliales incertae sedis*
Family *Trypetheliaceae*

●*Marcelaria purpurina* (Nyl.) Aptroot, Nelsen & Parnmen

Class *Eurotiomycetes*
Order *Pyrenulales*
Family *Pyrenulaceae*

Pyrenula anomala (Ach.) Vain.
°*Pyrenula xanthoglobulifera* Aptroot, Lücking & M. Cáceres

Class *Lecanoromycetes*
Order *Arctomiales*
Family *Arctomiaceae*

Arctomia leptospora (Malme) Otálora & Wedin

Order *Caliciales*
Family *Caliciaceae*

**Amandinea submontana* Marbach
°*Buellia curatellae* Malme
°*Cratiria obscurior* (Stirt.) Marbach & Kalb
Dirinaria aegialita (Afzel. ex Ach.) B.J. Moore
Dirinaria africana (Müll. Arg.) D.D. Awasthi
Dirinaria confluens (Fr.) D.D. Awasthi
Dirinaria consimilis (Stirt.) D.D. Awasthi
Dirinaria papillulifera (Nyl.) D.D. Awasthi
Dirinaria picta (Sw.) Clem. & Shear
Dirinaria pruinosa Kalb
Dirinaria purpurascens (Vain.) B.J. Moore
Dirinaria rhodocladonica Kalb, Schumm & Elix
Pyxine berteriana (Fée) Imshaug
°*Pyxine coccifera* (Fée) Nyl.
°*Pyxine cocoës* (Sw.) Nyl.
Pyxine eschweileri (Tuck.) Vain.
Pyxine petricola Nyl.
°*Pyxine subcinerea* Stirt.

Family *Physciaceae*

**Hyperphyscia adglutinata* (Flörke) H. Mayhofer& Poelt
Hyperphyscia syncolla (Tuck. ex Nyl.) Kalb
°*Physcia aipolia* (Humb.) Fürnr.
°*Physcia convexa* Müll. Arg.
°*Physcia manuelii* Moberg
**Physcia tribacia* (Ach.) Nyl.

Order *Candelariales*
Family *Candelariaceae*

°*Candelaria concolor* (Dicks.) Stein.

Order *Lecanorales*
Family *Lecanoraceae*

**Lecanora achroa* Nyl.
**Lecanora concilianda* Vain.
**Lecanora helva* Stizenb.

Family *Parmeliaceae*

**Bulbothrix regnelliana* Jungbluth, Marcelli & Elix
°*Canoparmelia amazonica* (Nyl.) Elix & Hale
°*Canoparmelia caroliniana* (Nyl.) Elix & Hale
°*Crespoa carneopruinata* (Zahlbr.) Lendemer & Hodkinson
°*Crespoa crozalsiana* (B. de Lesd. ex Harm.) Lendemer & Hodkinson
°*Crespoa scrobicularis* (Kremp.) Benatti & Lendemer
°*Myelochroa lindmanii* (Lynge) Elix & Hale
•*Neoprotoparmelia multifera* (Nyl.) Garima Singh, Lumbsch & I. Schmitt
Parmotrema argentinum (Kremp.) Hale
**Parmotrema confusum* Hale
°*Parmotrema consors* (Nyl.) Krog & Swinscow
°*Parmotrema dilatatum* (Vain.) Hale
Parmotrema melanochaetum (Kurok.) Blanco et al.
°*Parmotrema mesotropum* (Müll. Arg.) Hale
°*Parmotrema mordenii* (Hale) Hale
°*Parmotrema praesorediosum* (Nyl.) Hale
**Parmotrema sorediоaliphaticum* Estrabou & Adler
°*Parmotrema tinctorum* (Dèspr. ex Nyl.) Hale
°*Usnea subparvula* A. Gerlach & P. Clerc

Family *Ramalinaceae*

**Phyllopsora pyxinoides* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman
**Phyllopsora chlorophaea* (Müll. Arg.) Zahlbr.

Family *Ramboldiaceae*

°*Ramboldia russula* (Ach.) Kalb, Lumbsch & Elix

Order *Peltigerales*
Family *Collemataceae*

°*Leptogium austroamericanum* (Malme) C.W. Dodge
Leptogium chloromelum (Sw.) Nyl.
Leptogium cochleatum (Dicks.) Jørg. & James
Leptogium cyanescens (Rabenh.) Körb.
Leptogium diaphanum (Sw.) Mont.
Leptogium fusisporum (Tuck.) C.W. Dodge
°*Leptogium isidiosellum* (Riddle) Sierk
°*Leptogium marginellum* (Sw.) Gray
Leptogium phyllocarpum (Pers.) Mont.

Order *Ostropales*

Family *Graphidaceae*

°*Dyplolabia afzelii* (Ach.) A. Massal.
Sanguinotrema wightii (Taylor) Lücking

Order *Verrucariales*
Family *Verrucariaceae*

•*Agonimia opuntiella* (Buschardt & Poelt) Vězda

Class *Lichinomycetes*
Order *Lichinales*
Family Peltulaceae

**Peltula auriculata* Büdel, Schultz & Gröger

6.4 Identification Keys

We included in the keys all species currently reported to the Pantanal, that is, the species reported in the literature and those sampled and treated by us. However, for the microlichens group, only species that we collected and studied are included. Since a representative number of species known from old records were not recollected, we did not include them considering they may have old, often hidden, or wrong identification, which can be also different from the current concept. It is important to highlight that *Graphidaceae*, one of the most representative families in the area, is being treated separately because we found new species that need more studies.

6.5 Identification Key to the Groups of Lichens Found in the Pantanal

1a. Cyanobacteria as primary photobiont	Cyanolichens (Key A)
2b. Chloroccocoid algae as primary photobiont	2
2a. Thallus crustose, microfoliose, or squamulose	Microlichens (Key B)
2b. Thallus foliose or fruticose	3
3a. Thallus foliose, lobes usually narrower than 0.4 mm, spores brown, and mostly bicellular, rarely 4-celled	foliose *Caliciaceae* and *Physciaceae* (Key C)
3b. Thallus foliose or fruticose, lobes usually wider than 0.4 mm, spores hyaline, and simple	*Parmeliaceae* (Key D)

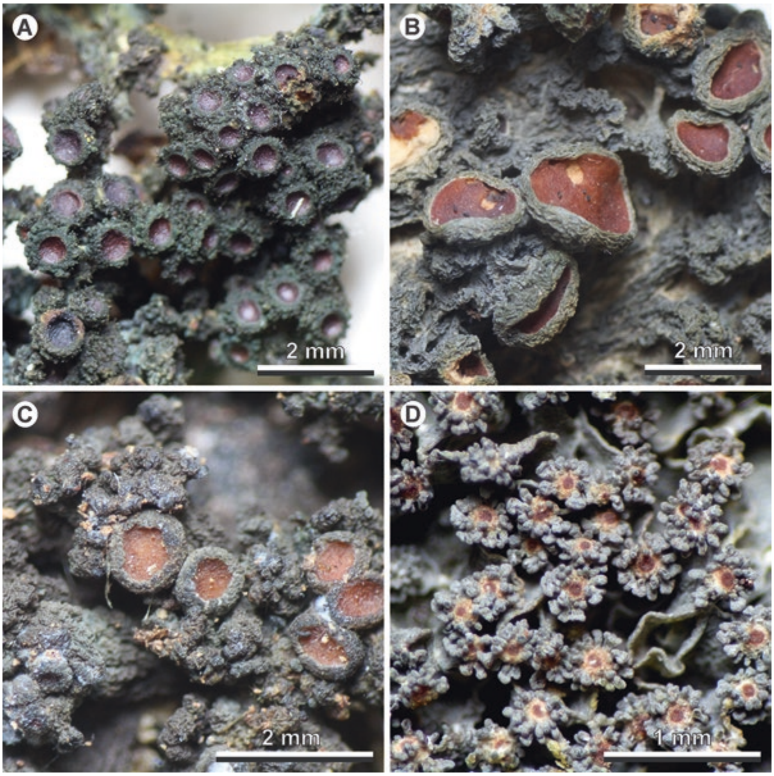


Fig. 6.2 Cyanolichens
(**a**) *Arctomia leptospora* (Malme) Otálora & Wedin. (**b**) *Leptogium chloromelum* (Sw.) Nyl. (**c**) *Leptogium fusisporum* (Tuck.) C.W. Dodge. (**d**) *Leptogium marginellum* (Sw.) Gray.

6.6 Key A – Cyanolichens

Identification Key to the Species of Cyanolichens Known from the Pantanal (Fig. 6.2)

1a. Thallus squamulose with ear-shaped	*Peltula auriculata*
1b. Thallus foliose	2
2a. Thallus with concentric ridges, attached on the substrate through rhizines that originate a hypothallus, and hereromerous	*Coccocarpia palmicola*
2b. Thallus without concentric ridges, attached on the substrate usually by hapterons, and homomerous	3
3a. Thallus with vegetative propagules (isidia and/or lobules)	4
3b. Thallus without vegetative propagules	11
4a. With lobules or lobuloid propagules	5
4b. With isidia or isidioid propagules	7

5a. Propagules present on the thallus and apothecia	*Leptogium diaphanum*
5b. Propagules restricted to the apothecia	6
6a. Apothecia marginal, up to 0.5 mm diam.	*Leptogium marginellum*
6b. Apothecia laminal, more than 1.0 mm diam.	*Leptogium phyllocarpum*
7a. Isidia usually granular, and ascospores transversely septate	8
7b. Isidia usually cylindrical, and ascospores muriform or submuriform	9
8a. Cortex with paraplectenchymatous cells	*Leptogium brebissonii*
8b. Cortex without paraplectenchymatous cells	*Arctomia leptospora*
9a. Thallus with smooth upper surface	*Leptogium cyanescens*
9b. Thallus with ridged or wrinkled upper surface	10
10a. Upper surface ridged, and lobes overlapping,	*Leptogium isidiosellum*
10b. Upper surface wrinkled, and lobes agglomerated	*Leptogium austroamericanum*
11a. Cortex with paraplectenchymatous cells	12
11b. Cortex without paraplectenchymatous cells	14
12a. Ascospores acicular, transversely septate	*Leptogium fusisporum*
12b. Ascospores fusiform, muriform to submuriform	13
13a. Upper surface with longitudinal to irregular ridges, and apothecia with thick paraplectenchymatous proper exciple	*Leptogium chloromelum*
13b. Upper surface distinctly striate, and apothecia with thick paraplectenchymatous thalline exciple	*Leptogium cochleatum*
14a. Apothecia immersed when young, with ascospores submuriform to muriform, 20–40 × 11–15 µm (Degelius 1974)	*Collema pustulatum*
14b. Apothecia sessile to stipitate, with ascospores transversely septate, (13–)15–24(–26) × 3.0–4.5 (–6.0) µm (Degelius 1954)	*Enchylium conglomeratum*

6.7 Key B – Microlichens

Identification Key to Some Epiphytic Species of Microlichens from the Pantanal (Figs. 6.3 and 6.4)

1a. Thallus sterile, without fruiting bodies	2
1b. Thallus fertile, with fruiting bodies	7
2a. Thallus yellow	3
2b. Thallus gray to whitish or green	4
3a. Thallus leprose/floccose/powdery	*Chrysothrix xanthina*
3b. Thallus microfoliose with soredia	*Candelaria concolor*
4a. Thallus squamulose, greenish	5
4b. Thallus byssoid, whitish to gray	6
5a. Squamules adnate, with tiny glassy hairs on the upper surface	*Agonimia opuntiella*
5b. Squamules ascending from a byssoid hypothallus	*Phyllopsora chlorophaea*
6a. Thallus forming distinct marginal lobules bordered by a black prothallus	*Phyllopsora pyxinoides*
6b. Thallus with entire margins and a pale prothallus	*Crypthonia albida*
7a. Ascomata closed or with narrow pore, rounded	8

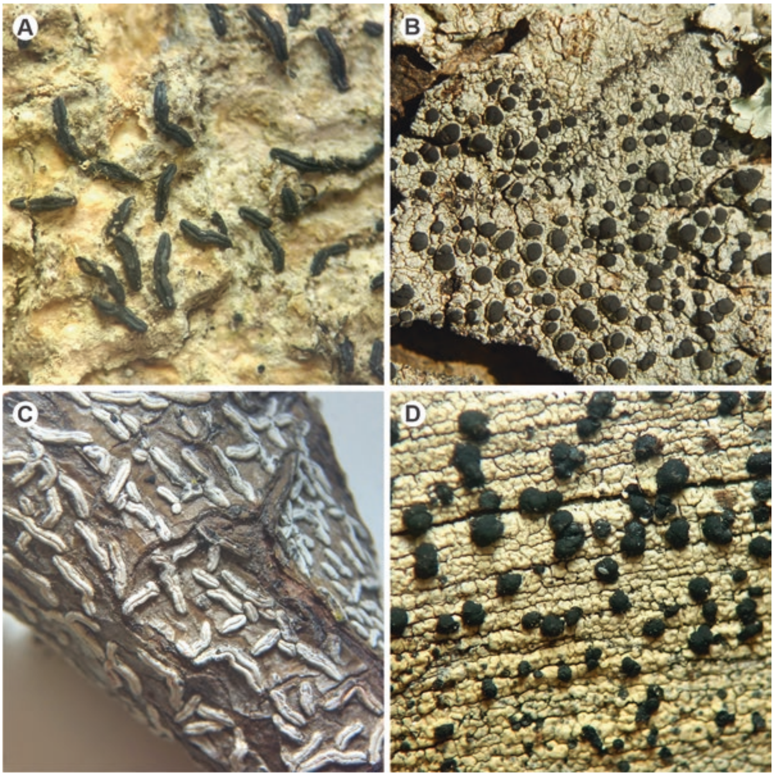


Fig. 6.3 Microlichens 01
(**a**) *Alyxoria varia* (Pers.) Ertz & Tehler. (**b**) *Cratiria obscurior* (Stirt.) Marbach & Kalb. (**c**) *Dyorigma afzelii* (Ach.) A. Massal. (**d**) *Buellia curatellae* (Malme) Marbach

7b. Ascomata with open disc or elongate to linear	11
8a. Ascomata apothecioid, immersed with narrow pore, and pale to brownish wall; thallus containing pockets of red crystals	*Sanguinotrema wightii*
8b. Ascomata perithecioid, with almost closed ostiole and black walls	9
9a. Ascomata and in part thallus covered by a layer of red, K+ purple pigment; ascospores hyaline	*Marcelaria purpurina*
9b. Ascomata not covered by pigment, black or thallus-covered; ascospores brown	10
10a. Ascomata fused into pseudostromatic groups, thallus UV-; ascospores 3-septate, small (17–20) μm	*Pyrenula anomala*
10b. Ascomata dispersed, thallus UV+ yellow (lichexanthone); ascospores muriform, large (more than 100 μm)	*Pyrenula xanthoglobulifera*
11a. Ascomata elongate to linear, often branched (lirellae)	12
11b. Ascomata round, with open disc (apothecia)	16

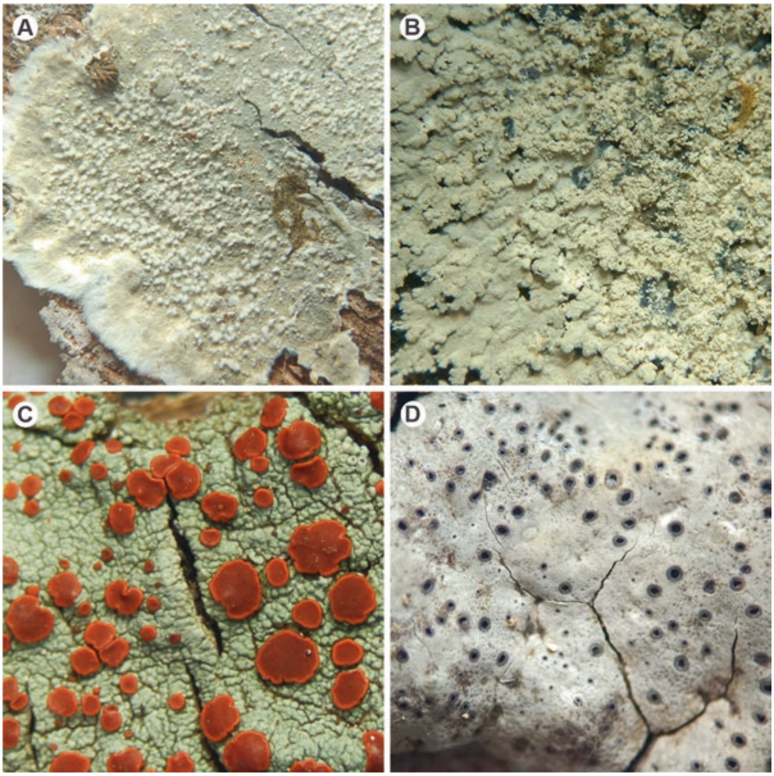


Fig. 6.4 Microlichens 02
(**a**) *Crypthonia albida* (Fée) Frisch & G. Thor. (**b**) *Phyllopsora pyxinoides* (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman. (**c**) *Ramboldia russula* (Ach.) Kalb. (**d**) *Sanguinotrema wightii* (Taylor) Lücking.

12a. Lirellae with disc exposed and black margins	*Alyxoria varia*
12b. Lirellae with disc concealed	13
13a. Lirellae with white coating which reacts C+ red	*Dyplolabia afzelii*
13b. Lirellae black or with pruina which is C-	14
14a. Lirellae with white pruina	*Opegrapha astraea*
14b. Lirellae epruinose, black	*Opegrapha rissoensis*
16a. Apothecia bright red, K+ purple	*Ramboldia russula*
16b. Apothecia not red	17
17a. Apothecia with pale to thallus-colored margin, containing algae (lecanorine), ascospores hyaline, one-celled (simple)	18
17b. Apothecia with brown-black margin not containing algae (lecideine), ascospores brown, 2-celled	21
18a. Ascospores around 50 per ascus	*Neoprotoparmelia multifera*
18b. Ascospores 8 per ascus	19
19a. Apothecial disc brown to reddish brown	*Lecanora concilianda*
19b. Apothecial disc beige to ochre	20

20a. Thallus greenish gray, containing atranorin and usnic acid	*Lecanora achroa*
20b. Thallus gray, containing atranorin but without usnic acid	*Lecanora helva*
21a. Thallus dark gray, irregular, K+ persistently yellow	*Amandinea submontana*
21b. Thallus pale gray, smooth, K+ yellow turning red after a few minutes	22
22a. Hymenium with numerous oil droplets	*Buellia curatellae*
22b. Hymenium without oil droplets	*Cratiria obscurior*

6.8 Key C – Foliose Caliciaceae and Physciaceae

Identification Key to the Foliose *Caliciaceae* and *Physciaceae* Species from the Pantanal (Fig. 6.5)

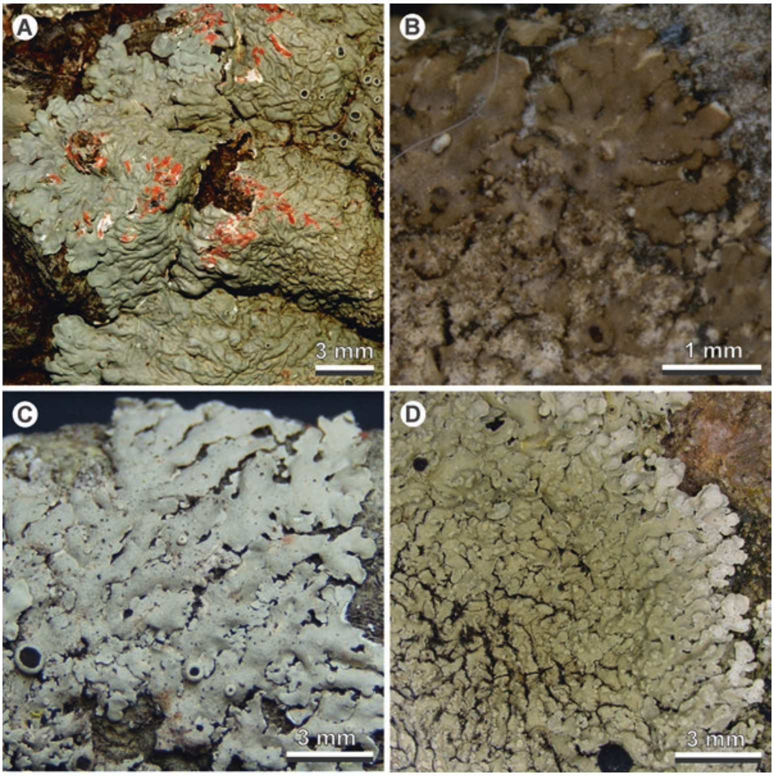


Fig. 6.5 Foliose Caliciaceae and Physciaceae
(**a**) *Dirinaria rhodocladonica* Kalb, Schumm & Elix. (**b**) *Hyperphyscia adglutinata* (Flörke) H. Mayrhofer & Poelt. (**c**) *Physcia aipolia* (Ehrh. ex Humb.) Fürnr. (**d**) *Pyxine cocoës* (Sw.) Nyl.

1a. Upper cortex UV+ yellow (lichexanthone present)	2
1b. Upper cortex UV- (lichexanthone absent)	6
2a. Soralia present	3
2b. Soralia absent	4
3a. Soralia marginal and crescent-shape; medulla yellow above	*Pyxine subcinerea*
3b. Soralia laminal and orbicular to irregular; medulla entirely white	*Pyxine cocoës*
4a. Medulla yellow above, K+ yellow to orange	*Pyxine berteriana*
4b. Medulla entirely white, K-	5
5a. Internal stipe reddish to brownish red, K+ reddish rose	*Pyxine petricola*
5b. Internal stipe white, K-	*Pyxine petricola* var. *convexula*
6a. Upper cortex K+ yellow (atranorin present)	7
6b. Upper cortex K- (atranorin absent)	16
7a. Rhizines present	8
7b. Rhizines absent	17
8a. Vegetative propagules present	9
8b. Vegetative propagules absent	13
9a. Phyllidia present; soralia and polysidiangia absent	*Physcia manuelii*
9b. Phyllidia absent; soralia or polysidiangia present	10
10a. Polysidiangia present; soralia absent	*Pyxine eschweileri*
10b. Polysidiangia absent; soralia present	11
11a. Soralia cinnabar-red	*Pyxine coccifera*
11b. Soralia white	12
12a. Soralia terminal at principal branches, labriform	*Physcia tribacia*
12b. Soralia marginal or at the tips of short lateral lacinulae, orbicular to capitate	*Physcia sorediosa*
13a. Maculae distinct and spotted	14
13b. Maculae absent	*Physcia kalbii*
14a. Lower surface black, except near the tips	*Physcia integrata*
14b. Lower surface pale to dark brown	15
15a. Saxicolous; lower surface with pinkish pigment	*Physcia convexa*
15b. Corticicolous; lower surface lacking pinkish pigment	14
16a. Soralia present; apothecia rare	*Hyperphyscia adglutinata*
16b. Soralia absent; apothecia frequent	*Hyperphyscia syncolla*
17a. Vegetative propagules present	18
17b. Vegetative propagules absent	22
18a. Isidia present; soralia and polysidiangia absent	*Dirinaria papillulifera*
18b. Isidia absent; soralia or polysidiangia present	19
19a. Soralia present; polysidiangia absent	*Dirinaria picta*
19b. Soralia absent; polysidiangia present	20
20a. Sekikaic acid present; divaricatic acid absent	*Dirinaria consimilis*
20b. Sekikaic acid absent; divaricatic acid present	21
21a. Apothecial disc with purple pruina	*Dirinaria pruinosa*
21b. Apothecial disc epruinose or with white pruina	*Dirinaria aegialita*
22a. Medulla with coccineus pigment	*Dirinaria rhodocladonica*
22b. Medulla totally white	23
23a. Saxicolous and strongly adnate to the substrate	*Dirinaria africana*
23b. Corticiclous and loosely adnate to the substrate	24
24a. Apothecial disc purplish pruinose	*Dirinaria purpurascens*
24b. Apothecial disc epruinose or whitish-pruinose	25
25a. Lower surface yellow	*Dirinaria melanocarpa*
25b. Lower surface black	*Dirinaria confluens*

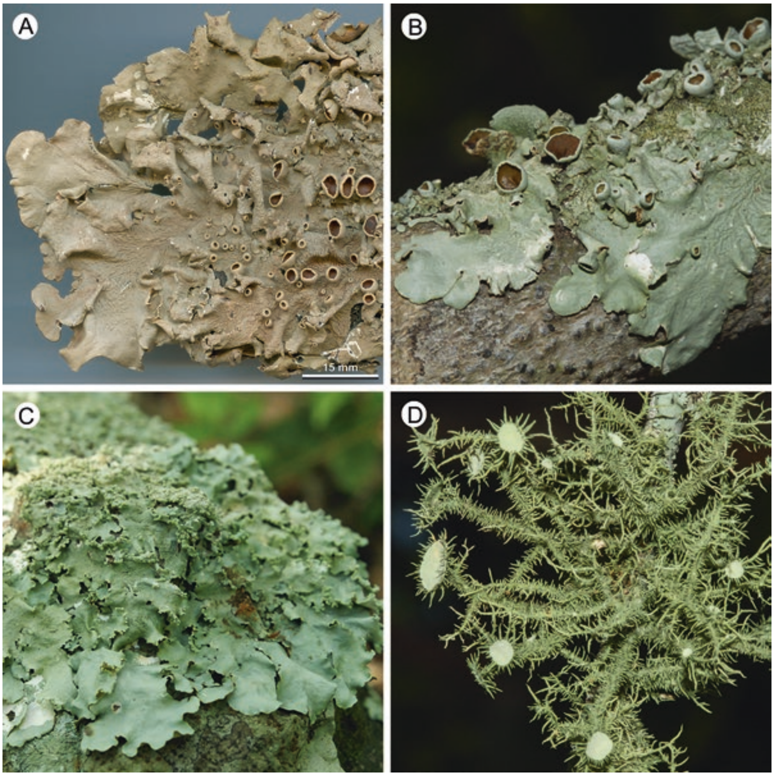


Fig. 6.6 Parmeliaceae
(**a**) *Parmotrema confusum* Hale. (**b**) *Parmotrema mesotropum* (Müll. Arg.) Hale. (**c**) *Parmotrema mordenii* (Hale) Hale. (**d**) *Usnea subparvula* A. Gerlach & P. Clerczz

6.9 Key D – Parmeliaceae

Identification Key to *Parmeliaceae* Species from the Pantanal (Fig. 6.6)

1a. Thallus fruticose, usneoid	*Usnea subparvula*
1b. Thallus foliose, parmelioid	2
2a. Lobes usually less than 5.0 mm wide, rhizines frequently present up to the margin	3
2b. Lobes usually more than 5.0 mm wide, rhizines frequently absent in a large marginal zone	8
3a. Thallus with marginal cilia	4
3b. Thallus without marginal cilia	15
4a. Marginal cilia bulbate, frequently without apices	*Bulbothrix regnelliana*
4b. Marginal cilia not bulbate	5
5a. Medulla yellow	*Myelochroa lindmanii*

5b. Medulla white	6
6a. Thallus with isidia or soredia	7
6b. Thallus without isidia or soredia	12
7a. Thallus isidiate	8
7b. Thallus sorediate	9
8a. Isidia ciliate; medulla K-, C+ rose (gyrophoric acid)	*Parmotrema melanochaetum*
8b. Isidia eciliate; medulla K+ red (lecanoric acid), C-	*Parmotrema tinctorum*
9a. Medulla K+ yellow or dirty yellow	10
9b. Medulla K-	11
10a. Thallus usually closely adnate to the substratum; medulla P+ slowly yellowish (atranorin)	*Parmotrema mordenii*
10b. Thallus usually loosely adnate to the substratum; medulla P+ orange (protocetraric acid)	*Parmotrema dilatatum*
11a. Soredia frequently on top of dactyls	*Parmotrema sorediοaliphaticum*
11b. Soredia usually formed in crescent-shaped soralia	*Parmotrema praesorediosum*
12a. Lobes ciliate	13
12b. Lobes eciliate	14
13a. Cilia short, tapered and thick; medulla UV-	*Parmotrema consors*
13b. Cilia long, uniform and thin; medulla UV+ greenish (alectoronic acid)	*Parmotrema argentinum*
14a. Medulla K+ dirty yellow, P+ orange (protocetraric acid)	*Parmotrema confusum*
14b. Medulla K-, P- (fatty acids)	*Parmotrema mesotropum*
15a. Upper surface smooth to slightly foveolate	16
15b. Upper surface scrobiculate	17
16a. Lower surface black, medulla with protocetraric acid (K+ yellow, P+ orange)	*Canoparmelia amazonica*
16b. Lower surface brown, medulla without protocetraric acid (K-, P-)	*Canoparmelia caroliniana*
17a. Thallus sorediate	18
17b. Thallus not producing propagules	*Crespoa scrobicularis*
18a. Lobes up to 2.5 mm wide	*Crespoa carneopruinata*
18b. Lobes up to 4.0 mm wide	*Crespoa crozalsiana*

6.10 Comments on the Species Treated in This Chapter

Agonimia opuntiella (Buschardt & Poelt) Vězda, Lichenes Rariores Exsiccati 33 (nos. 321-330): 4, no. 330. 1997.

Agonimia opuntiella is characterized by the greenish gray to brownish micro-squamulose thallus, squamules 0.5–1.5 mm, adnate, with tiny glassy hairs which are usually 17–21 × 5 μm, but a little longer in the Pantanal material (40–60 μm). Perithecia and pycnidia were not seen in our specimen. According to Smith et al. (2009), *A. opuntiella* differs from *A. tristicula* (Nyl.) Zahlbr. by the minute hairs along the thallus surface. See description in Aptroot (2011) and Smith et al. (2009).

Examined material: Corumbá municipality, beginning of the trail to Morro do Amolar, next to the margin of Baía do Taquaral, in a shaded place, on tree trunk, 18°02′48.90″S, 57°29′49.50″W, 89 m alt., 26.XI.2010, leg. A.A. Spielmann 8680 (CGMS).

Alyxoria varia (Pers.) Ertz & Tehler, Fungal Diversity 49(1): 53. 2011.

Fig. 6.3b

Alyxoria varia is characterized by its crustose thallus, with simple carbonized lirellae, not pruinose, with concealed disc, sometimes exposed. The ascospores are transversally septated, 6–7 cells, with two enlarged cells in the middle. The Pantanal material has ascospores of (27.5–)30–35(–37.5) × (–3.5)–5 µm, mostly within the interval cited by Ertz (2009). *A. varia* differs from *Opegrapha xerica* Torrente & Egea by shorter (14–20 µm) and less septate (4–6 cells) ascospores (Torrente and Egea 1992; Ertz 2009). See description in Ertz (2009) as *Opegrapha varia* Pers.

Examined material: Corumbá municipality, Fazenda Nhumirim, Pomar da sede-Pantanal, on goiabeira trunk [*Psidium guajava* L.], 18°59′01.8″S, 56°36′56.9″W, 90m alt., 26.X.1988, leg. V.J. Pott 684 (COR); idem, Sub-região Pantanal do Paraguai, Baía do Castelo, riparian forest in a rock outcrop, on tree trunk, 18°34′52.20″S, 57°31′36.50″W, 95m alt., 22.XI.2010, leg. T.H. Stefanello 28 (CGMS).

Amandinea submontana Marbach, Bibliotheca Lichenol. 74: 105. 2000.

Amandinea submontana is characterized by its crustose thallus, dark gray, with small black apothecia (around 0.2–0.4 mm), with clear hymenium, one-septate olive-brown ascospores, 12.5–15 × 5 µm and only atranorin in the thallus. According to Marbach (2000), this species resembles *A. leucomela* (Imshaug) P.F. May & Sheard, but differs mainly on the chemistry: *A. leucomela* has 6-O-methylarthotheline and lichexanthone, reacting UV+ on the thallus, while *A. submontana* has only atranorin (UV-). See description in Marbach (2000).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, riparian forest in a rock outcrop, on tree trunk, 18°34′52.20″S, 57°31′36.50″W, 95m alt., 22.XI.2010, leg. T.H. Stefanello 27 (CGMS).

Arctomia leptospora (Malme) Otálora & Wedin, Lichenologist 45: 293. 2013.

Fig. 6.2a

Arctomia leptospora is characterized by agglomerated branches that are covered by blackish granular isidia. The ascospores are transversely septate with (110–)125–175(–200) × 3–4(–5) µm (Malme 1924a). The thallus of *Arctomia leptospora* is greenish and homoiomerous, and cortices without paraplectenchymatous cells, as in *Collema*. The species was combined within *Arctomia* by Otálora & Wedin (2013), but previous molecular studies inferred that *A. leptospora* belongs to *Collemataceae* and further studies are necessary. See description in Malme (1924a).

Examined material: Corumbá municipality, Fazenda Nhumirim, Pomar da sede, on tree, 26. X.1988, leg. M.P. Marcelli 682 (COR); idem, Tromba dos Macacos, 02.XI.1993, leg. O. Yano s/n (COR).

Buellia curatellae Malme, Ark. Bot. 21A (no. 14): 18. 1927

Fig. 6.3d

Buellia curatellae is characterized by its usually cracked crustose thallus, pale gray, black, and small apothecia (0.4–0.6 mm), with inspersed hymenium, brown one-septate ascospores, 13–20 × 5 µm in the Pantanal material. The thallus reacts K+ yellow turning red, due to the presence of norstictic acid. This species is similar to *Buellia rechingeri* Zahlbr. which, according to Marbach (2000), has a cartilaginous-squamulose thallus and smaller ascospores (12)15–17(–18) × (4–)5–6 µm. See description in Marbach (2000).

Examined material: Rio Negro municipality, margin of the road MS-419, between Rio Negro and Rio Verde de Mato Grosso, in an open area, on a wooden fence pole, 19°17′55.83″S, 55°06′1.04″W, 165 m alt., 3.X.2013, leg. A.A. Spielmann 11132 (CGMS).

Bulbothrix regnelliana Jungbluth, Marcelli & Elix, Mycotaxon 104: 58 (2008)

This species is characterized by the lack of propagules, absence of laminal bulbs, cilia more frequently without apices, brown lower surface, coronate apothecia, ellipsoid ascospores 10–12 × 6–7 µm and medulla K+ yellow → orange, C-, KC-, P+ yellow, UV-.

It could be confused with *B. subcoronata* (Müll. Arg.) Hale and *B. viatica* Spielmann & Marcelli since they share the medullary chemistry and lack propagules, for instance. However, they can be distinguished by the lower surface color, the ascospores size, and the laminal ciliary bulbs. See Benatti (2012) for detailed comments and further differentiation.

Bulbothrix regnelliana was previously reported to the states of São Paulo (Jungbluth et al. 2008), Minas Gerais, and Rio Grande do Sul (Benatti 2012), and this is the first record to Mato Grosso do Sul state.

TLC: atranorin and norstictic acid.

Examined material: Corumbá, Sub-região Pantanal do Paraguai, on the bank of Taquaral Bay, 18° 02′ 42,3″ S, 57° 30′ 15,2″ W, 83 m alt., on thin branch of *Licania* sp. at the edge of the bay, 26.XI.2010, leg. L.S. Canêz et al. 3620 (CGMS).

Candelaria concolor (Dicks.) Stein., Flora, Regensburg 62: 364. 1879.

Candelaria concolor is characterized by the microfoliose, yellow thallus, formed by laciniae less than 0.5 mm wide, with granular soredia on their apices. Apothecia in this species are reported as rare (Awasthi 2007; Westberg and Arup 2010), and the Pantanal material was also found without this reproductive structure, having only soredia. This species is similar to *C. fibrosa* (Fr.) Müll. Arg., which usually has broader lobes, lacks soredia, and has numerous apothecia (Almborn 1966). See description in Almborn (1966) and Awasthi (2007).

Examined material: Corumbá municipality, Fazenda Nhumirim, Bordo de Salina – forest, on tree trunk, 18°59′01.8″S, 56°36′56.9″W, 90m alt., 10.IX.1988, leg. V.J. Pott 622 (COR).

Canoparmelia amazonica (Nyl.) Elix & Hale, Mycotaxon 27: 277. 1986.

Canoparmelia amazonica is different from other species of the genus due to its smooth upper surface, black lower surface, for presenting mostly simple isidia with brown apices and by its medullary chemistry: K+ yellow, C-, KC+ evanescent rose violet, P+ orange, UV-.

This species resembles *C. caroliniana* that also has isidia; however, it can be easily recognized because of its medullary chemistry. *Canoparmelia caroliniana* produces perlatolic acid (K-, P-) instead of protocetraric acid (K+, P+). Complete descriptions, additional data, and a helpful table about *Canoparmelia* species can be found in Jungluth (2006).

TLC: atranorin and protocetraric acid.

^{0}Examined Material: Corumbá, Morraria do Urucum, on fallen brunch, 19°12′08,2″ S, 57°36′04,6″ W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. 3348 (CGMS).

Canoparmelia caroliniana (Nyl.) Elix & Hale, Mycotaxon 27: 278. 1986.

Canoparmelia caroliniana presents smooth or slightly foveolate upper surface, isidiate, brown lower surface or with some black areas, concolour rhizines, and produces medullary perlatolic acid (KC+ evanescent pink) and cortical atranorin. For additional data, see Jungbluth (2006) and Spielmann & Marcelli (2008).

TLC: atranorin, perlatolic acid, traces of anziaic acid and triterpenes.

Examined Material: Brazil, Mato Grosso do Sul, Corumbá, Morraria do Urucum, on fallen brunch on trail, 19° 12′ 08,2″ S, 57° 36′ 04,6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. 3286 (CGMS).

Chrysothrix xanthina (Vain.) Kalb, Biblioth. Lichenol. 78: 144. 2001.

Chrysothrix xanthina is characterized by the bright yellow leprose thallus, with no separate reproductive structures. This species is very similar to *C. candelaris* (L.) Laundon, but according to Kalb (2001b), *C. xanthina* only occurs in the tropics and has smaller thallus granules (20–50 μm in diameter) than the former (75–200 μm in diameter). Differences in chemistry were also found, with some rare exceptions, as *C. candelaris* has calycin as the main substance, while *C. xanthina* produces more concentrations of pinastric acid. See description in Laundon (1981), as *C. candelaris*, and in Kalb (2001b).

Examined material: Corumbá municipality, on the border of Fazenda Nhumirim and Campo Dora, on a wooden fence pole, 18°59′01.8″S, 56°36′56.9″W, 90m alt., 11.IX.1988, leg. V.J. Pott 641 (COR); idem, Fazenda Nhumirim, Pomar da sede, on mangueira trunk [*Mangifera indica* L.], 18°59′01.8″S, 56°36′56.9″W, 90m alt., leg. V.J. Pott 690 (COR); Rio Negro municipality, margin of the road MS-419, between Rio Negro and Rio Verde de Mato Grosso, edge of Cerrado, 19°17′55.83″S, 55°06′1.04″W, 165m alt., 3.X.2013, leg. A.P. de Souza 42 (CGMS).

Cratiria obscurior (Stirton) Marbach & Kalb, Biblioth. Lichenol. 74: 186. 2000. Fig. 6.3b

Cratiria obscurior is characterized by the pale gray crustose thallus, the black lecideine apothecia, with clear hymenium, brown two-celled ascospores, 12.5–17.5 × 5 μm, excipulum K+ yellow-red forming red crystals, and thallus K+ red (norstictic acid). According to Marbach (2000), this species is very similar to *C. lauricassiae* (Fée) Marbach, which differs by its four-celled ascospores. Also similar to *C. obscurior* are *C. amphorea* (Eckfeldt) Marbach and *C. saltensis* (H. Magn.) Marbach, which differ by having inspersed hymenia. See description in Marbach (2000).

Examined material: Corumbá municipality, margin of Baía do Taquaral, riparian forest, on twig of *Licania* sp., 18°02′42.30″S, 57°30′15.20″W, 83m alt., 26.XI.2010, leg. L.S. Canêz 3605 (CGMS).

Crespoa carneopruinata (Zahlbr.) Lendemer & Hodkinson, North American Fungi 7(2): 2012.

This species is characterized by the scrobiculate upper surface, presence of orbicular and laminal soralia, lobes up to 2.5 mm, black lower surface, medulla K+ yellow, C-, KC-, P+ orange (stictic acid complex).

Crespoa carneopruinata was first reported to Mato Grosso do Sul state by Fleig & Riquelme (1991, as *Canoparmelia carneopruinata*, but here it is cited to the Pantanal for the first time. Additional data can be found in Jungbluth (2006).

Examined Material: Corumbá, Morraria do Urucum, on cortex, 19° 12′ 08,2″ S, 57° 36′ 04,6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz, A.A. Spielmann, A.P. Lorenz-Lemke & W.S. Fava 3251 (CGMS).

Crespoa crozalsiana (B. de Lesd. ex Harm.) Lendemer & Hodkinson, North American Fungi 7(2): 2012.

This species is characterized by the sublacinulate to lobate thallus, strong scrobiculate upper surface, orbicular soralia, laminal, atranorin as cortical constituents and stictic acid complex in the medulla (K+ yellow, C-, KC-, P+ orange).

Crespoa crozalsiana and *C. carneopruinata* are similar and it seems that the two differ only by the width of the lobes, that are up to 2.5 mm in *C. carneopruinata* and slightly wider in *C. crozalsiana* that are up to 4.0 mm. These two species could be synonyms, but a more thourough investigation is necessary. For additional information, see Jungbluth (2006) and Spielmann & Marcelli (2008).

TLC: atranorin, stictic, constictic (stictic complex).

Examined material: Corumbá, Morraria do Urucum, on cortex, 19° 12′ 08,2″ S, 57° 36′ 04,6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. (CGMS).

Crespoa scrobicularis (Kremp.) Benatti & Lendemer, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 25: 10. 1873.

This species is characterized by a very scrobiculate upper surface, narrow laciniae, propagules absent (only apothecia), and for presenting substances of the stictic acid complex.

Crespoa scrobicularis was reported to Brazil (as *Canoparmelia*) for several authors in different states (Ribeiro 1998, Eliasaro 2001, Jungbluth 2006, Spielmann 2006). Despite this, here in Mato Grosso do Sul state, *C. scrobicularis* was cited only to Ponta Porã in Osorio (1973) and it was found in Pantanal almost fifty years later.

TLC: atranorin and substances from stictic complex.

Examined material: Corumbá, Morraria do Urucum, on fallen branch, 19° 12′ 08,2″ S, 57° 36′ 04,6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. 3300, 3249, 3278 *p. parte* (CGMS).

Dirinaria aegialita (Afz. ex Ach.) B.J. Moore, The Bryologist 71: 248. 1968.

Dirinaria aegialita is characterized by the foliose thallus, slightly plicate; laciniae discrete to slightly confluent, palmatifid to irregularly branched, apices not flabellate and rounded; laminal polysidiangia with apical granular soredia; apothecia sessile to constricted at the base; disc plane to slightly convex, black, epruinose, or rarely whitish pruinose; ascospores *Dirinaria*-type, 2-celled, 13–17(–19) × 5–7(–8) µm (Awasthi 1975), but apothecia was not found in the studied material. The chemical constituents are atranorin and divaricatic acid. The other species with polysidiangia are *D. consimilis* and *D. pruinosa*, but the first has sekikaic acid and the last has purplish-pruinose apothecial disc. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, beginning of the trail to Morro do Amolar à margem da Baía do Taquaral, on rock, 18°02′48.90″S, 57°29′49.50″W, 89 m alt., 26.XI.2010, leg. L.S. Canêz 3636; 18°02′42.30″S, 57°30′15.20″W, 83m alt., leg. C.O. Dourado 77 (CGMS).

Dirinaria africana (Müll. Arg.) D.D. Awasthi, Biblioth. Lichenol. 2: 40. 1975.

Dirinaria africana is characterized by the foliose thallus strongly adnate, slightly plicate; laciniae confluent, subdichotomously branched, slightly flabellate, rounded apices, and dark-brown margins; vegetative propagules absent; apothecia immersed; disc plane, black, epruinose; ascospores *Dirinaria*-type, 12–18 × (5–)6–8 µm. The chemical constituents are atranorin and divaricatic acid. In Swinscow & Krog (1978) *D. africana* was treated as a synonym of *D. confluens*, but due to the characteristics presented by Awasthi (1975), it was considered a valid species. This is the first record of *D. africana* for the American continent. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, RPPN Eliezer Batista (Novos Dourados), topo do morro, on rock, 18°05′33.40″S, 57°29′31.40″W, 208m alt., 24.XI.2010, leg. L.S. Canêz 3566b, 3569 (CGMS); início da trilha, on rock, 18°05′40.20″S, 57°29′15.50″W, 95m alt., 24.XI.2010, leg. A.A. Spielmann 8741 (CGMS).

Dirinaria confluens (Fr.) D.D. Awasthi, Biblioth. Lichenol. 2: 28. 1975.

Dirinaria confluens is characterized by the foliose thallus loosely adnate, strongly plicate and verrucose in the central part; laciniae confluent, dichotomously to subdichotomously branched, flabellate, rounded apices; vegetative propagules absent; apothecia sessile to constricted at the base; disc plane to slightly convex, black, epruinose; ascospores *Dirinaria*-type, (14–)16–24 × (6–)8–10 µm. The chemical constituents are atranorin and divaricatic acid. A closely related species is *D. pruinosa,* which has purplish-pruinose apothecial disc. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, RPPN Eliezer Batista (Novos Dourados), on bark, 18°05′40.20″S, 57°29′15.50″W, 95m alt., 24.XI.2010, leg. C.S. Robles 45 (CGMS); idem, 58; 18°01′09.20″S, 57°32′03.80″W, 95m alt., leg. L.S. Canêz 3556 (CGMS); RPPN Acurizal, próximo à sede da ECOTROPICA, on bark 17°52′38.20″S, 57°33′12.00″W, 27.XI.2010, leg. T.S. Amaral 159 (CGMS).

Dirinaria consimilis (Stirt.) D.D. Awasthi, in Awasthi & Agarwal, J. Indian Bot. Soc. 49: 135. 1970.

Dirinaria consimilis is characterized by the foliose thallus, smooth to slightly plicate; laciniae discrete to slightly confluent, palmatifid to irregularly branched, apices not flabellate and rounded; laminal polysidiangia with apical granular soredia; apothecia sessile to constricted at the base; disc plane to slightly convex, black, epruinose, or rarely whitish pruinose; ascospores *Dirinaria*-type, 14–23 × 6–8 µm. The chemical constituents are atranorin and sekikaic acid. For comparisons with closely related species, see comments under *D. aegialita*. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai início da trilha para o Morro do Amolar à margem da Baía do Taquaral, on rock, 18°02′48.90″S, 57°29′49.50″W, 89m alt., 26.XI.2010, leg. C.O. Dourado 57 (CGMS); idem, 18°02′42.30″S, 57°30′15.20″W, 83m alt., 26.XI.2010, leg. L.S. Canêz 3626 (CGMS).

Dirinaria papillulifera (Nyl.) D.D. Awasthi, The Bryologist 67: 369. 1964.

Dirinaria papillulifera is characterized by the foliose thallus, slightly plicate to strongly plicate; laciniae discrete to slightly confluent, subdichotomously branched, flabellate, rounded apices; laminal to submarginal isidia present; apothecia sessile to constricted at the base; disc plane to slightly convex, black, epruinose; ascospores *Dirinaria*-type, 12–16 × 5.5–8 μm. The chemical constituents are atranorin and divaricatic acid. This is the only species with true isidia in *Dirinaria*. This is the first record of this species for the state of Mato Grosso do Sul. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Mandioré, on bark, 18°11′50.70″S, 57°30′39.70″W, 90m alt., 23.XI.2010, leg. A.A. Spielmann 8710, 8723 (CGMS); L.S. Canêz 3518, 3525, 3532, 3534 (CGMS); Baía do Castelo on bark, 18°35′17.30″S, 57°32′10.80″W, 86m alt., 22.XI.2010, leg. T.H. Stefanello 10 (CGMS).

Dirinaria picta (Sw.) Clem. & Shear, The Genera of Fugi. 323. 1931.

Dirinaria picta is characterized by the foliose thallus, not plicate; laciniae discrete, palmatifid to irregularly branched, apices not flabellate and rounded; laminal and hemispheric soralia, farinose soredia; apothecia sessile to constricted at the base; disc plane to slightly convex, black, epruinose; ascospores *Dirinaria*-type, (12–)14–17(–21) × 5–7(–9) μm. The chemical constituents are atranorin and divaricatic acid. *Dirinaria applanata* is the most closely related species, but the thallus of this species is strongly plicate and it has flabellate laciniae. This is the first record of this species for the state of Mato Grosso do Sul. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Mandioré, on bark, 18°11′50.70″S, 57°30′39.70″W, 90m alt., 23.XI.2010, leg. T.H.D. Leandro 30, 31, 33, 35, 40, 41, 42, 68 (CGMS), L.S. Canêz 3515, 3520, 3527, 3529 3538 (CGMS); Baía do Taquaral, on bark, 18°02′42.30″S, 57°30′15.20″W, 83m alt., 26.XI.2010, leg. C.O. Dourado 99, 103 (CGMS); L.S. Canêz 3611 (CGMS); Baía do Castelo, on bark, 18°35′17.30″S, 57°32′10.80″W, 86m alt., 22.XI.2010, leg. L.S. Canêz 3499 (CGMS); leg. T.H. Stefanello 9 (CGMS).

Dirinaria pruinosa Kalb, Biblioth. Lichenol. 78: 147. 2001.

Dirinaria pruinosa is characterized by the foliose thallus, not plicate to slightly plicate; laciniae discrete to slightly confluent, palmatifid to irregularly branched, apices not flabellate and rounded; laminal to marginal polysidiangia with apical granular soredia; apothecia sessile to constricted at the base; disc plane to slightly convex, black, purplish-pruinose; ascospores *Dirinaria*-type, (14–)20–25 × (6–)7–8 μm. The chemical constituents are atranorin and divaricatic acid. For comparisons with closely related species, see *D. aegialita* comment. This is the first record of this species for the state of Mato Grosso do Sul. See description in Kalb (2001b).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, RPPN Elizer Batista (Novos Dourados), início da trilha, on bark, 18°01′09.20″S, 57°32′03.80″W, 95m alt., 24.XI.2010, leg. L.S. Canêz 3554 (CGMS); Baía do Taquaral, início da trilha para o Morro do Amolar, próximo a margem da baía, 18°02′48.90″S, 57°29′49.50″W, 89m alt., 26.XI.2010, leg. L.S. Canêz 3637 (CGMS).

Dirinaria purpurascens (Vain.) B.J. Moore, The Bryologist 71: 251. 1968.

Dirinaria purpurascens is characterized by the foliose thallus loosely adnate to the substrate, slightly plicate; laciniae discrete to slightly confluent, palmatifid to irregularly branched, apices flabellate, truncate; vegetative propagules absent; apothecia sessile to constricted at the base; disc plane to slightly convex, black, purplish-pruinose; ascospores *Dirinaria*-type, (11–)14–18 × 5–7 μm. The chemical constituents are atranorin and divaricatic acid. For comparisons with closely related species, see *D. confluens* comment. This is the first record of this species for the state of Mato Grosso do Sul. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Mandioré, on bark, 18°11′50.70″S, 57°30′39.70″W, 90m alt., 23.XI.2010, leg. L.S. Canêz 3526, 3528 (CGMS); Nhecolandia, Baía do Jacaré, Fazenda Nhumirim, on bark, 10.IX.1988, leg. V.J. Pott 638, 639, 685 (COR); Morro São Domingos, on bark, 25.XI.1995, leg. E.F. da Rocha s/n (COR).

Dirinaria rhodocladonica Kalb, Schumm & Elix, Australasian Liquenology 86: 8. 2020

Fig. 6.5a

Dirinaria rhodocladonica is characterized by the foliose thallus, strongly plicate and verrucose in the central part; medulla white with coccineous pigment in the upper region; laciniae confluent, dichotomously to subdichotomously branched, flabellate, rounded to retuse apices; vegetative propagules not present; apothecia sessile to constricted at the base; disc plane to slightly convex, black, epruinose; ascospores *Dirinaria*-type, (12–)15–19 × 6–7 μm. The chemical constituents are atranorin and divaricatic acid. The main difference between *D. rhodocladonica* and *D. confluens* is the presence of a coccineous pigment in the medulla of the first species. See description in Awasthi (1975).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, RPPN Eliezer Batista (Novos Dourados), on bark, 18°05′40.20″S, 57°29′15.50″W, 95m alt., 24.XI.2010, leg. C.S. Robles 42 (CGMS); Rio Negro municipality, margem da Estrada MS-419, entre Rio Negro e Rio Verde do Mato Grosso, 19°17′55.83″S, 55°06′1.04″W, 165m alt., 3.X.2013, leg. A.A. Spielmann 11131, 11133 (CGMS).

Dyplolabia afzelii (Ach.) A. Massal., Neagenea Lich.: 6. 1854.

Fig. 6.3c

Dyplolabia afzelii is characterized by the brown to olive brown crustose thallus, mostly simple lirellae, (0.35–)0.75–1.75(–2.25) mm, with thick white coating C+ red (presence of lecanoric acid), laterally carbonized excipulum, clear hymenium, paraphyses branched and anastomosing, hyaline ascospores, 3-septate, 16–20 × 7.5

µm, with negative iodine reaction. Similar to *D. afzelii*, *D. ochrocheila* (Vain.) Rivas Plata & Lücking differs by its very long lirellae (10–30 mm) with a yellowish white cover and smaller ascospores (14–17 × 5–7 µm). The other three known species of this genus, *D. dalywaiana* Rivas Plata, Bawingan & Lücking, *D. oryzoides* (Leight.) Kalb & Staiger and *D. chumphonensis* J. Kalb & K. Kalb have submuriform to muriform ascospores (Kalb et al. 2016). See description in Staiger (2002).

Examined material: Corumbá municipality, Fazenda Nhumirim, Pomar da sede, on cajueiro trunk [*Anacardium occidentale* L.], 18°59′01.8″S, 56°36′56.9″W, 26.X.1988, leg. V.J. Pott 688 (COR).

Fellhanera vulgata (Malme) Lücking **comb. nov.**

MycoBank MB 835680

Bas.: *Bacidia vulgata* Malme, Ark. Bot. 27A(5): 10. 1935.

Tax. syn.: *Bacidia vulgata* f. *saxicola* Malme, Ark. Bot. 27A(5): 11. 1935.

This corticolous (and saxicolous) species has been related to the genus *Fellhanera*, but the combination has apparently never been validly published. *Fellhanera vulgata* is similar to the foliicolous *F. rhaphidophylli* (Rehm) Vězda and *F. paradoxa* (Vězda) Vězda. From the first it differs by the larger apothecia with distinct margins and from the second by the smaller, regularly 3-septate ascospores.

Examined material: Matto Grosso: Santa Anna da Chapada, 2 March 1894, Malme 2472 (S, holotype).

Crypthonia albida (Fée) Frisch & G. Thor, Mycol. Progress 9: 290. 2010.

Fig. 6.4a

Crypthonia albida is characterized by its crustose loose attached light green thallus, with pale prothallus, numerous felty-like white pseudoisidia, and the presence of psoromic acid as the major substance (thallus C-, K-, UV-, P+ strong yellow). According to Aptroot et al. (2009), psoromic acid is rare in *Arthoniales*, occurring for instance also in *Ancistrosporella psoromica* Komposch, Aptroot & Hafellner. In Arthoniaceae, besides *C. albida*, only three species of the related and similar genus *Herpothallon* have this substance: *H. australasicum* (Elix) Elix & G. Thor, *H. echinatum* Aptroot, Lücking & Will-Wolf and *H. globosum* G. Thor. The first differs from *C. albida* by the scattered red pigment in the prothallus and its substrate (foliicolous or lignicolous); *H. echinatum* has firmly attached thallus and cylindrical, compact pseudoisidia, whereas *H. globosum* has a red prothallus and red, globose pseudoisidia. See description in Aptroot et al. (2009) and Frisch & Thor (2010).

Examined material: Corumbá municipality, Morro São Domingos – Mineração Corumbaense, in Semidecidual forest area, 19°15′45.8″S, 57°36′11.6″W, 21.II.2001, leg. I.H. Ishii s/n (COR).

Hyperphyscia adglutinata (Flörke) H. Mayrhofer & Poelt, Herzogia 5(1–2): 62. 1979.

Fig. 6.5b

Hyperphyscia adglutinata is characterized by the small foliose thallus, upper surface gray brow to dark brown; laciniae confluent, irregularly branched, truncate, and ascending apices; laminal and maculiform soralia, slightly capitate, with granular soredia; apothecia sessile to constricted at the base; disc plane, brown to black;

ascospores *Pachysporaria* to *Physcia*-type, 18–23 × 8–11 µm (Moberg 1983), but in the studied material apothecia was not found. Only traces of skyrin were found as a chemical constituent. *Hyperphyscia syncolla* is a closely related species but lacks vegetative propagules. This is the first record of this species for the state of Mato Grosso do Sul. See description in Moberg (1987).

Examined material: Corumbá municipality, Base de Estudos do Pantanal (UFMS), Baía da Medalha, on bark, 19°34′32.90″S, 57°00′51.50″W, 95m alt., 21.VIII.2011, leg. A.A. Spielmann 9596 (CGMS); Fazenda Nhumirim, Pomar da Sede, on bark, 26.X.1988, leg. V.J. Pott 681a (COR).

Hyperphyscia syncolla (Tuck. ex Nyl.) Kalb, Lichenes Neotropici 6(230): 11. 1983.

Hyperphyscia syncolla is characterized by the small foliose thallus, verrucose in the central parts, upper surface gray brow to dark brown; laciniae confluent, irregularly branched, truncate, and ascending apices; vegetative propagules absent; apothecia sessile to constricted at the base; disc plane, brown to black; ascospores *Pachysporaria*-type, 15–21 × 7–11 µm. Only traces of skyrin were found as a chemical constituent. See description in Moberg (1987).

Examined material: Corumbá municipality, Morraria do Urucum, on bark, 19°12′08.20″S, 57°36′04.60″W, 733m alt., 3.IX.2010, leg. L.S. Canêz 3270 (CGMS).

Lecanora achroa Nyl., J. Bot., Lond. 14: 263. 1876.

Lecanora achroa is characterized by the green to greenish-gray crustose thallus, apothecia with thalline margin (lecanorine), 0.35–0.75 mm, disc beige, epruinose, yellowish hymenium with little dark crystals that dissolve in KOH, simple and ellipsoid spores, 9–12.5 × 5–6 µm and the presence of atranorin and usnic acid as major chemical compounds. This species is similar to *L. helva* and *L. leprosa* Fée, but differs on their main chemistry: while *L. achroa* has atranorin and usnic acid, *L. helva* is mentioned in the literature to produce 2’-O-methylperlatolic acid, and *L. leprosa* produces mainly substances from the ganga leoidin chemosyndrome (Galloway et al. 2001). See description in Galloway et al. (2001), Guderley (1999).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, on the river margin, ruderal environment, on the stipe of a carandá palm, 18°35′26.00″S, 57°32′44.70″W, 88m alt., 22.XI.2010, leg. T.H. Stefanello 57 (CGMS); idem, RPPN Eliezer Batista (Novos Dourados), beginning of the trail, 18°01′09.20″S, 57°32′03.80″W, 95m alt., 24.XI.2010, leg. L.S. Canêz 3565a (CGMS).

Lecanora concilianda Vain., Acta Soc. Fauna Flora Fenn. 7: 85. 1890.

Lecanora concilianda is characterized by the crustose verrucose thallus, apothecia with thalline margin (lecanorine), with crenulate margins, 0.25–0.55 mm, brown to reddish brown disc, amphitecium with large crystals, some dissolving in KOH, yellowish hypothecium, ascospores simple and ellipsoid, 12.5–17.5 × 6–9 µm. Thallus C-, K+ yellow, UV-, hymenium I+ blue persistent. No substances were detected in the Pantanal material. *Lecanora concilianda* is similar to *L. concilians* (Nyl.) Cromb., the latter having apothecia with darker discs (black-brown) and larger ascospores (14–20 × 9–12 µm) (Cáceres 2007). See description in Vainio (1890).

Examined material: Corumbá municipality, Morro Tromba dos Macacos, in a Cerrado forest area, on bocaiúva trunk, 19°12′45.3″S, 57°40′26.8″W, 02.XI.1993, leg. M.P. Marcelli 24809 (COR).

Lecanora helva Stizenb., Ber. Tät. St Gall. naturw. Ges.: 218 (1890) [1888-89].*

Lecanora helva is characterized by the crustose gray thallus, apothecia with thalline margin (lecanorine), 0.25–0.9 mm, beige to ochre disc, epruinose, with persistent margin, hymenium pale with small dark crystals dissolving in KOH, simple and ellipsoid spores, 10–12.5 × 5–6.2 μm, and atranorin as the main chemical compound. This species is morphologically similar to *L. achroa* and *L. leprosa*, differing regarding their chemistry (check on *L. achroa*). See description in Galloway et al. (2001), Guderley (1999).

Examined material: Rio Negro municipality, margin of the road MS-419, between Rio Negro and Rio Verde de Mato Grosso, in an open area, on a wooden fence pole, 19°17′55.83″S, 55°06′1.04″W, 165m alt., 3.X.2013, leg. A.A. Spielmann 11135 (CGMS).

Leptogium austroamericanum (Malme) C.W. Dodge, Ann. Missouri Bot. Gard. 20: 419. 1933.

Leptogium austroamericanum is characterized by the agglomerated lobes with irregular wrinkles on the upper surface, and granular to cylindrical isidia with withered appearance. *Leptogium cyanescens* is an isidiate species, as *L. austroamericanum*, but has smooth to rugulose upper surface. See description in Kitaura (2012).

Examined material: Corumbá municipality, Tromba dos Macacos, 02.XI.1993, s/c. 24817 (COR); idem, on *Aspidosperma subincanum*, 2.XI.1993, leg. M.P. Marcelli 24820 pr. min. p. (COR); idem, on bocaiuva tree, 02.XI.1993, leg. M.P. Marcelli 24824 (COR); idem, s/d, leg. M.P. Marcelli s/n. pr. max. p. (COR); idem, s/d, s/c, s/n (COR); idem, sub-region Paraguay Pantanal, Castelo Bay, 18°33′52.80″S, 57°34′29.30″ W, 92 m. alt., corticolous on riparian forest, on rock, 22.XI.2010, leg. T.H. Stefanello 79 (CGMS); idem, RPPN Rumo ao Oeste, Guaia Bay, 17°44′18.10″S, 57°41′27.80″ W, 91 m. alt., riparian forest, 28.XI.2010, leg. A.A. Spielmann 8813, (CGMS); idem, Brazil-Bolivia Frontier, Subregion Pantanal of Paraguay, margin of Mandioré Bay (Bolivia side), 18°11′50.70″S, 57°30′39.70″W, 90 m. alt., 23.XI.2010, leg. A.A. Spielmann 8726 pr. max. p. (CGMS).

Leptogium chloromelum (Sw.) Nyl., M Soc. Natl. Sci. Nat. Math. Cherb., 5: 333. 1857.

Fig. 6.2b

Leptogium chloromelum is characterized by the presence of overlapping branches, adpressed, and with irregular and longitudinal ridges on the upper surface. The subpedicellate apothecia have thick paraplectenchymatous proper exciple, as the apothecia of *L. phyllocarpum*. However, the apothecia of *L. phyllocarpum* are constituted by lobuloid structures, whereas the apothecia of *L. chloromelum* are smooth, without lobuloid structures. Both species, *L. chloromelum* and *L. phyllocarpum*, have fusiform ascospores, which are submuriform and muriform, respectively. See description in Kitaura (2012).

Examined material: Corumbá municipality, Tromba dos Macacos, on bocaiuva, 02.XI.1993, s/c, s/n (COR); idem, s/d, leg. M.P. Marcelli s/n. (COR 3152); s/d, leg.

M.P. Marcelli s/n. (COR 3176); idem, s/d, leg. M.P. Marcelli s/n (COR 3177); idem, Forte Coimbra, on calcareous substrate, s/d, leg. I.H. Ishii s/n (COR 6038).

Leptogium cochleatum (Dicks.) Jørg. & James, Lichenologist 15(2): 113. 1983.

Leptogium cochleatum is characterized by distinctly striate upper surface, subpedicellate apothecia on the lamina, and thick paraplectenchmatous thalline exciple. The surface of *Leptogium cochleatum* differs from the surfaces of *L. azureum* and *L. moluccanum* that are smooth. Furthermore, the apothecia of *L. azureum* are pedicellate, with pedicel c. 1 mm long. See description in Aragón et al. (2005).

Examined material: Corumbá Municipality, Reserva Acurizal, Córrego Fundão, 2.5 Km of waterfall, near to the Gaita local, aluvial soil with organic material, inclined relief, 17°54′00.8″ S, 57°33′45″ W, 09.V.2003, leg. V.J. Pott 6281 (CGMS).

Leptogium cyanescens (Rabenh.) Körb., Systema Lichenum Germaniae 420. 1855.

Leptogium cyanescens is constituted by smooth thallus, c. 100 μm thick, bluish, with cylindrical to flattened isidia on the lamina and margins of the lobes. *Leptogium cyanescens* differs from *L. denticulatum* by the presence of isidia. *Leptogium denticulatum* has denticules only on the margin of apothecia, whereas *L. cyanescens* is an isidiate species, and has apothecia with smooth margins. See description in Kitaura (2012).

Examined material: Corumbá Municipality, Morro do Urucum, on the border, corticolous, 19°12′08.20″S, 57°36′04.60″W, 730 m alt., 3.IX.2010, leg. A.A. Spielmann 8520 (CGMS).

Leptogium diaphanum (Sw.) Mont., Ann. Sci. Nat. Bot. Biol. Vég. 10: 134. 1848.

Comments: *Leptogium diaphanum* has a translucent thallus, 30–45 μm thick, and delicate lobules or lobuliform structures on both the thallus and apothecia.

Lobules are commonly found on the thallus of *L. diaphanum* which distinguishes this species from *L. cyanescens*, *L. isidiosellum* and *L. austroamericanum* that are exclusively isidiate species. See description in Cunha (2007).

Examined material: Corumbá Municipality, morraria do Urucum, on the trail, on cortex of tree, 19°12′08.20″S, 57°36′04.60″ W, 733 m. alt., 3.IX.2010, leg. L.S. Canêz 3236 pr. min. p., 3246, 3256 (CGMS).

Leptogium fusisporum (Tuck.) C.W. Dodge, Ann. Missouri Bot. Gard. 20: 418. 1933.

Fig. 6.2c

Leptogium fusisporum is characterized by the thallus constituted by branches, covered by paraplectenchymatous cells, with densely irregular ridges that originate cerebroid structures. The transversely septate ascospores have 30–50 × 5.0–7.5 μm (4–6 × 1 cells). Usually, this species is found sterile and was previously identified as *L. floridanum* Sierk, which is a species with fusiform and submuriform ascospores, 22–35 × 9–14 μm (Sierk 1964). See description in Sierk (1964).

Examined material: Corumbá Municipality, subregion Pantanal of Paraguay, Mandioré Bay, 18°11′50.70″S, 57°30′39.70″W, 90 m. alt. corticolous in riparian forest, 23.XI.2010, leg. T.H.D. Leandro 64, 65 (CGMS); idem, Mandioré Bay (Bolivia side), 18°11′50.70″S, 57°30′39.70″W, 90 m. alt., 23.XI.2010, leg. A.A. Spielmann 8718, 8720 (CGMS); idem, Brazil-Bolivia Frontier, subregion

Pantanal of Paraguay, margin of Mandioré Bay (Bolivia side), 18°11′50.70″S, 57°30′39.70″W, 90 m. alt., 23.XI.2010, leg. A.A. Spielmann 8726 pr. min. p., 8729 (CGMS); idem, margin of Taquaral Bay, corticolous on riparian forest, 18°02′42.30″S, 57°30′15.20″W, 83 m alt., 26.XI.2010, leg. C.O. Dourado 72 (CGMS).

Leptogium isidiosellum (Riddle) Sierk, Bryologist 67(3): 282. 1964.

Leptogium isidiosellum is characterized by irregular and longitudinal ridges on the upper surface, with cylindrical isidia on the lamina and margins of the lobes. The apothecia, when present, are constituted by thalline exciple with paraplectenchymatous cortex, 4–6 cells thick. *Leptogium isidiosellum* differs from *L. austroamericanum* and *L. cyanescens* mainly by the surface of the thallus. *Leptogium isidiosellum* has ridged upper surface, while *L. austroamericanum* has wrinkled upper surface, and *L. cyanescens* has smooth to rugulose upper surface. See descriptions in Sierk (1964) and Kitaura (2012).

Examined material: Corumbá municipality, Tromba dos Macacos, on *Aspidosperma subincarum*, 2.XI.1993, leg. M.P. Marcelli 24820 pr. max. p. (COR); idem, Fazenda Gaíva (Jaguaribe), Pantanal of Paraguay river, corticolous, open cerradão, with taboca (*Bambus* sp.) e *Zamia*, sandy soil, plane relief, 17°54′22.7″S, 57°38′40.0″W, alt. 155 m., 30.III.2003, leg. V.J. Pott 6110 (CGMS); idem, subregion Pantanal of Paraguay, Mandioré Bay, 18°11′50.70″S, 57°30′39.70″W, alt. 90 m, corticolous, on riparian forest, 23.XI.2010, leg. T.H.D. Leandro 49, 50 (CGMS).

Leptogium marginellum (Sw.) Gray, A Natur. Arrang. Brit. Plants 1: 401. 1821. Fig. 6.2d

Leptogium marginellum has thallus with irregular ridges, apothecia restricted to the margin of the lobes, with up to 0.5 mm diam., usually abundant. Lobules only on the margin of apothecia. When sterile, *L. marginellum* can be confused with *L. phyllocarpum* because of the ridged thallus. Both species are differentiated only with the presence of apothecia, which is abundant and marginal in *L. marginellum*, andlaminal and submarginal in *L. phyllocarpum*. See description in Kitaura (2012).

Examined material: Corumbá Municipality, Morraria do Urucum, on the trail, on cortex, 19°12′08.20″S, 57°36′04.60″ W, 733 m. alt., 3.IX.2010, leg. L.S. Canêz 3236 pr. max. p., 3265 (CGMS).

Leptogium phyllocarpum (Pers.) Mont., Ann. Sci. Nat. Bot. Biol. Vég., 10: 134. 1848.

Leptogium phyllocarpum is characterized by the upper surface with longitudinal to irregular ridges, and lobuloid structures restricted to the apothecia, with 1.0 mm diam. *L. phyllocarpum* has laminal and submarginal apothecia with lobuloid propagules that differs from *L. chloromelum,* which has only submarginal apothecia without lobuloid propagules. See description in Sierk (1964) and Cunha (2007).

Examined material: Corumbá Municipality, Morraria do Urucum, on the trail, on cortex of tree, 19°12′08.20″S, 57°36′04.60″ W, 733 m. alt., 3.IX.2010, leg. L.S. Canêz 3241, 3248 (CGMS).

Marcelaria purpurina (Nyl.) Aptroot, Nelsen & Parnmen, Glalia 5(2): 9. 2013.

Marcelaria purpurina is characterized by the olive-green, crustose thallus with patches of red pruina, the ascoma warts 0.5–0.9 mm diam. and covered by a thick red pruina, muriform, hyaline ascospores, 110–170 × 14–26 µm (Aptroot et al. 2013; ascospores not found in the examined material). According to Aptroot et al. (2013), this species differs from *M. benguelensis* (Müll. Arg.) Aptroot, Nelsen & Parnmen and *M. cumingii* (Mont.) Aptroot, Nelsen & Parnmen mainly by the red and not orange or yellow pruina, the generally larger ascomata and ascospores. See description in Aptroot et al. (2013).

Examined material: Rio Verde de Mato Grosso municipality, sítio Passarim, in an open area, riparian forest, on trunk in the margin of Verde river, 18°56′26.6″S, 54°55′16.6″W, 390m alt., 23.VIII.2015, leg. A.A. Spielmann 11937 (CGMS).

Myelochroa lindmanii (Lynge) Elix & Hale, Mycotaxon 29: 241, 1987.

This is a lichen with flat, adnate lobes, short cilia restricted to the lobe axils, and a yellow medulla (secalonic acids). It could be confused with *Canoparmelia* or *Parmotrema*; but no *Canoparmelia* species are known to develop a yellow medulla in Brazil, and although one can find some *Parmotrema* with yellow medulla, usually the loosely attached and wide lobes can be helpful to differentiate the genera. There was a proposition to classify this species in *Parmotrema* (Kurokawa & Arakawa 1997), but it was not widely accepted. Probably genetic data can help to accommodate it better in some other genus. For additional data, see Spielmann & Marcelli (2008).

Specimens examined: Corumbá, Urucum mountains, in fallen branch at the trail, 19°12′08.2″S, 57°36′04.6″W, 730 m alt., 03.IX.2010, leg. A.A. Spielmann et al. 8491 (CGMS).

Neoprotoparmelia multifera (Nyl.) Garima Singh, Lumbsch & I. Schmitt, in Singh, Aptroot, Rico, Otte, Divakar, Crespo, Cáceres, Lumbsch & Schmitt, MycoKeys 44: 41 (2018).

Neoprotoparmelia multifera is characterized by the crustose thallus (UV+ green) with lecanorine apothecia slightly convex, with brown disc, thaline margin thin, apothecia medulla UV+ green asci 64-spored, ascospores simple and hyaline ascospores, 6.2–7.5 × 1.7–2.5 µm. Species of *Neoprotoparmelia* Garima Singh, Lumbsch & I. Schmitt (formerly *Maronina* Hafellner & R.W. Rogers) are similar to *Protoparmelia* species, being together classified in a separate subfamily within *Parmeliaceae* (*Protoparmelioideae*) by Divakar et al. (2017) based on molecular data. According to these authors, the main differences among these genera are the distribution and the habitat where they occur: while *Neoprotoparmelia* consists of mostly tropical species growing on bark, *Protoparmelia* s. str. occurs in temperate regions, growing on siliceous rocks (Divakar et al. 2017). This is *N. multifera* in the strict sense, the occurrence of which is herewith confirmed for Brazil. No specimens of this species were found in the Northwest of Brazil, but it apparently occurs in the Central West. See description in Vainio (1890) as *Maronea multifera* (Nyl.) Vain and Santos *et al*. 2019.

Examined material: Corumbá municipality, margin of Baía do Taquaral, riparian forest, on twig of *Licania* sp., 18°02′42.30″S, 57°30′15.20″W, 83m alt., 26.XI.2010, leg. L.S. Canêz 3616 (CGMS).

Opegrapha astraea Tuck., Lichens of California (Berkeley): 33. 1866.

Opegrapha astraea is characterized by a very thin crustose thallus, with small lirellae (0.3–3.5 mm) with exposed disc in maturity, which is covered by a white pruina. Its lirellae has irregular carbonization, clear hymenium, I+ orange-red, olive green hypohymenium, hyaline and transversely septated spores, with a perispore and having 4 to 5 septa in the Pantanal material, 20–27.5 × 5–6 µm. We found the presence of atranorin and terpenes through TLC analysis in our material. According to Ertz (2009), *O. subcentrifuga* Nyl. is similar to *O. astraea* and probably belongs to the same group but differs by the small and 3-septate ascospores (11–14.2 × 3.2–3.9 µm). See description in Ertz (2009).

Examined material: Corumbá municipality, Morro Tromba dos Macacos, on tree trunk, 19°12′45.3″S, 57°40′26.8″W, 02.XI.1993, leg. M.P. Marcelli 24829 (COR).

Opegrapha rissoensis Redinger Ark. f. bot. 29A (19): 1940.

Opegrapha rissoensis is characterized by the small ascomatas (up to 0.5 mm), rounded to lirelliform, clear hymenium, I+ orange, excipulum with basal and irregular carbonization, spores with 4 septa, 20 × 2.5 µm, with isodiametric cells, baciliform and bifusiform conidia, many pycnidia along the thallus. The Pantanal material did not have pruina on the ascomatas. No chemical substance was detected in our material (TLC). See description in Redinger (1940).

Examined material: Corumbá municipality, Fazenda Nhumirim, Salina do 8, Reserva, Bordo de Salina – forest, on tree trunk, 18°59′01.8″S, 56°36′56.9″W, 10.IX.1988, leg. V.J. Pott 614 (COR).

Parmotrema argentinum (Kremp.) Hale, Phytologia 28: 334, 1974.

This species has ciliate lobes, ciliate apothecia and medulla producing alectoronic acid (UV+ greenish medulla). Relatively common in Mato Grosso do Sul, it is still much unrecorded for the Pantanal region. See descriptions in Canêz (2005) and Hale (1965).

Specimens examined: Corumbá, Urucum mountains, in fallen branch at the trail, 19°12′08.2″S, 57°36′04.6″W, 730 m alt., 03.IX.2010, leg. A.A. Spielmann et al. 8506 (CGMS).

Parmotrema confusum Hale, Bibliotheca Lichenologica 38: 113, 1990.

Fig. 6.6a

Parmotrema confusum can be recognized by the well-developed, substipitate, and imperforate apothecia with involute rim, eciliate lobes, and the production of protocetraric acid (medulla K+ dirty yellow, P+ orange). At first sight, this species can be confused with *Parmotrema mesotropum*, a lichen with negative medullary tests (only fatty acids). Some keys (e.g. Hale 1965, Sipman 2005) would lead to *Parmotrema zollingeri* (Hepp) Hale. Taking the revision of the group made by Elix (1998), one can discover that the medullary chemisty of *P. zollingeri* is quite complex, with fumarprotocetraric acid, succinprotocetraric acid, and protocetraric acid. Using the different chemistry of the synonyms of *P. zollingeri* studied, Elix (1998) recognized several of them as good species. But for some reason, *Parmelia latissima* var. *minima* Lynge was not included. This taxon was described by Lynge (1914), and inconclusively revised by Hale (1960). Only 30 years later, Hale (1990) reassessed it, concluding that it was a good species, with with a new name, *Parmotrema confusum* Hale.

This species was known only from the type, from Mato Grosso State, Brazil.

Specimens examined: Corumbá, Urucum mountains, in fallen branch at the trail, 19°12′08.2″S, 57°36′04.6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. 3277, 3278 *p.parte,* 3294, 3312, 3320, 3322, 3323, 3324, 3326, 3331, 3339, 3343, 3346 (CGMS).

Parmotrema consors (Nyl.) Krog & Swinscow, Lichenologist 15: 129, 1983.

The short, tapered, and thick cilia can be helpful to set apart this species from the other *Parmotrema*, together with the negative medullary reactions (only fatty acids found). For additional data about this and other species previously classified in *Canomaculina* Elix & Hale, see Spielmann & Marcelli (2009).

Specimens examined: Corumbá, Passo do Lontra, "Base de Estudos do Pantanal – UFMS", in the stipe of a "Buriti", at the roadside, 19°34′27.6″S, 57°01′23.0″W, 95 m alt., 21.VIII.2011, leg. A.A. Spielmann et al. 9436 (CGMS).

Parmotrema dilatatum (Vain.) Hale, Phytologia 28: 335, 1974.

This is a sorediate, eciliate species with medullary protocetraric and echinocarpic acids (K+ yellow, P+ orange), and cortical atranorin and usnic acid. Descriptions and comments can be found in Hale (1965) and Benatti & Marcelli (2010).

Specimens examined: Corumbá, Urucum mountains, in fallen branch at the trail, 19°12′08.2″S, 57°36′04.6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. 3303, 3335 (CGMS).

Parmotrema melanochaetum (Kurok.) Blanco et al., Mycologia 97: 157, 2005.

The abundant isidiate cilia and the medulla C+ rose (gyrophoric acid) are the main features to identify this species. Descriptions in Hale (1976), Marcelli (1993) and Jungbluth (2006).

Specimens examined: Corumbá, Urucum mountains, corticicolous, at the forest border, 19°12′08.2″S, 57°36′04.6″W, 730 m alt., 03.IX.2010, leg. A.A. Spielmann et al. 8500, 8547, 8549 (CGMS); idem, leg. L.S. Canêz et al. 3237, 3247 (CGMS); idem, Sub-região Pantanal do Paraguai, Baía do Mandioré, corticicolous, in riparian forest, 18°11′50.7″S, 57°30′39.7″W, 90 m alt., 23.XI.2010, leg. T.H.D. Leandro et al. 43 (CGMS).

Parmotrema mesotropum (Müll. Arg.) Hale, Phytologia 28: 337, 1974.

Fig. 6.6b

The eciliate lobes, imperforate apothecia, and negative spot tests in the medulla (fatty acids) are characteristics for this species. Usually the upper surface of the thallus is distinctly wrinkled, a feature also found in *Parmotrema confusum*, a common species. See descriptions in Hale (1965) and Jungbluth (2006).

Specimens examined: Corumbá, Sub-região Pantanal do Paraguai, RPPN Acurizal, próximo à sede da Ecotropica, corticícola, em tronco podre caído no chão da mata, 17°52′38.2″S, 57°33′12.0″W, 138 m alt., 27.XI.2010, leg. T.S. Amaral et al. 152 (CGMS); idem, Baía do Mandioré, 18°11′50.7″S, 57°30′39.7″W, 90 m alt., 23.XI.2010, leg. T.H.D. Leandro et al. 32, 34 (CGMS); idem, margem da Baía do Taquaral, 18°02′42.3″S, 57°30′15.2″W, 83 m alt., 26.XI.2010, leg. C.O. Dourado et al. 118 (CGMS).

Parmotrema mordenii (Hale) Hale, Phytologia 28: 337, 1974.

Fig. 6.6c

Remarkably similar to *Parmotrema praesorediosum*, this is a sorediate, saxicolous species recognized by the K+ yellow reaction (medulla with atranorin). A genetic study of this group is highly necessary. See descriptions in Hale (1971) and Spielmann & Marcelli (2009).

Specimens examined: Corumbá, Sub-região Pantanal do Paraguai, RPPN Rumo ao Oeste, Baía Guaíba, riparian forest, saxicolous at the border of the bay, 17°44′18.1″S, 57°41′27.8″W, 91 m alt., 28.XI.2010, leg. L.S. Canêz et al. 3648 (CGMS); idem, Baía do Taquaral, corticicolous in a branch of *Licania*, riparian forest, 18°02′42.3″S, 57°30′15.2″W, 83 m alt., 26/XI/2010, leg. C.O Dourado et al. 46 (CGMS).

Parmotrema praesorediosum (Nyl.) Hale, Phytologia 28: 338, 1974.

Similar to *Parmotrema mordenii*, in this species the medulla is K- (without atranorin). See descriptions in Jungbluth (2006) and Spielmann & Marcelli (2009).

Specimens examined: Corumbá, Sub-região Pantanal do Paraguai, RPPN Eliezer Batista (Novos Dourados), topo do morro, 18°05′33.4″S, 57°29′31.2″W, 208 m alt., 24.XI.2010, leg. L.S. Canêz et al. 3573 (CGMS).

Parmotrema sorediοaliphaticum Estrabou & Adler, Mycotaxon 66: 134, 1998.

The identity of this taxon is tentative. It belongs to a group of saxicolous, eciliate species that produces only fatty acids at the medulla. This species is a new record to Mato Grosso do Sul State, being previously known to Rio Grande do Sul (Canêz 2005), Argentina (Estrabou and Adler 1998) and Galápagos (Bungartz and Spielmann 2019). Full descriptions can be found in these references.

Specimens examined: Corumbá, Sub-região Pantanal do Paraguai, RPPN Acurizal, mata do fundão, saxicolous at the trail, shaded, 17°52′38.2″S, 57°33′12.0″W, 138 m alt., 27.XI.2010, leg. L.S. Canêz et al. 3642 (CGMS).

Parmotrema tinctorum (Dèspr. ex Nyl.) Hale, Phytologia 28: 339, 1974.

The isidiate, eciliate lobes and the medulla C+ reddish (lecanoric acid) are the main features of this species. A very common, cosmopolitan lichen.

Specimens examined: Corumbá, Urucum mountains, in fallen branch at the trail, 19°12′08.2″S, 57°36′04.6″W, 733 m alt., 03.IX.2010, leg. L.S. Canêz et al. 3338, 3345 (CGMS); idem, corticicolous at the forest border, leg. A.A. Spielmann et al. 8497 (CGMS).

Peltula auriculata Büdel, Schultz & Gröger, Plant Biology 2: 484, 2000.

Peltula auriculata is characterized by the squamulose thallus with ear-shaped, upper surface olive green, and spherical ascospores with 2.5–4.0 μm diam. The diversity of *Peltulaceae* is underestimated in the Pantanal as revealed by preliminar molecular studies still not published. *Peltula auriculata* is known to Roraima state (Schultz and Aptroot 2008), and reported here by the first time to Mato Grosso do Sul state.

Examined material: Corumbá municipality, sub-região Pantanal do Paraguay, RPPN Rumo ao Oeste, Baía Gaiba, 17°44′18.10″ S, 57°41′27.80″ W alt. 91 m, 28.XI.2010, leg. T.H. Stephanello 382, 383, 384, 385, 386 (CGMS).

Phyllopsora chlorophaea (Müll. Arg.) Zahlbr., Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 83: 133. 1909.

Phyllopsora chlorophaea is characterized by the squamulose thallus, formed by small ascending squamules less than 1 mm wide, with well-developed prothallus, white in herbarium but green when fresh. Its apothecia is brown, with dark reddish brown hypothecium and excipulum, simple ascospores, 10–11 × 2.5 μm. According to Swinscow & Krog (1981), *P. parvifoliella* (Nyl.) Müll. Arg. and *P. pyrrhomelaena* (Tuck.) Swinscow & Krog are similar species, having smaller ascospores: *P. parvifoliella*: 6–8 × 2–3 μm; *P. pyrrhomelaena*: 5–8 × 2.5–3 μm. No chemical substance was detected in our material (TLC). See description in Swinscow & Krog (1981) and Timdal (2008).

Examined material: Corumbá municipality, Morro Tromba dos Macacos, on tree trunk, 19°12′45.3″S, 57°40′26.8″W, 260m, 02.XI.1993, leg. M.P. Marcelli 24832 (COR).

Phyllopsora pyxinoides (Nyl.) Kistenich, Timdal, Bendiksby & S. Ekman, Taxon 67(5): 894. 2018.

Fig. 6.4b

Phyllopsora pyxinoides is characterized by the byssoid, squamulose to almost microfoliose thallus (squamules are connected in a rosette-like form), with a black hypothallus, lacking upper cortex, with laminal to marginal soredia and the presence of a few small, black apothecia without thalline margin (not found in the Pantanal material). The only similar species is *P. gossypina* (Sw.) Kistenich, Timdal, Bendiksby & S. Ekman, which has, however, a pale hypothallus and pinkish brown apothecia with a pale margin (Aptroot and Cáceres 2014, as *Crocynia gossypina*). See description in Brodo et al. (2001).

Examined material: Corumbá municipality, RPPN Acurizal, next to the head office of Ecotropica, 17°52′38.20″S, 57°33′12.00″W, 27.XI.2010, leg. T.S. Amaral 136, 137 (CGMS).

Physcia aipolia (Humb.) Fürnr., Naturhist. Topogr. Regensburg 2: 249. 1839.

Fig. 6.5c

Physcia aipolia is characterized by the foliose thallus, plane to convex in central parts, upper surface gray, with punctiform and abundant maculae; laciniae contiguous, irregularly branched, truncate apices, lower surface pale brown to dark brown, lower cortex prosoplectenchymatous to intermediate; vegetative propagules absent; apothecia sessile to constricted at the base; disc plane, brown to black, whitish-pruinose; ascospores *Physcia* to *Pachysporaria*-type, 20–22 × 8–11 μm. The chemical constituents are atranorin, zeorine and triterpenes. *Physcia convexa* is a closely related species, but it is saxicolous, and has white lower surface with pink pigment. See description in Moberg (1990) and Jungbluth (2010).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Mandioré, on bark, 18°11′50.70″S, 57°30′39.70″W, 90m alt., 23.XI.2010, leg. T.H.D. Leandro 36 (CGMS).

Physcia convexa Müll. Arg. Rev. Mycol. 10: 57. 1888.

Physcia convexa is characterized by the foliose thallus, convex in central parts, upper surface gray, with punctiform and abundant maculae; laciniae discrete to contiguous, irregularly to subdichotomously branched, subtruncate apices, white lower surface with pink pigment, lower cortex prosoplectenchymatous, with a thin layer of paraplectenchymatous cells bellow; vegetative propagules absent; apothecia sessile to constricted at the base; disc plane, dark brown, scarce whitish-pruinose; ascospores *Physcia*-type, 16–18 × 6–8 µm. The chemical constituents are atranorin, zeorine and triterpenes. This is the first record of this species for the state of Mato Grosso do Sul. See description in Moberg (1990) and Jungbluth (2010).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, RPPN Rumo ao Oeste, Baía Guaíba, on rock, 17°44′18.10″S, 57°41′27.80″W, 91m alt., 28.XI.2010, leg. LS. Canêz 3649 (CGMS), T.H. Stefanello 391, 392, 400, 406, 414 (CGMS).

Physcia manuelii Moberg, Nord. J. Bot. 10: 334. 1990.

Physcia manuelii is characterized by the foliose thallus, plane in central parts, upper surface green-grayish; laciniae discrete to contiguous, irregularly branched, rounded apices, lower surface white, lower cortex prosoplectenchymatous, with a more or less thin layer of paraplectenchymatous cells bellow; phyllidia marginal to laminal; apothecia sessile to constricted at the base; disc plane, black, white pruinose; ascospores *Pachysporaria*-type, (18–) 20–23(–25) × 6–11(–12) µm. Only atranorin was found as chemical constituent. This is the first record of this species for Brazil. See description in Moberg (1990).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, on bark, 18°33′52.80″S, 57°34′29.30″W, 92m alt., 22.XI.2010, leg. LS. Canêz 3510 (CGMS), T.H. Stefanello 88 (CGMS); idem, Baía do Mandioré, 18°11′50.70″S, 57°30′39.70″W, 90m alt., 23.XI.2010, leg. T.H.D. Leandro 47, 60, 89 (CGMS).

Physcia tribacia (Ach.) Nyl., Flora 57: 307. 1874.

Physcia tribacia is characterized by the foliose thallus, convex in central parts, upper surface subscrobiculate, gray; laciniae imbricate to contiguous, irregularly branched, apices irregular, lower surface white, lower cortex paraplectenchymatous; apothecia sessile to constricted at the base; disc plane, dark brown to black, without pruina; ascospores *Physcia* to *Pachysporaria*-type, (17–) 18–21 (–23) × (8–) 9–11(–12) µm. Only atranorin was found as a chemical constituent. This is the first record of this species to Mato Grosso do Sul state. See description in Moberg (1990). Jungbluth (2010) described the soralia as absent but pointed out the production of submarginal granules. The material from the Pantanal differs from typical material by the almost isidioid soredia and the pruinose thallus, and can represent a new taxon.

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, on bark, 18°33′52.80″S, 57°34′29.30″W, 92 m alt., 22.XI.2010, leg. T.H. Stefanello 70 (CGMS); idem, RPPN Rumo ao Oeste, Baía Guaíba, 17°44′18.10″S, 57°41′27.80″W, 91 m alt., 28.XI.2010, leg. L.S. Canêz 3651, 3652 (CGMS).

Porina cryptostomoides Lücking, Aptroot & Spielmann **nom. nov.**

MycoBank MB 835682

Porina cryptostoma Malme, Ark. Bot. 23A(1): 21. 1929; non Mont., Annls Sci. Nat. Bot. Sér. 3, 7: 176. 1847.

Examined material. Brazil. Mato Grosso do Sul: Corumbá; 29 July 1894, Malme s.n. (S-L 839, lectotype, here designated; MBT392540).

Pyrenula anomala (Ach.) Vain., Ann. Acad. Sci. fenn., Ser. A 6 (no. 7): 189. 1915.

Pyrenula anomala is characterized by the corticate, crustose thallus, UV-, the laterally fused, pseudostromatic black perithecia not covered by thallus, with separate apical ostioles, a clear hamathecium, gray-brown spores with usually 3 septa, 17.5–20 × 2.5–7.5(–8) μm. This species is similar to *P. arthoniotheca* Upreti, which has smaller ascospores. See description in Aptroot et al. (2008).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, in riparian forest, next to the river margin, on embaúba trunk [*Cecropia* sp.], 18°34′52.20″S, 57°31′36.60″W, 95m alt., 22.XI.2010, leg. L.S. Canêz 3494 (CGMS).

Pyrenula xanthoglobulifera Aptroot, Lücking & M. Cáceres, Bryologist 116: 303. 2013.

Pyrenula xanthoglobulifera is characterized by the crustose thallus with lichexanthone (UV+ yellow), the white pseudocyphellae on the thallus, erumpent to prominent perithecia with partial thalline cover and with apical ostioles, the inspersed hamathecium, brown, muriform, and large ascospores, 112 × 25 μm. This species is similar to *P. globifera* (Eschw.) Aptroot, but differs from this by the presence of lichexanthone and the thalline cover on the perithecia (Menezes et al. 2013). *Pyrenula lyoni* (Zahlbr.) Aptroot also has some similar characteristics, but the ostioles of the perithecia are lateral and it lacks lichenxanthone. See description in Menezes et al. (2013).

Examined material: Corumbá municipality, RPPN Rumo ao Oeste, Baía Gaiba, riparian forest in a rocky outcrop, on tree trunk, 17°44′18.10″S, 57°41′27.80″W, 91m alt., 28.XI.2010, leg. T.H. Stefanello 409 (CGMS).

Pyxine berteriana (Fée.) Imshaug, Trans Am. Micros. Soc. 76(3): 254. 1957.

Pyxine berteriana is characterized by the foliose thallus, upper surface brownish white to brownish gray; laciniae contiguous, irregularly to dichotomously branched, apices subtrucate and concave, medulla yellow in the upper layer and white in the lower layer; apothecia sessile to constricted at the base, *cocoës*-type; disc plane to convex, black, epruinose, white internal stipe; ascospores *Dirinaria*-type, 16–20 × 6–8 μm. The chemical constituents are lichexanthone and terpenes. See description in Imshaug (1957), Kalb (1987) and Jungbluth (2010).

Examined material: Corumbá municipality, Morraria do Urucum, on bark, 19°12′08.20″S, 57°36′04.60″W, 733m alt., 3.IX.2010, leg. L.S. Canêz 3291, 3302 (CGMS).

Pyxine coccifera (Fée.) Nyl., Mém. Soc. Imp. Sci. Nat. Cherbourgh 5: 108. 1857.

Pyxine coccifera is characterized by the foliose thallus, upper surface brownish gray; laciniae contiguous, irregularly branched, rounded apices, medulla yellow with a white layer below, with red pigment under the maculae; maculae red and irregular; soralia cinnabar red, orbicular to linear and marginal to submarginal, with granular soredia; apothecia sessile to constricted at the base, *obscurascens*-type; disc plane to convex, black, epruinose, white internal stipe; ascospores

Dirinaria-type, 14–18 × 6–8 µm. The chemical constituents are atranorin, chiodectonic acid, and triterpenes. Only this species has red maculae and soralia. See description in Kalb (1987), Jungbluth (2010).

Examined material: Rio Verde de Mato Grosso municipality, Sítio Passarim, on bark, 18°56′26.6″S, 54°55′16.6″W, 390m alt., 23.VIII.2013, leg. A.A. Spielmann 11939 (CGMS).

Pyxine cocoës (Sw.) Nyl., Mém. Soc. Imp. Sci. Nat. Cherbourgh 5: 108. 1857. Fig. 6.5d

Pyxine cocoës is characterized by the foliose thallus, upper surface brownish white; laciniae contiguous, irregularly branched, rounded apices; medulla totally white; soralia white, orbicular to irregular and laminal, with farinose to granular soredia; apothecia sessile to constricted at the base, *cocoës*-type; disc plane to concave, black, epruinose, with reddish brown internal stipe; ascospores *Dirinaria*-type, 14–19 × 7–9 µm. The chemical constituents are lichexanthone and triterpenes. *Pyxine subcinerea* differs by its crescent-shape soralia. See descriptions in Kalb (1987), Jungbluth (2010).

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, em poste de cerca, 18°35′26.00″S, 57°32′44.70″W, 88m alt., 22.XI.2010, leg. L.S. Canêz 3502 (CGMS); idem, RPPN Eliezer Batista (Novos Dourados), on rock, 18°05′29.70″S, 57°28′27.40″W, 87m alt., 24.XI.2010, leg. L.S. Canêz 3546 (CGMS); idem, Baía do Taquaral, on rock, 18°02′42.30″S, 57°30′15.20″W, 83m alt., 26.XI.2010, leg. L.S. Canêz 3607 (CGMS); idem, RPPN Rumo ao Oeste, Baía Guaíba, on rock, 17°44′18.10″S, 57°41′27.80″W, 91m alt., 28.XI.2010, leg. A.A. Spielmann 8815 (CGMS); L.S. Canêz 3644 (CGMS); T.H. Stefanello 402 (CGMS); idem, Fazenda Nhumirim, Pomar da sede, 26.X.1988, leg. V.J. Pott 692 (COR); Bolivia, Departamento Santa Cruz, Provícia Germán Busch Puerto Quijarro municipality, Baía do Mandioré, on rock, 18°11′50.70″S, 57°30′39.70″W, 90m alt., 23.XI.2010, leg. A.A. Spielmann 8733 (CGMS).

Pyxine eschweileri (Tuck.) Vain., Acta Soc. Fauna et Flora fenn. 7: 156. 1890.

Pyxine eschweileri is characterized by the foliose thallus, upper surface brownish gray, usually with reticulate maculae; laciniae contiguous, irregularly branched, rounded apices, medulla cream-colored to yellowish above with a white lower layer; marginal to submarginal polysidiagia, with irregular soralia and granular soredia; apothecia sessile to constricted at the base, *obscurascens*-type; disc plane to concave, black, epruinose, white internal stipe; ascospores *Dirinaria*-type, 2 and 3-septate, (14–)16–20(–24) × (4–)6–10 µm. The chemical constituents are atranorin and triterpenes. See description in Imshaug (1957), Kalb (1987), Jungbluth (2010).

Examined material: Corumbá municipality, Morraria do Urucum, on bark, 19°12′08.20″S, 57°36′04.60″W, 733m alt., 3.IX.2010, leg. L.S. Canêz 3285, 3305 (CGMS).

Pyxine petricola Nyl. in Cromb., Journ. Bot. Lond. 14: 263. 1876.

Pyxine petricola is characterized by the foliose thallus, upper surface gray; laciniae contiguous, irregularly to dichotomously branched, subrounded to rounded apices, medulla totally white; apothecia sessile to constricted at the base, *cocoës*-type; disc plane to convex, black, epruinose, reddish brown internal stipe; ascospores

Dirinaria-type, 14–18 × 5–7 µm. The chemical constituents are lichexanthone and terpenes. See description in Kalb (1987), Jungbluth (2010).

Examined material: Corumbá municipality, Base de Estudos do Pantanal (UFMS), estrada de acesso, on bark, 19°34′27.60″S, 57°01′23.00″W, 95m alt., 21.VIII.2011, leg. L.S. Canêz 9435, 9437, 9444 (CGMS); idem, Sub-região Pantanal do Paraguai, Baía do Castelo, on bark, 18°35′17.30″S, 57°32′10.80″W, 86 m alt., 22.XI.2010, leg. T.H. Stefanello 11 (CGMS); idem, 18°33′52.80″S, 57°34′29.30″W, 92 m alt., 22.XI.2010, leg. T.H. Stefanello 77, 90 (CGMS); idem, Baía do Mandioré, on bark, 18°11′50.70″S, 57°30′39.70″W, 90 m alt., 23.XI.2010, leg. T.H.D. Leandro 39 (CGMS); idem, RPPN Eliezer Batista (Novos Dourados), início da trilha, on bark, 18°01′09.20″S, 57°32′03.80″W, 95m alt., 24.XI.2010, leg. L.S. Canêz 3562, 3563, 3570 (CGMS); idem, Fazenda Nhumirim salina do oito, on bark, 10.IX.1988, leg. V.J. Pott 623 (COR); idem, Pomar da sede, on bark, 26.X.1988, leg. V.J. Pott 836, 837, 838 (COR); idem, Tromba dos Macacos, on bark, 24.VIII.1993, leg. M.P. Marcelli 24819, s/n (COR).

Pyxine subcinerea Stirt., Trans. New Zeland Inst. 30: 397. 1897.

Pyxine subcinerea is characterized by the foliose thallus, upper surface gray to brownish gray; laciniae contiguous, irregularly branched, rounded apices, medulla yellow above and with white lower layer; soralia marginal, white and with crescent-shape, with granular soredia; apothecia sessile to constricted at the base, *obscurascens*-type; disc plane, black, epruinose, white internal stipe; ascospores *Dirinaria*-type, (13–)14–19 × 6–8 µm. The chemical constituents are lichexanthone and triterpenes. For comparisons see the *P. cocoës* comment. See description in Kalb (1987), and Jungbluth (2010).

Examined material: Corumbá municipality, Morro do Urucum, on bark, 19°12′08.2″S, 57°36′04.6″W, 730m alt., 3.IX.2010, leg. A.A. Spielmann 8489 (CGMS); leg. L.S. Canêz 3296 (CGMS).

Ramboldia russula (Ach.) Kalb, Lumbsch & Elix, Nova Hedwigia 86(1-2): 37. 2008.

Fig. 6.4c

Ramboldia russula is characterized by the crustose continuous to aerolate thallus, having red apothecia with proper margin, with the same color as the disc, hymenium containing red pigment K+ purple and small crystals that dissolve in KOH, ascospores simple, ellipsoid and hyaline, 10–12.5 × 2.5–3 µm. Fumarprotocetraric acid (TLC) and lichexanthone (thallus UV+ yellow) were found in the Pantanal material. According to Kalb et al. (2008), other substances as protocetraric, confumarprotocetraric, and quaesitic acid can be found in minor concentrations in the thallus of this species. *R. russula* is similar to *R. haematites* (Fée) Kalb, Lumbsch & Elix, differing mainly by its chemistry, the latter having norstictic acid and lichexanthone as major substances, lacking fumarprotocetraric or other related acids (Kalb et al. 2008). This author also mentions that *R. russula* prefers more or less shady habitats, close to humid forests, while *R. haematites* is usually found in savannas and dry forests. See description in Vainio (1890) as *Lecidea russula* Ach.

Examined material: Rio Negro municipality, margin of the road MS-419, between Rio Negro and Rio Verde de Mato Grosso, Pantanal da Nhecolândia, on the edge of Cerrado forest, on a wooden fence pole, 19°17′55.83″S, 55°06′1.04″W, 165m alt., 3.X.2013, leg. A.P. de Souza 47 (CGMS).

Sanguinotrema wightii (Taylor) Lücking, Bot. J. Linn. Soc.: 441. 2015.

Fig. 6.4d

Sanguinotrema wightii is characterized by the crustose thallus with red crystals in the medulla, apothecia immersed in the thallus, visible as black pores, clear hymenium, brown and muriform ascospores, 17.5–22.5 × 10 μm. This species is similar to various *Leucodecton* species, but differs by the conspicuous red crystals in the thallus. See description in Frisch (2006), as *Leptotrema wightii* (Tayl.) Müll. Arg.

Examined material: Corumbá municipality, Sub-região Pantanal do Paraguai, Baía do Castelo, riparian forest in a rock outcrop, on tree trunk, 18°33′52.80″S, 57°34′29.30″W, 92m alt., 22.XI.2010, leg. T.H. Stefanello 84, 85 (CGMS).

Usnea subparvula A. Gerlach & P. Clerc, Lichenologist 49(3): 23. 2017.

Fig. 6.6D

Usnea subparvula is a shrubby-erect fruticose thallus, non-sorediate (often with apothecia) species characterized by the presence of spinulose fibrils, with lateral branches that are often somewhat wider at the ramification point, a thick cortex (8–10%), and the production of protocetraric acid (K−, P+ red) in the medulla.

Usnea parvula Motyka has a similar morphology to *U. subparvula*, with its numerous spinulose fibrils and irregular branches. It differs mainly by the K−, P− reacting medulla, the density of spinulose fibrils (*U. parvula*: 16–24/mm^2, *U. subparvula*: 10–15/mm^2) and distribution. *Usnea subparvula* is a common species in Mato Grosso do Sul; on the other hand *U. parvula* is more frequent in the Southern Brazil, not found so far in Mato Grosso do Sul state. See comments in Gerlach et al. (2017). This genus is reported for the first time from the Pantanal.

Specimens examined: Corumbá, sub-região Pantanal do Paraguai, on margin of Taquaral Bay, 18°02′42·3”S, 57°30’15·2”W, 83m, 2010, leg. A.A. Spielmann 8784 (CGMS).

Acknowledgments This study was financed in part by the Fundação Universidade Federal de Mato Grosso do Sul – UFMS/MEC – Brazil. We would like to thank Ph.D. João dos Santos Vila da Silva for his help with the map available in this chapter, and Dr. Matthias Schultz by the revision of *Peltula* specimens. Natalia M. Koch and Marcos J. Kitaura would like to thank CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) for their Post-doctoral PNPD scholarships and M.J.K. also to thank Fundect (Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) – Nº 04/2019 – PDCTR.

References

Almborn O (1966) Revision of some lichen genera in southern Africa I. Bot Not 119:70–112

Aptroot A (2011) New lichen records from Australia 73. *Agonimia opuntiella*. Australas Lichenol 68:3

Aptroot A (2012) A world key to the species of *Anthracothecium* and *Pyrenula*. Lichenologist 44(1):5–53

Aptroot A, Cáceres M (2014) A key to the corticolous microfoliose, foliose and related crustose lichens from Rondônia, Brazil, with the description of four new species. Lichenologist 46(6):783–799

Aptroot A, Lücking R (2016) A revisionary synopsis of the *Trypetheliaceae* (*Ascomycota*: *Trypetheliales*). Lichenologist 48(6):763–982

Aptroot A, van Herk CM (2006) Further evidence of the effects of global warming on lichens, particularly those with *Trentepohlia* phycobionts. Environm Pol 146:293–298

Aptroot A, Lücking R, Sipman HJM, Umaña L, Chaves JL (2008) Pyrenocarpous lichens with bitunicate asci. A first assessment of the lichen biodiversity inventory in Costa Rica. Bibliotheca Lichenol 97:1–162

Aptroot A, Thor G, Lücking R, Elix JA, Chaves JL (2009) The lichen genus *Herpothallon* reinstated. Bibliotheca Lichenol 99:19–66

Aptroot A, Nelsen MP, Parnmen S (2013) *Marcelaria*, a new genus for the *Laurera purpurina* group in the *Trypetheliaceae* (*Ascomycota*: *Dothideomycetes*). Glalia 5(2):1–14

Aragón G, Otálora MAG, Martínez I (2005) New data on the genus *Leptogium* (lichenized *Ascomycetes*) in the Iberan Peninsula. Nova Hedwigia 80(1-2):199–226

Archer AW (2007) Key and checklist for the lichen family *Graphidaceae* (lichenised *Ascomycota*) in the Solomon Islands. Syst Biodiversity 5(1):9–22

Arvidsson L, Galloway DJ (1979) The lichen genus *Coccocarpia* in New Zealand. Bot Not 132:239–246

Awasthi DD (1975) A monograph of the lichen genus *Dirinaria*. Bibliotheca Lichenol 2:1–108.

Awasthi DD (2007) A compendium of the Macrolichens from India, Nepal and Sri Lanka. Bishen Singh Mahedra Pal Singh, Dehra Dun, 580p

Baptista LRM (1996) Gustav Malme e a flora do Rio Grande do Sul. Ciência Ambiente 13:99–104

Barbosa TD (2019) *Caliciaceae* foliosas em Mato Grosso do Sul. Brazil Dissertação (mestrado):229p

Benatti MN (2012) A review of the genus *Bulbothrix* Hale: the species with medullary norstictic or protocetraric acids. MycoKeys 2:1–28

Benatti MN, Marcelli MP (2010) Espécies de *Parmotrema* (*Parmeliaceae, Ascomycota*) do litoral centro-sul do estado de São Paulo III. Grupos químicos equinocárpico e stíctico. Acta Bot Bras 24(2):304–321

Brako L (1989) Reevaluation of the genus *Phyllopsora* with taxonomic notes and introduction of *Squamacidia*, gen. nov. Mycotaxon 35(1):1–19

Brako L (1991) *Phyllopsora (Bacidiaceae)*. Flora Neotropica 55, New York Botanical Garden (for Organization for Flora Neotropica), Bronx, NY. 66pp

Brodo IM, Sharnoff SD, Sharnoff S (2001) Lichens of North America. Yale University Press, New Haven, pp 289–290

Bueno ML, Dexter KG, Pennington RT, Pontara V, Neves DM, Ratter JA, Oliveira-Filho AT (2018) The environmental triangle of the Cerrado domain: ecological factors driving shifts in tree species composition between forests and savannas. J Ecol 106(5):2109–2120

Bungartz F, Spielmann AA (2019) The genus *Parmotrema* (*Parmeliaceae*, *Lecanoromycetes*) in the Galapagos Islands. Plant Fungal Syst 64(2):173–231

Cáceres MES (2007) Corticolous crustose and microfoliose lichens of northeastern Brazil. Libri Botanici 22. Verlag, München. 168p

Canêz LS (2005) A família *Parmeliaceae* na localidade de Fazenda da Estrela, município de Vacaria, Rio Grande do Sul, Brasil. Dissertação (mestrado). Instituto de Botânica da Secretaria de Estado do Meio Ambiente. São Paulo. 292 p

Cunha IPR (2007) Fungos liquenizados do gênero *Leptogium* (*Ascomycetes*) no litoral sul do Estado de São Paulo. Dissertação de mestrado apresentada no Instituto de Biociências da Universidade Estadual Paulista

Degelius G (1954) The lichen genus *Collema* in Europe: Morphology, Taxonomy, Ecology. Symbolae Bot Upsalienses 13(2):1–499

Degelius G (1974) The lichen genus *Collema* with special reference to the extra-European species. Symbolae Bot Upsalienses 20:1–215

Diederich P, Ertz D, Eichler M, Cezanne R, van den Boom P, Fischer E, Killmann D, Van den Broeck D, Sérusiaux E (2012) New or interesting lichens and lichenicolous fungi from Belgium, Luxembourg and northern France. XIV Bull Soc Nat luxemb 113:95–115

Divakar PK, Crespo A, Kraichak E, Leavitt SD, Singh G, Schmitt I, Lumbsch HT (2017) Using a temporal phylogenetic method to harmonize family and genus-level classification in the largest clade of lichen-forming fungi. Fungal Diversity 84:101–117

Egea JM, Torrente P (1993) *Cresponea*, a new genus of lichenized fungi in the order *Arthoniales* (*Ascomycotina*). Mycotaxon 48:301–331

Eliasaro S (2001) Estudio taxonómico y florístico sobre las Parmeliaceae sensu stricto (Ascomycota Liquenizados) del Segundo Planalto del Estado de Paraná, Brazil. Buenos Aires. Tesis de Doctor (en Ciencias Biológicas). Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales. 267p.

Elix JA (1998) Clarification of the synonymy and chemistry of *Parmotrema zollingeri* and related species. Aus Lichenol 42:22–27

Ertz D (2009) Revision of the corticolous *Opegrapha* species from the Paleotropics. Bibliotheca Lichenol 102:1–176

Ertz D, Tehler A (2011) The phylogeny of *Arthoniales* (*Pezizomycotina*) inferred from nucLSU and RPB2 sequences. Fungal Diversity 49(1):47–71

Estrabou C, Adler MT (1998) Two new species of *Parmotrema* (*Parmeliaceae* sensu stricto, Lichenized *Ascomycotina*) from Argentina. Mycotaxon 66:131–136

Fleig M, Riquelme I (1991) Liquens de Piraputanga, Mato Grosso do Sul, Brazil. Acta Bot Bras 5(1):3–12

Frisch A (2006) The lichen family *Thelotremataceae* in Africa: A revision with special consideration of the taxa from Cameroon and Tanzania. Bibliotheca Lichenol 92:3–370

Frisch A, Thor G (2010) *Crypthonia*, a new genus of byssoid *Arthoniaceae* (lichenised Ascomycota). Mycol Progress 9(2):281–303

Frisch A, Kalb K, Grube M (2006) Contributions towards a new systematics of the lichen family *Thelotremataceae* III. Molecular phylogeny of the *Thelotremataceae*. Bibliotheca Lichenol 92:517–539

Galloway DJ, Johnson PN, Lumbsch HT (2001) Additional lichen records from New Zealand 35. Seven corticolous species of *Lecanora*, with notes on *L. caesiorubella* Ach. and *L. carpinea* (L.) Vain. Aus Lichenol 49:28–35

Gerlach A (2017) Taxonomy of the corticolous, shrubby, esorediate, neotropical species of *Usnea* Adans. (*Parmeliaceae*) with an emphasis on southern Brazil. Lichenologist 49(3):199–238

Giordani P, Brunialti G, Alleteo D (2002) Effects of atmospheric pollution on lichen biodiversity (LB) in a Mediterranean region (Liguria, northwest Italy). Environ Poll 118:53–64

Guderley R (1999) Die *Lecanora subfusca*-gruppe in Süd- und Mittleamerika. J Hattori Bot Lab 87:131–257

Hale ME Jr (1960) A revision of the South American species of *Parmelia* determined by Lynge. Contributions U S N Herbarium 36(1):1–41

Hale ME Jr (1965) A monograph of *Parmelia* subgenus *Amphigymnia*. Smithsonian Contributions Botany 36(5):358p

Hale ME Jr (1971) Morden-Smithsonian Expedition to Dominica: The Lichens (*Parmeliaceae*). Smithsonian Contributions Botany 4:1–25

Hale ME Jr (1976) A monograph of the lichen genus *Parmelina* Hale (*Parmeliaceae*). Smithsonian Contributions Botany 33:1–60

Hale ME Jr (1990) New species of *Parmotrema* (*Ascomycotina*: *Parmeliaceae*) from Tropical America. In Contributions to Lichenology. In honour of A. Henssen. Bibliotheca Lichenol 38:109–119

Hale ME Jr, Kurokawa S (1964) Studies on *Parmelia* subgenus *Parmelia*. Smithsonian Contributions Botany 36(4):121–191

Imshaug HA (1957) The lichen genus *Pyxine* in North and Middle America. Trans Am Microscopical Soc 76(3):246–269

Jungbluth P (2006) A família *Parmeliaceae* (fungos liquenizados) em fragmentos de cerrados do estado de São Paulo. Dissertação (mestrado). Instituto de Botânica. São Paulo. 323p

Jungbluth P (2010) Estudos taxonômicos em *Physcia* (Schreb.) Michx. e Pyxine Fr. PhD thesis. Instituto de Botânica. São Paulo. 228p

Jungbluth P, Marcelli MP, Elix JA (2008) Five new species of *Bulbothrix* (*Parmeliaceae*) from cerrado vegetation in São Paulo State, Brazil. Mycotaxon 104:51–63

Junk WJ, Nunes da Cunha C (2016) The Pantanal: A Brief Review of its Ecology, Biodiversity, and Protection Status. In: Finlayson CM et al (eds) The Wetland Book II: Distribution, Description, and Conservation. Springer, Dordrecht, pp 1–15

Junk WJ, Piedade MTF, Lourival R, Wittmann F, Kandus P, Lacerda LD, Bozelli RL, Esteves FA, Nunes da Cunha C, Maltchik L, Schöngart J, Schaeffer-Novelli Y, Agostinho AA (2014) Brazilian wetlands: their definition, delineation, and classification for research, sustainable management, and protection. Aquatic Conserv: Mar Freshw Ecosyst 24:5–22

Kalb K (1982a) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel II (N° 41-80). Neumarkt/Opf., 22 February 1982. 12 pp.

Kalb K (1982b) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel III (N° 81-120). Neumarkt/Opf., 2 April 1982. 12 pp.

Kalb K (1982c) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel IV (N° 121-160). Neumarkt/Opf., 16 August 1982. 12 pp.

Kalb K (1982d) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel V (N° 161-200). Newmarkt/Opf. 19 November 1982. – . 12 pp.

Kalb K (1983a) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel VI (N° 201-250). Neumarkt/OPf. 7 April 1983. 16pp

Kalb K (1983b) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel VII (N° 251-300). Newmarkt/OPf. 8 November 1983. 16 pp

Kalb K (1984) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikle VIII (N° 301-350). Neumarkt/OPf. 16 pp

Kalb K (1986) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel IX (N° 351-400). Neumarkt/Ofp. 16 pp

Kalb K (1987) Die Gattung *Pyxine*. Bibliotheca Lichenol 24:1–89

Kalb K (1988) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel X (N° 401-450). Neumarkt/OPf. 16 pp

Kalb K (1990) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel XI (N° 451-475). Neumarkt/OPf. 12 pp

Kalb K (1991) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel XII (N° 476-525). Neumarkt/OPf. 16 pp

Kalb K (2001a) Lichenes Neotropici ausgegeben von Klaus Kalb. Fascikel XIII (N° 526-575). Neumarkt/OPf. 17 pp

Kalb K (2001b) New or otherwise interesting lichens. I. Bibliotheca Lichenol 78: 14l-167

Kalb K, Staiger B, Elix JA (2004) A monograph of the lichen genus *Diorygma* – a first attempt. Symbolae Botanicae Upsalienses 34(1):133–181

Kalb K, Staiger B, Elix JA, Lange U, Lumbsch HT (2008) A new circumscription of the genus *Ramboldia* (*Lecanoraceae*, *Ascomycota*) based on morphological and molecular evidence. Nova Hedwigia 86(1-2):23–42

Kalb K, Archer AW, Sutjaritturakan J, Boonpragob K (2009) New or otherwise interesting lichens V. Bibliotheca Lichenol 99:225–246

Kalb K, Rivas-Plata E, Lücking R, Lumbsch HT (2011) The phylogenetic position of *Malmidea*, a new genus for the *Lecidea piperis*- and *Lecanora granifera*-groups (*Lecanorales*, *Malmideaceae*), inferred from nuclear and mitochondrial ribosomal DNA sequences, with special reference to Thai species. Bibliotheca Lichenol 106:143–168

Kalb J, Polyiam W, Plata ER, Bawingan PA, Kalb K, Lücking R (2016) 'Missing links' live? Novel taxa represent morphological transitions between distinctive phenotypes among extant *Graphidaceae* (lichenized *Ascomycota*: *Ostropales*). Phytotaxa 268(2):110–122

Kalb J, Schumm F, Elix JA (2020) Pigments and new lichen substances in the lichen genus *Dirinaria*. Australas Lichenol 86:6–9

Kistenich S, Timdal E, Bendiksby M, Ekman S (2018) Molecular systematics and character evolution in the lichen family Ramalinaceae (Ascomycota: Lecanorales). Taxon 67(5):871–904

Kistenich S, Bendiksby M, Ekman S, Cáceres MES, Hernández JE, Timdal E (2019) Towards an integrative taxonomy of *Phyllopsora* (*Ramalinaceae*). Lichenologist 51(4):323–392

Kitaura MJ (2012) Estudos taxonômicos de *Leptogium* (Ach.) S. F. Gray (*Collemataceae*, fungos liquenizados). Tese de Doutorado, Universidade Estadual Paulista, Botucatu.

Kitaura MJ, Bernardo CM, Koch NM, Rodrigues AS, Torres JM, Barbosa TD, Canêz LS, Spielmann AA, Honda NK, Fleig M, Lorenz AP (2019) *Leptogium* (*Collemataceae*, *Peltigerales*) from Mato Grosso do Sul state, Brazil: nine new records, three new taxa and a key for the species. Phytotaxa 399(2):127–146

Koch NM, Martins SMAM, Lucheta F, Müller SC (2013) Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. Ecol Indicators 34:22–30

Kondratyuk SY, Lőkös L, Farkas E, Jang SH, Liu D, Halda J, Persson PE, Hansson M, Kärnefelt I, Thell A, Hur JS (2019) Three new genera of the *Ramalinaceae* (lichen-forming *Ascomycota*) and the phenomenon of presence of 'extraneous mycobiont DNA' in lichen associations. Acta Botanica Hungarica 61(3–4):275–323

Kurokawa S, Arakawa S (1997) Revision of the Japanese Species of *Myelochroa* (*Parmeliaceae*). Bull Botanic Gardens Toyama 2:23–43

Laundon JR (1981) The species of *Chrysothrix*. Lichenologist 13:101–121

Lücking R, Kalb K (2018) Formal instatement of *Allographa* (*Graphidaceae*): how to deal with a hyperdiverse genus complex with cryptic differentiation and paucity of molecular data. Herzogia 31(1, Teil 2):535–561

Lücking R, Chaves JL, Sipman HJM, Umaña L, Aptroot A (2008) A First Assessment of the Ticolichen Biodiversity Inventory in Costa Rica: The genus *Graphis*, with notes on the genus *Hemithecium* (*Ascomycota*: *Ostropales*: *Graphidaceae*). Fieldiana Botany 46(1):1–126

Lücking R, Mangold A, Rivas-Plata E, Parnmen S, Kraichak E, Lumbsch HT (2015) Morphology-based phylogenetic binning to assess a taxonomic challenge: a case study in *Graphidaceae* (*Ascomycota*) requires a new generic name for the widespread Leptotrema wightii. Bot J Linn Soc 436:436–443

Lücking R, Moncada B, Hawksworth DL (2019) Gone with the wind: sequencing its type species supports inclusion of *Cryptolechia* in *Gyalecta* (*Ostropales*: *Gyalectaceae*). Lichenologist 51(4):287–299

Lynge B (1914) Die Flechten der ersten Regnellschen Expedition. Die gattungen *Pseudoparmelia* gen. nov. und *Parmelia* Ach. Ark Bot 13(13):1–172

Lynge B (1924) On South American *Anaptychiae* an *Physciae*. Vid Selsk Skrifter I Mat Naturv kl. 16:1-47. pl.I-V

Malme GOA (1897) Die flechten der Ersten Regnell'schen Expedition. I. Die gattung *Pyxine* (Fr.) Nyl. Bihang Till K. Svenska Vet.Akad. Handlingar 23(13):1–52

Malme GOA (1902) Die flechten der Ersten Regnell'schen Expedition. II. Die gattung Rinodina (Ach.) Sitz. Bihang Till K. Svenska Vet.-Akad. Handlingar 28(1):1–53

Malme GOA (1923) Die Flechten der Ersten Regnellschen Expedition. Die Gattungen *Bombyliospora*, *Megalospora, Catillaria* und *Rhizocarpon*. Ark Bot 18(12):1–17

Malme GOA (1924a) Die Collematazeen des Regnellschen Herbars. Ark Bot 19:1–29

Malme GOA (1924b) Die Flechten der Ersten Regnellschen Expedition. 2. *Astrotheliaceae*, *Paratheliaceae* und *Trypetheliaceae*. Ark Bot 19(1):1–34

Malme GOA (1925) Die Pannariazeen des Regnellschen Herbars. Ark Bot 20A(3):1–23

Malme GOA (1926) Die im Regnellschen Herbar aufbewahrten Arten der Flechtengattung Lecanactis (Eschw.) Wainio. Ark Bot 20B(2):1–6

Malme GOA (1927) Buelliae Itineris Regnelliani Primi. Ark Bot 21A(14):1–42

Malme GOA (1928) Lichenes Pyrenocarpi aliquot in Herbario Regnelliano asservati. Ark Bot 22A(6):1–11

Malme GOA (1929a) Pyrenulae et Anthracothecia Herbarii Regnelliani. Ark Bot 22A(11):1–40

Malme GOA (1929b) Porinae et Phylloporinae in Itinere Regnelliano Primo Collectae. Ark Bot 23A(1):1–37

Malme GOA (1934) Die Gyalectazeen der Ersten Regnellschen Expedition. Ark Bot 26A(13):1–10

Malme GOA (1935) Bacidiae Itineris Regnelliani Primi. Ark Bot 27A(5):1–40

Malme GOA (1936a) Lecideae expeditionis regnellianae primae. Ark Bot 28A(7):1–53

Malme GOA (1936b) Pertusariae expeditionis regnellianae primae. Ark Bot 28A(9):1–27

Malme GOA (1937) Lichenes nonnulli in Expeditione Regnelliana Prima collecti. Ark Bot 29A(6):1–35

Marbach B (2000) Corticole und lignicole Arten der Flechtengattung *Buellia* sensu lato in den Subtropen und Trope. Bibliotheca Lichenol 74:1–384

Marcelli MP (1993) Pequenas *Parmelia* s. l. (Liquens: *Ascomycotina*) ciliadas dos cerrados brasileiros. Acta Bot Bras 7(2):25–70

Marcelli MP (1998) History and current knowledge of Brazilian Lichenology. In: Marcelli, M.P. & M.R.D. Seaward (Eds). Lichenology in Latin America: history, current knowledge and applications, p. 25-45. CETESB. São Paulo

Marcelli MP (2006) Fungos liquenizados. In*:* Xavier Filho L, Legaz ME, Cordoba CV, Pereira EC Biologia de Líquens. Âmbito Cultural Edições, Ltda., Rio de Janeiro. 619 pages, pp. 25–74

Matos P, Vieira J, Rocha B, Branquinho C, Pinho P (2019) Modeling the provision of air-quality regulation ecosystem service provided by urban green spaces using lichens as ecological indicators. Sci Total Environ 665:521–530

Mayrhofer H (1987) Monographie der Flechtengattung *Thelenella*. Bibliotheca Lichenol 26: 1–106

Menezes AA, Xavier-Leite AB, Aptroot A, Cáceres MES (2013) New lichen species from the Caatinga in Chapada do Araripe, northeastern Brazil. Bryologist 116(3):302–305

Moberg R (1987) The genera *Hyperphyscia* and *Physconia* in East Africa. Nordic J Botany 7(6):719–728

Moberg R (1990) The lichen genus *Physcia* in Central and South America. Nordic J Botany 10:319–342

Morberg R (1983) The genus *Phaeophyscia* in East Africa. Nordic J Botany 3:509–516

Motyka J (1936) Lichenum generis *Usnea* studium monographicum. Pars systematica, volumen primum. Leopoli. p. 1–-304. Editio et proprietas auctoris

Motyka J (1938) Lichenum generis *Usnea* studium monographicum. Pars systematica, volumen secundum. Leopoli. p. 305–651. Editio et proprietas auctoris

Osorio HS (1973) Contribution to the lichen flora of Brazil. I. New or additional records. Rev Cienc Univ Lisboa, 2a ser, C (Cienc Nat) 17:447–450

Osorio HS (1992) Contribution to the Lichen Flora of Brazil. XXIX. Lichens from Ponta Porá, Mato Grosso do Sul. Comunicaciones Botánicas del Museo de Historia Natural de Montevideo 5 (98): 1–6

Otálora MA, Wedin M (2013) *Collema fasciculare* belongs in Arctomiaceae. The Lichenologist 45(3):295–304

Otálora MAG, Jørgensen Per M, Wedin M (2014) A revised generic classification of the jelly lichens, Collemataceae. Fungal Diversity 64:275–293

Purvis W (2000) Lichens. Natural History Museum, London/Smithsonian Institution, London, Washington D.C. 112 pp

Redinger K (1933a) Die Graphidineen der ersten Regnell'schen Expedition nach Brasilien 1892-95. I. Glyphis, Medusulina und Sarcographa. Ark Bot 25A(13):1–20

Redinger K (1933b) Die Graphidineen der ersten Regnell'schen Expedition nach Brasilien 1892-94 II. *Graphina* und *Phaeographina*. Ark Bot 26A, Nr 1:1–105

Redinger K (1935) Die Graphidineen der ersten Regnell'schen Expedition nach Brasilien 1892-94. III. *Graphis* und *Phaeographis*, nebst einem Nachtrage zu *Graphina*. Ark Bot 27A, Nr 3:1–103

Redinger K (1936) *Thelotremataceae* brasilienses imprimis ex herbario Regnelliano cognitae praetereaque in herbariis Krempelhuberi, Mülleri Arg., Nylanderi, Wainionis et Zahlbruckneri asservatae. Ark Bot 28A, 8:1–122

Redinger K (1940) Die Graphidineen der ersten Regnellschen Expedition Nach Brasilien 1892-94 – IV. *Opegrapha*. Ark Bot 29A(19):1–54

Ribeiro CH (1998) A família *Parmeliaceae* (*Ascomycota* liquenizados) em regiões montanhosas dos Estados de Minas Gerais, Rio de Janeiro e São Paulo. Dissertação (mestrado em Botânica). Instituto de Biociências, Universidade de São Paulo, 194p.

Rivas Plata E, Lücking R, Aptroot A, Sipman HJM, Chaves JL, Umaña L, Lizano D (2006) A first assessment of the Ticolichen biodiversity inventory in Costa Rica: the genus *Coenogonium* (*Ostropales*: *Coenogoniaceae*), with a world-wide key and checklist and a phenotypebased cladistic analysis. Fungal Diversity 23:255–321

Santos LA, Aptroot A, Lücking R, Cáceres ME (2019) High diversification in the *Neoprotoparmelia multifera* complex (*Ascomycota*, *Parmeliaceae*) in northeast Brazil revealed by DNA barcoding and phenotypical characters. Bryologist 122(4):539–552

Schultz M, Aptroot A (2008) Notes on poorly known, small cyanobacterial lichens from predominantly wet tropical to subtropical regions. Notizen über kaum bekannte, kleine cyanobakterielle Flechten überwiegend aus den feuchten Tropen und Subtropen. Sauteria 15:433–458

Sierk HA (1964) The genus *Leptogium* in North America North of Mexico. Bryologist 67:245–317

Sipman HJM (2005) Mason Hale's key to *Parmotrema*, revised edition: key to wide-lobed parmelioid species occurring in Tropical America (genera *Canomaculina*, *Parmotrema*, *Rimelia*, *Rimeliella*). Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin. http://www.bgbm.org/sipman/keys/Neoparmo.htm

Smith CW, Aptroot A, Coppins BJ, Flechter A, Gilbert OL, James PW, Wolseley PA (2009) The lichens of Great Britain and Ireland. British Lichen Society, London, 1046p

Spielmann AA (2006) Checklist of lichens and lichenicolous fungi of Rio Grande do Sul (Brazil). Caderno de Pesquisa Série Biologia 18(2):7–125

Spielmann AA, Canêz LS (2012) Breve histórico sobre a Taxonomia de liquens no Estado de Mato Grosso do Sul, Brazil. Glalia 4(1):53–60

Spielmann AA, Marcelli MP (2008) *Parmeliaceae* (*Ascomycota* liquenizados) nos barrancos e peraus da encosta da Serra Geral, Vale do Rio Pardo, Rio Grande do Sul, Brasil. II. Gêneros *Canoparmelia*, *Hypotrachyna*, *Myelochroa*, *Parmelinopsis* e *Relicina*. Iheringia, Série Botânica 63(2):193–212

Spielmann AA, Marcelli MP (2009) *Parmotrema* s.l. (*Parmeliaceae*, lichenized *Ascomycota*) from Serra Geral slopes in central Rio Grande do Sul State, Brazil. Hoehnea 36(4):551–595

Staiger B (2002) Die Flechtenfamilie *Graphidaceae*: Studien in Richtung einer natürlichen Gliederung. Bibliotheca Lichenologica 85:1–526

Staiger B, Kalb K (1995) Haematomma-studien. I. Die Flechtengattung Haematomma. Bibliotheca Lichenologica, 59, J. Cramer, Berlin, Stuttgart. pp 1–198

Swinscow TDV, Krog H (1978) The genus *Dirinaria* in East Africa. Norw J Bot 25:157–168

Swinscow TDV, Krog H (1981) The genus *Phyllopsora*, with a report on East African species. Lichenologist 13(3):203–247

Tibell L (1996) *Caliciales*. Flora Neotropica, 69, New York Botanical Garden, New York. 78 pp

Timdal E (2008) Studies on *Phyllopsora* (*Ramalinaceae*) in Peru. The Lichenologist 40(4):337–362

Torrente P, Egea JM (1992) New species of *Opegrapha* from South-Western Europe and Northern Africa. Mycotaxon 45:83–92

Vainio EA (1890) Étude sur la classification naturelle et la morphologie des Lichens du Brésil. Pars prima. Acta Societatis pro Fauna et Flora Fennica 7(1): i-xxix, 1-247

Westberg M, Arup U (2010) *Candelaria concolor* a rare lichen in the Nordic countries. Graphis Scripta 22:38–42

Zahlbruckner A (1931) Catalogus Lichenum Universalis. 8:1-612

Chapter 7
Hydrology and Vegetation Base for Classification of Macrohabitats of the Brazilian Pantanal for Policy-Making and Management

Catia Nunes da Cunha, Ivan Bergier, Walfrido Moraes Tomas, Geraldo Alves Damasceno-Junior, Sandra Aparecida Santos, Vivian Almeida Assunção, Ângela Lúcia Bagnatori Sartori, Arnildo Pott, Erica Cezarine de Arruda, Aurea da Silva Garcia, Rafaela Danilelli Nicola, and Wolfgang Johannes Junk

7.1 Introduction

Studies aimed at a macrohabitat classification of the Pantanal started some 20 years ago, within the German-Brazilian collaboration *Studies of Human Impacts on Forests and Floodplains in the Tropics (SHIFT)*. In 2011, Nunes da Cunha and Junk presented a new classification system for the macrohabitats of the Pantanal of Mato Grosso, which was updated in 2014 (Nunes da Cunha and Junk 2014). This system stimulated comparative scientific studies in the Pantanal and other large Brazilian

---

C. Nunes da Cunha (✉) · E. C. de Arruda · W. J. Junk
Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas INCT/INAU-UFMT,
Cuiabá, MT, Brazil

I. Bergier
Embrapa Pantanal & Embrapa Informática Agropecuária, Campinas, SP, Brazil

W. M. Tomas
Wildlife Laboratory, Embrapa Pantanal, Corumbá, MS, Brazil

G. A. Damasceno-Junior · A. Pott
Laboratório de Ecologia Vegetal, Instituto de Biociências, Federal University of Mato Grosso
do Sul, Campo Grande, MS, Brazil

S. A. Santos
Embrapa Pantanal, Corumbá, MS, Brazil

V. A. Assunção · Â. L. B. Sartori
Laboratório de Botânica, Instituto de Biociências, Universidade Federal de Mato Grosso do
Sul, Campo Grande, MS, Brazil

A. da Silva Garcia · R. D. Nicola
Wetlands International Brazil & Mupan, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_7

floodplains. It also provided the scientific basis for political discussions regarding public policies in the context of the Federal Law of the Pantanal (PLS 750/2011).

The Pantanal's macrohabitat classification enables a synthesis of knowledge about the structural components of its complex landscapes and those of other large Brazilian floodplains, such as the Amazonian *várzeas* and *igapós* (Junk et al. 2014b, 2015), as well as the floodplains of the Araguaia, Guaporé, and Paraná Rivers. The macrohabitat classification can be considered as an operational basis for scientific studies and activities related to the sustainable management and protection of large Brazilian wetlands (Junk et al. 2018). It is part of the Brazilian wetland classification system published in 2014 (Junk et al. 2014a, b) and recommended in 2018 by the National Wetland Council (CNZU) of the Ministry of the Environment.

Further studies on the ecological conditions in the southern Pantanal revealed the need for expansions of the classification system to include additional macrohabitats specific to the region. Here we present a complete classification system of the macrohabitats of the entire Brazilian Pantanal and discuss its implications for scientific studies and public policies related to sustainable management and protection.

7.2 The Position of the Pantanal Macrohabitat Classification Within the Brazilian Wetland Classification System: A Summary

A consortium of Brazilian and foreign scientists recently elaborated the following definition of Brazilian wetlands (Junk et al. 2014a, b). *Wetlands are ecosystems at the interface between aquatic and terrestrial environments; they may be continental or coastal, natural or artificial, permanently or periodically inundated by shallow water or consist of waterlogged soils. Their waters may be fresh, or highly or mildly saline. Wetlands are home to specific plant and animal communities adapted to their hydrological dynamics.* According to this definition, the Pantanal is a periodically inundated wetland.

The same authors defined the extent of wetlands as follows: *The extent of a wetland can be determined by the border of the permanently flooded or waterlogged area or, in the case of fluctuating water levels, by the limit of the area influenced during the mean maximum flood. The outer borders of wetlands are indicated by the absence of hydromorphic soils and or hydrophytes and or specific woody species that are able to grow in periodically or permanently flooded or waterlogged soils. The definition of a wetland area should include, if present, internal permanently dry areas as these habitats are of fundamental importance to the maintenance of the functional integrity and biodiversity of the respective wetland.*

This definition contains two innovative aspects:

1. The mean maximum water level of the rivers defines the extension of the inundation and therefore, the outer border of the wetlands. This definition is in agreement with the old Brazilian Forest Code (Brazilian law n° 4.771/1965), but it

contradicts the definition established in the current law regarding the protection of native vegetation (Brazilian law n° 12.651/2012). The latter considers the "regular level," that is, the level at which the river runs in its bed, that means at low water level, as the starting point for the definition of wetland borders along streams and rivers. However, the designation of this level as the wetland border does not take into account the dramatic economic and social impacts that extreme floods can create and which can in part be avoided by employing a definition based on mean maximum flood levels.

2. The inclusion of permanently terrestrial areas inside the floodplains recognizes their importance for the maintenance of biodiversity. In the Pantanal, many animals use these areas, represented by paleo-dykes (*capões*, *cordilheiras*), paleo-fans, and inselbergs, as periodic refuges during floods. Except inselbergs, the permanently terrestrial areas are part of the paleo-floodplain of the Pantanal that formed during the wetter periods of the Quaternary (Assine et al. 2015; McGlue et al. 2017; Guerreiro et al. 2018).

Periodic inundations and droughts, described as "flood pulses" (Junk et al. 1989), characterize the major part of Brazilian inland wetlands. Flood pulses are created by the annual rainy and dry seasons and are the principal driving force that determines the ecological conditions of wetlands. There are different types of flood pulses, with the Pantanal belonging to the group of wetlands subjected to a monomodal, predictable pulse of low amplitude (Table 7.1, Fig. 7.1). The impact of flood pulses on structures and processes of wetlands and their biodiversity are described by the Flood Pulse Concept (Junk et al. 1989), which treats the aquatic and terrestrial phases of the Aquatic-Terrestrial Transition Zone (ATTZ) as different stages of the same ecosystem. Their mutual influences form the basis for their specific

Table 7.1 Characterization of Brazilian wetlands according to their hydrological status

Wetlands without flood pulses			Wetland types
			Peatlands (*turfeiras*), headwater wetlands with some shrubs and palm trees (*veredas*), wet grasslands (*campos úmidos*), palm swamps (*buritizais*, *carnaubais*)
Flood pulsing wetlands			**Wetland types**
Predictability	**Frequency**	**Amplitude**	
Predictable	Monomodal	High	Wetlands along large rivers
Predictable	Monomodal	Low	Large interfluvial wetlands, wetlands with a low flood amplitude along rivers (e.g., those of the Pantanal), wetlands in coastal dunes (e.g., Lençóis Maranhenses)
Predictable	Polymodal	Variable	Tidal coastal wetlands
Unpredictable	Polymodal	Variable	Wetlands along small rivers, in small depressions, and in coastal dunes
Unpredictable	Multiannual	Low	Wetlands in the Brazilian semiarid Northeast
Variable	Variable	Variable	Wetlands in and around water bodies with fluctuating water levels because of anthropogenic influences

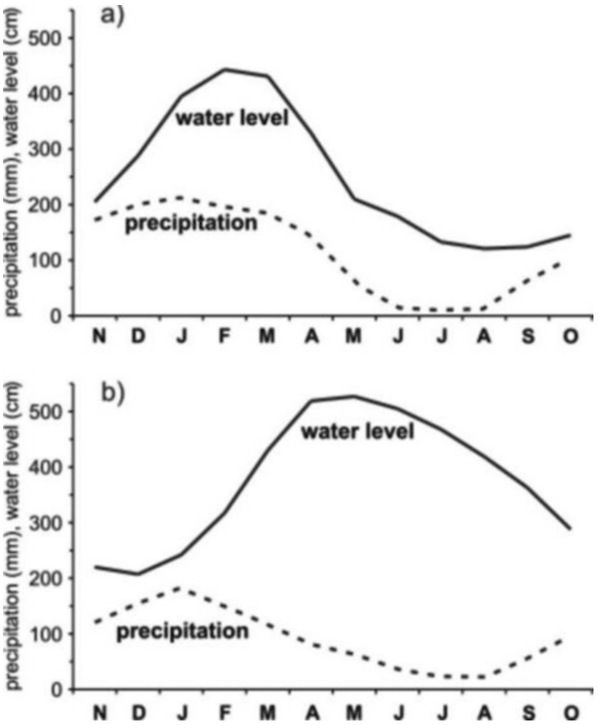


Fig. 7.1 (**a**) Mean monthly precipitation near Cuiabá (1933–1993) and the mean water level of the Cuiabá River in Cuiabá (1971–1988), northern Pantanal. (According to Zeilhofer 1996). (**b**) Mean monthly precipitation near Corumbá (1912–1971) and the mean water level of the Paraguay River in Ladário (1979–1987), southern Pantanal. (According to Hamilton et al. 1996)

characteristics. Changes in the rhythm, amplitude, and duration of flood pulses have serious consequences for wetlands as they result in changes in their ecological characteristics (Junk and Wantzen 2004).

Large floodplains are complex ecosystems composed of a large number of highly diverse landscape units, referred to in the classification system of Nunes da Cunha and Junk (2014) as functional units. An ecological characterization of these units is essential for the sustainable use of the floodplains and the maintenance of their biodiversity. *A functional unit is a large landscape unit in a floodplain, that is subjected to specific hydrological conditions during the annual cycle* (Junk et al. 2018). According to their hydrological status, five functional units can be distinguished. A sixth unit includes all areas strongly modified by humans, independent of the hydrological status of these areas (Fig. 7.2): (1) permanent aquatic areas, (2) predominantly aquatic areas, (3) predominantly terrestrial areas, (4) swamps, permanently water-saturated areas or areas covered by shallow water, (5) permanently terrestrial areas, and (6) anthropogenic areas.

Functional units can be subdivided into smaller units of subclasses and macrohabitats. A subclass is *a subunit of a functional unit with specific hydrological*

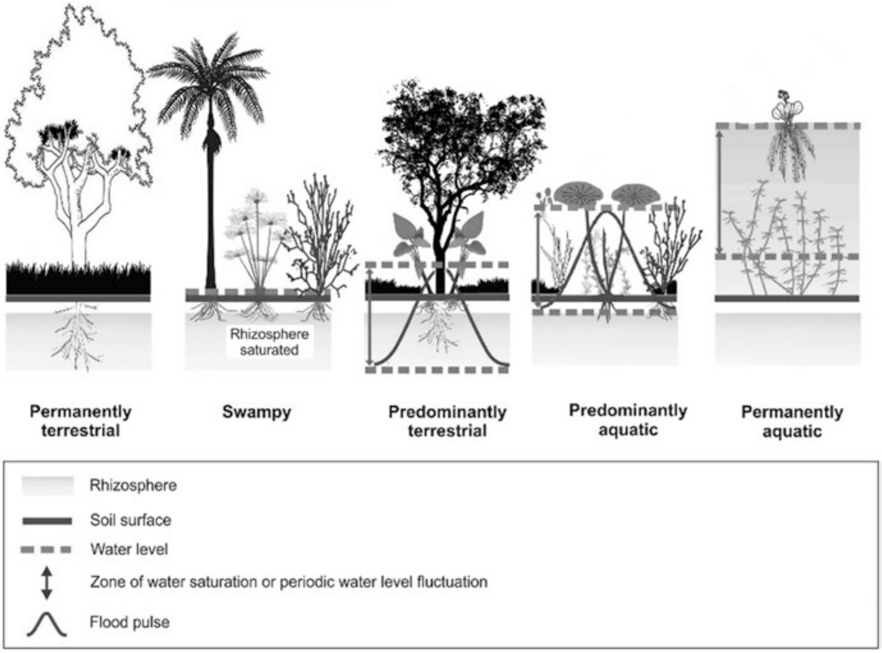


Fig. 7.2 The five functional units in large floodplains defined according to their hydrological status. Swampy, predominantly terrestrial and predominantly aquatic areas make up the ATTZ. (Adapted from Nunes da Cunha and Junk 2017)

conditions and a characteristic cover of higher vegetation. The smallest unit of the classification system is the macrohabitat, defined as *a subunit of a subclass, characterized by indicator plant species or groups of species.*

In the Brazilian wetland classification system, the Pantanal occupies the position of a class.

System: Inland wetlands

- **Subsystem:** Wetlands with fluctuating water level
  - **Order:** Wetlands subjected to predictable monomodal flood pulses of long duration
    - **Suborder:** Wetlands with flood pulses of low amplitude
      - **Class:** Brazilian Pantanal
        - **Functional units:** 6
          - **Subclasses:** 16
            - **Macrohabitats:** 74

Table 7.2 Summary of the actualized macrohabitat classification of the entire Brazilian Pantanal, basing on hydrological and botanical parameters

Functional units	Number of subclasses	Number of macrohabitats
1. Permanently aquatic areas	2	10
2. Predominantly aquatic areas (ATTZ, with a predominant aquatic phase)	2	8
3. Predominantly terrestrial areas (ATTZ, with a predominant terrestrial phase)	6	30
4. Swampy areas (permanently waterlogged or shallowly flooded)	2	7
5. Permanently terrestrial areas	2	10
6. Anthropogenic areas	2	9

Nunes da Cunha and Junk (2014) initially identified 56 macrohabitats in the Pantanal. After a workshop in April 2017, in Campo Grande, we added new macrohabitats exclusively occurring in the Pantanal of Mato Grosso do Sul, increasing the total number of macrohabitats to 74. In the following, we describe the macrohabitats in the entire Pantanal, as this information contributes to the scientific basis necessary for the formulation of a Federal Law of the Pantanal. The typology of the Pantanal is presented in Table 7.2.

7.3 General Description of the Pantanal's Subclasses and Macrohabitats

7.3.1 Functional Unit 1: Permanently Aquatic Areas

7.3.1.1 Subclass 1.1: River Channels

The permanently aquatic macrohabitats of the Pantanal are represented by river channels and perennial lakes. Rivers entering the Pantanal differ in their size and water quality, with the latter determined by the physical and chemical differences in the pedological characteristics of their catchment areas and the human impact therein (Figueiredo et al. 2012). Detailed studies are still needed for a better limnological characterization of these macrohabitats.

The central parts of river channels (Macrohabitat 1.1.1) are relatively homogeneous, and their main function is the transport of water as well as dissolved and solid materials. River channels are of biological importance because they provide refuge for aquatic organisms during the dry season and participate in the passive distribution and active migration of these species during the high-water period. As an example: The up-river spawning migrations of many fish species (*piracema*) along the Paraguay River and its tributaries have been well described (Ferraz de Lima 1987).

River shores (Macrohabitat 1.1.2) are biologically more active and more productive than the central parts of river channels because of their complex hydrogeomorphological structures, soil types, and the seasonal variations in both the duration of inundation and the vegetation structure. These factors contribute to the formation of complex food webs as well as a high diversity and abundance of organisms.

The rocky outcrops in some areas of the Paraguay River channel (Macrohabitat 1.1.3) contribute to the retardation of water discharge and are of fundamental importance for the maintenance of the hydrological regime of the Pantanal. Projects aimed at the channelization of the Paraguay River (hydrovia) that include the partial or total elimination of these obstacles to allow the passage of large ships would lead to dramatic changes in the hydrological regime of the Pantanal, reducing the total floodplain area and water storage capacity because of the accelerated water discharge (Ponce 1995).

7.3.1.2 Subclass 1.2: Lakes (*Lagoas, Lagos*, and *Baías*)

Other permanently aquatic habitats in the Pantanal are its numerous large and small lakes (baías, lagos, and lagoas, respectively), which differ in their origins and in their connectivity with the river system.

The geographer Wilhelmy (1958) distinguished: (a) lakes resulting from the inundation of the inner parts of meanders (*Umlaufseen*, Macrohabitat 1.2.4) and (b) lakes resulting from damming by natural levees (*Dammuferseen*, Macrohabitat 1.2.5), which are frequent in the sub-regions of the Paiaguás and Nhecolândia. Ab'Saber (1988) added to the classification of Wilhelmy large lakes situated at the border of elevations (*serranias*) surrounding the Pantanal (Macrohabitat 1.2.1). Examples include the Lagoas Mandioré, Gaíva, and Jacadigo at the Paraguay River, Baías Chacororé and Sinhá Mariana in the floodplain of the Cuiabá River and the smaller Baías de Acurizal and de Porto Fora. Furthermore, he added oxbow lakes (Macrohabitat 1.2.2). The intermediate-size lakes located in depressions in the subregion of Paiaguás have also been classified (Macrohabitat 1.2.3).

Güntzel et al. (2010) divide the Pantanal's lakes according to the frequency and duration of their connection with the river:

1. Lakes with low connectivity are largely isolated aquatic environments, but there is limited subterranean water exchange with rivers. Direct connections form only during exceptionally high floods.
2. Lakes of intermediate connectivity are those connected to a river by a narrow channel, whereby during the rainy season water runs from the river to the lake, which causes the latter to become more eutrophic.
3. In lakes with frequent and long-lasting connectivity, the water level varies according to that of the river.

Some lakes (such as the *lagoas* in Mato Grosso do Sul) have water levels and areas that fluctuate according to the amount of rainfall. Their borders are colonized by amphibious emergent herbaceous plants, such as *Diodia* spp., *Paspalidium* *geminatum* (Forssk.) Stapf, and *Reimarochloa* spp., and their deeper parts by submersed and free-floating aquatic macrophytes, such as *Salvinia auriculata* Aubl. and *Eichhornia azurea* (Sw.) Kunth (Allem and Valls 1987).

Studies on lakes of high alkalinity and salinity in the Pantanal of Nhecolândia have described their distinct spatial, physical, chemical, and biological characteristics. The distribution patterns of the lakes indicate differences in their genesis and in the environmental factors that have determined their features (Sakamoto 1997; Assine 2003; Bacani and Sakamoto 2007; Almeida et al. 2011; Oliveira et al. 2011; McGlue et al. 2017; Guerreiro et al. 2018).

In lakes with slightly brackish water (Macrohabitat 1.2.6), the pH varies between 7.0 during the rainy season and 8.3 during the dry season, unlike freshwater lakes in the same region, whose pH varies only from 7.8 to 7.6 during the rainy and dry season, respectively (Santos et al. 2012). The electrical conductivity of these brackish water lakes is in the range of 2.0–60.0 mS/cm, whereas that of freshwater lakes is considerably lower, 0.020–2.0 mS/cm (Bergier et al. 2016). The lakes of Macrohabitat 1.2.6 may be colonized by dense stands of *Typha domingensis* Pers., locally called *taboa* (Evans 2013). These lakes are common in Nhecolândia, where they are referred to as *baías salitradas* or *taboais* (Brum and Sousa 1985; Mourão et al. 1988; Calheiros and Oliveira 1999; Barbiéro et al. 2002; Santos et al. 2012).

Saline lakes (Macrohabitat 1.2.7) are disconnected from the local drainage system and are of high alkalinity and salinity because of the evaporation and geochemical processes resulting from the isolated groundwater table (Furian et al. 2013). These lakes are unsuitable for the growth of aquatic macrophytes and are colonized by alkali- and salt-tolerant bacteria, cyanobacteria and algae (McGlue et al. 2017; Guerreiro et al. 2018). The pH is frequently > 8 during the rainy season and reaches 10 or even higher values during the dry season (Santos et al. 2012). Electrical conductivity varies between 9 mS/cm during the rainy season and 20 mS/cm during the dry season. These lakes, whose depths rarely exceed 1 m, are endorheic, receiving their water from rain and surface runoff. They are surrounded by sandy elevations or paleo-levees covered by semi-deciduous forest or *cerradão*. During the dry season, sandy beaches frequently surround the lakes. In very dry years, the lakes may dry out completely (Brum and Sousa 1985; Mourão et al. 1988; Barbiéro et al. 2002; Medina-Júnior and Rietzler 2005; Almeida et al. 2011).

The study of sediment cores recently elucidated the origin of the saline lakes. The lakes of Nhecolândia developed during a wetter period about 10,000 years ago. Biogeochemical changes in the *salinas* started about 3000 years ago, not due to the impact of paleoclimatic events, such as longer dry periods, but to the hydrological isolation of the lakes (McGlue et al. 2017; Guerreiro et al. 2018).

However, given the variability in the Pantanal's lakes, broad geomorphological, limnological, and paleo-climatological studies are required for a better understanding and a more detailed classification of these important macrohabitats.

7.3.2 Functional Unit 2: Predominantly Aquatic Areas (ATTZ with a Predominant Aquatic Phase)

The macrohabitats of the ATTZ are characterized by aquatic and terrestrial phases whose features depend on the local hydrology. Environmental factors as well as the flora and fauna change depending on the water level, which is variable. Therefore, determinations of the boundaries of these areas are difficult and tend to be subjective, with the same areas often classified as predominantly aquatic and predominantly terrestrial. However, predominantly aquatic areas can be defined as those with a long aquatic phase.

Classifications are also based on the occurrences of higher plants. In areas with a long aquatic phase, the dominance of aquatic macrophytes is indicative of a predominantly aquatic macrohabitat, even though during the short terrestrial phase the same area is colonized by terrestrial plants. In areas with a long terrestrial phase, most of the plant species or communities occurring during the dry period are considered terrestrial, for instance, trees and shrubs, although many of them have developed adaptations to survive the aquatic or palustric phase. The dominance of these plants designates a macrohabitat as predominantly terrestrial even though during flood periods these same macrohabitats are colonized by aquatic macrophytes.

7.3.2.1 Subclass 2.1: Areas with Periodically Flowing Water (Small Water-Distribution Channels Inside the Floodplain)

Small channels and linear depressions, although they dry out during low-water periods, are of great importance for water distribution and outflow, fish migration, and the distribution of aquatic organisms inside the floodplain. *Bocas* and *furos* are temporary connections between lakes and river channels (Macrohabitat 2.1.1). Bocas, which may be formed naturally (Assine et al. 2015), or by humans (Galdino et al. 2006), increase both the water and the sediment supply to the adjacent floodplain (Bergier 2013).

Corixos (Macrohabitat 2.1.2) are old deep fluvial channels that dry out during the low-water period (Franco and Pinheiro 1982). Well-defined large *corixos* (*corixões*) (Carvalho 1986), include, for example, the Abobral River. *Vazantes* (Macrohabitat 2.1.3) are shallow channels covered by grasses and herbaceous plants during the terrestrial phase, and by aquatic macrophytes during high-water periods. A peculiar channel is the *landi* (Macrohabitat 2.1.4), which may be partially covered by flood-tolerant forest (Macrohabitat 3.5.4).

7.3.2.2 Subclass 2.2: Areas Periodically Covered by Standing Water

In deeply flooded (>2 m) areas (Macrohabitat 2.2.1), submersed aquatic macrophytes dominate, and because the dry periods are very short, there is no colonization by terrestrial plants. In areas covered by shallower water (Macrohabitat 2.2.2), there is typically a mixture of submerged, emergent, and floating-leaf plants. The high species richness of aquatic macrophytes (Pott et al. 2001) contributes substantially to primary production and provides food and shelter for a rich aquatic fauna. During the growth period, competition between macrophytes and algae for nutrients can result in the water sometimes being crystal clear (Fellerhoff et al. 2003).

Arrozais (wild rice fields, Macrohabitat 2.2.3) are areas inundated for 7–10 months of the year. They occur mostly along the Paraguay River in Mato Grosso do Sul, adjacent to the *morrarias* (hills) of Amolar and Urucum and in the large lakes of the Pantanal, such as Castelo, Gaíva and Mandioré. The inundation of these areas depends on the arrival of floodwaters from the north, not on the local rains that fall during the low-water period. Arrozais are characterized by monodominant stands of *Oryza latifolia* Desv. and *O. rufipogon* Griff., associated with *Leersia hexandra* Sw. and *Hymenachne amplexicaulis* (Rudge) Nees. The species composition in these areas varies considerably according to the annual and multi-annual variations in the inundation pattern. Any long-term change in the flood amplitude will eliminate this important macrohabitat, which contributes substantially to terrestrial and aquatic food webs via the high seed production of the wild rice.

In some depressions (Macrohabitat 2.2.4) more water accumulates than in the surroundings, resulting in the formation of shallow temporary lakes that dry out entirely during the dry season. During the aquatic phase, these lakes are colonized by amphibious aquatic macrophytes, such as *Helanthium tenellum* (Mart. ex Schult. & Schult. f.) Britton, *Echinodorus grandiflorus* (Cham. & Schltdl.) Micheli, *Eleocharis minima* Kunth, *E. acutangula* (Roxb.) Schult. and *Diodia kuntzei* K. Schum. During the short terrestrial phase of these areas, the dried-out areas are colonized by several species of grasses, such as *Reimarochloa brasiliensis* (Spreng.) Hitchc., *Steinchisma laxum* (Sw.) Zuloaga, *Setaria parviflora* (Poir.) Kerguélen, and *Digitaria fuscescens* (J. Presl) Henrard), as well as other herbaceous plants, such as *Richardia grandiflora* (Cham. & Schltdl.) Steud., together forming an important terrestrial macrohabitat consisting of “pure grassland” without shrubs and trees (*campo limpo* or, near Poconé, *campina*) (Oliveira 2009; Bao 2017). This area is listed twice in the classification system, as Macrohabitats 2.2 (Periodically aquatic areas) and 3.2 (Periodically terrestrial areas), due also to the differences in the respective species. This example shows how multi-annual wet and dry periods can change the occurrence and extension of macrohabitats in the ATTZ. In a multi-annual wet period the macrohabitat becomes mostly aquatic, and in a multi-annual dry period mostly terrestrial.

7.3.3 Functional Unit 3: Predominantly Terrestrial Areas (ATTZ with a Predominant Terrestrial Phase)

Macrohabitats in this functional unit are characterized by a terrestrial phase that is almost always longer than the aquatic phase. Most plants growing during the terrestrial phase are terrestrial. This group also includes all trees and shrubs. We used the terrestrial plants as the basis of the characterization. Aquatic macrophytes occur during the aquatic phase. Some of these macrohabitats can also be considered as predominantly aquatic or palustric such as Macrohabitats 2.2.4 and 3.2.4. and Macrohabitats 3.2.1 and 5.1.1.

7.3.3.1 Subclass 3.1: Areas Without or With Sparse Vegetation Cover

Despites the absence of higher vegetation, these areas represent macrohabitats with specific functions in the Pantanal. Sandy beaches (Macrohabitat 3.1.1) serve as resting places for many animals, such as capybaras (*Hydrochoaerus hydrochaeris*), caimans (*Caiman yacare*), and many birds. Species such as the black skimmer (*talha-mar*, *Rynchops niger*), large-billed tern (*trinta-réis-grande* (*Phaethusa simplex*), yellow-billed tern (*Trinta-réis-anão*, *Sternula [Sterna] superciliaris*), southern lapwing (*quero-quero*, *Vanellus chilensis*), pied plover (*batuíra-de-esporão*, *Hoploxypterus [Vanellus] cayanus*), and collared plover (*batuíra-de-coleira*, *Charadrius collaris*) use the sandbanks as nesting places. The role of the rocky outcrops (Macrohabitat 3.1.2) has yet to be studied, but the presence of a hard and persistent substrate in an otherwise soft and unstable environment characterized by constant deposition and erosion and offering a habitat for specialized organisms supports its denomination as distinct macrohabitat. The steep shores (*barrancos*, Macrohabitat 3.1.3) are used during the low-water period by kingfishers (*Megaceryle torquata*) for nesting and by otters as homes. In the aquatic phase, many aquatic invertebrates and some fish species also build their shelter in the rather stable sediments.

7.3.3.2 Subclass 3.2: Areas Covered with Grasses and Herbaceous Plants (Campo Limpo Natural)

Areas covered with grasses and other herbaceous plants, locally called *campos*, occur along the entire flooding gradient. In addition to the length of the periodic inundation, the factors that influence the vegetation include the soil conditions (sandy or clayey soils) and fluctuations in the groundwater level. Together they lead to changes in the dominant species during the rainy and dry seasons.

Grasslands in depressions periodically inundated by rainwater are dominated by *Elionurus muticus* (Spreng.) Kuntze), locally referred to as *capim-carona*. The macrohabitat itself is called *caronal* (Macrohabitat 3.2.1) (Santos et al. 2005). Annual burning of these grasslands is commonly conducted to provide fresh pasture for grazing cattle (see also Macrohabitat 5.1.1.).

Grasslands dominated by *Mesosetum chaseae* Luces (*grama-do-cerrado*) (Macrohabitat 3.2.2) occur on sandy and lixiviated soils that are poor in organic material and annually inundated for <3 months, but with an oscillating groundwater level. In wetter areas of this macrohabitat *Axonopus leptostachyus* (Flüggé) Hitchc. (*rabo-de-burro*) and *Paspalum plicatulum* Michx. (*capim-felpudo*) occur, and in dryer areas, *capim-carona* is found. These grasslands occur on large areas in the Pantanal of Nhecolândia and Aquidauana.

Andropogon hypogynus Hack. (*campo de capim-vermelho*) and *Axonopus leptostachyus* (Flüggé) Hitchc. (*campo de rabo-de-burro*) (Macrohabitat 3.2.3) dominate grasslands that are annually inundated for up to 3 months. They form large, highly lignified clusters (*macegas*) and are therefore little grazed by cattle. Consequently, ranchers burn these grasslands to stimulate regrowth, which is softer, but also favors the growth of *Axonopus purpusii* (Mez) Chase, or they plant the exotic grass *Urochloa humidicola* (Rendle) Morrone & Zuloaga. During the aquatic phase, *Leersia hexandra* Sw. may grow among the clusters (Schessl 1999).

Grasslands covered by *Axonopus purpusii* (Mez) Chase and *Reimarochloa brasiliensis* (Spreng.) Hitchc. (*campos de mimoso*, Macrohabitat 3.2.4) together with *Steinchisma laxum* (Sw.) Zuloaga and *Diodia kuntzei* K. Schum. are of high nutritional value for cattle and are highly grazed. These areas, which are annually inundated for about 6 months, develop in periodically flooded depressions, in the littoral zones of lakes and extensively in the floodplains near rivers. Terrestrial and aquatic phases are well pronounced and the floristic composition of the vegetation changes accordingly (Rebellato and Nunes da Cunha 2005), though the flora is more diverse in the aquatic than in the terrestrial phase (Rebellato et al. 2012).

During inundation, additional sediments and nutrients are deposited along the riverbanks, which are colonized by dense stands of semi-aquatic grasses such as *Louisiella elephantipes* (Nees ex Trin.) Zuloaga, and herbaceous plants, such as *Polygonum ferrugineum* Wedd., *Ludwigia* spp., and *Aspilia latissima* Malme (Macrohabitat 3.2.5). The lower sections of this highly productive macrohabitat are annually inundated for > 6 months.

7.3.3.3 Subclass 3.3: Areas Covered by Herbaceous Plants, Shrubs, and Small Groups of Trees

These are very dynamic macrohabitats, because most of the species have a high tolerance to floods and droughts. Multi-annual dry and wet periods, wildfires and anthropogenic impacts result in a reorganization of the spatial distribution of species such that many of these macrohabitats can be considered as successional stages.

Termite savannas (*campos de murunduns*, Macrohabitat 3.3.1) are a very characteristic landscape found in all Brazilian wetland savannas. In the Pantanal they occur mostly at its borders. Veloso and Góes-Filho (1982) referred to them as park savanna. The small earth mounds built by termites in these shallowly flooded grasslands may be as tall as 2 m, with a surface area of up to 20 m^2. The *cerrado* vegetation covering these terrestrial islands include the tree *Curatella americana* L. (*lixeira*). Areas between earth mounds are covered during the terrestrial phase by terrestrial grasses and herbaceous plants, and during the aquatic phase by palustric and aquatic macrophytes (Schessel 1999).

In grasslands (Macrohabitat 3.3.2) shallowly flooded for up to 3 months, there is often an invasion of shrubs, usually dominated by *Byrsonima cydoniifolia* A. Juss. (*canjiqueira*) or *Curatella americana* L. (*lixeira*). These areas are considered advanced stages of grasslands invaded by shrubs and trees locally called *campo sujo* (*campo sujo de canjiqueira* and *campo sujo de lixeira*)

Grasslands annually inundated for up to 6 months may be invaded by *Combretum lanceolatum* Pohl ex Eichler and *C. laxum* Jacq. (*pombeiro*) (Macrohabitat 3.3.3). Initially, these shrubs are found in isolated groups, but they gradually form dense monospecific stands that replace the grasslands valuable for cattle. Therefore, ranchers actively eliminate the shrubs, a process that in Mato Grosso State is called *limpeza de campo* (scrubbing of the grasslands).

In Mato Grosso do Sul there are areas shallowly flooded for periods ranging from a few weeks to a few months. Small elevations (about 20 cm tall), locally called *tacurus*, are a feature of this macrohabitat (Macrohabitat 3.3.4). Characteristic species are *Mimosa hexandra* Micheli, *Parkinsonia praecox* (Ruiz & Pav.) Hawkins, *Copernicia alba* Morong, *Fridericia* sp., *Cynophalla retusa* (Griseb.) Cornejo & Iltis, *Sarcomphalus mistol* (Griseb.) Hauenschild, *Castela coccinea* Griseb., and *Acrocomia aculeata (Jacq.)* Lodd. ex Mart. They belong to the *chaco arborizado*, a typical herbaceous vegetation characterized by spiny, succulent trees and shrubs 3–15 m in height.

7.3.3.4 Subclass 3.4: Areas Covered by Shrublands

Arbustal (shrubland) is the local name for areas densely covered by different species of shrubs. Frequently a single species is dominant and provides its name to the specific macrohabitat. Our studies (see Chap. 8 on monodominant stands) show that these formations are successional stages that begin with the invasion of a *campo limpo* ("scrubbed" grassland), proceed to *campo sujo*, and finally become *arbustal*. The latter stage may be stable for several decades because the dense plant cover hinders colonization by trees; however, long-term studies of this process are needed. Wildfires during multi-annual dry periods can eliminate these shrublands, thus controlling their proliferation. Because environmental legislation does not allow the use of fire as a control measure, these macrohabitats will likely expand.

Shrublands dominated by *Byrsonima cydoniifolia* A. Juss. (*canjiqueira*, Macrohabitat 3.4.1) occupy sandy soils annually inundated for up to 3 months. Their presence is favored by multi-annual dry periods, whereas during longer wet periods, they disappear (Pott and Pott 1994; Silva et al. 1998). Spiny shrublands (*espinheirais*, Macrohabitat 3.4.2) are dominated, for example, by *Mimosa* spp., *Byttneria* spp., and *Bauhinia bauhinioides* (Mart.) J.F. Macbr. These species grow to a height of 1.5–4.0 m in large areas of the north and southwest Pantanal that are annually inundated for up to 6 months. Herbaceous climbers cover the shrubs abundantly during the aquatic phase.

The *pombeiral* (Macrohabitat 3.4.3) is dominated by *Combretum lanceolatum* Pohl ex Eichler or by *C. laxum* Jacq. Both reach a height of about 4 m and tolerate flooding of up to 6 months. All shrublands are problematic for ranchers because they crowd out the valuable grasslands that are preferentially grazed by cattle. However, although ranchers devote considerable efforts to eradicating shrublands, removal is difficult, labor-intensive, and expensive.

Shrublands referred to as *barreiro* or *barreiral* (Macrohabitat 3.4.4) consist of low-density communities of shrubs and trees of *Prosopis rubriflora* Hassl. (*barreiro-preto*) or sometimes *Machaerium hirtum* (Vell.) Stellfeld. They occur in small depressions with saline and clayey soils experiencing shallow flooding of brief duration. This macrohabitat is under the influence of the Chaco in the Nabileque sub-region, which extends from Miranda to Porto Murtinho. In the sub-regions of Poconé, Nossa Senhora do Livramento, and Barão de Melgaço, the indicator species is *Machaerium hirtum* (Vell.) Stellfeld. *Barrerais* attract many animals, which consume the mineral-rich sediments (geophagy) (Coelho 2006).

7.3.3.5 Subclass 3.5: Areas Covered by Polyspecific Forests

Periodically inundated polyspecific (i.e., containing several species of trees) forests are scattered across many parts of the Pantanal, often along the shores of river channels and *corixos*, but also on higher-lying areas. Their successional stage differs depending on their position along the flooding gradient, ranging from pioneer riparian forests to fully developed floodplain forests (Nunes da Cunha and Junk 2001). Riparian forests of pioneer shrubs and trees are found in the lower areas of the natural levees near the river channel (Macrohabitat 3.5.1) and consist of *Alchornea castaneifolia* (Humb. & Bonpl. ex Willd.) A. Juss., *Sapium obovatum* Klotzsch ex Müll. Arg., and *Albizia inundata* (Mart) Barneby J.W. Grimes (*bigueiro*). In the middle part of the levee the forest is older and better structured (Macrohabitat 3.5.2) and made up mostly of *Banara guianensis* Aubl., *Mabea paniculata* Spruce ex Benth., *Pterocarpus santalinoides* L'Hér. ex DC., *Zygia cauliflora* (Willd.) Killip, *Spondias mombin* L., *Mouriri guianensis* Aubl., *Coccoloba mollis* Casar., *Eugenia inundata* DC., *Pouteria glomerata* (Miq.) Radlk., *Trichilia catigua* A. Juss., *Salacia elliptica* (Mart.) G. Don, and *Garcinia brasiliensis* Mart.

The highest parts of the levees (Macrohabitat 3.5.3) are shallowly flooded for short time periods. The soil is covered with a litter layer and colonized by few herbaceous plants, except in gaps. Characteristic tree species are *Handroanthus heptaphyllus* (Vell.) Mattos, *Nectandra amazonum* Nees, *Ocotea diospyrifolia* (Meisn.) Mez, and *Vitex cymosa* Bertero ex Spreng. Many species are deciduous during the dry season. During multi-annual dry periods, these forests are susceptible to wild fires.

A particular type of polyspecific forest grows along the drainage channels that transport water inside the floodplain (*landis*, Macrohabitat 3.5.4). These areas contain water for up to 8 months of the year and are colonized by highly flood-tolerant trees, such as *Calophyllum brasiliense* Cambess., *Leptobalanus parvifolius* (Huber) Sothers & Prance, *Alchornea discolor* Poepp., and *Vochysia divergens* Pohl.

A particular type of polyspecific forest, the Flooded Chaco forest (Macrohabitat 3.5.5), grows in periodically flooded depressions in the southern Pantanal and includes tree and shrub species from the Chaco forest. Characteristic species are *Gymnanthes discolor* (Spreng.) Müll. Arg., *Coccoloba rigida* Meisn., *Adelia membranifolia* (Müll. Arg.) Chodat & Hassl., *Phyllostylon rhamnoides* (J. Poiss.) Taub., *Sebastiania brasiliensis* Spreng., and *Machaonia brasiliensis* (Hoffmanss. ex Humb.) Cham. & Schltdl. The species *Tabebuia nodosa* (Griseb.) Griseb., *Schinopsis balansae* Engl., and *Aspidosperma quebracho-blanco* Schltdl. are present in smaller numbers.

A deciduous forest annually inundated for 1–2 months (Macrohabitat 3.5.6) grows on soils containing a high concentration of alkaline substances. This forest type occurs mostly in areas where the Paraguay River blocks the flow of the Taquari and in the Paiaguás sub-region. The mean canopy height is 12–15 m, with some emergent trees of 20–22 m. The most common tree species are *Phyllostylon rhamnoides* (J. Poiss.) Taub., *Cedrela fissilis* Vell., *Hymenaea courbaril* L., *Casearia gossypiosperma* Briq., *Pisonia zapallo* Griseb., and the acuri palm *Attalea phalerata* Mart. ex Spreng.

7.3.3.6 Subclass 3.6: Areas Covered by Monodominant Stands

Forests or savanna growing in the floodplain are often the result of the spread of single species (See Chap. 8 on monodominant stands). *Leptobalanus parvifolius* (Huber) Sothers & Prance (*pimenteira*, Macrohabitat 3.6.1) reaches heights of 5–8 m in areas that are annually inundated for up to 6 months. *Vochysia divergens* Pohl (*cambará*) is a highly flood-tolerant species (Arieira and Nunes da Cunha 2006) and spreads to the surrounding grasslands during multi-annual wet periods (Nunes da Cunha and Junk 2004) (Macrohabitat 3.6.2). The further expansion of this species is controlled by wildfires that occur during very dry periods. In the northern Pantanal, there are *cambará* forests of different age depending on their protection against fire. In old stands, several other species are associated with *V. divergens*, most of them from riparian forests, such as *Eugenia* spp., *Tocoyena foetida* Poepp., and *Psychotria carthagenensis* Jacq. Mature *cambará* forests are of high ecological value and merit protection because they serve as habitats for many different animal species. *Erythrina fusca* Lour. (*abobreiro*) forms monospecific forests along the Paraguay River and its lateral channels (Macrohabitat 3.6.3), where natural levees are poorly developed because of the low sediment load. The trees are annually inundated for > 6 months and to a depth of up to 6 m.

Tabebuia aurea (Silva Manso) Benth. & Hook. f. ex S. Moore (*paratudo*) forms monodominant savanna, the *paratudais* (Macrohabitat 3.6.4), which are characterized by a slightly developed understory of shrubs (Silva et al. 1998) and distinct herbaceous species (Soares and Oliveira 2009). *Copernicia alba* Morong, the *carandá* palm tree, is a Chaco species that grows in periodically flooded areas on clayey and sandy soils of high salinity (Prado 1993). It forms monodominant open savanna and has an understory of shrubs and trees as well as a variable and diversified stratum of grasses and herbaceous plants, when flooded for up to 3 months (Amador et al. 2012) (Macrohabitat 3.6.5). During longer inundations (up to 8 months), *C. alba* forests become denser (Macrohabitat 3.6.6).

Couepia uiti (Mart. & Zucc.) Benth. ex Hook. f. forms monodominant forests in periodically flooded savannas (*pateiro*, Macrohabitats 3.6.7) on sandy soils, frequently in the sub-regions of Abobral and Aquidauana (Allem and Valls 1987). *Curatella americana* L. (*lixeira*, Macrohabitat 3.6.8) forms open forests on sandy soils in shallowly inundated *campo cerrado*. *Lixeira* is a fire-tolerant pioneer species that can become invasive in grasslands depending on the depth and duration of flooding. In termite savannas (*campos de murunduns*, Macrohabitat 3.3.1), the tree grows on top of the termite mounds.

7.3.4 Functional unit 4: Swampy Areas (Permanently Waterlogged or Shallowly Flooded)

7.3.4.1 Subclass 4.1: Swamps Covered by Herbaceous Plants (*brejos*)

Swamps (*brejos*) are permanently waterlogged or shallowly flooded areas that are colonized by emergent palustric plants. Frequently, a single species dominates these areas, such as *Cyperus giganteus* Vahl (*piri*) in the *pirizal* (Macrohabitat 4.1.1), *Thalia geniculata* L. (*caeté*) in the *caetezal* (Macrohabitat 4.1.2), or *Canna glauca* L. (*cana-do-brejo*, Macrohabitat 4.1.3). In multispecies swamps, different species of grasses and sedges occur together with *Aeschynomene sensitiva* Sw., *A. fluminensis* Vell., and climbers such as *Cissus spinosa* Cambess. and *Ipomoea tenera* Meisn., among others (Macrohabitat 4.1.4). According to Silva et al. (2000), areas covered by swamps represent 7.4% of the vegetation of the Pantanal, 35.5% in the sub-region along the Paraguay River, 16.5% in the Abobral sub-region, and 14.8% in the Poconé sub-region. They have important ecological functions, filtering the water and providing refuge for animals (Pott et al. 2001). Swamps are difficult to study because of their difficult access and thus still require a better ecological characterization (but see monodominant stands Chap. 8). Nonetheless, they are strongly affected by human activities, such as drainage of small areas but also by natural changes in hydrology, as is the case in the Taquari delta (see Macrohabitat 4.1.5).

A specific type of swamp comprises the floating islands locally called *batumes* or *baceiros* (Macrohabitat 4.1.5). These islands develop on layers of floating organic material produced by aquatic macrophytes. Under permanently aquatic conditions, the decomposition of this material is retarded because of low oxygen concentrations. Palustric species colonize the organic layer, such as *Cyperus blepharoleptos* Steud., *Eleocharis plicarhachis* (Griseb.) Svenson, *Pityrogramma calomelanos* (L.) Link, and *Rhynchanthera novemnervia* DC. (Schessel 1999; Pott et al. 2001; Pivari et al. 2008). The roots and stolons of these plants stabilize the organic layer, which over time becomes thick enough to allow the growth of small shrubs. The layer follows the changes in the water level of the respective lakes, providing a stable, anoxic, swampy environment throughout the year. During periods of extreme drought, the layers may fall dry and decompose, or they may be destroyed by wildfires. This vegetation type exists in other wetlands as well, such as the Amazonian *várzeas*, where it was described by Junk and Piedade (1997).

Increased sediment load of the Taquari River, following the expansion of clearing and agriculture in the upper catchment, led in recent years to hydrological changes at the lower Taquari River delta. That has stimulated the development of different types of swamps over an area of about 11,000 km^2.

7.3.4.2 Subclass 4.2: Swamps Covered by Herbaceous Plants and Palms

These swamps are characterized by the presence of the palm *Mauritia flexuosa* L. f. (*buriti*, Macrohabitat 4.2.1). The trees reach a height of 5–20 m, forming forests (*buritizais*) that cover about 2% of the Pantanal, mainly in the standing water at the borders of the sub-regions of Barão de Melgaço, Paiaguás, Nhecolândia and Aquidauana (Silva et al. 2000). Eiten (1972) calls the *buritizais* "palm woodlands," separating them from other cerrado phytophysiognomies. The abundant fruits of these palm forests are an important food source for many animals. Parrots frequently build their nests in dead trees (personal communication Walfrido Tomas).

The palm forests growing in swamps of standing water differ from those growing in swamps along small streams, locally called *veredas*. They are also characterized by *Mauritia flexuosa* (Macrohabitat 4.2.2). The streams drain the areas along the eastern border of the Pantanal, in the sub-regions of Nhecolandia, Paiaguás, and Barão de Melgaço. The waterlogged soils of the *veredas* are colonized by palustric grasses, sedges, and aquatic macrophytes. *Buriti* palms grow in clusters within the *veredas* or in lines along the streams, together with *Xylopia emarginata* Mart. (*pindaíba-preta*), *Calophyllum brasiliense* (*guanandi*), and other trees adapted to swampy soils. The *buritizais* of the Aquidauana River are colonized by herbaceous species of the Pantanal; in contrast, those of the Coxim and Verde Rivers in Mato Grosso contain species of the *veredas* of the *cerrado* highlands.

7.3.5 Functional Unit 5: Permanently Terrestrial Areas

Permanently terrestrial areas play a very important role in the mosaic of Pantanal macrohabitats. They are colonized by strictly terrestrial plant and animal species. They also provide periodic refuge for many wetland animals during high-water periods in other areas, as well as food and nesting places for a wide range of species.

As such, permanently terrestrial areas are essential for the maintenance of biodiversity. This function has been taken into consideration by the Brazilian definition of wetland delimitation.

7.3.5.1 Subclass 5.1: Paleo-Deltas, Alluvial Terraces, and Paleo-Levees (*Capões*, *Cordilheiras*)

The Pantanal is the lowest part of the Upper Paraguay Basin, in which the rivers have deposited their sediments for several million years, forming large internal deltas. The largest delta, covering about 50,000 km^2, is that of the Taquari River (Assine 2005). These deltas reflect the different geological periods during which their sediments were deposited. For example, climatic changes during the Quaternary led to wetter and dryer periods and therefore to periods of higher and lower flood levels and changes in the sediment load (Ab'Saber 1988).

The results of these changes are the paleo-levees (*capões* and *cordilheiras*) in the Pantanal of Poconé and the paleo-terraces in the older parts of the river deltas, which reach a few meters above the actual flood level and are permanently dry. Ab'Saber (1988) also cited neotectonic processes in the formation of paleo-deltas and -levees, but additional studies are necessary to understand the genesis and age of these areas better.

Paleo-sediments are for the most part covered by savannas and forests. A typical savanna type is dominated by *Elionurus muticus* (*capim carona*, *campo limpo de caronal*, Macrohabitat 5.1.1), which grows in clusters. Its density depends on fire management and grazing. This macrohabitat is common on sandy soils in the sub-regions of Nhecolândia and Paiaguás. The same type of grassland can also occur in depressions periodically inundated by rainwater (Macrohabitat 3.2.1), but the associated species differ.

Another savanna type is dominated by *Mesosetum chaseae* (*grama-do-cerrado*, Macrohabitat 5.1.2), which grows on sandy soils, frequently in the sub-regions of Nhecolândia and Paiaguás. This perennial species tolerates nutrient-poor soils and hydrologic stress and is preferred by cattle, horses, and game animals. In the higher-lying areas of these sub-regions, grasslands are composed of *Paspalum lineare* Trin. (*fura-bucho*) and *Aristida* spp. (*barba-de-bode*), which are of low nutritional value.

The Pantanal's dense savanna forests (*cerradão*, Macrohabitat 5.1.3) are related to the savanna forests of the western and central region of the country, both floristically and structurally, but there are also floristic and physiognomic differences that have not yet been fully described. The most important tree species are *Qualea parviflora* Mart., *Q. grandiflora* Mart., *Alibertia edulis* (Rich.) A. Rich., *Byrsonima cydoniifolia* A. Juss., *Brosimum gaudichaudii* Trécul, *Kielmeyera coriacea* Mart. & Zucc., *Diospyros lasiocalyx* (Mart.) B. Walln., *Erythroxylum suberosum* A. St.-Hil., *Tocoyena formosa* (Cham. & Schltdl.) K. Schum., *Curatella americana* L., and *Hancornia speciosa* Gomes.

Forests with semi-deciduous species that shed their leaves during the dry season occupy paleo-levees (*capões* and *cordilheiras*) and high, recently formed levees

(Macrohabitat 5.1.4). The amount of leaf shedding is stronger in dry than in wet years. Characteristic species are *Trichilia stellatotomentosa* Kuntze, *Combretum leprosum* Mart., *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Trichilia elegans* A. Juss., *Astronium fraxinifolium* Schott, *Zanthoxylum rigidum* Humb. & Bonpl. ex Willd., *Albizia edwallii* (Hoehne) Barneby & J.W. Grimes, *Rhamnidium elaeocarpum* Reissek, *Tabebuia roseoalba* (Ridl.) Sandwith, *Vitex cymosa* Bertero ex Spreng., and *Enterolobium contortisiliquum* (Vell.) Morong. The *capões* of the sub-regions of Abobral and Paiaguás, in the Pantanal of Mato Grosso do Sul, are dominated by the trees and shrubs found in semi-deciduous forests. These species, which do not tolerate flooding, include *Rhamnidium elaeocarpum* Reissek, *Aspidosperma australe* Müll.Arg., *Senegalia tenuifolia* (L.) Britton & Rose, *Sideroxylon obtusifolium* (Humb. ex Roem. & Schult.) T.D. Penn., and *Priogymnanthus hasslerianus* (Chodat) P.S. Greene.

Deciduous forests (Macrohabitat 5.1.5) occur on alluvial terraces and are dominated by *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Tabebuia roseoalba* (Ridl.) Sandwith, *Combretum leprosum* Mart., *Casearia gossypiosperma* Briq., *Astronium urundeuva* (M. Alemão) Engl., *Anadenanthera colubrina* (Vell.) Brenan, *Spondias mombin* L., and *Cedrela fissilis* Vell. Emergent species such as *Astronium fraxinifolium* can reach a height of up to 35 m; lianas and bamboo (*Guadua paniculata* Munro) are abundant.

Some of these Pantanal forests exhibit unique floristic and ecological characteristics (Duarte 2007). They occur on more fertile soils and are generally dominated by the palm *Attalea phalerata* Mart. ex Spreng (*acuri*). The abundance of this palm has been attributed to its management by indigenous peoples during pre-Columbian times. Monodominant forests dominated by *Attalea phalerata* (acurizal) occur on capões (Macrohabitat 5.1.6) and *cordilheiras* in the sub-region of Nhecolândia of Mato Grosso do Sul (*babaçu* or *aguaçu*, Macrohabitat 5.1.7). Associated species include *Albizia niopoides* (Spruce ex Benth.) Burkart, *Anadenanthera colubrina* (Vell.) Brenan, and *Astronium fraxinifolium* Schott.

7.3.5.2 Subclass 5.2: Inselbergs (*Morros*)

Morros are rocky outcrops of the Serrana Province and the uplands (*planalto*) of Urucum-Amolar that emerge from Pantanal sediments. They may tower > 100 m above the floodplain and cover dozens of hectares. The deciduous forest that covers *morros* is relatively short (6–8 m), with a xerophytic physiognomy. Also present is the treelike cactus *Cereus bicolor* Rizzini & A. Mattos. In the lower parts of the *morros*, rock carvings indicate pre-Columbian human occupation in the area.

In Mato Grosso do Sul, *morros* occur along the Paraguay River, and in the subregion of Cáceres. These may reach a height of up to 1000 m and are covered by highly fertile soils deriving from limestone or basalt as well as soils deriving from rocks containing iron and manganese (Macrohabitat 5.2.1). The vegetation in this macrohabitat is deciduous, mainly consisting of *Acosmium cardenasii* H.S. Irwin &

Arroyo, *Senegalia polyphylla* (DC.) Britton, *Anadenanthera colubrina* (Vell.) Brenan, and *Jatropha vitifolia* var. *cnicodendron* (Griseb.) Pax.

Areas covered with *cerrado rupestre* (Macrohabitat 5.2.2) occur on the *morros* at the western border of the Pantanal, on soils derived from rocks rich in silica. Typical species include *Lafoensia pacari* A. St.-Hil., *Qualea grandiflora* Mart., *Hancornia speciosa* Gomes, *Himatanthus obovatus* (Müll. Arg.) Woodson, *Kielmeyera coriacea* Mart. & Zucc., and *Norantea goyasensis* Cambess. On tops occurs *Vellozia variabilis*.

On the highest parts of the *morros*, at the eastern border of the Pantanal, *campos rupestres* (Macrohabitat 5.2.3) occur on soils interspersed with rocks rich in iron (hematite) or silica. These grasslands may be interspersed or not with woody vegetation (*campos rupestres densos* and *campos rupestres abertos*, respectively). Characteristic grasses are *Trachypogon spicatus* (L. f.) Kuntze, *Axonopus* spp. and *Paspalum foliiforme* S.Denham. In the *campos rupestres densos*, *Aiouea trinervis* Meisn., *Qualea cryptantha* (Spreng.) Warm., *Styrax camporum* Pohl, and *Miconia ferruginata* DC. are common. There are also endemic species, such as *Aspilia grazielae* J.U. Santos.

7.3.6 Functional Unit 6: Anthropogenic Areas

7.3.6.1 Subclass 6.1: Paleo-Anthropic Areas

The paleo-anthropic areas, locally called *capões de aterro* (Macrohabitat 6.1.1), are represented by elevated areas inside the floodplain covering about 1 hectare. Pre-Columbian inhabitants of the Pantanal created these as refugia from floods, and their heights exceed the maximum flood level. The oldest mounds are estimated to be approximately 8,200 years old (Schmitz et al. 1998). Evidence of human occupation includes fish bones, and shells from aquatic mollusks used as food as well as ceramic fragments and graves. The accumulated shells contribute to both *aterro* stability and soil fertility, because their decomposition leads to the formation of beidellite, a mineral with a high ion-exchange capacity against lixiviation (Irion et al. 2011). Among the plant species growing in these areas are those useful for humans, such as *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. (palm), *Genipa americana* L., *Unonopsis guatterioides* (A. DC.) R.E. Fr., *Ficus* spp., *Cassia grandis* L. f. (canafístula), *Sapindus saponaria* L., and *Garcinia brasiliensis* Mart.

7.3.6.2 Subclass 6.2: Areas of Recent Anthropic Activities

Areas of recent anthropic activities in the Pantanal are still small but growing. Elevated roads (Macrohabitat 6.2.4) to and within the ranches and borrow pits (*caixas de empréstimo*, Macrohabitat 6.2.2) are increasingly modifying the water flux and the hydrology of many areas. The consequences for the vegetation have not yet been studied but are frequently visible as differences on both sides of roads, reflecting the changed inundation levels. Ranch houses are built on elevated sites (e.g., *capões* and *cordilheiras*), and the area around them is frequently used for subsistence agriculture (Macrohabitat 6.2.5). Birds, monkeys, and other wildlife also visit these plots. Small water reservoirs (*tanques*, *bebedouros*, Macrohabitat 6.2.1) constructed to provide water for cattle during low-water periods are also used by wildlife. Besides, some ranchers have dug small channels (Macrohabitat 6.2.3) to drain swampy areas or straightened natural channels. However, drainage and other activities modifying the hydrology of larger areas are detrimental to the Pantanal environment and should be controlled. Large projects, such as the canalization of the Paraguay River (Projeto Hidrovia), would be catastrophic for the Pantanal, as they will adversely impact large areas and their ecological functions (Hamilton 2002), modify the biodiversity, and alter the spatial arrangement of the macrohabitats in the affected areas. According to Ponce, (1995) the periodically flooded area (30%) of the Pantanal cover be eliminated.

Exotic grasses (*Urochloa decumbens* (Stapf) R.D. Webster, flood sensitive and *Urochloa humidicola* (Rendle) Morrone & Zuloaga, flood resistant) were introduced several decades ago to improve pasture quality and productivity. These areas were included as a specific macrohabitat (Macrohabitat 6.2.6). The influence of the grasses on the herbaceous stratum of native plants is already evident in several regions of the Pantanal. The presence of these exotics is irreversible and further studies are needed to understand their impact on the ecosystem better and to develop management options (Rebellato 2010).

Also, new areas adjacent to the floodplain are being drained for agricultural use (Macrohabitat 6.2.7), and older areas adjacent to the floodplain are being abandoned (Macrohabitat 6.2.8). The former divert water to supply mainly rice and corn plantations, thus severely changing the hydrology, the land micro-relief, and the natural plant communities. Abandoned agricultural plots are located mainly in the region of Miranda, Mato Grosso do Sul, except rice, rotated with native pasture. They are degraded areas with modified hydrology and micro-relief as well as substitution by secondary vegetation of herbaceous plants and shrubs. Dense stands of *Vernonanthura* spp. are frequent. Later, pioneer trees such as *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore (*paratudo*), and *Handroanthus heptaphyllus* (Vell.) Mattos (*piúva-do-campo*) enter the area.

7.4 Conclusions and Recommendations

The macrohabitat classification presented in this article is based on hydrological and botanical parameters. An inventory of higher plants of the Pantanal indicates the occurrence of 1903 species (Pott and Pott 1999). Currently, this number probably has increased to 2,000 species (see also Chap. 3 on checklist). Of the 1,903 species, 900 are herbaceous plants, among them 138 climbers, 11 epiphytes, and 15 parasites. 247 species are considered aquatic macrophytes, corresponding to 13 % of the total species number. The remaining 1,656 species, including all woody plants, are distributed in periodically flooded and permanently terrestrial areas, building the large number of macrohabitats. Species and characteristic plant and animal communities are associated with specific macrohabitats. Many animal species use different macrohabitats sometimes in different periods for feeding, relaxing or breeding. Therefore, the removal of a specific macrohabitat does affect not only the permanent residents but also many temporary visitors.

The Pantanal has a geo-ecological history of about 2.5 million years. The large majority of the actual geological formations is related to its genesis and is a result of paleoclimatic and paleogeographic changes occurring since the end of the Pleistocene (Ab'Saber 1988; Assine 2005). Major paleoclimatic changes resulted in several dryer and wetter periods that gave rise to the Pantanal complex, small-scale relief and the geomorphological basis of its large macrohabitat diversity. Only the areas along the river channels consist of recent sediments, as most of the Pantanal belongs to a paleo-floodplain made up of sediments strongly modified and lixiviated by the heavy rains that inundate the region (Assine et al. 2018).

Because of its large area, the Pantanal is composed of many sub-regions differing in their patterns of precipitation and influenced by rivers with different hydrological regimes. These rivers have formed large alluvial fans inside the Pantanal. They are composed of recent active parts and older, inactive parts, built during periods of different paleo-climatic conditions. These landscapes provide different environmental conditions for specific plant communities. The most recent information on the geology, geomorphology, and paleo-climate of the Pantanal can be found in Bergier and Assine (2016).

During recent decades, sedimentation processes were strongly accelerated by the increase in sediment load transported to the Pantanal from the surrounding uplands, due to the increased erosion of the soils as a result of agricultural activities. The most dramatic example is the Taquari River, which exceeded its channel, inundating the adjacent floodplain and modifying the vegetation over an area covering approximately 11,000 km^2 of its alluvial fan. The consequences on the vegetation have yet to be formally studied, but large, formerly macrohabitat-rich areas have clearly been transformed into monotonous hypoxic communities of floating aquatic macrophytes, which in part will become anoxic floating islands. Any new macrohabitat, which may arise from these changes, can easily be incorporated in the updated classification system presented here, as shown by the inclusion of various macrohabitats unique to Mato Grosso do Sul. Since many parts of the Pantanal must still be studied and considering the increase in human activities, another reform of the classification system may be necessary in a few years.

The discussion surrounding a proposed federal law for the Pantanal based on scientific knowledge also stimulated discussions on the classification of macrohabitats and the value of this classification system for the sustainable management and protection of the area. Macrohabitats as "management units," for instance in the Cadastro Ambiental Rural, were considered by representatives of agribusiness as too complex to be used in practice. However, a survey showed that a large majority of the macrohabitats established by the scientists were also recognized by ranchers of the Pantanal of Poconé (Duarte et al. 2017). Furthermore, the values attributed to the macrohabitats by the ranchers for cattle, wildlife, and fisheries were the same as those conferred by the scientists (Duarte et al. 2017). The recognition of the macrohabitats and their values by the ranchers, who own more than 90% of the Pantanal, increases the acceptance by the local population and underlines the practicality of the classification system (Junk et al. 2018). The applicability, however, depends also on the mapping of the macrohabitats, which is a complex task because of their small sizes.

The maintenance of macrohabitat diversity is a key element in the maintenance of the many ecosystem services provided by the Pantanal to the local population and society in general (Junk 2017). Low-density traditional cattle ranching takes these aspects into consideration. Any attempt to introduce intensive management methods, such as used in the highlands, into the complex environment of the Pantanal will seriously damage its ecological integrity.

In the Brazilian Pantanal, only about 5% of the area is under full protection in conservation units. These areas include the National Parks, Biological Reserves, and Private Reserves of Natural Patrimony. That is certainly insufficient. Indeed, according to Lourival et al. (2009) and Ide et al. (2012), at least 20% of the Pantanal should be fully protected. An analysis of four existing programs for the protection of the Pantanal concluded that none of the scenarios met the objective of protecting the habitats and their biodiversity in the target areas (Lourival et al. 2009). Close cooperation with traditional ranchers, the tourism sector, and non-governmental organizations involved in environmental protection will ensure the sustainable use of the natural resources of the Pantanal.

To reach sustainable use of the Pantanal, an interstate proposal should be forwarded that includes financially rewarding stakeholders who maintain all categories of the Pantanal environmental services, such as the maintenance of native pastures and forests as well as sustainable fish stocks; climate regulation; water purification; biodiversity conservation; and the maintenance of macrohabitat diversity (Junk 2017). The inclusion of local stakeholders in environmental protection (1) is cheaper and more efficient than purely governmental actions, (2) increases the local population's acceptance of environmental protection actions, and (3) builds a dense network of protected areas in the entire Pantanal that complements other governmental activities such as national parks and other permanently protected areas (APPs).

References

Ab'Saber AN (1988) O Pantanal Mato-grossense e a teoria dos refúgios. Rev Bras Geogr 50:9–57

Allem AC, Valls JFM (1987) Recursos forrageiros nativos do Pantanal Mato-Grossense. Brasília-DF, Embrapa-Cenargen, Documentos 8, 339p

Almeida TIR, Fernandes E, Mendes D, Sígolo JB (2011) Distribuição espacial de diferentes classes de lagoas no Pantanal da Nhecolândia, MS: uma contribuição ao estudo de sua compartimentação e gênese. In: Anais 1 Simpósio de Geotectonias – Pantanal. Embrapa Informática Agropecuária/INPE, p 155–164

Amador GA, Damasceno-Júnior GA, Casagrande JC, Sartori ALB (2012) Structure of two communities dominated by Copernicia alba and associations with soil and inundation in Pantanal wetland, Brazil. Oecologia Australis 16(4):846–858

Arieira J, Nunes da Cunha C (2006) Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae) no Pantanal Norte, MT, Brasil. Acta Bot Bras 20:568–580

Assine ML (2003) Sedimentação na bacia do pantanal mato-grossense, Centro Oeste do Brasil. Tese (de Livre Docência). Universidade Estadual Paulista. 105p

Assine ML (2005) River avulsions on the Taquari megafan, Pantanal wetland, Brazil. Geomorphology 7(3–4):357–371

Assine ML, Merino ER, Pupim FN, Azevedo Macedo H, Santos MGM (2015) The Quaternary alluvial systems tract of the Pantanal Basin, Brazil. Braz J Geol 45:475–489

Assine ML, Bergier I, Macedo HA, Pupim FN, Stevaux C, Silva A (2018) Anatomia funcional da paisagem. Ciência Pantanal 4:12–19

Bacani VM, Sakamoto AY (2007) Evolução do uso e ocupação do solo no Pantanal da Nhecolândia, MS, Brasil. Revista Eletrônica da associação dos Geógrafos Brasileiros 1:81–102

Bao F (2017) A vegetação campestre em gradientes inundáveis: composição florística, dinâmica do banco de sementes e de plântulas. Tese (em Ciências Biológicas – Biologia Vegetal). Universidade Estadual Paulista. 170p

Barbiéro L, Queiroz Neto JP, Ciornei G, Sakamoto AY, Capellari B, Fernandes E, Valles V (2002) Geochemistry of water and ground water in the Nhecolândia, Pantanal of Mato Grosso, Brazil: variability and associated processes. Wetlands 22:528–540

Bergier I (2013) Effects of highland land-use over lowlands of the Brazilian Pantanal. Sci Total Environ 463:1060–1066

Bergier I, Assine ML (2016) Dynamics of the Pantanal Wetland in South America. Springer. 243p

Bergier I, Krusche A, Guérin F (2016) Alkaline lake dynamics in the Nhecolândia landscape. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal Wetland in South America. Springer, pp 145–161

Brum PAR, Sousa JC (1985) Níveis de nutrientes minerais para gado, em lagoas (baías e salinas) no Pantanal Sul Mato-grossense. Pesqui. Agropecu. Bras. 20(12):1451–1454

Calheiros DF, Oliveira MD (1999) Pesquisa Limnológica no Pantanal: uma revisão. Acta Limnol. Brasil. In: Anais do II Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal. Embrapa-CPAP, Documentos, p 115–125

Carvalho NO (1986) Hidrologia da Bacia do Alto Paraguai. In: Anais do I Simpósio sobre Recursos Naturais e Sócio-Economico do Pantanal. Embrapa, p 43–49

Coelho IP (2006) Relações entre barreiros e a fauna de vertebrados no nordeste do Pantanal, Brasil. Dissertação (em Ecologia). Universidade Federal do Rio Grande do Sul. 56p

Duarte TG (2007) Florística, Fitossociologia e Relações Solo-Vegetação em Floresta Estacional Decidual em Barão de Melgaço, Pantanal de Mato Grosso. Tese (Botânica), Universidade Federal de Viçosa. 162p

Duarte TG, Nunes da Cunha C, Junk WJ (2017) Reconhecimento e apreciação da classificação dos macrohabitats do Pantanal Mato-grossense por pantaneiros de Poconé–MT. In: Nunes da Cunha C, Arruda EC, Junk WJ (Orgs.). Marcos Referenciais para a Lei Federal do Pantanal e gestão de outras áreas úmidas. EdUFMT, Carlini & Caniato, p 81–97

Eiten G (1972) The cerrado vegetation of Brazil. Bot Rev 38:201–341

Evans TL (2013) Habitat mapping of the Brazilian Pantanal using synthetic aperture radar imagery and object based image analysis. Dissertation (Dissertation in Science), University of Victoria, 173p

Fellerhoff C, Voss M, Wantzen K (2003) Stable carbon and nitrogen isotope signatures of decomposing tropical macrophytes. Aquat Ecol 37:361–375

Ferraz de Lima JA (1987) A pesca no pantanal de Mato Grosso (Rio Cuiabá: a importância dos peixes migradores). Acta Amazônica 16(17):87–94

Figueiredo DM, Dores EFG, Paz AR, Souza CF (2012) Availaility, uses and management of water in the Brazilian Pantanal. In: Ioris AAR (Org.). Topical wetland management: the South-American Pantanal and the international experience. 1 ed. Ashgate Publishing Company. p 59–98

Franco M, Pinheiro R (1982) Geomorfologia, In: Brasil. Ministério das Minas e Energia Secretaria Geral. Projeto RADAMBRASIL. Folha SE.21 – Corumbá e parte da Folha SE.20 Rio de Janeiro (Levantamento de Recursos Naturais, 27)

Furian S, Martins ERC, Parizotto TM, Rezende-Filho AT, Victoria RL, Barbiéro L (2013) Chemicaldiversity and spatial variability in myriad lakes in Nhecolândia in the Pantanal wetlands of Brazil. Limnol Oceanogr 58:2249–2261

Galdino S, Vieira LM, Pellegrin LA (2006) Impactos ambientais e socioeconômicos na bacia do Rio Taquari – Pantanal. Embrapa Pantanal. 356p

Guerreiro RL, McGlue MM, Stone JR, Bergier I, Parolin M, Caminha SFS, Warren LV, Assine ML (2018) Paleoecology explains Holocene chemical changes in lakes of the Nhecolândia (Pantanal-Brazil). Hydrobiologia 815:1–19

Güntzel AM, Panarelli EA, da Silva WM, Roche KF (2010) Influence of connectivity on Cladocera diversity in oxbow lakes in the Taquari River floodplain (MS, Brazil). Acta Limnol Bras 22(1):93–101

Hamilton SK, Sippel SJ, Melack JM (1996) Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. Archiv fur Hydrobiologie 137:1–23

Hamilton SK (2002) Human impacts on hydrology in the Pantanal wetland of South America. Water Sci Technol 45(11):35–44

Ide CN, Gonçalves FV, Lastoria G, Val HC, Silva JB, Steffen JL, Val LAA, Ribeiro ML, Gabas SG, Broch SAO (2012) Soil and water conservation in the Upper Paraguai River basin: examples from Mato Grosso do Sul, Brazil. In: Ioris AAR (Org.). Topical Wetland Management: the South-American Pantanal and the international experience. 1 ed. Ashgate Publishing Company. p. 99–172

Irion G, Buchas H, Junk WJ, Nunes da Cunha C, Morais JO, Kasbohm J (2011) Aspects of the geological and sedimentological evolution of the Pantanal plain during the Pleistocene. In: Junk WJ, da Silva CJ, Nunes da Cunha C, Wantzen KM (Orgs.). The pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft. p 47–70

Junk WJ (2017) Ecoturismo: uma opção de manejo sustentável para o Pantanal? In: Irigaray CTJH, Braun A, Irigaray M (Orgs.). Pantanal legal: a Tutela Jurídica das Áreas Úmidas e do Pantanal Mato-Grossense. EdUFMT, Carlini & Caniato Editorial

Junk WJ, Piedade MTF (1997) Plant life in the floodplain with special reference to herbaceous plants. In: Junk WJ (ed) The Central Amazon floodplain: ecology of a pulsing system, Ecological studies, vol 126. Springer, pp 147–186

Junk WJ, Wantzen CM (2004) The flood pulse concept: new aspects, approaches and applications – an update. In: Welcomme R, Petr T (eds) Proceedings of the 2nd Large River Symposium (LARS), Pnom Penh, Cambodia [Food and Agriculture Organization & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 2004/16]: 117–149.

Junk, WJ, Wittmann F, Schöngart J, Piedade MTF (2015) A classification of the major habitats of Amazonian black-water river floodplains and a comparison with their white-water counterparts. Wetlands Ecology and Management 23(4):677–693

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain-systems. Can Spec Publ Fish Aquat Sci 106:110–127

Junk WJ, Piedade MTF, Lourival R, Wittmann F, Kandus P, Lacerda LD, Bozelli RL, Esteves FA, Nunes da Cunha C, Maltchik L, Schöngart J, Schaeffer-Novelli Y, Agostinho AA (2014a) Brazilian wetlands: their definition, delineation, and classification for research, sustainable management, and protection. Aquat Conserv Mar Freshw Ecosyst 24(1):5–22

Junk WJ, Piedade MTF, Lourival R, Wittmann F, Kandus P, Lacerda LD, Bozelli RL, Esteves FA, Nunes da Cunha C, Maltchik L, Schoengart J, Schaeffer-Novelli Y, Agostinho AA, Nóbrega

RLB (2014b) Parte I: Definição e Classificação das Áreas Úmidas (AUs) Brasileiras: Base Científica para uma Nova Política de Proteção e Manejo Sustentável. In: Nunes da Cunha C, Piedade MTF, Junk WJ (Orgs.). Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats. EdUFMT. p 13–76

Junk WJ, Piedade MTF, Nunes da Cunha C, Wittmann F, Schöngart J (2018) Macrohabitat studies in large Brazilian floodplains to support sustainable development in the face of climate change. Ecohydrol Hydrobiol 18:334–344

Lourival R, Mccallum H, Grigg G, Arcangelo C, Machado R, Possingham H (2009) A systematic evaluation of the conservation plans for the Pantanal Wetland in Brazil. Wetlands 29:1189–1201

McGlue MM, Guerreiro RL, Bergier I, Silva A, Pupim FN, Oberc V, Assine ML (2017) Holocene stratigraphic evolution of saline lakes in Nhecolândia, southern Pantanal wetlands (Brazil). Q Res 88:472–490

Medina-Júnior PB, Rietzler AC (2005) Limnological study of a Pantanal saline lake. Braz J Biol 65(4):651–659

Mourão GM, Ishii IH, Campos ZMS (1988) Alguns fatores limmnológicos relacionados com a ictiofauna de baías e salinas do Pantanal da Nhecolândia, MS, Brasil. Acta Limnol Bras 2:181–198

Nunes da Cunha C, Junk WJ (2001) Distribution of wood plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. Int J Ecol Environ Sci 27:63–79

Nunes da Cunha C, Junk WJ (2004) Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. Appl Veg Sci 7:103–110

Nunes da Cunha C, Junk WJ (2014) A Classificação dos Macrohabitats do Pantanal Mato-grossense. In: Nunes da Cunha C, Piedade MTF, Junk WJ (Orgs.). Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats. EdUFMT. p 77–122

Nunes da Cunha C, Junk WJ (2017) Classificação dos macrohabitats do Pantanal matogrossense para fins de gestão. In: Nunes da Cunha C, Arruda EC, Junk WJ (eds) Marcos Referenciais para a Lei Federal do Pantanal e Gestão de Outras Áreas Úmidas. EdUFMT, Carlini&Caniato, p 73–79

Oliveira PC (2009) Banco de sementes de campos savânicos inundáveis no Pantanal de Mato Grosso. Dissertação (em Ecologia e Conservação da Biodiversidade). Universidade Federal do Mato Grosso. 79p

Oliveira APG, Ribeiro AA, Wassouf Junior ER, Souza GF, Bernadi I, Penatti NC, Almeida TIR, Paranhos Filho AC (2011) Uso de Sensoriamento Remoto na quantificação das lagoas do Pantanal da Nhecolândia, Mato Grosso do Sul. In: Anais XV Simpósio Brasileiro de Sensoriamento Remoto – SBSR. INPE, p 369

Pivari MO, Pott VJ, Pott A (2008) Macrófitas aquáticas de ilhas flutuantes (baceiros) nas sub-regiões do Abobral e Miranda, Pantanal, MS, Brasil. Acta Botanica Brasilica 22(2):563–571

Ponce VM (1995) Hydrological and Environmental Impact of the Paran'a-Paraguay Waterway on the Pantanal of Mato Grosso (Brazil). San Diego State University, San Diego, 125p

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa. 320p

Pott A, Pott VJ (1999) Flora do Pantanal, listagem atual de Fanerógamas. In: Anais II Simpósio sobre Recursos Naturais e Socio-econômicos do Pantanal, Corumbá, 1996. Corumbá: Embrapa. pp 297–325

Pott A, Nunes da Cunha C, Pott JV, Silveira EA, Sartori ALB (2001) Avaliação Ecológica Rápida Componente Botânica Parque Nacional do Pantanal Mato-grossense e Entorno. Plano de Manejo do Parque Nacional do Pantanal Mato-grossense. ANEXO 4

Prado DE (1993) What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco, V. Candollea 48(1):145–172

Rebellato L (2010) Padrões sazonais e espaciais de distribuição e diversidade de herbáceas no Pantanal de Poconé-MT. 2010. Doutoral thesis. Ecologia (Conservação e Manejo da Vida Silvestre) Universidade Federal de Minas Gerais

Rebellato L, Nunes da Cunha C (2005) Efeito do "fluxo sazonal mínimo da inundação" sobre a composição e estrutura de um campo inundável no Pantanal de Poconé, MT, Brasil. Acta Botanica Brasilica 19:789–799

Rebellato L, Nunes da Cunha C, Figueira JEC (2012) Respostas da comunidade herbácea ao pulso de inundação no Pantanal de Poconé, Mato Grosso. Oecologia Australis 16:797–818

Sakamoto AY (1997) Dinâmica hídrica em uma lagoa “salina” e seu entorno no pantanal da Nhecolândia: Contribuição ao estudo das relações entre o meio físico e a ocupação, fazenda São Miguel do Firme, MS. Tese (doutorado na Faculdade de Filosofia, Letras e Ciências Humanas). Universidade de São Paulo. 183p

Santos SA, Crispim SMA, Comastri Filho JA, Pott A, Cardoso EL (2005) Substituição de Pastagem Nativa de Valor Nutritivo por Forrageiras de Melhor Qualidade no Pantanal. Circular Técnica, 62. Embrapa Pantanal. ISSN 1517-1965. 5p

Santos KRDS, Rocha ACR, Sant’Anna CL (2012) Diatoms from shallow lakes in the Pantanal of Nhecolândia, Brazilian wetland. Oecologia Australis 16:756–769

Schessl M (1999) Floristic composition and structure of floodplain vegetation in the northern Pantanal of Mato Grosso, Brazil. Phyton 39:303–338

Schmitz PI, Rogge JH, Rosa AO, Beer MV (1998) Aterros indígenas no Pantanal do Mato Grosso do Sul. Instituto Anchietano de Pesquisas. 270p

Silva JSV, Abdon MM, Boock A, Silva MP (1998) Fitofisionomias dominantes em parte das sub-regiões do Nabileque e Miranda, Sul do Pantanal. Pesquisa Agropecuária Brasileira 33:1713–1719

Silva MP, Mauro R, Mourão G, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Revista Brasileira de Botânica 23(2):143–152

Soares JJ, Oliveira AKM (2009) O paratudal do Pantanal de Miranda, Corumbá-MS, Brasil. Revista Árvore 33(2):339–347

Veloso PH, Góes-Filho L (1982) Fitogeografia Brasileira. Classificação fisionômica-ecológica da vegetação neotropical. Boletim Técnico Projeto RADAMBRASIL, Série Vegetação. 85p

Wilhelmy H (1958) Umlaufseen and dammuferseen tropischer Tiefland flusse. Zeitschr für Geomorphologie, N.F. 2:27–54

Zeilhofer P (1996) Geooekologische Charakterisierung des noerdlichen Pantanal von Mato Grosso. Brasilien, Anhand Multitemporaler Landsat Thematic Mapper-Daten. Herbert Utz-Verlag, Muenchen

Chapter 8
Monodominant Stands in the Pantanal

Geraldo Alves Damasceno-Junior, Rosa Helena da Silva, Darlene Gris, Evaldo Benedito de Souza, Maíra da Rocha, Daniel Armando Manrique Pineda, Gisaine de Andrade Amador, Allan Henrique de Almeida Souza, Jens Oldeland, and Arnildo Pott

8.1 Introduction

Monodominance is defined as the phenomenon that a single species, in comparison to all other species in the stand, covers most of the area of the stand. For some authors, this limit is more than 50% (Connell and Lowman 1989), and for others, over 60% (Torti et al. 2001). Other related terms are oligodominant or mono-oligodominant, and hyperdominant, as, e.g., applied to 227 tree species of the Amazon rain forest which together account for half of all trees (ter Steege et al. 2013). Monodominance is commonly found outside the tropics in biomes such as Taiga (Rozhkov and Shvidenko 2010). In the tropics, monodominant stands occur, e.g., in Central Africa, Malaysia (Peh et al. 2011), New Guinea, Costa Rica, Guyana,

---

G. A. Damasceno-Junior (✉) · R. H. da Silva · E. B. de Souza · D. A. Manrique Pineda · G. d. A. Amador · A. H. de Almeida Souza · A. Pott
Laboratório de Ecologia Vegetal, Instituto de Biociências, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil

D. Gris
Laboratório de Ecologia Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

Grupo de Pesquisa em Ecologia Florestal – Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, AM, Brazil

M. da Rocha
Laboratório de Ecologia Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

MAUA Working Group, National Institute for Amazonian Research (INPA), Manaus, Amazonas State, Brazil

J. Oldeland
Biodiversity, Evolution, and Ecology of Plants, Institute of Plant Sciences and Microbiology, University of Hamburg, Hamburg, Germany

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_8

Panama, and Brazil (Connell and Lowman 1989; Nascimento and Proctor 1997a; Marimon et al. 2001). Monodominance has interested researchers for decades, especially in the tropics where it contrasts with highly diverse forest stands in which 1 ha may harbor more than 900 species (Wilson et al. 2012; ter Steege et al. 2019).

The causes of monodominance in tropical environments have been attributed to many features (Hart et al. 1989). Peh et al. (2011) reviewed the causes of classical monodominance in tropical forests and distinguished between ecological and evolutionary explanations. As ecological causes, they highlighted, for example, shade tolerance and seedling survival under a closed canopy (Torti et al. 2001) and slow decomposition rates that lead to a low nutrient availability. As evolutionary causes, they highlighted, for example, large seeds to overcome deep leaf litter, or ectomycorrhizal association, and masting that leads to predation satiation. Other ecological causes are associated with edaphic features such as higher levels of soil fertility (Van Der Velden et al. 2014) or with a high concentration of particular ions such as Mg in the soil, e.g., *Peltogyne gracilipes* in Amazonia (Nascimento and Proctor 1997b). Another feature that is related to local monodominance in hyperdiverse forests such as Amazonia is the coppicing ability (ter Steege et al. 2019). In most cases, the causes of monodominance are a combination of different features (Peh et al. 2011). In seasonally flooded environments, monodominance has been primarily attributed to inundation (Nascimento and Cunha 1989; Arieira and Nunes da Cunha 2006; Ribeiro and Brown 2006), as in the case of *Tabebuia cassinoides* (Lam.) DC. in the south and southwest of Brazil (Galvão et al. 2002; Kolb and Joly 2009), *Vochysia divergens* in the Pantanal (Nascimento and Cunha 1989), *Prioria copaifera* in Central America (Lopez and Kursar 1999), *Taxodium distichum* in the USA (Mitsch et al. 1991), and *Melaleuca quinquenervia* in Australia (Franklin et al. 2007). The latter also became a dominant invasive in the Everglades in Florida (Richardson 2010). Most publications on monodominant stands are about trees and shrubs, but there are also herbaceous species (Rocha et al. 2015).

The Pantanal is, perhaps, the richest tropical floodplain in the world in terms of monodominant stands. In this chapter, we have recorded about 27 species that can be considered monodominant in parts of the Pantanal wetland.

The suffix “al” is a collective used in the Portuguese language that means “a lot/many.” This suffix is popularly used to name most of these formations in the Pantanal, and the inhabitants have a local name for each one of them. For example, a monodominant stand formed by the tree *Tabebuia aurea*, locally known as *paratudo*, is called *Paratudal*.

The most conspicuous monodominant stands in the Pantanal are formed by the trees and shrubs *Erythrina fusca*, *Tabebuia aurea*, *Handroanthus heptaphyllus*, *Vochysia divergens*, *Byrsonima cydoniifolia*, *Leptobalanus parvifolius*, *Couepia uiti*, and *Combretum laxum*. Herbaceous species, mostly grasses and sedges, are also common as monodominant, and we highlight *Oryza latifolia*, *O. rufipogon*, *Hymenachne amplexicaulis*, *H. pernambucensis*, *Paspalum repens*, *Cyperus giganteus*, *Typha domingensis*, *Elionurus muticus*, and *Andropogon hypogynus*. Among these, the only species with dominance not related to inundation is *E. muticus*; in extremely sandy areas, it is inundated only in exceptional flooding events. The final group of monodominant species in the Pantanal are the palms, mainly *Copernicia alba*, *Attalea phalerata*, *A. speciosa*, and *Mauritia flexuosa*. The first one is associated with the most floodable environments, the second occurs in intermediately floodable conditions, the third only occurs on well-drained soils, and the latter occurs on wet but relatively well-aired soils.

A frequent feature of Pantanal monodominant species are grayish (*B. cydoniifolia*, *C. alba*, *C. uiti*, *L. parvifolius*, *Paspalum carinatum*, *T. aurea*, *Zanthoxylum rigidum*), light-green (*A. hypogynus*, *E. muticus*, *H. pernambucensis*), or dark-green but very shiny leaves (*Eichhornia* spp., *V. divergens*), common in pioneer and heliophilous plants, interpreted as an adaptation to excessive sunlight (radiation load). The only shade-tolerant species are *A. phalerata*, *A. speciosa*, and *C. laxum*. *Cecropia pachystachya*, a pioneer species, forms monodominant patches in post-burn gaps (Arruda et al. 2016); it also has light-green leaves. The erect green shoots of the monodominant *Cyperus giganteus* and *Typha domingensis* are aerial stems, with shiny leaves.

In this chapter, we will describe the common species and the landscapes of these monodominant stands in the Pantanal, with information from the literature when available and, in many cases, including our field observations.

8.2 Monodominant Trees and Shrubs

8.2.1 **Tabebuia aurea** *(Silva Manso) Benth. & Hook.f. ex S.Moore (Bignoniaceae) – "Paratudo"*

Tabebuia aurea is a tree of 7–15 m in height with a trunk of 20–50 cm (or even more) in diameter at breast height. It has a thick bark (3–4 cm) and yellow flowers that mainly bloom in August/September and which create a unique landscape when the monodominant formation, locally known as *Paratudal*, is flowering (Fig. 8.1). This species is native to Argentina, Paraguay, Bolivia, Suriname, Peru, and Brazil and is cultivated as an ornamental in many countries such as the USA, French Polynesia, and India (GBIF 2019a). It occurs in savannas with well-drained soils such as the Cerrado vegetation, Caatinga, seasonally flooded areas such as riparian forests, and seasonally flooded savannas, forming monodominant stands (Pott and Pott 1994). Inside the Cerrado domain, it has as a characteristic tortuous trunk, and it occurs on deep to shallow soils with rocky outcrops, being recorded by Ratter et al. (2003) in 67% of 376 sample plots in the Cerrado domain. In flooded areas, it presents a straighter trunk, though it keeps a similarly thick corky bark to protect against fire. In Cerrado areas, this species occurs on soils with pH from 4 to 5, a low fertility, and a high aluminum saturation (Ribeiro and Brown 2002).

Tabebuia aurea monodominant stands are recorded in the Brazilian Pantanal and Paraguayan Chaco (Pott and Pott 1994), occurring on soils with a medium to high fertility and a low aluminum saturation (Ribeiro and Brown 2002), being flooded

Fig. 8.1 Monodominant stand of *Tabebuia aurea* (*Paratudal*), flowering, on the Miranda River floodplain. (Picture by Adriano Afonso Spielmann)

from 30 to nearly 180 days per year (Bueno et al. 2014) with flooding levels ranging from 0.4 to 2.25 m (near riverbanks) (Manrique-Pineda et al. 2021). These stands cover 1.7% of the total Pantanal area and are more frequent in subregions bordering the Chaco biome, such as Nabileque (covering 14%), Miranda (6.4%), and Abobral (3.5%) (Silva et al. 2000) (see the chapter on "Vegetation Mapping" Chap. 2).

The most curious aspect of this monodominant species is that its occurrence is associated with small earth mounds that permit it to escape higher levels of inundation. These small earth mounds are locally called *murundus*, in general varying from 0.035 to 0.95 m in height (Manrique-Pineda et al. 2021), sometimes more (Fig. 8.2). They are different from the *murundus* that occur in Central Brazil but both usually occur spread over grasslands (Neto et al. 1986; Oliveira-Filho 1992). Not all *T. aurea* individuals grow on earth mounds, especially not in less inundated areas. Depending on the location, each earth mound has one *T. aurea* tree, but this can vary, as well as a few other trees and shrubs. At the landscape scale, *T. aurea* individuals occur only on *murundus* in lower and more flooded areas and without *murundus* in higher parts of the landscape. These murundus protect *T. aurea* populations from fire and flood in areas with a high frequency of fire and high levels of inundation (Manrique-Pineda et al. 2021). The origin of these *murundus* is not yet well studied and clarified. In the Pantanal, there are *murundus* of biotic (ants, termites, earthworms, and humans) and abiotic (hydrological/geomorphological action) origin (Werger 1983; Ponce and Nunes da Cunha 1993). Some authors have mentioned the possible biotic origin of these *murundus* in *Paratudal* (Soares and Oliveira 2009). In preliminary observations, we found murundus with and without termites but we did not see a behavior that could be related to the origin of all these earth mounds. That must be better investigated. However, this edaphic fauna

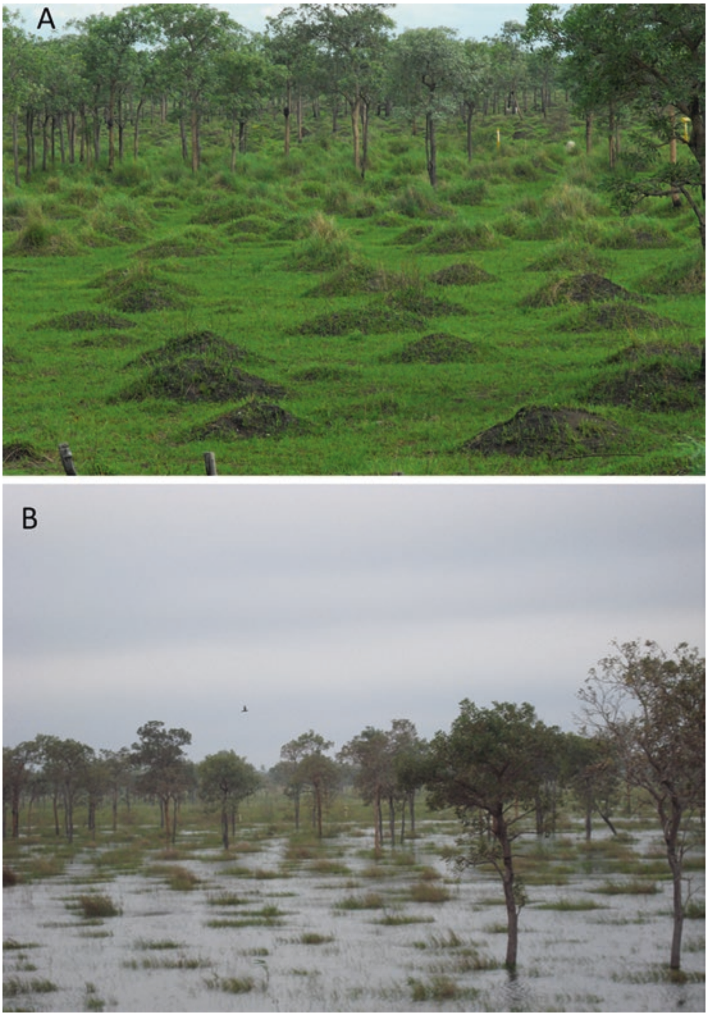


Fig. 8.2 Earth mounds (*murundus*) with monodominant stands of *Tabebuia aurea* in the subregion of Miranda, Pantanal. (**a**) During the dry season, after a fire (Picture by Paulo Robson de Souza). (**b**) During the wet season. (Picture by Geraldo Alves Damasceno-Junior)

probably contributed to the better soil structure of the mound top compared with the in-between heavy clay. One noteworthy aspect is that in many subregions where *murundus* occur, such as Miranda and Abobral, the floodplain is more erosive than depositional (M. Assine, pers. comm.). Thus, it is possible that the *murundus* of these *Paratudal* stands have their origin in differential erosion, where over many generations of trees their root system could have avoided sediment loss at that point. Indeed, cattle trampling at their sleeping sites can also flatten *murundus*, and trees can bend over or fall. A striking adaptation to the expansive clays is the very ramified and superficial type of the root system in *T. aurea* rather than the usual deep taproot in these trees.

The flowering and fruiting of this species is massive, and thousands of seeds are produced every year (G.A. Damasceno-Junior pers. obs.). The seeds are anemochoric, and many do land among *murundus*, others on them, as well as on the road embankment, or some are first trapped by neighboring trees and then may drop on mounds. However, their seedlings do not survive flood, even when they grow on the *murundus* (Ribeiro and Brown 2006), whereas on the road they succeed. Thus, the recruitment is episodic and only occurs in years with low or without inundation, as shown by the dendrochronological analysis of growth rings (G.A. Amador, unpublished data). The Pantanal populations of *T. aurea* seem to be genetically adapted to such conditions. Once recruited, they can grow relatively faster than Cerrado genotypes and thus escape from the next inundation (Ribeiro and Brown 2006). Besides, the levels of herbivory in the Pantanal are lower than in Cerrado, and this also contributes to the massive recruitment of this species (Ribeiro and Brown 2006). This too might give those seedlings a minimal but as yet unknown size advantage to escape the negative effects of flooding. Probably because of these features, the population structure of this species is not the usual inverted J (Bueno et al. 2014). The growth of this species is negatively affected by El Niño-Southern Oscillation events (Leite 2012), as it does its recruitment in cohorts.

At 18 months of age, the seedlings of *T. aurea* already have a sort of lignotuber or xylopodium to resprout post-fire (Pott and Pott 1994). That is an important feature, because the subregions where these stands occur, Nabileque, Miranda, and Abobral, are among the most fire prone in the Pantanal, belonging to the corridor of fire and flood of the Pantanal (see the chapter on “Fire” Chap. 18). Monodominant stands of *T. aurea* in these subregions have a fire regime with a frequency that varies from 2 to 9 repetitions in an interval of 15 years. The combination of repeated fires and high levels of inundation favors the monodominance of this species (Manrique-Pineda et al. 2021). It also needs certain levels of Zn and K in the soil to maintain the high number of individuals (Damasceno-Junior et al. 2021).

These monodominant stands are of the species poorest in tree species, the numbers ranging from 6 to 13 in plots of 1.3 to 1.5 ha reaching 36 species in a sampling spread over an area of 40 km in radius (Soares and Oliveira 2009; Bueno et al. 2014; Manrique-Pineda et al. 2021). Some flood-tolerant companion trees are *Laetia americana*, *Phyllanthus chacoensis*, and *Prosopis rubriflora*. On the other hand, the richness of herbaceous species is high in this hyperseasonal savanna; a survey recorded 78 species, where *Microstachys hispida* and *Andropogon hypogynus* are the most important (Bueno et al. 2014). However, in multiannual dry periods, the grassland can be overtaken by shrubs and young trees of various species from adjacent/near dry forests, such as *Casearia aculeata*, which in wetter years are set back again.

8.2.2 Byrsonima cydoniifolia *A. Juss. (Malpighiaceae) – "Canjiqueira"*

Byrsonima cydoniifolia is a shrub or treelet of 1 to 6 m in height, very branched from the base (Fig. 8.3), with yellow flowers that mainly bloom from September to December (Pott and Pott 1994) and drupe fruits that disperse from September to April (Damasceno-Junior et al. 2010). This monodominant formation is locally known as *Canjiqueiral*. In South America, this species occurs in Bolivia, Paraguay, and Brazil, where it can be found from Mato Grosso do Sul and São Paulo to Maranhão States. Besides the Pantanal, it also occurs in the Cerrado and Caatinga domains (Mamede and Francener 2015), with records in the Amazonian domain and the Andean lowlands in Bolivia (up to 1500 m a.s.l.) (Missouri Botanical Garden 2015). It is always associated with sandy soils and is considered as an "invasive" plant by the Pantanal ranchers, because it can spread in flooded grasslands, shading out some grasses and increasing its dominance in dry years (Pott and Pott 1994). Monodominant savanna of *B. cydoniifolia* is recorded from seven subregions of the Pantanal. It covers 19.1% of the Nabileque subregion, 3.5% of Miranda, and 1.8% of Abobral and is less abundant in northern parts where it occurs with 0.8% in Cáceres and Poconé and 0.03% in Paiaguás subregions, covering 2.3% of the Brazilian Pantanal (Silva et al. 2000) (see the chapter on "Vegetation Types" Chap. 2). In the Abobral and Miranda subregions, these monodominant stands can also be found in ancient and sand-silted channels, occurring side by side with monodominant stands of *Tabebuia aurea* (Pott et al. 2011). In the Paiaguás and Poconé

Fig. 8.3 Monodominant stand of *Byrsonima cydoniifolia* (*Canjiqueiral*) on floodable grassland in the subregion of Abobral, Pantanal. The tree in the right foreground is *Tabebuia aurea*. (Picture by Paulo Robson de Souza)

subregions, it can also occur side by side with monodominant stands of *Curatella americana* (Padilha et al. 2008). It also occurs as monodominant in the Araguaia wetland in southern Amazonia (Marimon and Lima 2001).

Byrsonima cydoniifolia is pollinated by species of the Centridini (a tribe of large apid bees), mainly by *Epicharis nigrita*, a bee that collects only oil (Sazan et al. 2014), and builds an underground waterproof tube to nest (Gaglianone 2005), wherein it survives floods. This plant has a low self-compatibility, and most of its pollination comes from pollen carried over long distances. The apomixis is low, and the reproductive success comes mainly from cross-pollination (Sazan et al. 2014). One remarkable aspect of this species is that its massive fructification is not as much consumed by birds as expected (I.M. Ilha pers. comm.). This species is consumed by feral pigs (*Sus scrofa*) and fishes. When the massive fruiting occurs during the flood season, the fruits first sink and, after some time, they begin to ferment and float and are massively dispersed by water (G.A. Damasceno-Junior pers. obs.).

Byrsonima cydoniifolia can survive a fire, resprouting from the base, except when very young (Pott and Pott 1994). These authors also observed that this species is little browsed by cattle in the Pantanal, except new regrowth, which is a source of protein and minerals. Its leaf and bark extract has an allelopathic effect (Amador 2013). The richness of woody species in this *Canjiqueiral* formation is low; only nine species were found in a total of 3 ha sampled in the Miranda and Paraguai subregions. The main species besides *B. cydoniifolia* were *Tabebuia aurea*, *Handroanthus heptaphyllus*, and *Erythroxylum anguifugum* in the Miranda subregion (Amador 2013) and *Curatella americana*, *Terminalia corrugata*, and *Qualea parviflora* in the Paiaguás and Poconé subregions (Padilha et al. 2008). On the other hand, the herbaceous stratum is very rich, with 181 species from 120 genera and 36 botanical families recorded in two areas in the Miranda and Paraguai subregions. During the dry season, the species with the highest cover was *Richardia grandiflora* (Rubiaceae) and during flooding *Axonopus purpusii* (Poaceae) (Amador 2013).

Densities of *B. cydoniifolia* varied from 53 to 68 individuals per hectare (Amador 2013). The density of this species increases on soils with lower contents of Ca and Mg and higher levels of fine sand (Damasceno-Junior et al. 2010). Data on girth growth of this species analyzed from annual growth rings showed that in the Nhecolândia subregion, it grows nearly 0.33 to 0.99 cm.yr.$^{-1}$ and growth is faster during the first 9 years (Mattos et al. 2016). In the Poconé subregion, this species has a mean radial increment of 0.15 cm.yr.$^{-1}$, with the highest rate at 29 years old. It can reach a life span of 97 years (Costa 2013).

8.2.3 **Erythrina fusca** ***Lour. (Fabaceae) – "Abobreiro"***

In the floodplains of the Cáceres subregion, we recorded monodominant stands of the tree species *Erythrina fusca*, known as "Abobral" (Pott et al. 2011; Nunes da Cunha and Junk 2014), as this species is popularly known as *abobreiro* (and also as *eritrina* and *mulungu*) (Fig. 8.4). It is the most widespread species of the genus

Fig. 8.4 Flowering monodominant stand of *Erythrina fusca* on the margin of the Paraguay River, at low water, near the Taiamã Ecological Station (TES)

Erythrina, occurring in Oceania, Asia, Central and South America, and some islands in Africa (Russo and Baguinon 1997; Parrini and Raposo 2010). In Brazil, it occurs sparsely in riparian forests, mainly in the Pantanal and Amazonia; however, its occurrence as a monodominant is recorded along the banks of the Aquidauana River and covering larger areas in low-lying freshwater swamps in the Cáceres subregion, mostly at the Taiamã Ecological Station (TES) and nearby areas (Russo and Baguinon 1997; Pott et al. 2011).

Erythrina fusca is a deciduous, heliophytic, hygrophytic, and secondary pioneer tree and can reach 20–30 meters in height, but usually has only half that size in the Pantanal, with a globose crown, a short and very branched trunk with light, soft, and clear wood (Pott and Pott 1994; Lorenzi 2002). However, in the Pantanal, it behaves as a primary pioneer (Gris et al. 2020). Isolated trees can reach a basal stem diameter of over 80 cm.

This species has a rich connection with the fauna: the flowers are visited by 20 species of birds, most of them with destructive behavior. Among these species, the members of Trochilidae (hummingbirds) and Icteridae families and occasionally *Brotogeris chiriri* (Vieillot, 1818) are the possible pollinators (Parrini and Raposo 2010). The petals and seeds are food for birds such as *Saltator coerulescens* (Vieillot, 1871) and insects; and during pod dehiscence, the seeds fall into the water, being quickly ingested by fish (Pott and Pott 1994; Parrini and Raposo 2010).

At the TES, the monodominant stands of *E. fusca* are found on the banks of the Paraguay River and especially of the *Bracinho* (Paraguay River anabranch), in areas with low sediment loads, at undeveloped marginal levees, extending to the interior of the TES area (Nunes da Cunha and Junk 2014; Frota et al. 2018). Forests dominated by *E. fusca* may be subjected to floods up to 6 m deep and for up to 8 months (Nunes da Cunha and Junk 2014). In these stands, found near the Paraguay River and *Bracinho* anabranch, *E. fusca* dominates with approximately 77% of the number of trees in the community, coexisting with ten other species, while the herbaceous stratum is very homogeneous, dominated mainly by grasses such as *Hymenachne amplexicaulis* (Gris 2017). The occurrence of some tree species, such as *Calophyllum brasiliense* and *Alchornea discolor*, is related to the *E. fusca* patches in riparian forests of the Paraguay River (Olivo-Neto et al. 2020).

The dominance of *E. fusca* in this subregion of the Pantanal seems to be favored by the local environmental factors since it is tolerant of low soil fertility and higher flood levels; besides that, prolonged periods of flooding increase the germination rates of the species (Gris 2017). One feature that can further the monodominance is the strong allelopathic effect of this species. Leaf extracts of *E. fusca* reduced the percentage of germination and the germination speed index of *Lactuca sativa* seeds to a similar degree as the effect of 2,4-dichlorophenoxyacetic acid (which is a powerful herbicide) (Gris et al. 2019).

E. fusca has clear annual growth rings in its wood, and their analysis revealed that it is a very fast-growing species, with a maximum diameter increment of 1.6 cm/year at 7 years old. This was measured in individuals of up to 54 years old. In years with *El Niño*-Southern Oscillation (ENSO) events, the species reduces its growth rate (Gris et al. 2020). The recruitment of seedlings in this species appears to be reduced in years with a lower minimum inundation, and, as a consequence, the population structure of this species does not have an inverse J distribution of age (Gris et al. 2020). Larger cohorts are recruited in favorable years with a higher minimum inundation level. Thus, changes in global and local environmental conditions, mainly leading to decreases in flood levels (such as reduced rainfall or waterway and hydroelectric construction), can show drastic adverse effects on this unique monodominant formation.

8.2.4 **Leptobalanus parvifolius** *(Huber) Sothers & Prance (Chrysobalanaceae) – "Pimenteira"*

Leptobalanus parvifolius is a tree with usually branched trunks between 3 and 7 m tall, and apparently, it resprouts from its roots, as shown by a certain alignment of individuals (Fig. 8.5). It produces flowers from May to June, sometimes until November or February, with fruits mainly in October and December, consumed by birds and fishes during the flood, and abundant seeds (Pott and Pott 1994). It occurs from the south of Colombia and Venezuela to Bolivia and Central Brazil, including the Pantanal floodplain (GBIF 2020c). It occurs as a monodominant in the Pantanal and the Araguaia region that belongs to Amazonia (Pott and Pott 1994; Marimon and Lima 2001). In the Pantanal, these monodominant stands are called *Pimenteiral*. The species seems to be less frequent along the southern boundary of the Pantanal,

Fig. 8.5 Inside view of a monodominant stand of *Leptobalanus parvifolius*, known as *Pimenteiral*, with visible flood level marks on the barks of the trunks (see arrow) and apparent root sprouting as shown by a certain alignment. (Picture by Evaldo Benedito de Souza)

perhaps due to deficient records, while in the northern part, it usually occurs in association with *Vochysia divergens*. In the Poconé subregion, it has been mentioned as the most common species inside monodominant stands of *V. divergens*, and there it spreads rapidly in wet multi-year periods, invading native grasslands (Nunes da Cunha et al. 2007).

In the southern parts of the Pantanal, *L. parvifolius* can occur on earth mound edges and in riparian forests in association with *Inga vera*, or along seasonal streams forming a hedge, often associated with *Calophyllum brasiliense*. It is considered an invasive woody plant, undesired by ranchers (see the chapter on "Encroachment" Chap. 11). Despite being a riparian species, it may occur at fair distances from a river, just as its associated species *Combretum lanceolatum* and *Vochysia divergens* (Pott et al. 2011). *Leptobalanus parvifolius* can also be seen colonizing roadside drainage dykes, or occurring on the plains, along with *Couepia uiti*; then mostly *Leptobalanus parvifolius* dominates over *C. uiti*. The canopies of these monodominant stands are dense, and stands are little colonized by other trees or shrubs. Thus, in arrangements with older and higher trees, groups of *Leptobalanus* often are used as shelter by cattle and native fauna.

Leptobalanus parvifolius occurs on sandy and silty soils of low fertility (Arieira et al. 2016), often forming compact monodominant stands. Its habitat is characterized by intermittent water systems with periodically flowing water in areas that can stay flooded during 6–8 months. There it grows in linear arrangements, in association with woody plants such as *C. brasiliense*, *Erythroxylum anguifugum*, and *Alchornea discolor* (the local name of such a wooded groove is *landi*) (Pott and Pott 1994; Nunes da Cunha et al. 2007). But it can also occur at sites with a higher amplitude of flooding (Pott and Pott 1994). Thus, *L. parvifolius* is one of the most flood-tolerant monodominant species. *Leptobalanus parvifolius*, as well as some other monodominant species in the Pantanal, build stands that are considered evergreen pioneer forests under fluvial influence (also see the chapter on "Vegetation Types" Chap. 2).

The growth and dominance of *L. parvifolius* may be even faster and more vigorous than that of other common species in the Pantanal, such as *Vochysia divergens*, *B. cydoniifolia*, and *Combretum laxum*. In an experiment evaluating the growth of woody species in grasslands in the Poconé subregion, *L. parvifolius* was among those with the highest number of individuals and highest basal area after 7 years of protection against bovine cattle grazing (Nunes da Cunha and Junk 2004). The succession of this vegetation occurs sequentially over time but also depends on the frequency of fire and flood events which can change the direction of the events (Pott et al. 2011).

Physiologically, *Leptobalanus parvifolius* is a superior performer, with high photosynthetic rates during the dry season, compared with other monodominant flood-tolerant species such as *V. divergens* and *B. cydoniifolia* (Dalmagro et al. 2016). According to the authors, the species has the highest CO_2 ratio between intercellular space and environment, being highly efficient in water use during the dry season, and with a lower leaf water potential (1.9 MPa) than other species (e.g., *V. divergens*, *B. cydoniifolia*, *Curatella americana*, *Duroia duckei*, *Alchornea discolor*, and *Tocoyena formosa*). In contrast, *L. parvifolius* appeared to undergo both metabolic and stomatal limitations since the stomatal conductance declined in response to seasonal flooding (Dalmagro et al. 2016).

8.2.5 **Couepia uiti** *(Mart. & Zucc.) Benth. ex Hook.f. (Chrysobalanaceae) – "Pateiro"*

Couepia uiti is a South American species found in the Amazonian domain, but it is also quite frequent in the Cerrado and Caatinga (Brasil 2020). Often mentioned as a tree or treelet and sometimes as a shrub due to its plenty ramifications at the ground level (Fig. 8.6), *C. uiti* reaches 3–5 m in height with a crown width of up to 5 m. The crown is dense and low, often touching the ground. This characteristic protects it against fire, but younger individuals with undeveloped crowns are susceptible to fire. The crown is a shelter for duck, and from this originates its popular name *pateiro* (*pato,* meaning duck) (Pott and Pott 1994); a monodominant stand is called a *Pateiral*. It flowers from August to November. The primary pollinators are bees and wasps, and the fruits are produced only through cross-pollination (Paulino-Neto 2007). The *C. uiti* fruits have a creamy pulp, that is appreciated by the native fauna, and has high potential as food (Pott and Pott 1994) and can be used in culinary (Damasceno Junior et al. 2010).

Considered an invader of native pastures in several subregions (Allem and Valls 1987), *C. uiti* was evaluated as having a medium level of aggressiveness as an

Fig. 8.6 Dense ramification at the ground level in *Couepia uiti* in the subregion of Nhecolândia, Pantanal. (Picture by Evaldo Benedito de Souza)

Fig. 8.7 Monodominant stand of *Couepia uiti* with young (foreground) and adult (background) individuals spreading in floodable grasslands in the subregion of Abobral, Pantanal. (Picture by Evaldo Benedito de Souza)

invader (Junk and Nunes da Cunha 2012). However, in sandier subregions, some ranchers consider this species as the most unwanted invader, due to its rapid dispersion strongly increasing occupation from year to year (Allem and Valls 1987). Apart from not being grazed (Pott and Pott 1994), the shading of its dense and low canopy prevents the growth of grasses and makes it difficult for cattle to access the small clearings within formations of *C. uiti* (Fig. 8.7).

Fig. 8.8 *Couepia uiti* underground sprouting (c. 15 cm) 25 days after cutting in the subregion of Nhecolândia, Pantanal floodplain. (Picture by Evaldo Benedito de Souza)

The expansion of this species occurs during multiannual flood cycles in phases with extended flood periods (Pott and Pott 1994; Santos and Comastri Filho 2012). *C. uiti* spreads on lower flooded areas, mainly in the flood channels and seasonal streams (*corixos* and *vazantes*), on riverbanks, and in swamps (Allem and Valls 1987; Pott and Pott 1994). It is generally dominant in sandy areas on riverbanks (Prance and Schaller 1982) forming narrow groves, or even spreading across the grasslands in large patches, a few hundred meters wide. When monodominant stands of *C. uiti* are associated with seasonal watercourses (*corixos* and *vazantes*), it is almost always accompanied by *Leptobalanus parvifolius* (*pimenteira*) in the highest part of the terrain. It can also be associated with *Byrsonima cydoniifolia* (*canjiqueira*). Due to the domed shape of the crown, this is a conspicuous and easily recognizable monodominance in the floodable grasslands.

The sprouting capacity of this species makes it difficult to control its invasion in pastures by cutting or fire (Fig. 8.8). Even though it is not fire resistant, it can sprout naturally after fires. Besides flooding, the capacity to resprout may be a leading factor of its spreading over pastures since cattle trampling could stimulate a substantial increase in branches by sprouting at the ground level.

8.2.6 Vochysia divergens *Pohl (Vochysiaceae) – "Cambará"*

In the Pantanal, *Vochysia divergens* (Vochysiaceae) is popularly known as *Cambará*, and its monodominant stands are called *Cambarazal*. It is a tree of 7–25 m in height with a trunk diameter of 30–80 cm (Nascimento and Cunha 1989). It has a straight trunk, shiny leaves, and yellow flowers (Fig. 8.9) that attract hummingbirds. This species occurs in Paraguay, Bolivia, Peru, and Brazil from Mato Grosso do Sul to

Fig. 8.9 *Vochysia divergens* flowering in the Pantanal. Picture by Paulo Robson de Souza

the North and Northeast, mainly in riparian forests and flooded environments, such as the Araguaia wetlands (Marimon and Lima 2001; Brasil 2020).

The *Cambarazais* monodominant stands are very common in the northern Pantanal subregions, covering nearly 9.3% of the Barão de Melgaço, 6.4% of the Poconé, 5.6% of the Paraguai subregions, and 3.1% of all Pantanal (Silva et al. 2000; Arieira and Nunes da Cunha 2006), expanding during years with high levels of inundation (Nunes da Cunha and Junk 2004). Thus, it is a monodominant species associated with deeply flooded areas in the Pantanal, abundant on riversides and in riparian forests (Fig. 8.10).

This species has a strong ability to colonize grasslands (see the chapter on "Encroachment" Chap. 11) and has reduced rangelands for cattle over the last 30 years, causing financial losses to local ranchers. The spreading of this monodominant species is associated with the interannual cycles of inundation in the Pantanal, increasing in years with higher flooding due to its ability to grow underwater without shedding leaves (Nunes da Cunha and Junk 2004). Its seeds can even germinate in the water, inside the winged fruits (C. Nunes da Cunha, pers. comm.); thus, they are both anemochoric and hydrochoric. Along the Paraguay River, it is more frequent in areas flooded between 80 and 100 days per year, but they can remain underwater until 140 days (Damasceno-Junior et al. 2005). However, where the riparian forests on the Paraguay River are inundated up to 270 days per year, this species is not the most flood tolerant among the monodominant species (Damasceno-Junior et al. 2005).

The physiological mechanism of flood tolerance of this species is associated with a higher photosynthetic rate than highland Cerrado species under high soil moisture conditions, but a lower performance under inundation (Dalmolin et al. 2013). Probably this explains the good performance of this species in years of inundation but not in extremely inundated areas. On banks of the Cuiabá River, in 2001,

Fig. 8.10 Monodominant stands of *Vochysia divergens* (*Cambarazal*) flowering along abandoned river branches, near the Cuiabá River and the National Park of the Pantanal; the brown patches are floating meadows. (Picture by Fabio Edir dos Santos Costa)

we observed some *V. divergens* trees with exposed root systems exhibiting two branching strata, probably grown to adjust to flood level changes. However, the abundance of *V. divergens* decreases in dry years, mainly because of fire events (see the chapter on "Fire" Chap. 18) that can sharply increase its mortality rate, mainly in young individuals (Nunes da Cunha and Junk 2004). Besides, the photosynthetic rate decreases significantly under dry conditions (Dalmolin et al. 2018). In the twentieth century, the Pantanal experienced a rather semiarid period of 14 years without flooding between 1960 and 1974, and during that dry period, *V. divergens* tended to disappear from the Pantanal (Veloso 1972).

The number of species in these stands decreases with increased flooding, and despite having strong dominance of *V. divergens*, the older stands are the richest monodominant formation in tree species recorded in the Pantanal, with 83 tree and shrub species in 4 ha (Arieira and Nunes da Cunha 2006). These monodominant stands typically form forests, not savanna, as formed by the other tree species that occupy large areas in the Pantanal. When higher ocean surface temperatures and *El Niño-Southern Oscillation* (ENSO) reduce the rainfall in the northern Pantanal (Thielen et al. 2020), the diameter increment of *V. divergens* also decreases, according to dendrochronological analysis applied in this species to reconstruct past climatic changes (Fortes et al. 2018).

8.2.7 Curatella americana *L. (Dilleniaceae) – "Lixeira"*

This Neotropical savanna tree is widespread in the Llanos of Colombia and Venezuela, and Brazil, where it is abundant in the Cerrado and the Pantanal. It is particularly abundant in the Pantanal, occurring scattered, or as increasingly dense monodominant stands (Fig. 8.11). For its scabrous coriaceous leaves, it is called *lixeira* (meaning sandpaper), and the stand is called *Lixeiral*. It can be associated with several tree species, such as *Byrsonima cydoniifolia* and *Myrcia palustris* (Padilha et al. 2008). Its bark has various layers of fire insulation, but even after top kill, it resprouts from the lignotuber and root buds (see the chapter on "Fire" Chap. 18). It grows on earth mounds sourrounded by the flat landscape (*campos de murundu)*, and also in floodable grasslands (*campos de lixeiro*), is frequent on the edge of *cordilheiras*, i.e., paleolevees, wherefrom it has increased over grasslands in the Pantanal (see the chapter on "Encroachment" Chap. 11). In the dry period of 1960–1974 (Veloso 1972), it even grew in dried pond beds. Nowadays, in some places in the Poconé subregion, paradoxically *C. americana* is fringing on stands of *V. divergens* that, in contrast, benefits from a set of wet years.

Curatella americana is brevi-deciduous, and the fallen leaves remain undecomposed for months. At leaf change, around August/September, the bee-pollinated flowers appear. The seeds are mature at the onset of the rains and are carried by birds attracted by the white aril contrasting with the red fruit when opened (Pascotto et al. 2012). Once established, the tree persists under recurrent fires. Though flood tolerant, its size is smaller in floodable areas. The combined effect of fire and flood often results in dwarfed multi-stems (1–2 m tall) from post-burn regrowth. Leaves on young sprouts generally have twice the average size of leaves on older branches;

Fig. 8.11 Monodominant stand of *Curatella americana* (*Lixeiral*) in the Pantanal. The dark trunks are signs of fire. Picture by Geraldo Alves Damasceno-Junior

they are browsed by cattle and tapir (*Tapirus terrestris*). Its wood presents annual growth rings and attains its maximum annual diametric increment at 74 years old (Costa 2013).

8.2.8 **Handroanthus heptaphyllus** *(Vell.) Mattos (Bignoniaceae) – "Piúva"*

This tall tree (10–25 m) forms low-density stands (*Piuval*) on river floodplains. It is a species of the Atlantic Forest distributed from Ceará to Rio Grande do Sul in Brazil and also occurring in Bolivia, Paraguay, and Argentina. For its open canopy, it is one of the jabirus (*Jabiru mycteria*) preferred nesting sites. It is also an excellent roosting tree for bats (Aguirre et al. 2003). The understory is variable, composed of open grassland or most often of shrubs and small trees, once this tree functions as nucleation for ornithochorous plants. Many of them are riparian species, such as *Genipa americana*, emerging from seeds dropped by the parakeets that nest collectively under the jabiru nest, strengthening it.

This majestic tree also occurs scattered throughout the Pantanal, either in riparian vegetation or in floodable grasslands, where it sometimes is hit by lightning for being the highest emerging point (Damasceno-Junior et al. 2005). Like *Tabebuia aurea*, flowering is massive and synchronized (Fig. 8.12), producing numerous anemochoric seeds. It germinates better in clayey soils, in light conditions, or in the understory, but the seedlings develop better in sunny conditions and on sandy soils (Bocchese et al. 2008; Borges et al. 2014). It grows in fire-prone zones, being quite fire sensitive when young, but it can regrow from the base, becoming more tolerant as the bark thickens (A. Pott pers. obs.). The root system tends to be horizontal, an adaptation to flooded habitats. The growth of this species increases in years with *La Niña* events, and it also responds clearly to variation in climate, which makes this species a good model for dendrochronological studies (Leite 2012). This species can occur in flooding gradients in areas that remain flooded from 60 to 270 days per year (Damasceno-Junior et al. 2005). The bark is rich in secondary compounds such as iridoids and triterpenes, some of them with antioxidant activity (Garcez et al. 2007). Wood extracts also contain lapachol and similar compounds (Schmeda-Hirschmann and Papastergiou 2003). It makes good wood for barrels of *cachaça* (Brazilian rum) (Bortoletto et al. 2016).

8.2.9 **Inga vera** *Willd. (Fabaceae) – "Ingá"*

This species has a wide Neotropical distribution, occurring from Mexico to Uruguay in different domains such as Amazonia, Cerrado, Caatinga, and Atlantic Forest (GBIF 2020b). For Pantanal standards, this is a small to medium-sized tree (3–10 m

Fig. 8.12 Monodominant stand of *Handroanthus heptaphyllus* (*Piuval*) in floodable savanna in the Miranda subregion of the Pantanal. Picture by Arnildo Pott

tall), with a broad, evergreen canopy, often hanging down to the ground on riversides. Outside the Pantanal, it can reach 25 m in height (Pennington 1997). It forms monodominant belts (*Ingazal*) on riverbanks flooded up to 4 months. The best flooding belt of this species on the Paraguay River has floods from 50 to 180 days per year (Damasceno-Junior et al. 2005). The species often occurs gregariously with few seedlings underneath, except in gaps. Large bees and hummingbirds pollinate the flowers, but some other birds feed on the nectar and stamens (Pennington 1997). Fruiting (Fig. 8.13) occurs in the rainy season. *Inga vera* seeds have a sweet aril, and are dispersed by birds, mammals, and fishes.

Despite its thin bark, it is a relatively fire-resistant species, being one of the most common trees in burned areas along the Paraguay River (Arruda et al. 2016). The litter is mostly removed by the floods, except where shallow outcropping roots trap debris. Only scattered grass grows under the dense stands, leaving little fuel to be burned. Few other plants occur underneath, and thus it seems allelopathic. Away from watercourses, it is sparse and does not occupy grasslands. Nevertheless, near watercourses, it can act as a pioneer species growing in between grasses on recently deposited riverbanks. Sometimes it is smothered by vines and lianas. This species has annual growth rings (Ishii 1998). It seems to be recruited from seedlings only in very dry years (Damasceno-Junior 1997), as seedlings are rare after the flood, although it can survive inundation up to 270 days per year, as along the Paraguay

Fig. 8.13 *Inga vera* with fruit. Picture by Geraldo Alves Damasceno-Junior

River. When flooded, this species presents alcoholic fermentation as an alternative metabolic pathway (Okamoto 1998), and that probably explains its high abundance on riversides near running water that can wash the roots, removing the toxic effect of the alcohol. It has a remarkable ability to resprout after disturbances, such as extreme flooding (Damasceno-Junior et al. 2004).

At the beginning of the twentieth century, the steamships on the Paraguay River used *Inga* wood bought from riverine people. Nevertheless, *I. vera* is still one of the main species of these riparian forests (Damasceno-Junior et al. 2005), which shows its resilience.

8.3 Monodominant Tree Palms

8.3.1 Copernicia alba *Morong (Arecaceae) – "Carandá"*

This palm is a conspicuous element of the Gran Chaco landscape in Paraguay, Bolivia, and Argentina and the Pantanal in Brazil. It occurs from central and northern Beni in Bolivia, the center and northwest of Paraguay, and the north and northwest of Argentina to the provinces of Santa Fé and Corrientes in the south (Moraes 1991). In Brazil, it covers areas in Mato Grosso do Sul State, around the Miranda and Paraguay Rivers (Pott and Pott 1994), and it decreases in dominance towards the northern parts of the Pantanal.

This heliophyte palm produces a high number of fruits, dispersed by birds, mammals, and fishes (*pacu*). It covers extensive areas with monodominant stands, locally known as *Carandazal* (Fig. 8.14). The stands occur as open or dense monodominant patches or associated with deciduous trees such as *Tabebuia aurea*, *Astronium*

Fig. 8.14 Monodominant stands of *Copernicia alba* (*Carandazal*) in two situations: (**a**) on the bank of the Paraguay River; (**b**) in the Miranda subregion in seasonally flooded grasslands. The lack of dead leaf sheaths indicates past wildfires. Pictures by Geraldo Alves Damasceno-Junior

fraxinifolium, and *Machaerium hirtum* (Amador et al. 2012). *Copernicia alba* is most common on plains and lower-lying areas with deep and moist soils. Sometimes it also occurs in shallow and dry soils such as the hills around the Pantanal (Silva 2018). This species has an affinity with alkaline soils and can be considered an indicator of calcareous and/or saline soils (Pott and Pott 1994). The monodominance of *C. alba* is associated with soils with base saturation above 75%, in some cases reaching 95% (Amador et al. 2012), mainly because of Ca saturation. Its density increases on soils with pH higher than 5.7, higher inundation, and high levels of Mg (Damasceno-Junior et. al 2021). This species can survive up to 8 months of flooding, to 0.5 m deep (Pott and Pott 1994), or even deeper if the water is flowing. It is resistant to recurrent fire (Cisz et al. 2013), except if the flames reach its apical meristem (Silva 2018).

Sometimes *C. alba* can replace all the woody riverine vegetation; extensive areas of that vegetation occur on the banks of rivers such as the Paraguay River (Fig. 8.14a). *C. alba* also can colonize bare areas, or areas with only herbaceous species, and areas with some trees and shrubs (Fig. 8.14b), and can coexist with other typical monodominant species such as *Tabebuia aurea*.

Despite being monodominant, stands of this species can be considered as one of the richest floodable communities in the Pantanal. A survey in two areas of *Carandazal* in the Pantanal yielded 22 tree and shrub species and 178 herbaceous species (Amador et al. 2012). Flooding in these stands was associated with a decreasing number of tree and shrub species and changes in the composition of associated species (Amador et al. 2012). This species probably does not show a continuous process of recruitment (Arrúa and Negrelle 2014), and the events of recruitment are not yet understood.

8.3.2 Mauritia flexuosa *L.f. (Arecaceae) – "Buriti"*

This palm species occurs from Panama to the north and center of South America, being very frequent in the Amazonian and Cerrado domains; its known southern limit of distribution does not cross the Tropic of Capricorn (GBIF e). Two types of stands of this palm species occur along rivers and around springs in the Cerrado domain. The first is a swamp with a savanna physiognomy, known as *Vereda*, with a continuous grass stratum and a discontinuous tree stratum formed almost exclusively by *M. flexuosa*, on saturated hydromorphic soils. The second type has a floodable riparian forest physiognomy also formed by monodominant stands of *M. flexuosa*, known as *Buritizal* (IBGE 1992; Ribeiro and Walter 2008). These two notable and very similar physiognomies occur in the eastern zone of the Pantanal plain (Moreira et al. 2017). At a superficial glance, *Veredas* can resemble *Buritizais*, but the similarities are restricted to the presence of *Mauritia flexuosa*. *Buritizais* of riparian forest contain many associated tree species, while trees are less frequent in

Veredas (Pott et al. 2011; Moreira et al. 2017). The tree species that co-occur together with *Mauritia flexuosa* in the floodable riparian forests also occur widespread in the riparian forests along the Pantanal rivers (Moreira et al. 2017). The species composition of the herbaceous-shrubby stratum of the *Veredas* on the floodplain at Rio Verde/Coxim is only 30% similar to the *Buritizais* and shares more species with the upland *Veredas* (Moreira et al. 2017).

The *Buritizais* in the Pantanal (Fig. 8.15) were classified by Eiten (1972) as "palm woodland," distinguishing them from upland *Veredas*. *Buritizais* occur in the subregions of Barão de Melgaço, Paiaguás, Aquidauana, Miranda, and Nhecolândia (Silva et al. 2000), the two latter along the Aquidauana and Taquari Rivers. Most often, the herbaceous stratum is formed by aquatic plants that are typical of the Pantanal (Fig. 8.15), not *Vereda* (Pott et al. 2011), because of the wet and dry conditions, while true *Veredas* are permanently wet (Moreira et al. 2017).

Fig. 8.15 Monodominant stand of *Mauritia flexuosa* (*Buritizal*) at the eastern edge of the Pantanal plain. Here under wet and dry regime, the herbaceous stratum is formed by aquatic plants that are typical of the Pantanal, not of *Vereda*. Picture by Evaldo Benedito de Souza

8.3.3 Attalea phalerata *Mart.* ex *Spreng.* *(Arecaceae) – "Acuri"*

This palm species grows up to 2–12 m in height; its stem circumference, including the dead leaf sheaths that remain on the tree after leaf fall, can be up to 1.5–2 m (Fig. 8.16). When old, these sheaths begin to fall off, and the trees then look thinner. The species occurs in many environments in South America, from the lowlands of Peru, Ecuador, and Colombia, and the Bolivian Amazon region, to Brazilian Amazonia (Amazonas, Pará, Acre, and Rondônia). It also occurs in the Cerrado domain in Central Brazil, reaching Paraguay (GBIF 2020a). It is a pioneer species that can grow in the understory of semideciduous and riparian forests and *cerradão* woodland, generally associated with humid but not necessarily floodable areas. This is the most common palm of the Pantanal and the third most common species in surveys in the Pantanal (see the chapter on "Woody Vegetation" Chap. 9), forming monodominant stands known as *Acurizal* (Fig. 8.16). *Attalea phalerata* is also recorded in semideciduous and deciduous, riparian forests, and in *cerradão* (Pott and Pott 1994; Damasceno-Junior et al. 1999; Negrelle 2016). In riparian forests, the species only occurs in areas with shallow flooding, a habitat that is common on the banks of the Miranda River, but it is rare in riparian forests of the Paraguay River, where flooding can last up to 270 days per year (Damasceno-Junior et al. 2005); towards Cáceres, it becomes more frequent. Generally, this species is recorded along the Paraguay River in ancient terrain where people lived and built

Fig. 8.16 *Attalea phalerata*, the tallest is a remnant of seasonal forest, and the shortest is a regenerating individual. Picture by Paulo Robson de Souza

higher terraces to avoid flooding. Thus, it can be considered an indicator of those archeological sites that are very common along the Paraguay River (Schmidt 1942).

This species also was recorded as a monodominant (Fig. 8.17) in the Barão de Melgaço, Paiaguás, and Abobral subregions, forming monodominant rings like high dense belts around islets of deciduous forests, locally known as *capão* (Damasceno-Junior et al. 1999; Negrelle 2016) (Fig. 8.18). The "capões" are surrounded by wet and dry natural grasslands. The edge zone of capões is subjected to annual flooding, while the center because of its elevated topography is rarely flooded (Damasceno-Junior et al., 1999). In dry years, fires can occur (Rivaben et al. 2021). Fire in these "capões" often starts at the edges, close to the seasonally flooded and burned grasslands. *Attalea phalerata* individuals are the first to burn (Damasceno-Junior et al. 1999; Rivaben et al. 2021). Being a fire- and flood-tolerant species, *Attalea phalerata* can benefit from the interaction between fire and flooding, showing an increase in the density of individuals and thus increasing its monodominance (Rivaben et al. 2021). The species prefers soils of medium to high fertility (Pott and Pott 1994). As a pioneer species, its monodominance is, in some cases, associated with disturbance (Fig. 8.19). In the Abobral subregion, this species also becomes fully monodominant on the islets after deforestation.

Fig. 8.17 Monodominant stands of *Attalea phalerata* (*Acurizal*) in the subregion of Paiaguás, Pantanal. Many of these areas have been under traditional shifting cultivation by riverine people. Picture by Geraldo Alves Damasceno-Junior

Fig. 8.18 Forested islet (*capão*) with *Attalea phalerata* forming a belt around the central dry forest; *Attalea phalerata* also occurs in the understory of the central dry forest, in the Abobral subregion of the Pantanal. Picture by Paulo Robson de Souza

Fig. 8.19 *Attalea phalerata* in regrowth and regeneration after deforestation of paleolevees for cultivated pasture in the Paiaguás subregion. Picture by Geraldo Alves Damasceno-Junior

8.3.4 Attalea speciosa *Mart.* ex *Spreng.* *(Arecaceae) – "Babaçu"*

This palm can reach 30 m in height and 44 cm in diameter (Moraes 2014). It is an Amazonian species and can also be found in the Cerrado (JBRJ 2010). Monodominant stands of this species can be found in many areas of Brazil, e.g., in Maranhão where it has a relevant economic value (Araújo et al. 2016). *Attalea speciosa* forms the monodominant *Babaçual* on some sandy ridges next to ponds in the Nhecolândia and Aquidauana subregions and on the upper watershed (Fig. 8.20). These monodominant stands are very isolated in the Pantanal, suggesting that the species is spread by indigenous people. The fruits may also have been carried by water to the plain, although they seem somewhat large. This palm has a strong history of usage by traditional and indigenous populations in South America. It is most likely that pre-Columbian inhabitants have brought it into the Pantanal (Levis et al. 2012; Araújo et al. 2016). The external edges of the stands are covered with Cerrado woodland further down in the floodable gradient with grassland. The formation is a closed forest, colonized by a few seasonal forest trees such as *Astronium fraxinifolium*, but recurrent fires hinder the succession. *Attalea speciosa* is very fire prone because of the amount of fuel from its large leaves; the seedling and the young palm survive fires because of their deep underground hypocotyl (Pott et al. 2011). This palm can also increase its abundance under high levels of disturbance (Montúfar et al. 2011).

Fig. 8.20 Monodominant stand of *Attalea speciosa* (*Babaçual*) in the Kadiwéu Indigenous Reserve. Picture by Geraldo Alves Damasceno-Junior

Some Additional Arboreal/Shrubby Species

A few additional pioneer trees, shrubs, and palms may also occur as monodominants, e.g., *Xylopia aromatica* (Annonaceae), *Sapium obovatum* (Euphorbiaceae), *Zanthoxylum rigidum* (Rutaceae), and *Sesbania virgata* (Fabaceae). *Xylopia aromatica* stands (*Pindaival*) occur in the eastern zones of Nhecolândia, Paiaguás, and Barão de Melgaço; however, many stands have been cleared to enhance the native pasture or to cultivate the exotic forage grass *Urochloa humidicola*.

Sapium obovatum stands (*Saranzal*) are common on riverbanks such as the Paraguay River. The species is an evergreen, dark-green-leaved medium-sized tree (4–12 m tall); it is fire sensitive, abundant in riparian forests, often being dominant in patches or belts of intermediate successional stages.

Zanthoxylum rigidum stands grow mostly on earth mounds but can spread to floodable grasslands, as happened in the late 1980s near Porto Jofre in the Poconé subregion, nowadays taken over by *Vochysia divergens*. *Sesbania virgata* is spreading since 2018 with the begginig of dry pluriannual period. It becomes monodominant mainly on pond beds that stayed without inundation or with weak inundation for a set of dry years.

The short palm *Bactris glaucescens* (Arecaceae), known as *tucum*, is another riverine species which forms nearly monospecific thickets (*Tucunzal*). The flood-tolerant tree *Calophyllum brasiliense* (Calophyllaceae) is colonizing dead riparian forest of the silted, permanently overflown lower Taquari River (Armando Lacerda, pers. comm.). Thus, it seems that a new type of monodominant forest is developing (*Landizal*), but in the Pantanal so far, it only occurs in riparian forests and forest islands in deep-flooded zones.

The *Espinheiral* is a dense thorn scrub of entangled *Bauhinia bauhinioides* (Fabaceae), *Byttneria filipes* (Malvaceae), and other flood-tolerant spiny shrubs and vines (*Cissus spinosa*, Vitaceae), mainly on floodplain swamps of the Miranda River, e.g., along the Corixo Mutum (an abandoned anabranch of the Miranda River). Small areas of *Espinheiral* also occur in the *Tabebuia aurea* savanna; these are the last patches to dry out and are thus important as a source of water for the fauna and as a nesting site for waterfowl. In the *Espinheiral*, there is little grass undergrowth, so fires generally do not penetrate these monostands beyond the native peripheric tall grasses, such as *Andropogon hypogynus*, or scandent plants, e.g., *Rugoloa hylaeica*.

Another important monodominant species is *Combretum laxum*, a scandent shrub that is strongly encroaching in grasslands in the northern Pantanal. This aspect is discussed in the chapter on "Encroachment" Chap. 11.

8.4 Herbaceous Monodominant Formations

8.4.1 **Cyperus giganteus** *Vahl (Cyperaceae) – "Piripiri or Piri"*

Native to the American continent, this species is a giant sedge (2–3 m tall), a perennial, aquatic herb that is propagated by seeds or rhizomes. It is common in all subregions of the Pantanal, commonly occurring in small permanent or temporary

Fig. 8.21 Monodominant stand of *Cyperus giganteus* (*Pirizal*), a flooded habitat, in the subregion of Miranda, Pantanal. Picture by Geraldo Alves Damasceno-Junior

ponds, lakes, and river floodplains. It grows on sandy or clayey soils as a rooted aquatic macrophyte (Fig. 8.21) or as a floating meadow in shallow waters and forms herbaceous monodominant formations called *Pirizal* (Pott and Pott 2000; Lorenzi 2008). This sedge has the C_4 type of photosynthesis (Rodrigues and Estelita 2003). Despite being an aquatic macrophyte, it can die when rooted under inundation conditions for more than 3 or 4 months (G.A. Damasceno-Junior pers. obs.; Fig. 8.22). When floating, it can resist longer periods of inundation because of aerenchyma inside its roots and rhizomes (Rodrigues and Estelita 2002, 2004). This species is similar in appearance and ecology to *C. papyrus* L. in African wetlands with similar flooded habitats (Terer et al. 2012).

Cyperus giganteus stands survive fires. Fires do not affect the dominance of *C. giganteus* since it rapidly regrows from its rhizomes. But with fires, we observed a decrease in species diversity in the community and changes in the floristic composition because some species are fire resistant and others germinate after burning. These changes are noticeable both in the upper stratum of the vegetation, near the inflorescences, and in the lower stratum, close to the water surface (Rocha et al. 2015). While observing the community along trails, we recorded in the upper stratum a wide variety of emergent vines (e.g., *Cissampelos pareira*, *Odontocarya tamoides*, *Funastrum clausum*, *Rhabdadenia madida*, and *Ipomoea* spp.), and tops of shrubs, e.g., *Ludwigia tomentosa*, *Bauhinia bauhinioides*, *Discolobium*

Fig. 8.22 Monodominant stand of *Cyperus giganteus* (*Pirizal*), dead after 3 months deeply flooded in the subregion of Miranda, Pantanal. The pale-green small plant in the front is *Pistia stratiotes*, indicating water above the soil surface. (Picture by Paulo Robson de Souza)

pulchellum, and *Ipomoea carnea*, whereas intermingled in the lower stratum, both emergent vines and herbaceous species commonly found in the floodplain or floodable grasslands in the Pantanal were observed (*Ricciocarpos natans*, *Leersia hexandra*, *Pityrogramma calomelanos*, *Ceratopteris pteridoides*, *Echinodorus paniculatus*, *Salvinia auriculata*, *Pistia stratiotes*, *Utricularia gibba*, *Eichhornia azurea*, *Cyperus* spp., *Nymphaea* spp., *Lemna* spp., *Wolffiella* spp., *Eleocharis* spp., and *Pontederia* spp.). These species of the lower stratum remain present during both the flooding season and during the dry season in areas where the *Pirizal* stays flooded (where the soil surface stays submerged). However, in *Pirizais* where the soil partially or totally dries in the dry period, immigration of ruderal species from the nearby roadside can occur. The *Pirizal* also shows changes in the floristic composition according to the different flooding regimes of the Pantanal rivers and also due to the characteristics (vegetation and soil) of each subregion. *Pirizal* covers 3.8% of the Nabileque subregion, 2.7% of the Abobral, and 2.2% of the Poconé, covering 1.2% of the whole Pantanal (Silva et al. 2000).

8.4.2 **Oryza** ***spp. (Poaceae) – “Arroz”***

Oryza latifolia Desv.) and *O. rufipogon* Griff. are two species of wild rice. They are aquatic herbs that occur in the Pantanal and have a broad distribution from Mexico to Paraguay, mainly in Amazonia and the Pantanal (Pott and Pott 2000). They occur as monodominant stands along the Paraguay River, called *Arrozal*. These species are 1–1.8 m tall during the dry season and can reach 4–6 m during flooding (Figs. 8.23 and 8.24). In general, *O. latifolia* (the most studied species) can be found flowering and fruiting from February to August in the Pantanal (Pott and Pott 2000). However, in monodominant stands, flowering is concentrated in April and May, and fruiting is at the end of May and the beginning of July (Bertazzoni and Damasceno-Junior 2011). This species occurs in patches, and its monodominance at the landscape level is seasonal: it increases as the water level rises, from 30% to 40% of cover when the river level is low up to 80–100% of cover (Fig. 8.23) when the water attains the maximum (Bertazzoni and Damasceno-Junior 2011). At maximum inundation, this species has ripe grains that are released onto the water; then it lodges its stems and other species increase and become dominant (Bertazzoni and Damasceno-Junior 2011). Species such as *Hymenachne amplexicaulis* (Rudge) Nees or *Leersia hexandra* Sw. (both Poaceae) start to grow faster after the rice has lodged its stems

Fig. 8.23 Monodominant stands of *Oryza latifolia* (*Arrozal*) in areas flooded by the Paraguay River, western edge of the Pantanal near the *Amolar* mountain range, Corumbá, Mato Grosso do Sul. Picture by Geraldo Alves Damasceno-Junior

Fig. 8.24 Monodominant stand of *Oryza rufipogon* (*Arrozal*) along the Paraguay River, near the Amolar mountain range, Corumbá, Mato Grosso do Sul. Picture by Geraldo Alves Damasceno-Junior

and become monodominant in the same place where *O. latifolia* was flowering and fruiting (G.A. Damasceno-Junior, pers. obs.). These and other species belong to an assembly of species that can exhibit seasonal monodominance. The dominance of *O. latifolia* seems to be correlated to the highest levels of the Paraguay River since in years with deep inundation it is easier to find patches of monodominant *O. latifolia* stands. In years with more shallow inundation, the most common patches are of *O. rufipogon* (G.A. Damasceno-Junior pers. obs.). The flooded grasslands in which these two rice species occur are very rich in species: up to 120 other species have been recorded (Rosa Helena da Silva, unpublished data). The main associated species in the monodominant *Oryza* stands and their neighboring areas are aquatic herbs and subshrubs, such as *Ipomoea carnea*, *Echinochloa polystachya*, *Polygonum acuminatum*, *Ricciocarpos natans*, *Eichhornia crassipes*, *Pontederia rotundifolia*, *Pistia stratiotes*, *Paspalum repens*, *Commelina longicaulis*, *Marsilea crotophora*, *Salvinia auriculata*, *Vigna lasiocarpa*, *Azolla filiculoides*, *Cyperus blepharoleptos* (previously named as *Oxycaryum cubense*), and *Ludwigia helminthorrhiza* (Catian et al. 2012; Cunha et al. 2012).

8.4.3 Elionurus muticus *(Spreng.) Kuntze (Poaceae) – "Capim-Carona"*

This medium-sized tussock grass is dominant in flood-free or exceptionally flooded areas, called *Caronal* (Fig. 8.25), mainly in the Nhecolândia and Aquidauana subregions, on very sandy, low-fertility soils (Pott et al. 2011). However, though nonflooded, the water table can reach the surface in the rainy season, and probably therefore, the short rhizomes of *E. muticus* tend to grow upwards to escape waterlogging. In wetter years, the grass does not survive in the lower-lying edges and depressions, as we observed in 1988. Thus, it seems quite a stable community, and in fact, we have seen sites where the *Caronal* has remained unchanged for decades. Where cattle is excluded, several species that are preferentially grazed increase, such as *Trachypogon spicatus*, *Desmodium barbatum*, and *D. guaraniticum*. *Elionurus muticus* contains volatile oil in its leaves and is very flammable, even when green, and when intentionally burned or hit by wildfires, the flames can reach up to 6 m high. Few tree species succeed under such harsh conditions, e.g., *Mouriri elliptica*, a Cerrado treelet with a corky bark even on its branches. Near the transition with Cerrado woodland, other fire-tolerant sparse trees may appear, such as *Bowdichia virgilioides*, *Curatella americana*, *Diptychandra aurantiaca*, *Eugenia pantanalensis*, and *Pseudobombax longiflorum*. On slightly higher ground (*murundu*), there are small islets with short trees or palms, such as *Attalea phalerata*, *Dipteryx alata*, and *Zanthoxylum rigidum*.

Fig. 8.25 Grasslands dominated by *Elionurus muticus* (*Caronal*) in the Nhecolândia subregion with Cerradão vegetation in the background. (Picture by Alexandre de Mattos Martins Pereira)

8.4.4 Andropogon hypogynus *Hack. (Poaceae) – "Capim-Vermelho"*

This species is a 1–2 m tall tussock grass, perennial with short rhizomes, and it can be found with flowers and fruits throughout the year (Zanin and Longhi-Wagner 2011). It occurs nearly all over the Cerrado domain and also in savannas in northern South America such as Venezuela, Colombia, and Roraima State in Brazil (Brasil 2020). It is very frequent in *Veredas* (wet grasslands in the Cerrado domain) (Moreira et al. 2011), and it is abundant throughout the Pantanal. Without cattle or fire, it becomes monodominant within a few years (Fig. 8.26). Its dominance is also related to high levels of organic matter, clay, and Mn in the soils (Amador 2013), but it can also be found on sandy soils mainly at the dystrophic Planosol and Cambisol soil groups (Schessl 1999). The monodominant stands of this species are very fire prone and can have more than 50% cover of dry and dead organic matter during the dry season (Fig. 8.26). Probably it was very common and determining the physiognomy of the vegetation in parts of the Pantanal before cattle ranching and management with fire and grazing became common practice. As the tussocks grow, they expand and shade out smaller associated species. It is common in areas flooded for about 3 months with water levels from 0.5 to 1.0 m (Schessl 1999; Nunes da Cunha and

Fig. 8.26 Monodominant stand of *Andropogon hypogynus* in a 4-year ungrazed natural grassland in the Nhecolândia subregion, Pantanal. (Picture by Alexandre de Mattos Martins Pereira)

Junk 2011), and it can also occur in herbaceous strata of *Tabebuia aurea* and *Byrsonima cydoniifolia* monodominant stands (Amador 2013).

8.4.5 **Andropogon bicornis** ***L. (Poaceae) – "Capim Rabo-de-Burro"***

This tussock grass (0.8–1.7 m high) can occur in almost all wetlands from the South of the USA to northern Argentina and Uruguay, from 0 to 2500 m a.s.l. (GBIF 2020d). This species often forms dense populations in swamps, the margins of rivers and streams, and in disturbed environments (Zanin and Longhi-Wagner 2011). It has flowers and fruits throughout the year but can increase flowering after fire events (Munhoz and Felfili 2005; Zanin and Longhi-Wagner 2011). It is a C_4 grass (Bezerra et al. 2019), and it forms dense bunches, regrowing from short rhizomes after fires. When mature, the culms become brown-reddish with white-topped inflorescences; that gives it its popular name *rabo-de-burro*, meaning donkey tail. Its wind-blown diaspores spread far. This species becomes monodominant in floodable grasslands, mainly in degraded areas left under- or ungrazed, on nearly any soil type, but it seems to prefer soils with higher silt and P contents and cation exchange capacity (Haase 1990). It is one of the macrohabitats (see the chapter on "Macrohabitats" Chap. 7) burned for grazing or being replaced by cultivated pasture, as the leaf blade has sharp edges. In the Pantanal, this species is very often found growing on histosols (Pivari et al. 2008), increasing its cover during the wet season (Santana et al. 2019). It has potential as an ornamental (Stumpf et al. 2009).

8.4.6 **Paspalum lineare** ***Trin.*/Paspalum carinatum** ***Humb. & Bonpl. ex Flüggé (Poaceae) – "Fura-Bucho"***

Paspalum lineare is a perennial cespitose grass from 0.1 to 1.5 m high that can be found in savannas from Central America to South America, and in Brazil mainly in the Cerrado, Amazonian, and Atlantic Rain Forest domains (Brasil 2020). It is known in Brazil as *fura-bucho*. It is a C_4 grass (Magnusson et al. 1999). In the eastern sandy zones of the Nhecolândia and Paiaguás subregions and in earth mound grasslands (*campos de murundu*) in the northern part of the Poconé subregion, there are areas dominated by the medium-sized tussock grasses *Paspalum lineare*/*P. carinatum*. Their density is low with a high proportion of bare soil between tussocks. Such areas are characterized by soils of low fertility and forage with a low nutritional value. Aggravated by the absence of permanent water bodies, these areas are consequently scanty in fauna (A. Pott pers. obs.). For example, in the Pantanal, very low Ca and organic matter contents in the soils can result in the scarcity of palms and consequently of macaws and parrots. While *Paspalum lineare* increases its cover in undisturbed areas (Eugênio et al. 2011), it is sensitive to frequent fires (Jancoski et al. 2019). As a consequence, in the Pantanal, *P. lineare* is replaced by *P. carinatum* in burned and grazed areas. But the low calcium preference for *P. lineare* is relative to the soil conditions in Pantanal. In wet grassland of the Cerrado in Brasília, on very acid soils, *P. lineare* occupies the sites with higher moisture and more Na, Ca, and Fe (Munhoz et al. 2008). In Cerrado grassland near the Pantanal, in Santo Antônio do Leverger, *P. carinatum* varied from 29% (in the dry season) to 36% (in the rainy season) of the diet of bovine cattle (Bauer et al. 2008).

8.4.7 **Paspalum wrightii** *Hitchc. and Chase (Poaceae) – "Capim Macega-Branca"*

Paspalum wrightii is a perennial cespitose 1.6–3 m high grass. It occurs from the South of the USA across Central America into South America where it can be found in Venezuela, Guiana, Bolivia, Paraguay, Argentina, and Brazil. In Brazil, it occurs in Amazonia, the Cerrado, and the Pantanal (JBRJ 2010; GBIF f). This is the dominant grass of the *Tabebuia aurea* floodable savanna, surviving flood and fire. It is an important forage in native pastures in the Miranda and Nabileque subregions of the Pantanal (Allem and Valls 1987). It has vigorous, sharp-pointed rhizomes enabling it to grow in the high-plasticity clay; it also is able to punch through nursery bags. It is less dominant in sandy soils, where other grasses are more frequent, such as *A. hypogynus* and *Sorghastrum setosum*. Its dominance increases in soils with high pH, and higher levels of organic matter, base saturation, clay, Mn and P (Amador 2013). In the Pantanal, it can also be found in monodominant stands of *Copernicia alba* (Amador et al. 2012). It also occurs around big lakes at the western border of the Pantanal (Cunha et al. 2012). *Paspalum wrightii* substitutes *Andropogon hypogynus* as a monodominant species in wetter areas (Schessl 1999).

8.4.8 **Eichhornia** *spp./***Pontederia** *spp. (Pontederiaceae) – "Camalote/Aguapé"*

There are two water hyacinth species, *Eichhornia crassipes* (Mart.) Solms and *E. azurea* (Sw.) Kunth, and both have the local name *camalote*, or *aguapé* elsewhere in Brazil, and are distributed in all states of the country (Brasil 2020). These species, especially *E. crassipes*, spread nearly all over the world in many types of ecosystems, in the USA, Europe, Asia, Oceania, and Africa, mainly because of their ability to colonize open waters and also as a result of the global warming that provides conditions for this species to invade temperate waters (Thomaz 2002). Because of its invasibility, *E. crassipes* has, nowadays, an extent of occurrence of 57.28% of the world area (Murphy et al. 2019). Monodominant stands of *Eichhornia* species in the

Pantanal are called *Camalotes* or *Camalotal* (Pivari et al. 2008). *E. crassipes* is a free-floating species (or rooted in shallow water, and then it has no longer inflated petioles), while *E. azurea* is an anchored floating plant. Additionally, there are some species such as *Pontederia rotundifolia* having a similar habit as *E. azurea*, while *P. reflexa* is a rooted macrophyte. These species can be part of the seed bank and emerge as aquatic species in floodable environments (Ferreira et al. 2016). *E. crassipes* seeds can stay alive in the seed bank for 20 years (EPPO 2008). Both *E. crassipes* and *E. azurea* form dense monodominant stands and occur in water bodies all over the Pantanal. The species of *Eichhornia* are frequently found as monodominant in oxbow lakes (Schessl 1999). *Pontederia parviflora* is more abundant in seasonal ponds and flooded grasslands, disappearing in the dry season. These species are important structuring elements for the environment to the aquatic fauna (Padial et al. 2008) and can be used as a shelter, foraging place, and as transport medium by young fishes (Sazima and Zamprogno 1985). Because of their ability of rapid vegetative growth and colonization of open water bodies, these species have become important problems in electric power reservoirs (Mormul et al. 2009). These species are used as indicators of the environment in the classification of wetlands (see the chapter on "Macrohabitats" Chap. 7). Even while floating, these species can grow out over histosols and occasionally grow as epiphytes (Pivari et al. 2008). *Eichhornia crassipes* has been suggested to remove heavy metals such as Pb, Cd, and Zn from waters (Mahamadi and Nharingo 2010). For *E. crassipes*, its cover seems to increase with increasing levels of nutrients in the water, especially phosphorus (Meza-Lopez and Siemann 2017). The petiole of *E. crassipes* can be used for handicrafts by traditional and indigenous people of the Pantanal (Bortolotto and Guarim Neto 2006).

8.4.9 **Typha domingensis** ***Pers. (Typhaceae) – "Taboa"***

Cattail is called *taboa* in Brazil, and the monodominant stand *Taboal*. It is a perennial emergent aquatic herb with 1 cm thick rhizomes that are able to survive hazards such as occasional fires. This species is spread worldwide in tropical and temperate environments, found in sparse patches in all subregions of the Pantanal and in the upper watershed. It colonizes disturbed or constructed ponds, regardless of soil type, but increases with eutrophication, e.g., from cattle dung. The spike produces 200,000–300,000 seeds, dispersed by wind or by water, being able to germinate submerged, and then the hypocotyl floats and is carried to a muddy shore where the seedling roots down (Pott and Pott 2000). This species benefits from shallow waters until 40 cm of inundation; under higher levels of inundation, its dominance decreases (Chen et al. 2010). The dominance and expansion of *T. domingensis* are also promoted by high P availability, a low soil redox potential (Li et al. 2010), and a high nitrogen level (Grace 1988). Despite being also found in brackish environments, salinity above 7 ppt results in deterioration of *Typha* stands (Glenn et al. 1995). It can also increase its cover after a fire but gets back to the initial state 3 years after

(Ponzio et al. 2004). Its dry phytomass is used as biosorbent for metals in wastewater (Abdel-Ghani et al. 2009).

8.4.10 Thalia geniculata *L. (Marantaceae) – "Caeté"*

The fireflag is widespread in Africa and the Americas (GBIF 2019b; Brasil 2020). In the Pantanal, it forms the *Caetezal*, an emergent aquatic monodominant stand, present throughout the Pantanal. Together with *Cyperus giganteus* stands, *Caetezal* covers 1.2% of all Pantanal vegetation (Silva et al. 2000), occurring in depressions with water during almost the whole year and that during the flooding period are inundated up to 1.5 m for 3–5 months (Schessl 1999). *Caetezais* are indicative of those environments (see the chapter on "Macrohabitats" Chap. 7). Plant size (1–4 m) and leaf blade width vary according to flood level and soil fertility (A. Pott pers. obs.). Stands are not monospecific, as many associated aquatic plants grow interspersed. Those associated species benefit when *T. geniculata* starts to wilt. This often occurs before the soil starts to dry up. This species survives fires and the dry season because of its starchy rhizomes. Its rhizome is aerenchymatic and grows preferably in the top 10 cm of the soil (Schessl 1999). Its occurrence is associated with soils with high base saturation and organic carbon content (Haase 1990), but these soils must keep moist during the dry season (Haase and Beck 1989; Haase 1990; Pott et al. 2011). This species can be a food resource for the fauna, being part of the marsh deer diet (Tomas and Salis 2000). Their flowers have a specialized pollination mechanism called explosive secondary pollen presentation that is triggered mainly by bees and hummingbirds (Davis 1987). The species can be used for wastewater treatment (Pincam et al. 2020). The aerial parts of *T. geniculata* contain compounds that are active against *Plasmodium falciparum* and *Leishmania donovani* (Lagnika et al. 2008).

8.4.11 Aspilia latissima *Malme (Asteraceae) – "Mirassol," "Malmequer"*

This subshrub (1–2 m tall) can be dominant in floodplains of the Paraguay, Cuiabá, and Miranda Rivers, on loamy and clayey soils. The local people call such stands *Malmequerzal* (*Malmequerzais* – Plural). These stands often are located near riverbanks in the same environment where we can find *Polygonum acuminatum*, *Commelina longicaulis*, and *Louisiella elephantipes* (Lehn et al. 2012). As the species name suggests, it has broad leaves that shade out smaller plants, but this species is also very competitive because of its vegetative propagation. This species can be part of seed banks in flooded grasslands in the Pantanal (Souza et al. 2019). Leaf extracts of this species show activity against many species of fungi and bacteria, such as *Candida albicans*, *C. parapsilosis*, *C. tropicalis*, *Pseudomonas aeruginosa*, *Enterococcus faecalis*, *Escherichia coli*, and *Staphylococcus aureus* (Souza et al. 2015). This species also has an acaricidal effect against ticks such as *Rhipicephalus* (*Boophilus*) *microplus* (Santos et al. 2013).

8.4.12 **Heliconia marginata** *(Griggs) Pittier (Heliconiaceae) – "Pacova"*

This herb (1-2 m tall) with orange flowers is distributed from Panama to the Pantanal mainly in Amazonic environments, in Bolivia, Peru, and in the states of Amazon, Acre, Mato Grosso, and Mato Grosso do Sul in Brazil (JBRJ 2010; GBIF 2017). It forms *Pacoval* monodominant stands in stripes along rivers. This community has been named *Heliconietum* by Veloso (1972) and is a successional stage before woody vegetation. This species has rhizomes, whereby it survives fires. The leaves are grazed by capybara, and the flowers are visited by hummingbirds.

8.5 Possibilities of Economical Use

Although the Pantanal is a wetland with limited agricultural potential, the occurrence of several extensive monodominant stands may provide an opportunity for economical use. Most of the species reported here have possibilities to be used economically and are suggested for land restoration within the WebAmbiente hotsite (Brasil Embrapa/MMA 2018).

Paratudo (*Tabebuia aurea*) is a name allusive to medicinal properties, meaning "for everything" in Portuguese, or *paratodo* in Spanish. Other products, such as chemical compounds of the bark and leaves (see the chapter on "Metabolomics" Chap. 17), can also be extracted and used. Some species, such as *T. aurea*, *Handroanthus heptaphyllus*, and *Vochysia divergens*, can, with appropriate studies on growth rates, also be used as sources of timber. Other species may also be suitable as a source of timber, but more dendrochronological studies are needed, particularly to elucidate the considerable variation in diameter and volume increment that seems to exist between the different Brazilian wetlands, as has been demonstrated for *Calophyllum brasiliense* (Rosa et al. 2017).

Byrsonima cydoniifolia stands are just like a giant orchard in the Pantanal, without need to be planted, and no necessity to use pesticides or fertilizers. The fruit pulp is edible and can be used for juice, ice cream, and cakes (Pott and Pott 1994; Damasceno-Junior et al. 2010). The fruits contain trans-piceatannol stilbenoid derivatives and resveratrol, flavonoids, and gallic acid derivatives, with potent anti-inflammatory and antihyperalgesic effects (Santos et al. 2017). The fruits also contain high-quality oils with bioactive compounds (Marcelino et al. 2019) and have great potential as an organic gourmet commodity because of their nutraceutical potential that is stronger than grape as an antioxidant (Santos et al. 2017) and is readily produced.

Vochysia divergens is also a medicinal plant, as the bark is rich in sericic acid with activity against some bacteria such as *Staphylococcus aureus* (Hess et al. 1995). The leaves show no signs of herbivory, except a specific caterpillar. That may be related to endophytic fungi with potent biological activity detected in the leaves; they also show antimicrobial activity against clinical pathogens (Noriler et al. 2018).

Curatella americana leaves are used to polish pots and objects of horn and timber. The bark contains tannin. The crossed-fiber wood is used for stamp mills, troughs, and domestic water containers. The seed aril is edible, and the leaves are used as a medicine against tonsillitis (G.A. Damasceno-Junior pers. obs.).

Attalea phalerata has been used by the local people before the arrival of the Europeans. The fruit pulp and nuts are edible, and it is possible to grind its pulp into flour for human use together with fish in the traditional culinary; the heart of palm is sold at traditional markets (Damasceno-Junior et al. 2010). It is also consumed by peccaries, coatimundi, and psittacines and is one of the essential foods of hyacinth macaws to raise their offspring. The leaves are used to cover buildings.

Attalea speciosa is also a useful palm: the seeds contain an edible oil, and the leaves are used to cover roofs. The pulp is used to make flour (Araújo et al. 2016).

Mauritia flexuosa produces fruits with edible pulp, rich in carotenoids. The petioles are used to make various pieces of furniture. It provides the nesting sites for macaws.

Copernicia alba shows a high production of fruits every year that also can be used as food.

The species of *Oryza* are grazed by cattle and wildlife in the Pantanal (Allem and Valls 1987; Pott and Pott 2000) and were used by many native ethnicities, such as the Guató indigenous people, as food in the past (Matos 1875; Métraux 1942; Susnik 1982; Oliveira 1996). All grains of these species are red after harvesting and processing. The whole grains of *O. latifolia* are a significant source of proteins, carbohydrates, lipids, and fibers (Barbosa et al. 2017). Since the seeds of the *Oryza* species can be used as food, and in order to improve the income of riverine inhabitants by selling it as gourmet rice, it has been promoted by the Federal University of Mato Grosso do Sul as well as by NGOs (Bortolotto et al. 2017).

The C_4 sedge *Cyperus giganteus* produces a high amount of biomass that can be used for many purposes, such as cellulose production, ornamentals, and handicrafts.

Elionurus muticus contains sesquiterpenoids of essential oil with activity against some bacteria, such as *Bacillus cereus*, *Pseudomonas aeruginosa*, and *Staphylococcus aureus*; the interesting aspect of this is that the concentration and activity of these sesquiterpenoids can vary during the year (Hess et al. 2007).

8.6 Future Studies on Monodominant Stands in the Pantanal

While we consider the considerable economic potential of these species, some studies need be done to provide knowledge to be used in their management, such as on dendrochronology, biochemical composition and bioactivity, nutraceutical potential and food technology of fruits and other edible parts, reproductive biology, autecology, etc. Part of that is underway in ongoing projects of the UFMS (see the chapter on “Food Plants” Chap. 19).

We also consider it fundamental to understand the effects of inundation levels that help to maintain these populations, their soil preferences, their areas of recruitment, and the influences of flood and fire, to evaluate the possibilities to use these factors in the management of these species.

Acknowledgments The authors thank the Universidade Federal de Mato Grosso do Sul for the facilities in doing this work, to the CNPq (National Council for Scientific and Technological Development) for the grants to GADJ (process 307429/2019-9), AP (process 3031 91/2017), the scholarship to MR (process 554066/2010-6), CAPES (Coordination for Higher Education Staff Development) for the scholarship to DG, EBS, and DAMP, and to the FUNDECT (Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul) for the scholarship to GAA. We are also grateful to the INAU/CNPq project (Nr. 610033/2009-3) for the fundings of some of the results shown here.

References

Abdel-Ghani NT, Hegazy AK, El-Chaghaby GA, Lima EC (2009) Factorial experimental design for biosorption of iron and zinc using *Typha domingensis* phytomass. Desalination 249:343–347

Aguirre LF, Lens L, Matthysen E (2003) Patterns of roost use by bats in a Neotropical savanna: implications for conservation. Biol Conserv 111:435–443

Allem AC, Valls JFM (1987) Recursos Forrageiros Nativos do Pantanal Mato-Grossense. EMBRAPA, Brasilia

Amador GA (2013) Aspectos Ecológicos da estrutura da vegetação em áreas inundáveis dominadas por *Byrsonima cydoniifolia* e *Tabebuia aurea* no Pantanal. Mato Grosso do Sul, Brasil. PhD Thesis, Universidade Federal de Mato Grosso do Sul.

Amador GA, Damasceno-Junior GA, Casagrande JC, Sartori ALB (2012) Structure of two communities dominated by *Copernicia alba* and associations with soil and inundation in Pantanal Wetland, Brazil. Oecologia Australis 16:846–858

Araújo FR, González-pérez SE, Lopes MA, Viégas IDJM (2016) Ethnobotany of babassu palm (Attalea speciosa Mart.) in the Tucuruí Lake protected areas mosaic - eastern Amazon. Acta Bot Brasilica 30:193–204

Arieira J, Nunes da Cunha C (2006) Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae), no Pantanal Norte, MT, Brasil. Acta Bot Brasilica 20:569–580

Arieira J, Penha J, Nunes da Cunha C, Couto EG (2016) Ontogenetic shifts in habitat-association of tree species in a neotropical wetland. Plant Soil 404:219–236

Arruda WDS, Oldeland J, Paranhos Filho AC, Pott A, Cunha NL, Ishii IH, Damasceno-Junior GA (2016) Inundation and fire shape the structure of riparian forests in the Pantanal, Brazil. PLoS One 11:e0156825

Arrúa RD, Negrelle RRB (2014) Estructura poblacional, regeneración y producción potencial de cera de *Copernicia alba* Morong ex Morong, Britton en tres sitios de la región del Chaco, Paraguay. Iheringia – Ser Bot 69:277–284

Barbosa MM, Macedo MLR, Hiane PA, Damasceno-Junior GA, Braga Neto JA, Mendonça LABM, de Guimarães RCA, do Nascimento VA (2017) Proteins of *Oryza latifolia* from Brazilian Pantanal: impact on the use of aminoacids and weight gain of animals. Int J Dev Res 07:16885–16891

Bauer MO, Penso S, de Abreu JG, Gondim CA, Chichorro JF, Vasconcelos LV (2008) Composição botânica da dieta de bovinos em pastagem natural do cerrado mato-grossense. Ciência Anim Bras 9:346–356

Bertazzoni EC, Damasceno-Junior GA (2011) Aspectos da biologia e fenologia de *Oryza latifolia* Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Bot Brasilica 25:476–786

Bezerra MAO, Mozeto AA, de Oliveira PE, Volkmer-Ribeiro C, Rodrigues VV, Aravena R (2019) Late Pleistocene/Holocene environmental history of the southern Brazilian Pantanal wetlands. Oecologia Aust 23:712–729

Bocchese RA, Kleber A, De Oliveira M, Melotto AM, Fernandes V, Laura VA (2008) Effects of soil structure on germination of *Tabebuia heptaphylla* seeds. Cerne 14:62–67

Borges VP, de Costa MAPC, Ribas RF (2014) Emergencia e crescimento inicial de *Tabebuia heptaphylla* (Vell.) em ambientes contrastantes de luz. Rev Árvore 38:523–531

Bortoletto AM, Corrêa AC, Alcarde AR (2016) Fatty acid profile and glycerol concentration in cachaças aged in different wood barrels. J Inst Brew 122:293–298

Bortolotto IM, Guarim Neto G (2006) O uso do camalote, *Eichhornia crassipes* (Mart.) Solms, Pontederiaceae, para confecção de artesanato no Distrito de Albuquerque, Corumbá, MS, Brasil. Acta Bot Brasilica 19:331–337

Bortolotto IM, Hiane PA, Ishii IH, de Souza PR, Campos RP, Gomes RJB, da Farias CS, Leme FM, Arruda R d C d O, de Corrêa-da-Costa LBL, Damasceno-Junior GA (2017) A knowledge network to promote the use and valorization of wild food plants in the Pantanal and Cerrado, Brazil. Reg Environ Chang 17:1329–1341

Brasil (2020) Flora do Brasil 2020 em construção. Jard Botânico do Rio Janeiro. http://www.reflora.jbrj.gov.br/reflora/listaBrasil/PrincipalUC/PrincipalUC.do#CondicaoTaxonCP. Last accessed 27/05/2020

Brasil Embrapa/MMA (2018) WebAmbiente. https://www.webambiente.gov.br/publico/inicio.xhtml

Bueno M, Damasceno-Junior G, Pott A, Pontara V, Seleme E, Fava W, Salomão A, Ratter J (2014) Structure of arboreal and herbaceous strata in a Neotropical seasonally flooded monodominant savanna of *Tabebuia aurea*. Braz J Biol 74:325–337

Catian G, Leme FM, Francener A, Carvalho FS, Pott A, Pott VJ (2012) Macrophyte structure in lotic-lentic habitats from Brazilian Pantanal. Oecologia Aust 16(4):782–796

Chen H, Zamorano MF, Ivanoff D (2010) Effect of flooding depth on growth, biomass, photosynthesis, and chlorophyll fluorescence of *Typha domingensis*. Wetlands 30:957–965

Cisz ME, Falkowski MJ, Orr B (2013) Small-scale spatial patterns of *Copernicia alba* Morong near Bahia Negra, Paraguay. Nat Resour 4:369–377

Connell JH, Lowman MD (1989) Low-diversity tropical rain forests: some possible mechanisms for their existence. Am Nat 134:88–119

Cunha N, Delatorre M, Rodrigues R, Vidotto C, Gonçalves F, Scremin-Dias E, Damasceno-Júnior G, Pott V, Pott A (2012) Structure of aquatic vegetation of a large lake, western border of the Brazilian Pantanal. Braz J Biol 72:519–531

Costa CP (2013) Padrões da distribuição de plantas arbóreo-arbustivas em meso-escala no Pantanal de Mato Grosso. PhD Thesis, Universidade de Brasília.

Dalmagro HJ, Lathuillière MJ, Vourlitis GL, Campos RC, Pinto OB, Johnson MS, Ortíz CER, de Lobo FA, Couto EG (2016) Physiological responses to extreme hydrological events in the Pantanal wetland: heterogeneity of a plant community containing super-dominant species. J Veg Sci 27:568–577

Dalmolin A, Dalmagro H, de Lobo FA, Antunes M, Ortíz C, Vourlitis G (2013) Photosynthetic light and carbon dioxide response of the invasive tree, *Vochysia divergens* Pohl, to experimental flooding and shading. Photosynthetica 51:379–386

Dalmolin Â, Almeida Lobo F, Vourlitis G, Dalmagro H, Antunes Junior M, Rodriguez Ortiz C (2018) Physiological adjustments of an invasive tree species to extreme hydrological events in a tropical seasonal wetland. Trees 32:1365–1375

Damasceno-Junior GA (1997) Estudo floristico e fitossociologico de um trecho de mata ciliar do Rio Paraguai, Pantanal-MS, e suas relações com o regime de inundação. Dissertation, Universidade Estadual de Campinas.

Damasceno-Junior GA, Bezerra MAO, Bortolotto IM, Pott A (1999) Aspectos florísticos e fito-fisionômicos dos capões do Pantanal do Abobral. In: II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal, pp 203–214

Damasceno-Junior GA, Semir J, dos Santos FAM, de Leitão-Filho HF (2004) Tree mortality in a riparian forest at Rio Paraguai, Pantanal, Brazil, after an extreme flooding. Acta Bot Brasilica 18:839–846

Damasceno-Junior GA, Semir J, dos Santos FAM, de Leitão-Filho HF (2005) Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200:119–135

Damasceno-Junior GA, Souza PR, Bortolotto IM, Ramos MIL, Hiane PA, Braga Neto JA, Ishii IH, Costa DC, Ramos-Filho MM, Gomes RJB, Barbosa MM, Rodrigues RB (2010) Sabores do Cerrado e Pantanal: Receitas e boas práticas de aproveitamento. Editora UFMS, Campo Grande

Damasceno-Junior GA, Oldeland J, Amador GA, Casagrande JC, Twerski A (2021) Environmental drivers of three neighbouring monodominant stands in Pantanal wetland. J Veg Sci 32(3) e13023

Davis MA (1987) The role of flower visitors in the explosive pollination of *Thalia geniculata* (Marantaceae), a Costa Rican Marsh Plant. Bull Torrey Bot Club 114:134–138

Eiten G (1972) The cerrado vegetation of Brazil. Bot Rev 38:201–341

EPPO (2008) Data sheets on quarantine pests: *Eichhornia crassipes*. EPPO Bull 38:441–449

Eugênio CUO, Munhoz CBR, FelfiLi JM (2011) Dinâmica temporal do estrato herbáceo-arbustivo de uma área de campo limpo úmido em Alto Paraíso de Goiás, Brasil. Acta Bot Brasilica 25:497–507

Ferreira FA, Catian G, Pott A (2016) Diaspore bank of aquatic macrophytes maintaining species diversity in a Neotropical pond. Acta Sci Biol Sci 38:419–427

Fortes CF, Nunes da Cunha C, Rosa SA, Paixão E, Junk WJ, Schöngart J, Paixão E, Junk WJ (2018) Dendrochronological records of a pioneer tree species containing ENSO signal in the Pantanal, Brazil. Braz J Bot 41:167–174

Franklin DC, Brocklehurst PS, Lynch D, Bowman DMJS (2007) Niche differentiation and regeneration in the seasonally flooded Melaleuca forests of northern Australia. J Trop Ecol 23:457–467

Frota AVB, Ikeda-Castrillon SK, Kantek DLZ, Silva CJ (2018) Macrohabitats da Estação Ecológica de Taiamã, no contexto da Área Úmida Pantanal mato-grossense, Brasil. Bol Mus Para Emílio Goeldi – Ciênc Nat 12:239–254

Gaglianone MC (2005) Nesting biology, seasonality, and flower hosts of *Epicharis nigrita* (Friese, 1900) (Hymenoptera: Apidae: Centridini), with a comparative analysis for the genus. Stud Neotrop Fauna Environ 40:191–200

Galvão F, Roderjan C, Kuniyoshi Y, Ziller S (2002) Composição Florística e Fitossociologia de caxetais do litoral do Estado do Paraná-Brasil. Floresta 32 (1): 17-39

Garcez FR, Garcez WS, Mahmoud TS, de Figueiredo PO, Resende UM (2007) Novos constituintes químicos das cascas do caule de *Tabebuia heptaphylla*. Quim Nova 30:1887–1891

GBIF (2019a) *Tabebuia aurea* (Silva Manso) S.Moore. Species 2000 ITIS Cat Life. https://www.gbif.org/species/4091191. Last accessed 23/10/2019

GBIF (2020a) *Attalea phalerata* Mart. ex Spreng. https://www.gbif.org/species/2732758

GBIF (2020b) *Inga vera* Willd. https://www.gbif.org/occurrence/download/0057395-200613084148143 GBIF Occurrence Download https://doi.org/10.15468/dl.94fjpe

GBIF (2020c) *Licania parvifolia* Huber. https://www.gbif.org/species/2985492. Last accessed 24/06/2020

GBIF (2017) GBIF Occurrence Download *Heliconia marginata*. Licence CC BY 40. https://www.gbif.org/occurrence/download/0001115-171109162308116

GBIF (2019b) GBIF Occurrence Download *Thalia geniculata*. License CC BY-NC 40. https://www.gbif.org/occurrence/download/0038246-181108115102211

GBIF (2020d) GBIF Occurrence Download *Andropogon bicornis*. Licence CC BY-NC 40. https://www.gbif.org/occurrence/download/0037525-200613084148143

GBIF (2020e) GBIF Occurrence Download *Mauritia flexuosa*. https://doi.org/10.15468/dl.sb746b

GBIF (2020f) GBIF Occurrence Download *Paspalum wrightii*. https://www.gbif.org/occurrence/download/0036934-200613084148143. Last accessed 11/08/2020

Glenn E, Thompson TL, Frye R, Riley J, Baumgartner D (1995) Effects of salinity on growth and evapotranspiration of *Typha domingensis* Pers. Aquat Bot 52:75–91

Grace JB (1988) The effects of nutrient additions on mixtures of *Typha latifolia* L. and *Typha domingensis* Pers. along a water-depth gradient. Aquat Bot 31:83–92

Gris D (2017) Monodominance of *Erythrina fusca* Lour.: influence of environmental factors, chemical ecology and dendroecology. PhD Thesis, Universidade Federal de Mato Grosso do Sul.

Gris D, Boaretto AG, Marques MR, Geraldo, Damasceno-Junior A, Carlos, Carollo A (2019) Secondary metabolites that could contribute to the monodominance of *Erythrina fusca* in the Brazilian Pantanal. Ecotoxicology 28:1232–1240

Gris D, Paixão E, Arruda RCO, Ishii IH, Marques MR, Damasceno-Junior GA (2020) Growth and establishment of monodominant stands affected by ENSO and flooding in the Pantanal. Sci Rep 10:1–13

Haase R (1990) Community composition and soil properties in northern Bolivian savanna vegetation. J Veg Sci 1:345–352

Haase R, Beck SG (1989) Structure and composition of savanna vegetation in northern Bolivia : a preliminary report. Brittonia 41:80–100

Hart TB, Hart JA, Murphy PG (1989) Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. Am Nat 133:613–633

Hess SC, Brum RL, Honda NK, Cruz AB, Moretto E, Cruz RB, Messana I, Ferrari F, Filho VC, Yunes RA (1995) Antibacterial activity and phytochemical analysis of *Vochysia divergens* (Vochysiaceae). J Ethnopharmacol 47:97–100

Hess SC, Peres MTLP, Batista AL, Rodrigues JP, Tiviroli SC, Oliveira LGL, Santos CWC, Fedel LES, Crispim SMA, Flach A, Pantaroto S (2007) Evaluation of seasonal changes in chemical composition and antibacterial activity Artigo. Química Nova 30:370–373

IBGE (1992) Manual técnico da vegetação brasileira. Fundação Brasileira de Geografia e Estatística, Rio de janeiro.

Ishii IH (1998) Estudos dendrocronológicos e determinação da idade de árvores de matas ciliares do Pantanal sul-mato-grossense. PhD Thesis, Universidade Federal de São Carlos.

Jancoski HS, Pinto JRR, Nogueira DS, Mews HA, Abad JCS, Scalon MC, Marimon BS (2019) Fine-scale effects of fire on non-woody species in a southern Amazonian seasonal wetland. Wetl Ecol Manag 27:267–281

JBRJ (2010) Flora do Brasil 2020 em construção. http://floradobrasil.jbrj.gov.br/reflora/listaBrasil/PrincipalUC/PrincipalUC.do;jsessionid=050814FBF0CBEFC9C2D795C0ED76C7DC#CondicaoTaxonCP. Last accessed 14/08/2019

Junk WJ, Nunes da Cunha C (2012) Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction?. Wetlands Ecology and Management 20 (2):111–122

Kolb RM, Joly CA (2009) Flooding tolerance of *Tabebuia cassinoides*: metabolic, morphological and growth responses. Flora Morphol Distrib Funct Ecol Plants 204(7):528–535

Lagnika L, Attioua B, Weniger B, Kaiser M, Sanni A, Vonthron-Senecheau C (2008) Phytochemical study and antiprotozoal activity of compounds isolated from *Thalia geniculata*. Pharm Biol 46:162–165

Lehn CR, ML B, Kufner DCL, Scremin-Dias E, Pott VJ, Damasceno-Junior GA (2012) Fitossociologia de Macrófitas Aquáticas associadas ao Rio Miranda, Pantanal, MS, Brasil. Rev Biol Neotrop 8:23–31

Leite PTP (2012) Dendroecologia de Tabebuia aurea (Manso) Benth. & Hook e *Tabebuia heptaphylla* (Vell.) Toledo (Bignoniaceae) no Pantanal de Mato Grosso, Brasil. Dissertation, Universidade Federal de Mato Grosso.

Levis C, de Souza PF, Schietti J, Emilio T, da Pinto JLPV, Clement CR, Costa FRC (2012) Historical human footprint on modern tree species composition in the Purus-Madeira interfluve, Central Amazonia. PLoS One 7:e48559

Li S, Lissner J, Mendelssohn IA, Brix H, Lorenzen B, McKee KL, Miao S (2010) Nutrient and growth responses of cattail (*Typha domingensis*) to redox intensity and phosphate availability. Ann Bot 105:175–184

Lopez OR, Kursar TA (1999) Flood tolerance of four tropical tree species. Tree Physiol 19:925–932

Lorenzi H (2002) Árvores brasileiras: Manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Instituto Plantarum de Estudos da Flora, Nova Odessa SP Brasil

Lorenzi H (2008) Plantas daninhas do Brasil : terrestres, aquáticas, parasitas e tóxicas. Instituto Plantarum de Estudos da Flora, Nova Odessa SP Brasil

Magnusson WE, De Araújo MC, Cintra R, Lima AP, Martinelli LA, Sanaiotti TM, Vasconcelos HL, Victoria RL (1999) Contributions of C3 and C4 plants to higher trophic levels in an Amazonian savanna. Oecologia 119:91–96

Mahamadi C, Nharingo T (2010) Utilization of water hyacinth weed (*Eichhornia crassipes*) for the removal of Pb(II), Cd(II) and Zn(II) from aquatic environments: an adsorption isotherm study. Environ Technol 31:1221–1228

Mamede MCH, Francener A (2015) *Byrsonima* in Lista de Espécies da Flora do Brasil. Jard Botânico do Rio Janeiro

Manrique Pineda DA, de Souza EB, Paranhos Filho AC, Encina CCC, Damasceno-Junior GA (2021) Fire, flood and monodominance of Tabebuia aurea in Pantanal. For Ecol Manag 479:118599. https://doi.org/10.1016/j.foreco.2020.118599

Marcelino G, Donadon JR, Caires ARL, Michels FS, Oliveira LCS, Cortes MR, Maldonade IR, Cavalheiro LF, Nazário CED, Maróstica Júnior MR, Santos NMD, Batista PB, Pott A, Nunes ÂA, Figueiredo PS, Hiane PA, Nascimento VA, Guimarães RCA (2019) Characterization and oxidative stability of oils and bioactive compounds of the fruits of *Byrsonima cydoniifolia* A. Juss. at different ripening stages. J Sci Food Agric 99:2855–2864

Marimon BS, de Lima ES (2001) Caracterização fitofisionômica e levantamento florístico preliminar no Pantanal dos Rios Mortes-Araguaia, Cocalinho, Mato Grosso, Brasil. Acta Bot Brasilica 15:213–229

Marimon BS, Felfili JM, Haridasan M (2001) Studies in Monodominant Forests in Eastern Mato Grosso, Brazil: Ii. a Forest in the Areões Xavante Indian Reserve. Edinb J Bot 58:483–497

Matos RJC (1875) Viagem de Porto Feliz a Cidade de Cuyaba: 22 de junho de 1826. Rev Trimest do Inst Histórico Geogr e Ethnogr do Bras 38:367–441

Mattos PP, Domene VD, Salis SM, Braz EM (2016) Crescimento diamétrico de canjiqueira (*Byrsonima cydoniifolia*) no Pantanal da Nhecolândia, Corumbá, MS. Comunicado técnico 382/100. Embrapa Florestas/Embrapa Pantanal. Colombo, PR, Brazil.

Métraux A (1942) The native tribes of eastern Bolivia and western Matto Grosso. Smithsonian Institution, Washington, DC.

Meza-Lopez MM, Siemann E (2017) Nutrient enrichment increases plant biomass and exotic plant proportional cover independent of warming in freshwater wetland communities. Plant Ecol 218:835–842

Missouri Botanical Garden (2015) Tropicos | Name – *Byrsonima cydoniifolia* A. Juss. https://www.tropicos.org/Name/19500177?projectid=13&langid=66. Last accessed 10/07/2019

Mitsch WJ, Taylor JR, Benson KB (1991) Estimating primary productivity of forested wetland communities in different hydrologic landscapes. Landsc Ecol 5:75–92

Montúfar R, Anthelme F, Pintaud JC, Balslev H (2011) Disturbance and resilience in tropical American palm populations and communities. Bot Rev 77:426–461

Moraes M (1991) Contribución al estudio del ciclo biológico de *Copernicia alba* en una estancia ganadera (Espíritu, Beni, Bolivia). Ecol en Boliv 18:1–20

Moraes RM (2014) Palmeras útiles de Bolívia. Las espécies mayormente aprovechadas para diferentes fines y aplicaciones. La Paz: Herbário Nacional de Bolívia - Universidade Mayor de San Andrés, Plural Ediciones

Moreira SN, Pott A, Pott VJ, Damasceno-Junior GA, Moreira SN, Pott A, Pott VJ, Damasceno-Junior GA (2011) Structure of pond vegetation of a Vereda in the Brazilian Cerrado. Rodriguésia 62:721–729

Moreira SN, Pott VJ, de Souza EB, Pott A (2017) Are *Mauritia flexuosa* L. f. palm swamps in the Brazilian Pantanal true veredas? A floristic appraisal. Bol Mus Para Emílio Goeldi Cienc Nat 12:221–238

Mormul RP, Ferreira FA, Michelan TS, Carvalho P, Silveira MJ, Thomaz SM (2009) Aquatic macrophytes in the large, sub-tropical Itaipu Reservoir, Brazil. Rev Biol Trop 58:1437–1451

Munhoz CBR, Felfili JM (2005) Fenologia do estrato herbáceo-subarbustivo de uma comunidade de campo sujo na Fazenda Água Limpa no Distrito Federal, Brasil. Acta Bot Brasilica 19:979–988

Munhoz CBR, Felfili JM, Rodrigues C (2008) Species-environment relationship in the herb-subshrub layer of a moist Savanna site, Federal District, Brazil. Braz J Biol 68:25–35

Murphy K, Efremov A, Davidson TA, Molina-navarro E, Fidanza K, Camila T, Betiol C, Chambers P, Tapia J, Varandas S, Springuel I, Kennedy M, Paulo R, Dibble E, Hofstra D, András B, Gebler D, Baastrup-spohr L, Urrutia-estrada J (2019) World distribution, diversity and endemism of aquatic macrophytes. Aquat Bot 158:103127

Nascimento MT, Da Cunha CN (1989) Estrutura e composição florística de um cambarazal no pantanal de Poconé-MT. Acta Bot Brasilica 3:3–23

Nascimento MT, Proctor J (1997a) Population dynamics of five tree species in a monodominant peltogyne forest and two other forest types on Maraca Island, Roraima, Brazil. For Ecol Manag 94:115–128

Nascimento MT, Proctor J (1997b) Soil and plant changes across a monodominant rain Forest boundary on Maraca Island, Roraima, Brazil. Glob Ecol Biogeogr Lett 6:387

Negrelle RRB (2016) Tree species composition and structure in an area representative of "acuri forest" at Pantanal matogrossense, Brasil. Ciencia Florest 26:589–600

Neto MDA, Furley PA, Haridasan M, Johnson CE (1986) The Murundus of the Cerrado Region of Central Brazil. J Trop Ecol 2:17–35

Noriler SA, Savi DC, Aluizio R, Palácio-Cortes AM, Possiede YM, Glienke C (2018) Bioprospecting and structure of fungal endophyte communities found in the Brazilian biomes, Pantanal, and Cerrado. Front Microbiol 9:1–14

Nunes da Cunha C, Junk WJ (2004) Year-to-year changes in water level drive the invasion of Vochysia divergens in Pantanal grasslands. Appl Veg Sci 7:103–110

Nunes da Cunha C, Junk WJ (2014) A Classificação dos Macrohabitats do Pantanal Matogrossense. In: da Nunes, Cunha, Catia, Fernandez, Matia Tereza P, Junk WJ, editor. Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats. Cuiabá: EdUFMT. pp. 77–122

Nunes da Cunha C, Junk WJ, Leitão Filho HDF (2007) Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology. Amazoniana 19:159–184

Nunes da Cunha C, Junk WJ (2011) A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to national and international wetland classification systems. In: Junk WJ, da Silva CJ, da Nunes Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia-Moscow, pp 127–141

Okamoto JM (1998) Ecofisiologia da germinação e do metabolismo respiratório de quatro espécies do gênero *Inga* Mill. (Mimosaceae) submetidas à hipóxia e anóxia. Dissertation, Universidade Estadual de Campinas.

Oliveira-Filho AT (1992) Floodplain 'Murundus' of Central Brazil : evidence for the termite-origin hypothesis. J Trop Ecol 8:1–19

Oliveira JE (1996) Guató: Argonautas do Pantanal. EDIPUCRS, Porto Alegre

Olivo-Neto AM, Da Silva CJ, Castrillon SKI, Lazaro WL, Damasceno-Junior GA, Gris D, Pereira TDC, Sander NL (2020) Spatial distribution of single specie dominant forests of *Erythrina fusca* Lour. At the Taiamã Ecological Station, Pantanal, Mato Grosso, Brazil. Trop Ecol 61:248–257

Padial A, Bini L, Thomaz S (2008) The study of aquatic macrophytes in Neotropics: a scientometrical view of the main trends and gaps. Braz J Biol 68:1051–1059

Padilha DC, Salis SM, Crispim SMA (2008) Fitossociologia das Espécies Lenhosas em Campo Cerrado no Pantanal de Poconé e Paiaguás. Bol Pesqui e Desenvolv – Embrapa 81

Parrini R, Raposo MA (2010) Aves explorando flores de *Erythrina fusca* (Leguminosae, Fabaceae) durante a estação seca no Pantanal de Mato Grosso. Iheringia Série Zool 100:97–101

Pascotto MC, Ten Caten H, Oliveira JPF (2012) Birds as potential seed dispersers of *Curatella Americana* L. (Dilleniaceae) in the Brazilian Cerrado. Ornitol Neotrop 23:585–595

Paulino-Neto, HF (2007) Pollination and breeding system of Couepia uiti (Mart. and Zucc.) Benth (Chrysobalanaceae) in the Pantanal da Nhecolândia. Brazilian Journal of Biology 67(4):715–9

Peh KS-HH, Lewis SL, Lloyd J (2011) Mechanisms of monodominance in diverse tropical tree-dominated systems. J Ecol 99:891–898

Pennington TD (1997) In: Linklater R (ed) The genus *Inga* botany. The Royal Botanic Gardens, Kew, London

Pincam T, Brix H, Jampeetong A (2020) Growth performance of tropical wetland species (*Cyperus involucratus* Rottb. and *Thalia geniculata* L.) in anaerobic digester effluent and their water treatment efficiency. Ecol Eng 143:105667

Pivari MO, Pott VJ, Pott A (2008) Macrófitas aquáticas de ilhas flutuantes (baceiros) nas sub-regiões do Abobral e Miranda, Pantanal, MS, Brasil. Acta Bot Brasilica 22:563–571

Ponce VM, Nunes da Cunha C (1993) Vegetated Earthmounds in tropical savannas of Central Brazil: a synthesis: with special reference to the Pantanal do Mato Grosso. J Biogeogr 20:219

Ponzio KJ, Miller SJ, Lee MA (2004) Long-term effects of prescribed fire on Cladium jamaicense Crantz and Typha *domingensis* Pers. densities. Wetl Ecol Manag 12:123–133

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa, Corumbá

Pott VJ, Pott A (2000) Plantas aquáticas do Pantanal. Embrapa, Brasília

Pott A, Oliveira A, Damasceno-Junior G, Silva J (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71:265–273

Prance GT, Schaller GB (1982) Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. Brittonia 34:228–251

Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian cerrado vegetation III: comparison of the woody vegetation of 376 areas. Edinb J Bot 60:57–109

Ribeiro SP, Brown VK (2002) Tree species monodominance or species-rich savannas? The influence of abiotic factors in designing plant communities of the Brazilian Cerrado and Pantanal Matogrossense a review. Ecotropica 8:31–45

Ribeiro SP, Brown VK (2006) Prevalence of monodominant vigorous tree populations in the tropics: herbivory pressure on Tabebuia species in very different habitats. J Ecol 94:932–941

Ribeiro JF, Walter BMT (2008) As principais fitofisionomias do Bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: Ecologia e Flora. Embrapa Informação Tecnológica, Brasilia, pp 151–212

Richardson CJ (2010) The Everglades: North America's subtropical wetland. Wetl Ecol Manag 18:517–542

Rivaben RC, Pott A, Bueno ML, Parolin P, Neyra MOC, Oldeland J, Silva RH, Damasceno-Júnior GA (2021) Do fire and flood interact to determine forest islet structure and diversity in a Neotropical wetland? Flora 281:151874. https://doi.org/10.1016/j.flora.2021.151874

Rocha M, Santos Júnior CC, Damasceno-Junior GA, Pott V, Pott A (2015) Effect of fire on a monodominant floating mat of *Cyperus giganteus* Vahl in a Neotropical wetland. Braz J Biol 75:114–124

Rodrigues AC, Estelita MEM (2002) Primary and secondary development of *Cyperus giganteus* Vahl rhizome (Cyperaceae). Rev Bras Botânica 25:251–258

Rodrigues AC, Estelita MEM (2003) Origin and structure of the Kranz tissue in bracts of *Cyperus giganteus* Vahl (Cyperaceae). Rev Bras Botânica 26:445–452

Rodrigues AC, Estelita MEM (2004) Anatomia da raiz de *Cyperus giganteus* Vahl (Cyperaceae) em desenvolvimento. Rev Bras Botânica 27:629–638

Rosa SA, Barbosa ACMC, Junk WJ, Nunes da Cunha C, Piedade MTF, Scabin AB, Ceccantini GCT, Schöngart J (2017) Growth models based on tree-ring data for the Neotropical tree species *Calophyllum brasiliense* across different Brazilian wetlands: implications for conservation and management. Trees – Struct Funct 31:729–742

Rozhkov VA, Shvidenko AZ (2010) The first digital maps of biological productivity parameters. Eurasian Soil Sci 43:1296–1304

Russo RO, Baguinon NT (1997) Erythrina fusca Loureiro. In: der Faridah Hanum IVMLJG (ed) Plant resources of South-East Asia no 11: auxiliary plants, Leiden, pp 121–123

Santana FJM, Pérez-Buitrago N, Pérez-Cárdenas N (2019) Variación estacional de la composición florística en sabanas inundables en Arauca, Colombia. Caldasia 41:404–421

Santos SA, Comastri-Filho JA (2012) Práticas de limpeza de campo para o Pantanal. Comunicado Técnico 92. Embrapa Pantanal, Corumbá.

Santos LB, Souza JK, Papassoni B, Borges DGL, Damasceno-Junior GA, de Souza JME, Carollo CA, de Borges FA, dos Santos LB, Souza JK, Papassoni B, Borges DGL, Damasceno-Junior GA, de Souza JME, Carollo CA, de Borges FA (2013) Efficacy of extracts from plants of the Brazilian Pantanal against *Rhipicephalus* (*Boophilus*) *microplus*. Rev Bras Parasitol Veterinária 22:532–538

Santos VS, Nascimento TV, Felipe JL, Boaretto AG, Damasceno-Junior GA, Silva DB, Toffoli-Kadri MC, Carollo CA (2017) Nutraceutical potential of *Byrsonima cydoniifolia* fruits based on chemical composition, anti-inflammatory, and antihyperalgesic activities. Food Chem 237:240–246

Sazan MS, Bezerra ADM, Freitas BM (2014) Oil collecting bees and *Byrsonima cydoniifolia* A. Juss. (Malpighiaceae) interactions: the prevalence of long-distance cross pollination driving reproductive success. An Acad Bras Cienc 86:347–358

Sazima I, Zamprogno C (1985) Use of water hyacinths as shelter, foraging place, and transport by young piranhas, *Serrasalmus spilopleura*. Environ Biol Fish 12:237–240

Schessl M (1999) Floristic composition and structure of floodplain vegetation in the northern Pantanal of Mato Grosso, Brazil. Phyton (B Aires) 39:303–336

Schmeda-Hirschmann G, Papastergiou F (2003) Naphthoquinone Derivatives and Lignans from the Paraguayan Crude Drug “Tayï Pytá” (*Tabebuia heptaphylla*, Bignoniaceae). Technical University of Berlin

Schmidt M (1942) Estudos de etnologia brasileira : peripécias de uma viagem entre 1900 e 1901: seus resultados etnológicos. Ed. Nacional, São Paulo

Silva RH (2018) Estabelecimento de protocolo para uso sustentável de *Copernicia alba* Morong ex Morong & Britton na bacia do rio Paraguai, MS. Universidade Federal de Matro Grosso do Sul. PhD Thesis, Universidade Federal de Mato Grosso do Sul.

Silva MP, Mauro R, Mourão G, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Rev Bras Botânica 23:143–152

Soares JJ, de Oliveira AKM (2009) O paratudal do Pantanal de Miranda, Corumbá-MS, Brasil. Rev Árvore 33:339–347

Souza EB, Damasceno-Junior GA, Pott A (2019) Soil seed bank in Pantanal riparian forest: persistence, abundance, functional diversity and composition. Oecologia Aust 23:891–903

Souza JME, Chang MR, Brito DZ, Farias KS, Damasceno-Junior GA, Turatti ICC, Lopes NP, Santos EA, Carollo CA, Souza JME, Chang MR, Brito DZ, Farias KS, Damasceno-Junior GA, Turatti ICC, Lopes NP, Santos EA, Carollo CA (2015) Antimicrobial activity of *Aspilia latissima* (Asteraceae). Brazilian J Microbiol 46:1103–1110

Stumpf ERT, Barbieri RL, Fischer SZ, Heiden G, Neitzke RS (2009) Uso ornamental de *Andropogon bicornis* L. (Poaceae). Ceres 56:186–192

Susnik B (1982) Los aborígenes del Paraguay: cultura material. Mus etnográfico Ändres Barbero 4:64–67

ter Steege H, Pitman NCA, Sabatier D, Baraloto C, Salomão RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE, Molino J-F, Monteagudo A, Núñez Vargas P, Montero JC, Feldpausch TR, Coronado ENH, Killeen TJ, Mostacedo B, Vasquez R, Assis RL, Terborgh J, Wittmann F, Andrade A, Laurance WF, Laurance SGW, Marimon BS, Marimon B-H, Guimarães Vieira IC, Amaral IL, Brienen R, Castellanos H, Cárdenas López D, Duivenvoorden JF, Mogollón HF, de Matos FDA, Dávila N, García-Villacorta R, Stevenson Diaz PR, Costa F, Emilio T, Levis C, Schietti J, Souza P, Alonso A, Dallmeier F, AJD M, Fernandez Piedade MT, Araujo-Murakami A, Arroyo L, Gribel R, PVA F, Peres CA, Toledo M, Aymard CGA, Baker TR, Cerón C, Engel J, Henkel TW, Maas P, Petronelli P, Stropp J, Zartman CE, Daly D, Neill D, Silveira M, Paredes MR, Chave J, de Lima Filho DA, Jørgensen PM, Fuentes A, Schöngart J, Cornejo Valverde F, Di Fiore A, Jimenez EM, Peñuela Mora MC, Phillips JF, Rivas G, van Andel TR, von Hildebrand P, Hoffman B, Zent EL, Malhi Y, Prieto A, Rudas A, Ruschell AR, Silva N, Vos V, Zent S, Oliveira AA, Schutz AC, Gonzales T, Trindade Nascimento M, Ramirez-Angulo H, Sierra R, Tirado M, Umaña Medina MN, van der Heijden G, Vela CIA, Vilanova Torre E et al (2013) Hyperdominance in the Amazonian tree flora. Science 342:325

ter Steege H, Henkel TW, Helal N, Marimon BS, Marimon-Junior BH, Huth A, Groeneveld J, Sabatier D, de Coelho LS, de Filho DAL, Salomão RP, Amaral IL, de Matos FDA, Castilho CV, Phillips OL, Guevara JE, de Carim MJV, Cárdenas López D, Magnusson WE, Wittmann F, Irume MV, Martins MP, da Guimarães JRS, Molino JF, Bánki OS, MTF P, NCA P, Mendoza AM, Ramos JF, Luize BG, Moraes de Leão Novo EM, Núñez Vargas P, TSF S, Venticinque EM, Manzatto AG, NFC R, Terborgh J, Casula KR, Honorio Coronado EN, Montero JC, Feldpausch TR, Duque A, FRC C, Arboleda NC, Schöngart J, Killeen TJ, Vasquez R, Mostacedo B, Demarchi LO, Assis RL, Baraloto C, Engel J, Petronelli P, Castellanos H, de Medeiros MB, Quaresma A, Simon MF, Andrade A, Camargo JL, Laurance SGW, Laurance WF, Rincón LM, Schietti J, Sousa TR, de Sousa Farias E, Lopes MA, Magalhães JLL, Mendonça Nascimento HE, Lima de Queiroz H, Aymard CGA, Brienen R, Revilla JDC, Vieira ICG, Cintra BBL, Stevenson PR, Feitosa YO, Duivenvoorden JF, Mogollón HF, Araujo-Murakami A, Ferreira LV, Lozada JR, Comiskey JA, de Toledo JJ, Damasco G, Dávila N, Draper F, García-Villacorta R, Lopes A, Vicentini A, Alonso A, Dallmeier F, VHF G, Lloyd J, Neill D, de Aguiar DPP, Arroyo L, Carvalho FA, de Souza FC et al (2019) Rarity of monodominance in hyperdiverse Amazonian forests. Sci Rep 9:13822

Terer T, Muasya AM, Dahdouh-Guebas F, Ndiritu GG, Triest L (2012) Integrating local ecological knowledge and management practices of an isolated semi-arid papyrus swamp (Loboi, Kenya) into a wider conservation framework. J Environ Manag 93:71–84

Thielen D, Schuchmann KL, Ramoni-Perazzi P, Marquez M, Rojas W, Quintero JI, Marques MI (2020) Quo vadis Pantanal? Expected precipitation extremes and drought dynamics from changing sea surface temperature. PLoS One 15:1–25

Thomaz SM (2002) Fatores ecológicos associados à colonização e ao desenvolvimento de macrófitas aquáticas e desafios de manejo. Planta Daninha 20:21–33

Tomas WM, Salis SM (2000) Diet of the marsh deer (*Blastocerus dichotomus*) in the Pantanal wetland, Brazil. Stud Neotrop Fauna Environ 35:165–172

Torti SD, Coley PD, Kursar TA (2001) Causes and consequences of monodominance in tropical lowland forests. Am Nat 157:141–153

Van Der Velden N, Ferry Slik JW, Hu Y-HY-H, Lan G, Lin L, Deng X, Poorter L, Slik JWF, Hu Y-HY-H, Lan G, Lin L, Deng X, Poorter L (2014) Monodominance of *Parashorea* chinensis on fertile soils in a Chinese tropical rain forest. J Trop Ecol 30:311–322

Veloso HP (1972) Aspectos fito-ecológicos da Bacia do Alto Paraguai. Universidade de São Paulo, São Paulo

Werger MJA (1983) Tropical grasslands, savannas, woodlands: natural and manmade. In: Holzner W, Werger MJA, Ikusima I (eds) Man's impact on vegetation. Dr. W. Junk Publication, The Hague/Boston, pp 107–137

Wilson JB, Peet RK, Dengler J, Pärtel M (2012) Plant species richness : the world records. J Veg Sci 23:796–802

Zanin A, Longhi-Wagner HM (2011) Revisão de *Andropogon* (Poaceae – Andropogoneae) para o Brasil. Rodriguésia 62:171–202

Chapter 9
Composition and Distribution of Woody and Palm Vegetation in the Pantanal Wetland

Evaldo Benedito de Souza, Arnildo Pott, Florian Wittmann, Pia Parolin,
Heike Markus-Michalczyk, Marcelo Leandro Bueno,
and Geraldo Alves Damasceno-Junior

9.1 Introduction

The distribution of tree, shrub, and palm species at a broad geographic scale is influenced by climatic factors, such as rainfall pattern and temperature, soil type, relief, and species traits, like dispersal capacity. However, owing to the location in the middle of the continent and its relatively small size with a slightly variable climatic regime (Marengo et al. 2015), climatic factors, such as temperature and rainfall, do not seem to determine the occurrence or absence of species in certain areas in the Pantanal. Even small variations in temperature and rainfall can affect the population densities of arboreal species across the floodplain. In the Pantanal, differences of composition were reported to be mostly associated with soil type (Pott 1994), inundation (Damasceno-Junior et al. 2005), and biogeographic factors, i.e., the influence of adjacent biomes (Adámoli 1982; Prado and Gibbs 1993a; Pott et al. 2011).

E. B. de Souza (✉) · A. Pott · G. A. Damasceno-Junior
Laboratório de Ecologia Vegetal, Instituto de Biociências, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil

F. Wittmann
Department of Wetland Ecology, Institute for Geography and Geoecology, Karlsruhe Institute for Technology, Karlsruhe, Germany

P. Parolin
Université Côte d'Azur, INRAE, CNRS, ISA, Sophia Antipolis, France

H. Markus-Michalczyk
NIOZ Royal Netherlands Institute for Sea Research, Estuarine and Delta Systems, Yerseke, The Netherlands

M. L. Bueno
Universidade Estadual de Mato Grosso do Sul, Laboratório de Macroecologia e Evolução (LAME), Mundo Novo, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_9

The soils of the Pantanal are in their majority Planosols, distributed throughout the wetland, with a wider occurrence in the central and southern parts; Spodosols, in the central-west subregions of Paiaguás and Nhecolândia; and Plinthosols, concentrated in the north. At low topographies occur Argisols, Gleysols, Latosols, Luvisols, Neosols, Vertisols, and Chernosols (Spera et al. 2000). The prevailing plant physiognomies can be excellent indicators of soil types in the Pantanal. Cerrado woodlands (*cerradão*) in the northern Pantanal, for example, become established on Spodosols (Salis et al. 2006). In contrast, deciduous seasonal forests are associated with Vertisols and Plinthosols (Damasceno-Junior et al. 2009; Bueno et al. 2014). Vertisols are moderately drained and have elevated contents of clay that are rich in calcium and magnesium. Luvisols are non-hydromorphic mineral soils, with relatively high proportions of clay and high base saturation (Pott 1994; Spera et al. 2000).

The Pantanal soils have diverse origins that are influenced by the different hydrologic regimes of each subregion (Cunha 1981; Soares et al. 2006; Couto and Oliveira 2010; Beirigo et al. 2011). Due to the various characteristics that distinguish soil types in the Pantanal (structural, drainage, availability of nutrients, cation exchange capacity, etc.), they may cause stands that differ in plant species composition (Cunha 1981; Soares et al. 2006; Zeilhofer 2006; Beirigo et al. 2011; Bazzo et al. 2012).

The proportion of flooded areas and the length of the period of flooding increases as the altitude decreases within the floodplain. This decrease in altitude and, consequently, the increase in flooding area occur more pronounced from the east to the west of the Pantanal. The largest flooded areas with longest floods are located to the west, on the axis of the Paraguay River (Padovani 2010). In this way, the altitudinal gradient can be an indirect factor that affects the composition of woody species on a large geographic scale inside the wetland.

In general, the vegetation is distributed over a subtle but well-defined topographic gradient. Such distribution is mainly driven by the levels of flood tolerance of the species (Nunes da Cunha 2001; Damasceno-Junior et al. 2005; Bueno et al. 2014). However, several species can occur all over the gradient, showing a high plasticity (Adámoli and Pott 1996; Nunes da Cunha 2001; Damasceno-Junior et al. 2005). These aspects can be easily demonstrated at local scales. The effect of altitude and, consequently, of inundation on species composition is less obvious when considered at broader geographic scales encompassing the whole plain. This results mainly from the presence of species that do not tolerate the long flooding in areas that are homogeneously flooded over wide stretches of land but can persist on small, slightly elevated pieces of terrain that are consequently flooded more shortly. Some isolated points in subregions of shallow floods can also stay flooded for more than 6 months and allow the establishment of hydrophilous species.

The levels of endemism in the flora of the Pantanal floodplain are comparatively low, and the vegetation is an aggregate of species from adjacent domains. This results from the fact that the formation of the Pantanal is relatively young, ~2.5 Ma (Ussami et al. 1999), and that is in contrast with the other biomes in Brazil, such as the Cerrado, Atlantic Forest, and Amazon. Besides, the strong climatic variability subjecting the area to constant drought and super wet events can hinder the evolution of endemic species. The influence of the immigration of species from vegetation domains adjacent to the Pantanal is very evident. Nevertheless, some species that occur in the uplands and nearby hills do not succeed to become established and maintain viable populations within the plain, even though their seeds arrive dispersed by wind, birds, and water. Thus, species establishment on the floodplain depends as much on the requirements of the species as on the availability of suitable habitats. Most woody species that occur in the flooded area of Pantanal have wide distributions occurring in all Brazilian phytogeographic domains. Specifically, the domains that influence the Pantanal vegetation are the Cerrado, Chaco, Amazon, and Atlantic Forest (Adámoli 1982; Damasceno-Junior et al. 2009; Pott et al. 2011; Pontara et al. 2016; Bueno et al. 2017; Bueno et al. 2018b).

The vegetation of the Pantanal is considered as originating predominantly from the Cerrado. Adámoli (1982) estimated that 70% of the Pantanal is covered by Cerrado vegetation. Later, Silva et al. (2000), interpreting satellite images with field inspection, determined that 36% of all vegetation types are typical representants of the Cerrado, with 22% *cerradão* (Cerrado woodlands) and 14% *cerrado sensu stricto*. The more extensive contact area of the Pantanal plain with the adjacent Cerrado may be a determinant factor for this feature. The proportion of *cerrados* in other formations (e.g., seasonal forests) varies per subregion, with the highest proportions in the eastern part of the plain (Silva et al. 2000a) (see the Chap. 2 on "Mapping").

In the most accepted classification, the Pantanal is divided into 11 subregions (Fig. 9.1), with distinctive edaphic aspects, relief, soil, and vegetation (Silva and Abdon 1998). Therefore, each subregion can be characterized according to its dominant vegetation types. Some vegetation types are most common or even exclusive to specific subregions, emphasizing the landscape differences over the plain. Even so, species composition may be similar in areas with similar environmental characteristics, even when they are geographically distant.

The subregions in the Pantanal are often distinguished by the dominance of certain vegetation types. However, there is also a remarkable heterogeneity within each subregion, with vegetation mosaics and abrupt shifts in the local species composition and in the structure of different types of vegetation. Sometimes such a shift is not so apparent when changes in species composition and vegetation structure occur over a gradient or continuum. In general, the abrupt differences are driven by a fine-scale topographic variation and flooding regime that determine the species location along the environmental gradient (Pott and Silva 2015). The characterization and identification of vegetation types and their structural and floristic differences can be given by the presence or absence and, more often, by the frequency of occurrence of some species (Nunes da Cunha and Junk 2011; Pott et al. 2011; Wittmann et al. 2017). In this chapter, we investigate the distribution patterns of woody and palm species and their correlations with soil types and altitudinal categories within the Pantanal wetland. We also analyze the overlap of the Pantanal species composition with the vegetation of other wetland regions in Brazil.

9.2 Methods

We compiled and reviewed 50 publications with surveys of tree, shrub, and palm species at 70 locations, which comprised a total of 492 species within the Pantanal wetland (Fig. 9.1). To compile the data, we used Web of Science, university data repositories, and printed symposium annals, conference, and congress proceedings. The compilation was made between September 2019 and January 2020. We georeferenced the data. For growth form determination of the tree or shrub species, we considered the classifications used in the surveys (when present), as well as the database of Flora do Brasil (Brasil 2020). We did not consider species that grow as subshrubs; thus, we included only tall shrub species and tree species, even those occasionally classified as shrubs, or shrubs occasionally classified as trees, and tree palms. Taxa names were verified on the website Flora do Brasil 2020 (Brasil 2020) and *Taxonomic Name Resolution Service* (Boyle et al. 2013).

We analyzed the distribution of species as a function of altitude (height above sea level) and soil type. Soil type information was obtained from the site AMBDATA (INPE 2010). We obtained the altitudinal data from the *Banco de Dados Geomorfométricos do Brasil*, available at the site TOPODATA (INPE 2011). Within

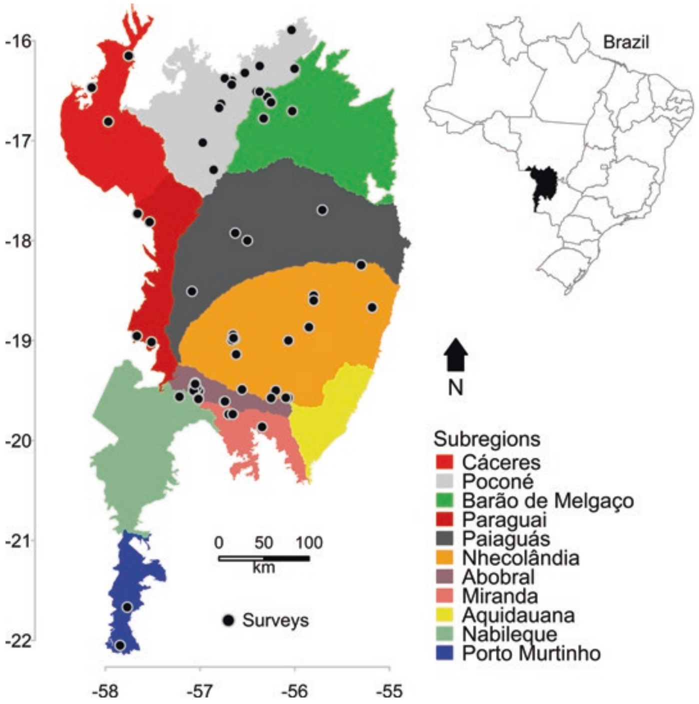


Fig. 9.1 Locations of surveys of shrub, palm, and tree species within the subregions of the Brazilian Pantanal wetland

the plain, we distinguished the following altitudinal categories: 80–100, 100–130, 130–170 m; in the survey, no site over 170 m asl was recorded. The altitude categories were delimited in order to secure that each altitudinal category comprised approximately a similar area size (Fig. 9.2). For comparisons of species composition between altitudinal category and soil type, we utilized permutational multivariate analysis of variance (PERMANOVA) with 1000 permutations and pairwise-permanova for differences between groups (Anderson 2001), with Bonferroni corrections for p-value adjustment. For a better visualization of species distribution along altitudinal category and soil type, we applied hierarchical cluster analyses based on absence/presence matrices using Ward's minimum variance method (Ward 1963).

We also calculated the relative species frequency in the altitudinal categories and soil types. To evaluate frequency, we considered only soil types which contained at least three surveys. We did not consider species abundances due to the discrepancies in methods and sampling effort in the surveys, since several surveys only contained a species list, but no abundance data.

Species similarity of the woody flora of the Pantanal wetland as compared to all other Brazilian biomes was investigated based on floristic inventories compiled by

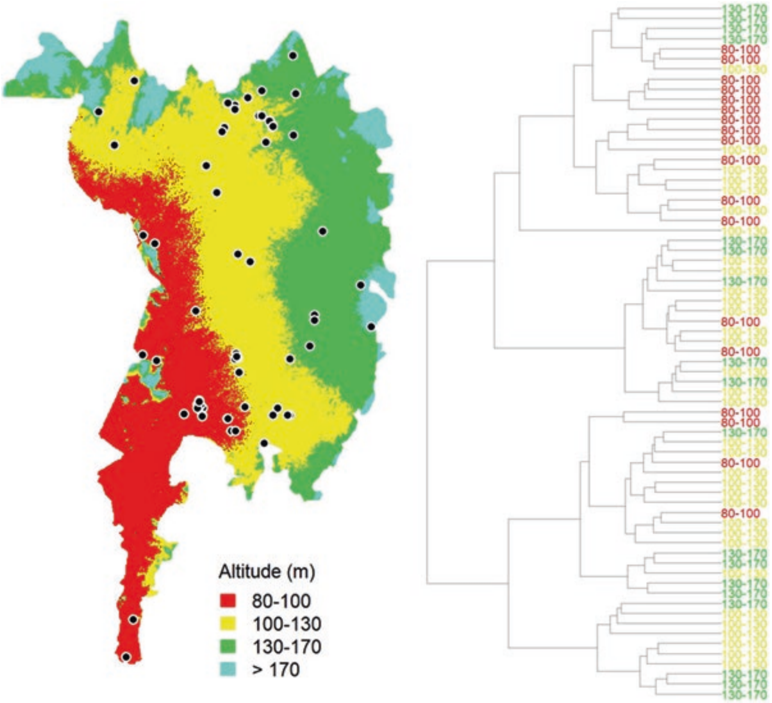


Fig. 9.2 Hierarchical cluster of the floristic relations between altitudinal categories in the Brazilian Pantanal wetland. Colors in the dendrogram indicate the altitudinal categories

Wittmann et al. (2017) for the Cerrado, Atlantic Forest, Amazonia, Caatinga, and Pampas. We restricted this analysis only to the 28 surveys that were conducted in episodically or periodically flooded areas of the Pantanal. We calculated the Bray-Curtis disimilarity index of species composition between vegetation domains and built a hierarchical cluster (average method or UPGMA) of the floristic relations utilizing the absolute species frequency (number of occurrences/number of surveys) in each vegetation domain.

9.3 Results and Discussion

9.3.1 Altitude

Our analyses showed differences in species composition between the altitudinal categories of 80–100 and 100–130 m and between 80–100 and 130–170 m (PERMANOVA: $F = 2.13$; $R^2 = 0.06$; p-value < 0.01; pairwise p-values < 0.05). However, there was no difference between the categories 100–130 and 130–170 m (pairwise p-value > 0.05). This indicates a higher singularity in species composition in the lower parts of the Pantanal wetland (80–100 m), mainly in the Paraguay, Abobral, Nabileque, and Porto Murtinho subregions, which are the regions where seasonal floods last longest (Fig. 9.2).

Some species frequencies varied markedly along the altitudinal gradient. Examples are typical species of the *cerrados* or seasonal forests, such as *Curatella americana*, *Terminalia corrugata*, *Dipteryx alata*, *Astronium fraxinifolium*, and *Protium heptaphyllum*, that were more frequent at higher altitudes and rare or even absent at lower altitudes (Fig. 9.3). When present at low altitudes, their occurrence is restricted to areas of slightly higher elevation, such as macro mounds, locally called *capões* (Ponce and Nunes da Cunha 1993) and paleolevees, possibly due to their flood intolerance. However, during dry years, some species, e.g., *C. americana* and *Byrsonima cydoniifolia*, tend to advance over floodable grasslands (see the Chap. 11 on "Encroachment"). *Curatella americana* does not germinate during the flood; but depending on the duration of the flood, the seed can remain viable and germinate post-flood. *Dipteryx alata* has a lower flood tolerance than *C. americana* and loses viability during and particularly after the flood (Oliveira et al. 2019).

Species generally associated with riparian forests, edges of forest islets, or monodominant formations, such as *Tabebuia aurea* and *Leptobalanus parvifolius*, seem to prefer the lowest altitudes of the Pantanal. Further examples are *Cecropia pachystachya*, *Inga vera*, *Andira inermis*, *Erythroxylum anguifugum*, *Zanthoxylum rigidum*, *Handroanthus heptaphyllus*, and *Coccoloba cujabensis* (Fig. 9.3). The majority of species showed wide distributions within and even outside the plain (see the section of the "Habitat Generalist Species").

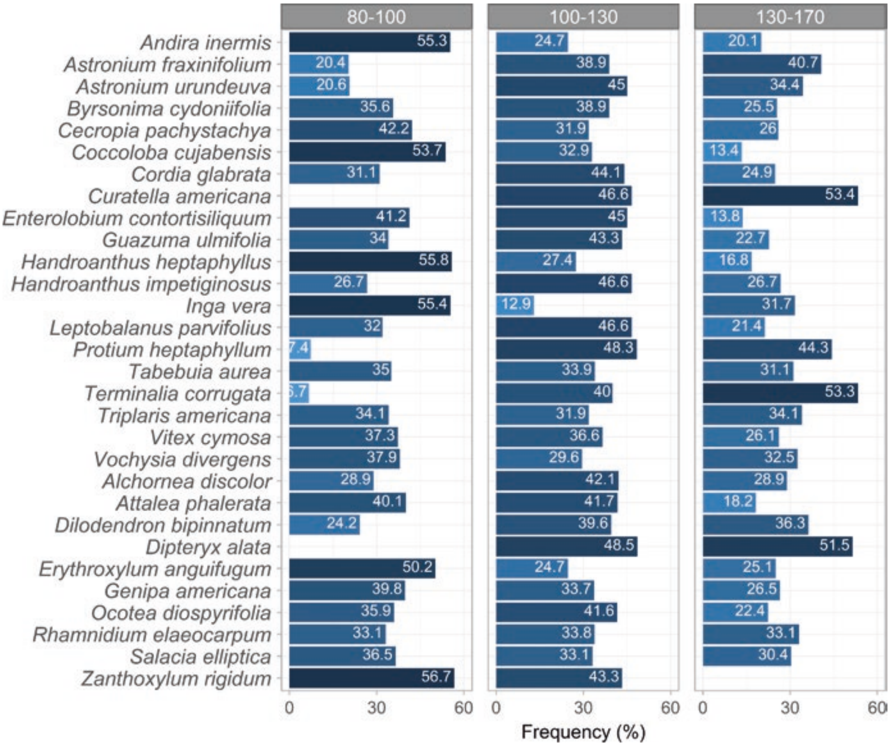


Fig. 9.3 Frequency distributions of shrub, palm, and tree species in three altitudinal categories (m) in the Brazilian Pantanal wetland

9.3.2 Soil

Our analysis showed that the species composition varied significantly between soil types (PERMANOVA: F = 2.26; p-value = 0.001). We observed that the floristic composition on Spodosols was significantly different from that on Vertisols, Gleysols, and Luvisols; Vertisols in addition differed from Luvisols and Planosols, while Planosols differed from Gleysols (Table 9.1).

While Vertisols occur in areas dominated by deciduous forests, the distribution of Spodosols geographically clustered the savanna woodlands (*cerradão*). *Cerradão* can establish on well-drained mesotrophic and eutrophic soils (Spodosols and Neosols) (Salis et al. 2006; Lima-Júnior 2007). In turn, unlike Spodosols, Gleysols are associated mainly with riparian forest and *Vochysia divergens* woodlands (*Cambarazal*). Gleysols consequently differ from Planosols because they are associated with the *cerrados* and less often with semideciduous forest (Beirigo et al. 2011). The same pattern characterizes the difference between Planosols and Vertisols, the latter being mainly associated to the semideciduous forest.

Table 9.1 *P*-values from pairwise comparisons of the composition of woody and palm species of areas with different soil types in the Brazilian Pantanal wetland using permutational multivariate ANOVA with 1000 permutations and the Bonferroni method for *p*-value adjustment. Significant differences ($p < 0.05$) in bold

	Spodosols	Gleysols	Luvisols	Planosols	Plinthosols
Gleysols	**0.015**	–	–	–	–
Luvisols	**0.030**	0.659	–	–	–
Planosols	0.135	**0.045**	0.285	–	–
Plinthosols	1.000	0.554	1.000	1.000	–
Vertisols	**0.015**	0.165	**0.015**	**0.015**	0.105

Semideciduous forests are found on Vertisols and Plinthosols (Soares et al. 2006; Damasceno-Junior et al. 2009; Beirigo et al. 2011). In this type of vegetation, the palm *Attalea phalerata* is almost omnipresent. This species is a good indicator of calcareous clay soils that are relatively rich in nutrients (Negrelle 2016). However, to the north of the plain, deciduous forests may occur, to smaller extents, upon Cambiosols and Planosols (Beirigo et al. 2011). Planosols are typical *cerrado sensu stricto* soil and also support *cerradões*. In turn, Plinthosols in the Pantanal wetland are also occupied by *cerrado sensu stricto*, *Cambarazal*, *Pimenteiral* (*Leptobalanus parvifolius* woodland), and *Pirizal* (monodominant formation of *Cyperus giganteus*) (Beirigo et al. 2011).

Luvisols are eutrophic, well-drained, mineral soils with high contents of clay and high base saturation and are preferentially colonized by seasonal forests (Beirigo et al. 2011). Luvisols are also recorded in *Cambarazal* and *cerradão* and occupy small patches in the floodplain (Soares et al. 2006). Vertisols commonly can support semideciduous forest (*capão*) (Damasceno-Júnior et al. 1999) and savanna (*Tabebuia aurea* monodominant stands) (Bueno et al. 2014) (Fig. 9.4).

The most frequent species on Spodosols were *Astronium fraxinifolium*, *Curatella americana*, *Tabebuia aurea*, *Protium heptaphyllum*, and *Dipteryx alata*, species typical of *cerrados* (Bueno et al. 2018a). Gleysols, in turn, had *Ocotea diospyrifolia*, *Inga vera*, *Genipa americana*, and *Triplaris americana*, which are species commonly reported to occur in riparian forests (Damasceno-Junior et al. 2005). The most frequent trees on Luvisols were *Vitex cymosa*, *D. alata*, *I. vera*, *Rhamnidium elaeocarpum*, and *T. americana*. Planosols, the prevalent soils in the Pantanal, showed *Handroanthus impetiginosus*, *A. fraxinifolium*, *T. aurea*, *A. urundeuva*, *Celtis iguanaea*, and *Cordia glabrata*. The most frequent trees on Plintosols were *A. fraxinifolium*, *Cecropia pachystachya*, *D. alata*, *Guazuma ulmifolia*, *Leptobalanus parvifolius*, *Byrsonima cydoniifolia*, *Vochysia divergens*, and *Celtis iguanaea*. *Inga vera*, *Cecropia pachystachya*, *Erythroxylum anguifugum*, *G. americana*, *Attalea phalerata*, and *Handroanthus heptaphyllus* grow on Vertisols, usually found in riparian forests (Fig. 9.5).

Taking into account only the most frequent species (Fig. 9.5), soil type does not seem to clearly determine the species composition, except Spodosols and Gleysols, that carried, respectively, species from the *cerrados* (e.g., *A. fraxinifolium*, *T. aurea*, *D. alata*, *C. americana*) and riparian forest (*G. americana*, *I. vera*, *O. diospyrifolia*).

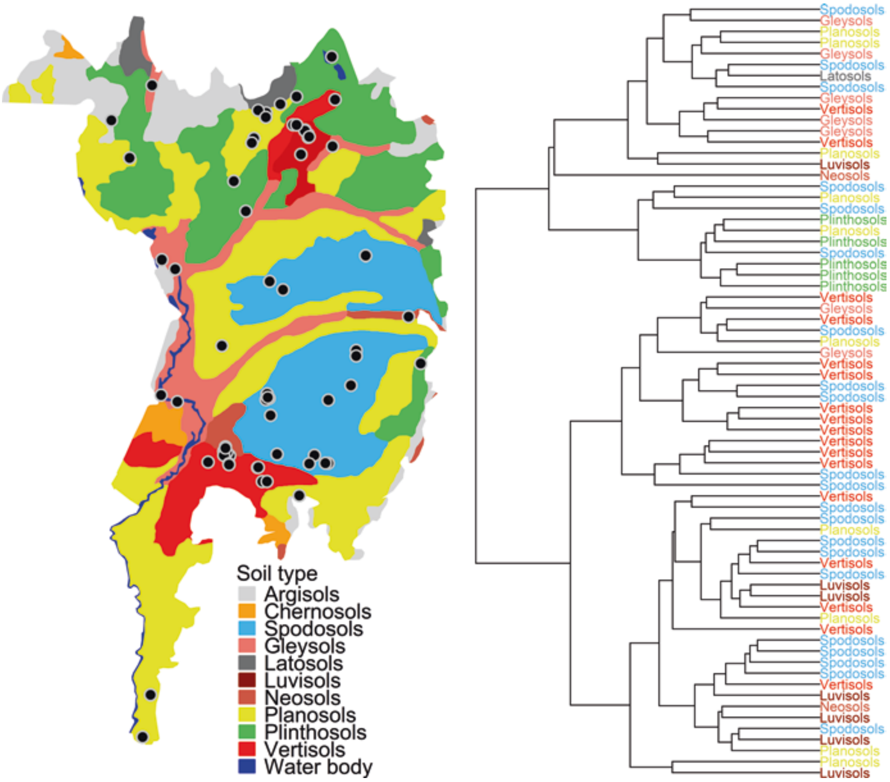


Fig. 9.4 Hierarchical clustering (Ward's method) showing the floristic relationship between soil types in the Brazilian Pantanal wetland. Colors in the dendrogram indicate the soil types

Nevertheless, it has to be considered that, in general, the most frequent species are those with wider amplitudes of ecological suitability; thus, they can occur in various habitats with different soil types and physiognomies. Some soil types were poorly represented (Latosols and Neosols) or were not represented (Argisols and Chernosols) in the surveys.

9.4 Main Woody and Palm Vegetation Types in the Wetland and Upland Influences

The frequency at which species occur in each vegetation type and all over the floodplain can help to characterize the vegetation types of each subregion and their relation with other biomes. The Cerrado was the biome with the lowest dissimilarity with the Pantanal, followed by Caatinga and Atlantic Forest (Table 9.2). Although the Cerrado was repeatedly reported to be the biome of highest floristic relationship

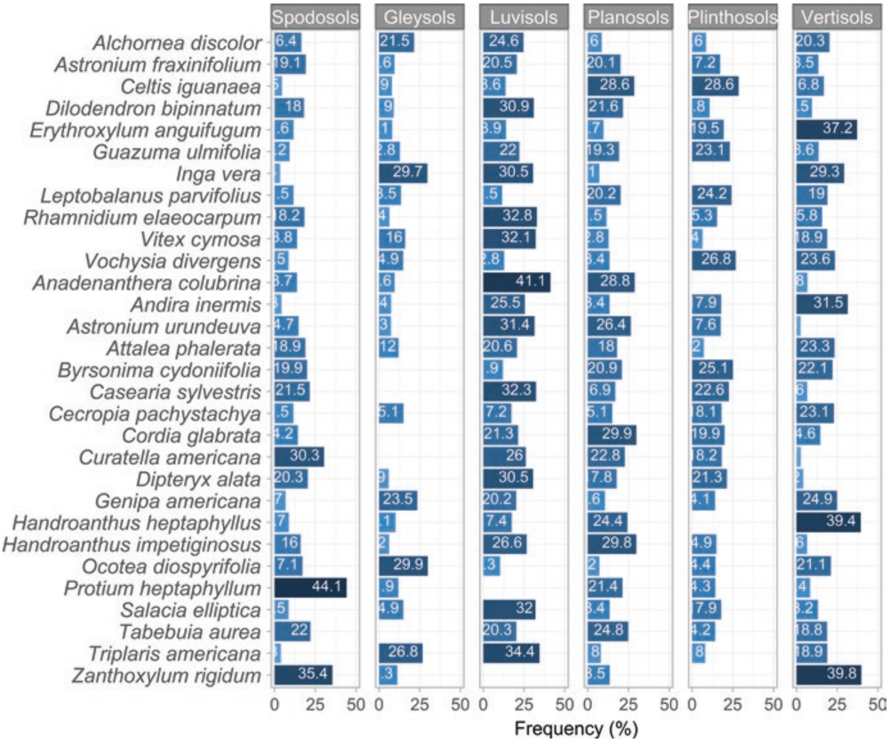


Fig. 9.5 Frequency distribution of the main woody and palm species on the soil types of the Brazilian Pantanal wetland

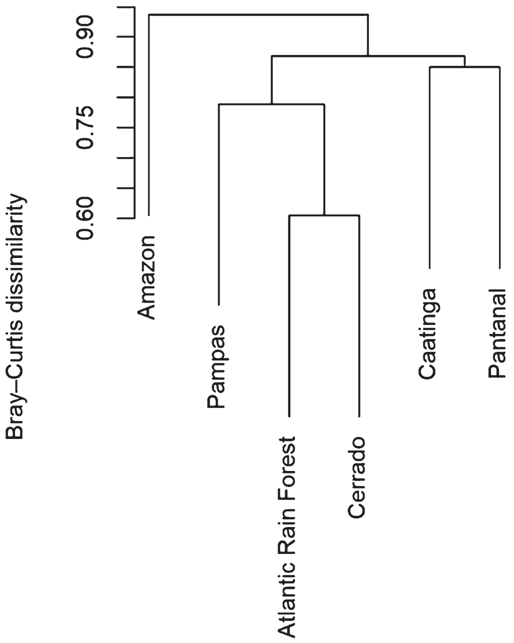
Table 9.2 Differences of woody and palm species composition (Bray-Curtis dissimilarity) between flood-prone vegetation of the Brazilian vegetation domains

	Amazon	Atlantic Forest	Caatinga	Pampas	Cerrado
Atlantic Forest	0.934				
Caatinga	0.952	0.897			
Pampas	0.992	0.697	0.932		
Cerrado	0.900	0.604	0.816	0.881	
Pantanal	0.907	0.854	0.850	0.913	0.801

to the Pantanal (Adámoli 1982; Ratter et al. 1988; Silva et al. 2000b; Pott et al. 2011; Pott and Silva 2015), a considerable floristic relationship also exists to the Caatinga (Fig. 9.6), a characteristic of the Pantanal vegetation that has been only slightly explored.

The *cerrados* are the main type of vegetation inside the Pantanal (Adámoli 1982; Silva et al. 2000a). The subregions with the highest representations of *cerrados* are in the northern and eastern parts, while the *cerrado* vegetation is scarce in the southwest region (Paraguay, Nabileque, and Porto Murtinho subregions) mainly due to

Fig. 9.6 Hierarchical clustering of the floristic relations of wetland woody and palm species of Brazilian domains using the method of group average in the matrix of species frequencies



edaphic conditions (Adámoli 1982; Pott et al. 2011). The *cerradão* is dominant in Cáceres and Nhecolândia with 36.85% and 33.5% cover, respectively (Silva et al. 2000a), and with a high heterogeneity in some places. The *cerrados* vegetation contingent in the northern regions can be related to the adjacent Cerrado north of the plain, at altitudes of c. 180 m, where species such as *Qualea grandiflora*, *Q. parvifolia*, *Anadenanthera colubrina*, *Vatairea macrocarpa*, *Lafoensia pacari*, *Curatella americana*, *Terminalia argentea*, *Tabebuia aurea*, *Callisthene fasciculata*, and *Luehea paniculata* are some of the most abundant (Morais et al. 2019).

Such Cerrado vegetation types include the *murundu* grasslands that are also common in Central Brazilian *cerrados* (Furley 1986; Oliveira-Filho 1992) and also present in the floodplain of the Araguaia River, one of the largest Brazilian floodplains (Marimon et al. 2012). *Murundus* or micro mounds are approximately rounded earth mounds, up to several meters in diameter (Ponce and Nunes da Cunha 1993), and 5–70 cm above the floodable ground. Besides, forest islets on the *capões* (macro mounds) and paleolevees also occur. *Capões* and paleolevees are mainly covered by species of seasonal semideciduous forests (Rodrigues et al. 2012) and are less associated with *cerrados* than *murundu* grasslands. Therefore, although both vegetation types are small islets of woody vegetation in a floodable grassland landscape, the species composition or at least the species abundance is remarkably different (Marimon et al. 2012; Rodrigues et al. 2012; Morais et al. 2014).

Between the vegetation of *cerrado sensu stricto* and seasonal semideciduous forest close to the eastern edge of the floodplain (Nhecolândia and Paiaguás subregions), a palm species characterizes two similar vegetation types. The first is the

Buritizal (monodominant forest stand of *Mauritia flexuosa*; see the Chap. 8 on "Monodominant Stands"). Similarly, *veredas* (savanna monodominant stand of *Mauritia flexuosa*; see the Chap. 8 on "Monodominant Stands") also occur in these same subregions of the floodplain (Fig. 9.7) (IBGE 2012; Ribeiro and Walter 1998; Moreira et al. 2017). *Veredas* are not considered in the habitat classifications of the Pantanal. In consequence, both *veredas* and *buritizais* in the Pantanal have been classified as "swamps with *Mauritia flexuosa* (*Buritizal*)" (Nunes da Cunha and Junk 2011) or "*Mauritia flexuosa* palm land (*Buritizal*)" (Pott et al. 2011) or "swamps of herbaceous plants and palms" (Nunes da Cunha et al. 2015).

Some areas with *cerradão* inside the floodplain (such as in the Barão de Melgaço subregion) may be considered transitions between *cerradão* and seasonally dry forests, with up to 20% of the species belonging to the seasonally dry forest (Rodrigues et al. 2012). Such a transition can be the consequence of relatively high concentrations of calcium and magnesium in the soil (Prado et al. 1992). Riparian forests of the Miranda River at the southeastern edge also have floristic similarities with seasonal forests (deciduous and semideciduous) on calcareous soils of the Serra da Bodoquena plateau (Baptista-Maria et al. 2009; Pott et al. 2014).

The seasonally dry forests in the Pantanal also have some relations with the Neotropical dry forests (Damasceno-Junior et al. 2009; Damasceno-Junior et al. 2018). Neotropical dry forests are found in northeastern Brazil, in the Caatinga

Fig. 9.7 *Veredas*; open woodland of *Mauritia flexuosa* at the eastern edge of the Pantanal wetland (Picture by Evaldo Benedito de Souza)

biome, extending and scattering towards the Cerrado (Prado and Gibbs 1993b; Pennington et al. 2000; Bueno et al. 2018b). In seasonally dry forests in the Pantanal of the Barão de Melgaço subregion, from a total of 106 species, 24.5% are typical from dry forests, and 28% have wide distributions (Duarte 2007). A striking characteristic of these forests is the dominance of *Attalea phalerata*, varying between 24% and 64% of the individuals in the community (Duarte 2007; Negrelle 2016). All the subregions of the Pantanal contain species common to the Caatinga. Some species shared between the Caatinga and the Pantanal are, for example, *Aspidosperma pyrifolium*, *Anadenanthera colubrina*, *Astronium urundeuva*, *Amburana cearensis*, *Handroanthus impetiginosus*, and others. Curiously, some species such as *Crateva tapia* that are rare in Brazilian riparian forests occur in the Pantanal and elevated swamps of the Caatinga.

These Pantanal-Caatinga relationships reinforce the hypothesis that these dry forests in the Pantanal are relict formations, an evidence of a more direct connection with the Caatinga during the Pleistocene dry climate, being part of the South American Pleistocene Arch (Prado and Gibbs 1993b; Damasceno-Junior et al. 2009; Neves et al. 2015). However, in some investigations on floristic relations within the South American Pleistocene Arch, the Pantanal has been ignored or has been included as belonging to the Cerrado biome and not as an independent biome (Prado and Gibbs 1993b; Santos et al. 2012; Neves et al. 2015; Wittmann et al. 2017).

In turn, deciduous forests are established mainly in the northeast of the floodplain. However, they also may be found strictly on the hills (Urucum and Amolar mountain ranges) in the more floodable areas of the Paraguay subregion, in the western center of the floodplain (Prance and Schaller 1982; Ratter et al. 1988; Damasceno-Junior 1997).

Another vegetation type that is common also in the Brazilian northeast region (Campos et al. 2017) is forested savanna dominated by *Attalea speciosa* (Silva et al. 2000a), also called *Attalea speciosa* palm lands (Pott et al. 2011). In the Pantanal floodplain, they are found in central Nhecolândia, Barão de Melgaço, and in the north of the Cáceres subregions. *Attalea speciosa* stands occupy 0.3% of the floodplain (Silva et al. 2000a). But there is no record of such formations in other Pantanal subregions. The origin of this species on the plain can be attributed to pre-Columbian humans that promoted its dispersal (Pott et al. 2011). That seems to have also influenced the spread of other species, such as *Sapindus saponaria*, the palm *Acrocomia aculeata*, and many useful plants (Pott and Pott 1999). *Acrocomia aculeata*, for example, is present in several other subregions and is one of the typical species of dry forests (Pott et al. 2011). It is also quite frequent in areas of *cerrados* and seasonal semideciduous forest (Rodela 2006), except in the eastern part where it is somewhat scarce.

We highlight the Amazon species component in the Pantanal, primarily due to the entrance of those species via the Paraguay River. In more prolonged and higher-lying flood parts of the Paraguay subregion, the dominant woody formations are riparian forests, *Vochysia divergens* woodland, and seasonal semideciduous forest that can be found on the *capões* or paleolevees scattered in the flat grasslands or shrublands. Less common are floodable savannas of *Copernicia alba* and *Tabebuia* *aurea* (Silva et al. 2000a). These differences in environmental conditions bring about differences in the types of vegetation and thus differences in species composition between altitudinal levels (Fig. 9.2). A similar pattern can be seen in the frequencies of some dry forest species that are more frequent in higher-lying areas (Fig. 9.3). The southwestern part of the floodplain (Paraguay, Abobral, and Nabileque subregions) has the highest proportion of flooded area due to the influence of the Paraguay River, making the riparian forests longer flooded than in any other subregion (Hamilton et al. 1996; Silva et al. 2000a). Inundation in these forests can vary from 30 to more than 270 days per year (Damasceno-Junior et al. 2005).

Some 30% of the species of the riparian forest of the Paraguay River have geographic distributions that are markedly linked to Amazonia (Damasceno-Júnior 1997). Another 20% have their distributions linked to the Argentinian and Paraguayan Humid Chaco, probably because of the proximity to that domain (Spichiger et al. 2005). Of the other species, some 20% have wide distributions, and only four are shared with the Cerrado riparian flora. More intense and prolonged floods can explain this scarcity of species from the Cerrado in the riparian forests of the Paraguay subregion. Although the Chiquitano Dry Forest in Eastern Lowland Bolivia represents the narrowest transition between the Amazon and the Chaco (Killeen et al. 2006), the Andean tropical forest is, probably via the connectivity along gallery forests, the main floristic connection between the Amazon and the Chaco (Trujillo-Arias et al. 2017). In the same way, the floodable forests of the Paraguay River can be a floristic Amazon-Chaco corridor without the presence of *cerrado* in between.

The species composition of riparian forests of the Paraguay subregion is similar to others, both in the Pantanal (e.g., Miranda River) and elsewhere (Paraná River, south of the Pantanal). A curiosity is that some species of these riparian forests of the Paraguay River also occur in seasonal semideciduous forest islets in other subregions. Such coincidence happens because islet edges are flood prone and, thus, contain some of the flood-tolerant species that also occur in the Paraguay River margins, such as *Inga vera*, *Cecropia pachystachya*, *Vochysia divergens*, *Ocotea suaveolens*, *Leptobalanus parvifolius*, and *Couepia uiti*. Many species that are frequent in the riparian forests of the Paraguay River also occur in riparian forests outside the Pantanal (*I. vera*, *Genipa americana*, and *Hymenaea courbaril*) and floodable forests of the Amazon region (e.g., *Casearia aculeata*, *Zygia inaequalis*, *Mouriri guianensis*, *Vitex cymosa*, and *V. divergens*) (Damasceno-Junior 1997; Damasceno-Junior et al. 2004; Damasceno-Junior et al. 2005; Oliveira et al. 2014; Bueno et al. 2018a).

One intrinsic characteristic of riparian forests throughout the floodplain is the abundance of early successional species. The dynamics of rivers, with fast erosion on concave banks and deposition on convex banks, gives a successional character to these forests, and that allows the high abundance of early successional species, such as *Cecropia pachystachya* (Pott and Pott 1994). We observed large strips of riparian forests with predominantly *C. pachystachya*, making it one of the most frequent and conspicuous species along the Miranda River (Fig. 9.8). This species is also an indicator of fire occurrence in these forests (Arruda et al. 2016).

Fig. 9.8 *Cecropia pachystachya*, emergent in riparian forest of the Miranda River, Abobral subregion in the Pantanal wetland (Picture by Evaldo Benedito de Souza)

Chaquenian influence is evident in the southwestern part of the floodplain (Paraguay, Nabileque, and Porto Murtinho subregions). Despite a predominance of Chaquenian species (e.g., *Diplokeleba floribunda*, *Microlobius foetidus*, and *Tabebuia nodosa*), some Cerrado species are still found in this region. Southwards from the city of Corumbá in the Mato Grosso do Sul State, near the Jacadigo Lake, a few Cerrado species (e.g., *Tabebuia aurea*, *Cordia glabrata*, *Casearia aculeata*, *Randia heteromera*, and *Celtis iguanaea*) were recorded. However, approximately 22% of the species occurring there are Chaquenian (*Aspidosperma quebracho-blanco*, *Tabebuia nodosa*, *Capparicordis tweediana*, *Cynophalla retusa*, *Anisocapparis*). That leads to conclusion that this vegetation is a Chaco-Pantanal transition (Prado et al. 1992; Maria et al. 2018; Sartori et al. 2018). Other species recorded there also occur in vegetation presently considered Chaquenian in the Porto Murtinho subregion (Maria et al. 2018; Sartori et al. 2018).

Steppic Park Savanna (*Copernicia alba* monodominant stands) and Steppic Forested Savanna (Chaco) are the main vegetation types in the Porto Murtinho subregion (Amador et al. 2012). Prado et al. (1992) described this subregion as a Chaco-Pantanal transition, with formations with different strengths of relation with the Chaco *sensu stricto* in Bolivia, Paraguay, and Argentina, also having elements of semideciduous and riparian forests.

The main vegetation types in the Porto Murtinho subregion are named after their dominant species. The *Schinopsis balansae* parkland (locally known as *Quebrachal*), for example, constitutes groupments dominated by *S. balansae* of up to 20 m high (Spichiger et al. 2005). This vegetation type is similar to the Argentinian Chaco, and some associated species are the same (such as *Prosopis ruscifolia*). But these parklands also contain elements of deciduous forest (e.g., *Astronium urundeuva*, *Handroanthus impetiginosus*, and *Pseudobombax* sp.). Formations of semideciduous forest with a dominance of *Aspidosperma quebracho-blanco* are also present; they are physiognomically similar, but floristically distinct from the Paraguayan and Argentinian Chaco (Prado et al. 1992). One of the most frequent vegetation types in the southern part of the Porto Murtinho subregion occurs on isolated rocky outcrops and is dominated by *Schinopsis brasiliensis*, with characteristic species of the Caatinga semideciduous forest and the Cerrado, such as *Anadenanthera colubrina*, *Sterculia striata*, *Cnidoscolus vitifolius*, and *Amburana cearensis*.

Although the vegetation of the Porto Murtinho subregion in the past has been considered quite distinct from the Chaco *sensu stricto* of Bolivia, Paraguay, and Argentina (Prado et al. 1992), it is relevant to point out that in recent surveys, it has been shown to be floristically much more closely related. Indeed, 68 new species of Chaquenian origin were reported (Sartori et al. 2018). Furthermore, the vegetation types of some parts of the Porto Murtinho subregion are much more distinct from the formations of other domains in Brazil than from the Chaco domain (Sartori et al. 2018; Baptista et al. 2020).

Besides the floristic resemblances with the Chaco, the flood dynamics of the Porto Murtinho subregion are quite different from those of the other Pantanal regions. The floodplain area is smaller and much narrower in this subregion, and other environmental conditions prevail (Adamoli 2000). These particularities counteract the current, widely accepted delimitation of the southern boundary of the Pantanal and the integration of the Porto Murtinho subregion into the Pantanal wetland. Therefore, the Porto Murtinho subregion should have a name that clearly distinguishes it from the other Brazilian biomes, to provide the basis for the delimitation and use of specific criteria for conservation actions (Adamoli 2000; Sartori et al. 2018).

9.5 Habitat Generalists: Species with Higher Frequencies in the Floodplain and with Wide Geographic Distributions

Usually, species with high frequencies of occurrence (e.g., the species in Fig. 9.9) have a wide-ranging tolerance to environmental conditions. That is, they are habitat generalists. Generalist species are less sensitive to environmental changes and, due to their higher tolerance, they are less sensitive to reductions in local populations. Despite being generalists for a broad set of environmental variables, such species also can be specialists in some determined gradient (Ainsworth and Drake 2020).

Most tree, palm, or shrub species occurring in the Pantanal have wide distributions and are present in various biogeographic domains (Pott and Ratter 2011). Some species considered to be part of the Cerrado flora (Mendonça et al. 1998; Bueno et al. 2018a; Françoso et al. 2020) are among the most frequent species on

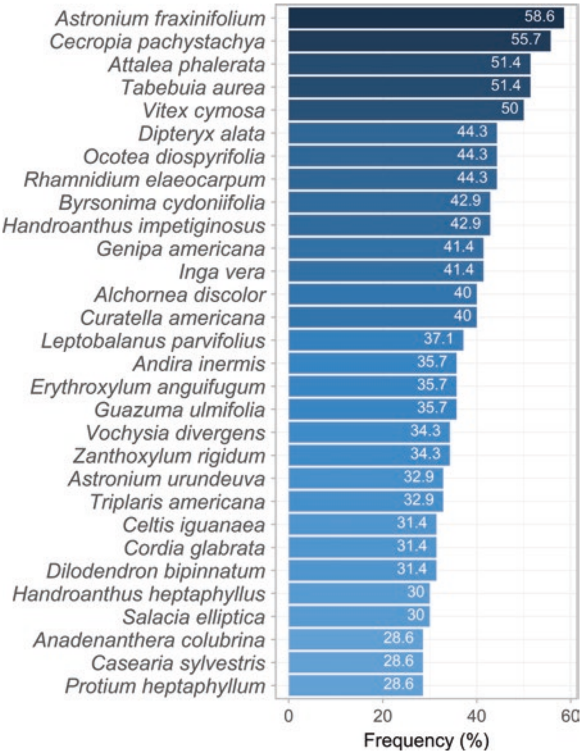


Fig. 9.9 Frequency distribution of the main woody and palm species in 70 surveys in the Brazilian Pantanal wetland

the floodplain. In the surveys we analyzed here, some of the most frequent species were *Astronium fraxinifolium* (58.6% of the surveys), *Cecropia pachystachya* (55.7%), *Attalea phalerata* (51.4%), *Tabebuia aurea* (51.4%), *Vitex cymosa* (50%), and others (Fig. 9.9).

Among the most frequent species, *Astronium fraxinifolium* is a species of wide distribution, occurring mainly in the Cerrado and Caatinga biomes. It is a typical species in seasonal forests and *cerradão* (Prado and Gibbs 1993b; Bueno et al. 2014; Bueno et al. 2018a; Damasceno-Junior et al. 2018). It prefers flood-free soils; consequently, it is more frequent in subregions with higher altitudes in the Pantanal. It can be found in lower subregions, but then it is restricted to elevated terrains, such as forest islets and paleolevees, and even on hummocks of the *Tabebuia aurea* savanna, and also on riverbanks with brief or running floods.

Cecropia pachystachya is a species of the initial succession stage, colonizing especially convex river margin sedimentations, and also forest gaps opened by fire, flood, or wind. This species can also colonize floating Histosols, banks build-up by *Cyperus blepharoleptos* and locally known as *Baceiros* (described as floating meadows in the Chap. 4 of “Aquatic Plants”). These banks can navigate the Paraguay

River and are frequently colonized by this tree species. Reason for its commonness in the plain is the high number of seeds produced almost year-round, and the formation of a potentially persistent seed bank (Souza et al. 2019). It has been observed as monodominant in the silted delta of the lower Taquari River (Louzada et al. 2020).

Attalea phalerata is a typical palm tree of seasonally dry forests and lowland semideciduous forests. Its occurrence is noticeable on the edges of forest islets. Its presence, forming a surrounding belt around the forest islets, is strongly determined by the effect of the interaction between the dynamics of fire and floods. This species is also widespread in riparian forests and on paleolevees. It can form monodominant patches (locally known as *Acurizal*), exclusive to the western zone of the plain (see the Chap. 8 on "Monodominant Stands"). *Attalea phalerata* is also frequent outside the plain, for example, in the seasonal riparian forests of the Serra da Bodoquena plateau (Baptista-Maria et al. 2009). Its high frequency can be associated with a wide range of dispersers, from rodents to birds (Galetti and Guimarães 2004). The palm was not recorded in surveys in the Porto Murtinho subregion.

Vitex cymosa is originally from the Andean montane forest and is very frequent in floodable forests of the *várzea* (floodplain) in the central Amazon (Parolin 2010). In the Pantanal, it is one of the deciduous trees found mainly in riparian forests in the subregions of Paraguay, Barão de Melgaço, and Poconé (Pott et al. 2011). This species is a component of the semideciduous forest islets of the Abobral subregion. It was also recorded in the Porto Murtinho subregion.

Tabebuia aurea has a wide distribution, preferring warm and dry climates that correspond to the present climatic conditions of Neotropical savannas (Collevatti et al. 2014). However, that preference for dry climates contrasts with the conditions available to its monodominant formations, locally known as *Paratudal* (see the Chap. 8 on "Monodominants") in the subregions of Nabileque, Miranda, and Abobral (Ribeiro and Brown 2002; Soares and Oliveira 2009; Bueno et al. 2014). There, the duration of the dry season is minimized by floods providing waterlogged and moist soils for a few months after the rainy season. Nevertheless, although somewhat flood tolerant, it avoids deep, prolonged floods, growing on 0.5–1.5 m high conic earth mounds.

In terms of abundance (not treated here), besides the species mentioned above, others such as *Curatella americana*, *Vochysia divergens*, and *Copernicia alba* are cited as most common in the Pantanal (Pott and Silva 2015). Considering the entire plain, these species are very abundant in some subregions, often forming extensive monodominant forested savannas (see the Chap. 8 on "Monodominants") or patches, and are almost absent in others. An example is *C. americana*; it is much more frequent in the subregions towards the north and east of the plain, being the dominant species in Cerrado formations. But in the western part, close to the Paraguay River, in the Nabileque and Porto Murtinho subregions, its occurrence is scarce. An exception is the transition from upland Cerrado to the Pantanal Nabileque subregion that is dominated by *C. americana* inside the Kadiwéu indigenous reserve (G.A. Damasceno-Junior per. obs.). Similarly, *C. alba* and *T. aurea* are two of the most abundant species in these subregions, but their abundances are reduced northeastwards, restricted to small groupments or isolated individuals. The same happens with *Vochysia divergens* that diminishes its occurrence drastically southwards.

Because they are the most frequent species on the plains, they are also more available and highly targeted for human use. Some of these species are of frequent human use, mainly the use of wood for the construction of fences and corrals, in addition to the production of firewood and coal. The main species used for these purposes are *T. aurea*, *H. impetiginosus*, *H. heptaphyllus*, *D. alata*, *Astronium fraxinifolium*, *C. americana*, *Guazuma ulmifolia*, and *C. alba*. Other uses are handicrafts and utensils from palm leaves. However, the biggest threat is the removal of vegetation for the implementation of agricultural activities, especially pastures. This is especially true in the eastern part of the plain, the region least affected by flooding. The most threatened formations are the seasonal dry forest and semideciduous forest, which have a high frequency of several of these species. Many of these species are also considered pasture invaders, which leads farmers to withdraw (pasture cleaning), either in areas with native pasture or in cultivated pastures, which can be a trigger for the exacerbation of deforestation in the Pantanal (Junk and Nunes da Cunha 2012).

As described above, most woody species in the Pantanal originate from the adjacent vegetation domains, have wide geographic distributions, and are tolerant of a wide range of environmental conditions. The level of environmental tolerance of the species can be critical in determining ecosystem functions. Habitat generalist species can play a central role in ecological relationships and therefore in ecosystem functions. Their presence makes ecosystems more resilient and resistant under climatic changes (Richmond et al. 2005; Aslan 2019). Considering the annual periodic flooding and pluriannual hydrologic fluctuations, besides fires (Oliveira et al. 2014; Arruda et al. 2016), the Pantanal is expected to contain a large contingent of habitat generalist species. Knowing which species belong to this category and how they respond to climate change is an essential step for conservation actions.

9.6 Habitat Specialists: Species with Limited Distributions in the Pantanal or That Are Restricted to Its Border

The species composition in the Pantanal is also defined by barriers to the occurrence of tree species by effects of climate, soil, inundation, fire, and species traits. It is noteworthy that some species which are common in riverine forests and swamps in the upland of Pantanal rivers are found only in the border zone and were never recorded inside the Pantanal. Besides the riverine forests and swamps, the main vegetation types in the highlands around the Pantanal are Cerrado, semideciduous forests, and deciduous forests. All these vegetation types also occur here and there inside the Pantanal. There are 541 tree and palm species recorded to occur in the border zone that are considered Cerrado species and 497 species that are recorded for the highlands of Mato Grosso do Sul State only that are typical for seasonal semideciduous and deciduous forests (Bueno et al. 2018a; Damasceno-Junior et al. 2018). Even at similar environments in the border zone and deep in the Pantanal, quite a number of species are not found inside the Pantanal. We will highlight some of these species below.

Mauritia flexuosa is the palm with the broadest distribution in South America, very frequent in Amazonia and the Brazilian Cerrado (Rull and Montoya 2014). On the uplands, it occurs almost exclusively in *veredas*. Inside the floodplain, *M. flexuosa* occurs mainly in the eastern edge, in the Barão de Melgaço, Paiaguás, Aquidauana, Miranda, and Nhecolândia subregions (Silva et al. 2000a); the latter two are along the Aquidauana and Taquari Rivers (Pott et al. 2011). However, *M. flexuosa* does not advance over the middle of the plain. Westwards, along the Aquidauana River, we only observed it up to near the junction with the Miranda River, where it is replaced by another palm, *Copernicia alba* (Moreira et al. 2017). This is probably due to *M. flexuosa* preferring hydromorphic or swampy soils without flood pulses or soils with very low flood pulses only where its pneumatophore system can help to get oxygen (Parolin 2012; Galeano et al. 2015). Consequently, wherever flooding pulses reach more than approximately 1 m, it disappears.

Additional species that occur in the highlands and were not found inside the floodplain are *Erythrina similis* and *E. speciosa*. These two species are found in swamps with calcareous soils in Corumbá (Paraguay subregion) and the Serra da Bodoquena. These two environments are seasonally flooded and are very close to the Pantanal wetlands, but these species were never recorded there.

Salix humboldtiana Willd. has a wide distribution ranging from southern North America to southern South America. It forms characteristic riparian forests along watercourses (FAO 2014; GBIF 2019). High genetic variation among populations relates to climatic conditions and in particular to the precipitation pattern associated with the geological configuration of rivers (Hernández-Leal et al. 2019). *Salix* is a species-rich genus characteristic for floodplains comprising gallery forests, riparian forests, and diverse wetland types (Karrenberg et al. 2002). However, *S. humboldtiana* is only recorded on the Aquidauana River on sandy levees at the entrance to the Pantanal (Fig. 9.10) and was also recorded on the Paraguay River after the transition from the Pantanal to Chaco. This pioneer species, adapted to physical disturbance, settles on bare ground, e.g., in the central Amazonian white-water floodplain (*várzea*). *Salix humboldtiana* withstands prolonged inundation at low-lying sites with high sedimentation rates. After *S. humboldtiana* has become established, inundation and sedimentation are reduced. This facilitates *Cecropia latiloba* to form monospecific stands at low to middle elevations along watercourses (Parolin et al. 2002), comparable to *C. pachystachya* in the Pantanal (Fig. 9.8). However, *Cecropia* regenerates from potentially persistent seed banks (Souza et al. 2019), whereas *Salix* showed a very short seed viability (Karrenberg et al. 2002; Parolin et al. 2002). Thus, the window of opportunity for *Salix* establishment in the Pantanal may be too small.

Species such as *Guarea kunthiana* and *Tapirira guianensis* are also common along the rivers before they enter the Pantanal. *Tapirira guianensis* is one of the

Fig. 9.10 Researchers Geraldo Alves Damasceno-Junior and Heike Markus-Michalczyk collecting *Salix humboldtiana* on sandy levees of the Aquidauana River at the entrance to the Pantanal wetland

most common species in gallery forests in Brazil and in nearly all headwaters of Pantanal rivers (Silva Junior et al. 1998; Damasceno-Junior et al. 2001; Costa Junior et al. 2008). Pollen of *Tapirira* was recorded in Baía Negra, inside the Pantanal, having been very abundant from 1300 to about 2000 ybp (Bezerra et al. 2019). Probably relatively recent changes in climatic conditions prevented the present occurrence of this species inside the Pantanal. *Guarea kunthiana* is quite common in rivers of headwaters of the Pantanal, especially in the Serra da Bodoquena in bottom parts of valley headsprings (G.A. Damasceno-Junior pers. obs.). The occurrence of this species is associated with high-fertility soils that provide sufficient humidity all year round. The stronger seasonality of the Pantanal lowlands may act as a barrier for this species.

On the other hand, there are many dry environments inside the Pantanal, such as *cerrados* and seasonally dry forests. Likewise, some species quite common in headwaters in these environments are not recorded inside the Pantanal. That is the case in *Sterculia striata*, which is recorded in deciduous forests in the Urucum Hills, and on the border of the Pantanal in the Poconé subregion and the Rio Negro ranchlands (Damasceno-Junior 2005). The distribution of these species permits us to hypothesize that the Pantanal can be a filter of distribution for some groups of wetland and dryland species. Many explanations are possible for this phenomenon. One possibility is the variation between dry and wet seasons that can be very pronounced in some years. All in all, the vegetation of the Pantanal is adapted to frequent changes – due to the natural dynamics and drastic annual variations of the floodplain system.

However, more pronounced and extreme changes in climatic conditions, such as an increase in the frequency of *El Niño* events (Gris et al. 2020), can represent a risk, reducing the growth and regeneration of populations adapted to the current conditions.

References

Adámoli J (1982) O Pantanal e suas relações fitogeográficas com os cerrados. Discussão sobre o conceito do "Complexo do Pantanal." XXXII Congr Nac Botânica, pp 109–119

Adamoli J (2000) O Limite sul do Pantanal. In: III Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal Os Desafios do Novo Milênio. Embrapa Pantanal, Corumbá, pp 1–15

Adámoli J, Pott A (1996) Estudo fitossociológico e ecológico do Pantanal dos Paiaguás. In: II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal, pp 215–225

Ainsworth A, Drake DR (2020) Classifying Hawaiian plant species along a habitat generalist-specialist continuum: Implications for species conservation under climate change. PloS One 15: e0228573. https://doi.org/10.1371/journal.pone.0228573

Amador GA, Damasceno-Junior GA, Casagrande JC, Sartori ÂLB (2012) Structure of two communities dominated by Copernicia alba and associations with soil and inundation in Pantanal wetland, Brazil. Oecologia Aust 16:846–858. https://doi.org/10.4257/oeco.2012.1604.09

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46

Arruda WDS, Oldeland J, Paranhos Filho AC, Pott A, Cunha NL, Ishii IH, Damasceno-Junior GA (2016) Inundation and fire shape the structure of riparian forests in the Pantanal, Brazil. PLoS One 11:e0156825. https://doi.org/10.1371/journal.pone.0156825

Aslan CE (2019) Implications of non-native species for mutualistic network resistance and resilience. PLoS One 14:1–15. https://doi.org/10.1371/journal.pone.0217498

Baptista MSP, Assunção VA, Bueno ML, Casagrande JC, Sartori ÂLB (2020) Species representativeness of Fabaceae in restrictive soils explains the difference in structure of two types of Chaco vegetation. Acta Bot Brasilica 34:559–569. https://doi.org/10.1590/0102-33062020abb0064

Baptista-Maria VR, Rodrigues RR, Damasceno-Junior G, Maria FS, Souza VC (2009) Composição florística de florestas estacionais ribeirinhas no estado de Mato Grosso do Sul, Brasil. Acta Bot Brasilica 23:535–548. https://doi.org/10.1590/S0102-33062009000200025

Bazzo JC, Freitas DAF , Silva MLN, Cardoso LE, Santos SA (2012) Aspectos Geofísicos E Ambientais Do Pantanal Da Nhecolândia. Rev Geogr 29:141–161

Beirigo RM, Torrado PV, Stape J, Couto EG, Andrade GRP (2011) Solos da Reserva Particular do Patrimônio Natural Sesc Pantanal. Rio de Janeiro, SESC, 2011. 75 pp.

Bezerra MAO, Mozeto AA, Oliveira PE, Volkmer-Ribeiro C, Rodrigues VV, Aravena R (2019) Late Pleistocene/Holocene environmental history of the southern Brazilian Pantanal wetlands. Oecologia Aust 23:712–729. https://doi.org/10.4257/oeco.2019.2304.02

Boyle B, Hopkins N, Lu Z, Raygoza Garay JA, Mozzherin D, Rees T, Matasci N, Narro ML, Piel WH, Mckay SJ, Lowry S, Freeland C, Peet RK, Enquist BJ (2013) The taxonomic name resolution service: an online tool for automated standardization of plant names. BMC Bioinformatics 14:16. https://doi.org/10.1186/1471-2105-14-16

Brasil (2020) Flora do Brasil 2020 em construção. In: Jard. Botânico do Rio Janeiro. http://www.reflora.jbrj.gov.br/reflora/listaBrasil/PrincipalUC/PrincipalUC.do#CondicaoTaxonCP. Accessed 27 May 2020

Bueno M, Damasceno-Junior G, Pott A, Pontara V, Seleme E, Fava W, Salomão A, Ratter J (2014) Structure of arboreal and herbaceous strata in a neotropical seasonally flooded monodominant savanna of Tabebuia aurea. Braz J Biol 74:325–337. https://doi.org/10.1590/1519-6984.16612

Bueno ML, Rezende VL, Pontara V, Oliveira-Filho AT (2017) Floristic distributional patterns in a diverse ecotonal area in South America. Plant Ecol 218:1171–1186. https://doi.org/10.1007/s11258-017-0759-1

Bueno ML, Oliveira-Filho AT, Pontara V, Pott A, Damasceno-Junior GA (2018a) Tree flora of the Cerrado of Mato Grosso do Sul state. Iheringia – Ser Bot 73:53–64. https://doi.org/10.21826/2446-8231201873s53

Bueno ML, Dexter KG, Pennington RT, Pontara V, Neves DM, Ratter JA, Oliveira-Filho AT (2018b) The environmental triangle of the Cerrado Domain: ecological factors driving shifts in tree species composition between forests and savannas. J Ecol 106:2109–2120. https://doi.org/10.1111/1365-2745.12969

Campos JLA, Albuquerque UP, Peroni N, Araújo EL (2017) Population structure and fruit availability of the babassu palm (Attalea speciosa Mart. ex Spreng) in human dominated landscapes of the northeast region of Brazil. Acta Bot Brasilica 31:267–275. https://doi.org/10.1590/0102-33062016abb0255

Collevatti RG, Lima-Ribeiro MS, Terribile LC, Guedes LBS, Rosa FF, Telles MPC (2014) Recovering species demographic history from multi-model inference: the case of a Neotropical savanna tree species. BMC Evol Biol 14:1–13. https://doi.org/10.1186/s12862-014-0213-0

Costa Junior RF, Ferreira RLC, Rodal MJN, Feliciano ALP, Marangon LC, Silva WC (2008) Estrutura fitossociológica do componente arbóreo de um fragmento de floresta ombrófila densa na mata sul de Pernambuco, Nordeste do Brasil. Ciência Florest 18:173–183

Couto EG, Oliveira VA de (2010) The soil diversity of the Pantanal. Pantanal Mato Grosso Ecol Biodivers Sustain Manag Large Neotrop Seas Wetl 71–102

Cunha NG (1981) Classificação e fertilidade de solos da planície sedimentar do rio Taquari, Pantanal Matogrossense. Embrapa Pantanal, Circular técnica nº 4

Damasceno-Junior GA (1997) Estudo floristico e fitossociologico de um trecho de mata ciliar do Rio Paraguai, Pantanal-MS, e suas relações com o regime de inundação. Biblioteca Digital da Unicamp

Damasceno-Junior GA (2005) Estudo floristico e fitossociologico de um gradiente altitudinal no planalto residual do Urucum, Mato Grosso do Sul, Brasil. Biblioteca Digital da Unicamp

Damasceno-Júnior GA, Bezerra MADO, Bortolotto IM, Pott A (1999) Aspectos florísticos e fitofisionômicos dos capões do Pantanal do Abobral. In: II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal, pp 203–214

Damasceno-Junior GA, Nakajima JN, Resende UM (2001) A floristic survey of the Rio Negro, Rio Aquidauana and Rio Miranda Watersheds (Headwaters) of the Pantanal, Mato Grosso do Sul, Brasil. In: Willink PW, Chernoff B, Alonso LE, Montambault JR (eds) A biological assessment of the aquatic ecosystems of the Pantanal, Mato Grosso do Sul. Brasil. Conservation International, Washington, DC, pp 34–43

Damasceno-Junior GA, Semir J, Santos FAM, Leitão-Filho HF (2004) Tree mortality in a riparian forest at Rio Paraguai, Pantanal, Brazil, after an extreme flooding. Acta Bot Brasilica 18:839–846. https://doi.org/10.1590/S0102-33062004000400014

Damasceno-Junior GA, Semir J, Santos FAM, Leitão-Filho HF (2005) Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200:119–135. https://doi.org/10.1016/j.flora.2004.09.002

Damasceno-Junior GA, Pott A, Pott VJ, Silva JSV (2009) Florestas estacionais no Pantanal: considerações florísticas e subsídios para conservação. Geografia 34:697–707

Damasceno-Junior GA, Pott A, Neves DRM, Sciamarelli A, Fina BG (2018) Woody flora of dry forests of Mato Grosso do Sul: State of the art. Iheringia – Ser Bot 73:65–79. https://doi.org/10.21826/2446-8231201873s65

Duarte TG (2007) Florística, fitossociologia e relações solo-vegetação em floresta estacional decidual em Barão de Melgaço, Pantanal de Mato Grosso. Universidade Federal de Viçosa

FAO (2014) Poplars and willows: tress for society and the environment. CABI and FAO, Rome

Françoso RD, Dexter KG, Machado RB, Pennington RT, Pinto JRR, Brandão RA, Ratter JA (2020) Delimiting floristic biogeographic districts in the Cerrado and assessing their conservation status. Biodivers Conserv 29:1477–1500. https://doi.org/10.1007/s10531-019-01819-3

Furley PA (1986) Classification and distribution of Murundus in the Cerrado of Central Brazil. J Biogeogr 13:265–268

Galeano A, Urrego LE, Sánchez M, Peñuela MC (2015) Environmental drivers for regeneration of Mauritia flexuosa L.f. in Colombian Amazonian swamp forest. Aquat Bot 123:47–53. https://doi.org/10.1016/j.aquabot.2015.02.001

Galetti M, Guimarães PR (2004) Seed dispersal of Attalea phalerata (Palmae) by Crested caracaras (Caracara plancus) in the Pantanal and a review of frugivory by raptors. Ararajuba 12:133–135

GBIF (2019) Salix humboldtiana Willd. In: GBIF Backbone Taxon. Checkl. dataset. https://doi.org/10.15468/39omei. Accessed 18 Nov 2020

Gris D, Paixão E, Arruda RCO, Ishii IH, Marques MR, Damasceno-Junior GA (2020) Growth and establishment of monodominant stands affected by ENSO and flooding in the Pantanal. Sci Rep 10:1–13. https://doi.org/10.1038/s41598-020-60402-x

Hamilton SK, Sippel SJ, Melack JM (1996) Inundation patterns in the Pantanal Wetland of South America determined from passive microwave remote sensing. Arch für Hydrobiol 137:1–23

Hernández-Leal MS, Suárez-Atilano M, Piñero D, González-Rodríguez A (2019) Regional patterns of genetic structure and environmental differentiation in willow populations (Salix humboldtiana Willd.) from Central Mexico. Ecol Evol 9:9564–9579. https://doi.org/10.1002/ece3.5475

IBGE (2012) Manual técnico da vegetação brasileira. Rio de Janeiro: IBGE. Disponível em: https://biblioteca.ibge.gov.br/visualizacao/livros/liv63011.pdf. Accessed 15 May 2020

INPE (2010) AMBDATA: Variáveis ambientais para modelagem de distribuição de espécies. In: Grup. Model. para Estud. da Biodiversidade. http://www.dpi.inpe.br/Ambdata/index.php. Accessed 27 May 2020

INPE (2011) TOPODATA – Banco de Dados Geomorfométricos do Brasil. http://www.dsr.inpe.br/topodata/. Accessed 27 May 2020

Junk W, Nunes da Cunha C (2012) Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction? Wetl Ecol Manag 20:111–122. https://doi.org/10.1007/s11273-011-9246-y

Karrenberg AS, Kollmann J, Edwards PJ (2002) Pollen vectors and inflorescence morphology in four species of Salix 235:181–188. https://doi.org/10.1007/s00606-002-0231

Killeen TJ, Chavez E, Peña-Claros M, Toledo M, Arroyo L, Caballero J, Correa L, Guillén R, Quevedo R, Saldias M, Soria L, Uslar Y, Vargas I, Steininger M (2006) The Chiquitano dry forest, the transition between humid and dry forest in eastern lowland Bolivia. In: Pennington RT, Lewis GP, Ratter JA (eds) Neotropical Savannas and seasonally dry forests. CRC Press; Taylor & Francis Group, Boca Raton, pp 213–233

Lima-Júnior GA (2007) Flora e estrutura do estrato arbóreo e relações solo-vegetação de cerradão em Barão De Melgaço, Pantanal de Mato Grosso, Brasil. Universidade Federal de Viçosa

Louzada RO, Bergier I, Assine ML (2020) Landscape changes in avulsive river systems: case study of Taquari River on Brazilian Pantanal wetlands. Sci Total Environ 723:138067. https://doi.org/10.1016/j.scitotenv.2020.138067

Marengo JA, Alves LM, Torres RR (2015) Regional climate change scenarios in the Brazilian Pantanal watershed. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal Wetland in South America. Springer, pp 1–13

Maria VRB, Maria FS, Silva SM (2018) Wood flora of Bodoquena and Maracaju Plateau, middle-southeastern region of Mato Grosso do Sul state, Brazil. Iheringia – Ser Bot 73:34–52. https://doi.org/10.21826/2446-8231201873s34

Marimon BS, Marimon-Junior BH, Mews HA, Jancoski HS, Franczak DD, Lima HS, Lenza E, Rossete AN, Moresco MC (2012) Florística dos campos de murundus do pantanal do araguaia, Mato Grosso, Brasil. Acta Bot Brasilica 26:181–196. https://doi.org/10.1590/S0102-33062012000100018

Mendonça RC, Felfili JM, Walter BM., Silva Junior MC, Rezende AV, Filgueiras TS, Nogueira P (1998) Flora vascular do bioma Cerrado. In: Cerrado: Ambiente e Flora. Embrapa, Planaltina. Brasilia, pp 289–556

Morais RF, Morais FF, Lima JF (2014) Composição e estrutura da comunidade arbórea e arbustiva em murundus no Pantanal de Poconé, Mato Grosso. Rev árvore 38:443–451

Morais FF, Monteiro R, Ikeda-Castrillon SK (2019) Estrutura da comunidade arbórea de uma área de cerrado, sudoeste do estado de Mato Grosso, fronteira Brasil – Bolívia. Equador 8:332–349

Moreira SN, Pott VJ, Souza EB, Pott A (2017) Are *Mauritia flexuosa* L. f. palm swamps in the Brazilian Pantanal true veredas? A floristic appraisal. Bol Mus Para Emílio Goeldi Cienc Nat 12:221–238

Negrelle RRB (2016) Tree species composition and structure in an area representative of “acuri forest” at pantanal matogrossense, Brasil. Cienc Florest 26:589–600. https://doi.org/10.5902/1980509822759

Neves DM, Dexter KG, Pennington RT, Bueno ML, Oliveira Filho AT (2015) Environmental and historical controls of floristic composition across the South American Dry Diagonal. J Biogeogr 42:1566–1576. https://doi.org/10.1111/jbi.12529

Nunes da Cunha C (2001) Distribution of woody plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. Int Journey Ecol Environ Sci 27:63–70

Nunes da Cunha C, Piedade MTF, Junk WJ (2015) Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats. EdUFMT, Cuiabá

Nunes da Cunha C, Junk WJ (2011) A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to national and international wetland classification systems. In: Junk WJ, Silva CJ, Nunes da Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia-Moscow, pp 127–141

Oliveira MT, Damasceno-Junior GA, Pott A, Paranhos Filho AC, Suarez YR, Parolin P (2014) Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence. For Ecol Manage 331:256–263. https://doi.org/10.1016/j.foreco.2014.08.011

Oliveira PC, Parolin P, Borghetti F (2019) Can germination explain the distribution of tree species in a savanna wetland? Austral Ecol 44:1373–1383. https://doi.org/10.1111/aec.12811

Oliveira-Filho AT (1992) Floodplain ‘Murundus’ of Central Brazil: evidence for the termite-origin hypothesis. J Trop Ecol 8:1–19

Padovani CR (2010) Dinâmica espaço-temporal das inundações do Pantanal. Escola Superior de Agricultura “Luiz de Queiroz”

Parolin P (2010) Flood-tolerant trees of Amazonian floodplains also tolerate drought. Rev Pesqui 61:7–38

Parolin P (2012) Diversity of adaptations to flooding in trees of Amazonian floodplains. Pesqui Bot 63:7–28

Parolin P, Oliveira AC, Piedade MTF, Wittmann F, Junk WJ (2002) Pioneer trees in Amazonian floodplains: three key species form monospecific stands in different habitats. Folia Geobot 37:225–238. https://doi.org/10.1007/BF02804233

Pennington RT, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and quaternary vegetation changes. J Biogeogr 27:261–273. https://doi.org/10.1046/j.1365-2699.2000.00397.x

Ponce VM, Nunes da Cunha C (1993) Vegetated earthmounds in tropical Savannas of Central Brazil: a synthesis: with Special Reference to the Pantanal do Mato Grosso. J Biogeogr 20:219. https://doi.org/10.2307/2845673

Pontara V, Bueno ML, Scremin-Dias E (2016) Evitação do alagamento em Triplaris gardneriana Wedd. (Polygonaceae): Crescimento e aspectos morfo-anatômicos. Acta Sci Biol Sci 38:341–346. https://doi.org/10.4025/actascibiolsci.v38i3.31267

Pott A (1994) Ecossistema Pantanal. In: Puignau JP (ed) Utilizacion y manejo de pastizales. IICA-PROCISUR, Montevideo, pp 31–44

Pott A, Pott VJ (1999) Flora do Pantanal: Listagem atual de fanerógamas. In: Anais do II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal. Embrapa Pantanal, Corumbá, pp 297–325

Pott A, Pott Vali J (1994) Plantas do Pantanal. Embrapa, Corumbá

Pott A, Ratter JA (2011) Species diversity of terrestrial plants and human impact on the vegetation of the Pantanal. In: Junk WJ, Silva CJ, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia-Moscow, pp 281–300

Pott A, Silva JSV (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I, Assine M (eds) Dynamics of the Pantanal wetland in South America. The handbook of environmental chemistry. Springer, Cham, pp 111–131

Pott A, Oliveira A, Damasceno-Junior G, Silva JSV (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71:265–273. https://doi.org/10.1590/S1519-69842011000200005

Pott A, Damasceno-junior GA, Pereira M (2014) Características da Bacia Hidrográfica do Rio Miranda. Rev GeoPantanal 16:125–140

Prado DE, Gibbs PE (1993a) Patterns of species distributions in the dry seasonal forests of South America. Source Ann Missouri Bot Gard 80:902–927. https://doi.org/10.2307/2399937

Prado DE, Gibbs PE (1993b) Patterns of species distributions in the dry seasonal forests of South. Ann Missouri Bot Gard 80:902–927

Prado DE, Gibbs PE, Pott A, Pott VJ (1992) The Chaco-Pantanal transition in southern Mato Grosso, Brazil. In: Furley PA, Proctor J, Ratter JA (eds) Nature and dynamics of forest-savanna boundaries. Chapman & Hall, pp 451–470

Prance GT, Schaller GB (1982) Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. Brittonia 34:228. https://doi.org/10.2307/2806383

Ratter JA, Pott A, Pott VJ, Cunha CN, Haridasan M (1988) Observations on woody vegetation types in the Pantanal and at Corumbá, Brazil. Notes RBG Edinburgh 45:503–525

Ribeiro SP, Brown VK (2002) Tree species monodominance or species-rich savannas? The influence of abiotic factors in designing plant communities of the Brazilian Cerrado and Pantanal Matogrossense: a review. Ecotropica 8:31–45

Ribeiro JF, Walter BMT (1998) Fitofisionomias do bioma Cerrado. In: Sano SM, de Almeida SP (eds) Cerrado: ambiente e flora. Embrapa-CPAC, Planaltina, pp 87–166

Richmond CE, Breitburg DL, Rose KA (2005) The role of environmental generalist species in ecosystem function. Ecol Modell 188:279–295. https://doi.org/10.1016/j.ecolmodel.2005.03.002

Rodela LG (2006) Unidades de vegetação e pastagens nativas do Pantanal da Nhecolândia, Mato Grosso do Sul. Universidade de São Paulo

Rodrigues NB, Júnior GAL, Costa RB, Silva FHB, Cunha CN (2012) Composição florística, fitossociologia e diversidade de uma Floresta Estacional Decidual em Cáceres, Pantanal de Mato Grosso. Multitemas 41:19–33

Rull V, Montoya E (2014) Mauritia flexuosa palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. Quat Sci Rev 99:17–33. https://doi.org/10.1016/j.quascirev.2014.06.007

Salis SM, Assis MA, Crispim SMA, Casagrande JC (2006) Distribuição e abundância de espécies arbóreas em cerradões no Pantanal, Estado do Mato Grosso do Sul, Brasil. Rev Bras Botânica 29:339–352. https://doi.org/10.1590/S0100-84042006000300002

Santos RM, Oliveira-Filho AT, Eisenlohr PV, Queiroz LP, Cardoso DBOS, Rodal MJN (2012) Identity and relationships of the Arboreal Caatinga among other floristic units of seasonally dry tropical forests (SDTFs) of north-eastern and Central Brazil. Ecol Evol 2:409–428. https://doi.org/10.1002/ece3.91

Sartori ALB, Pott VJ, Pott A, Carvalho FS (2018) Checklist of angiosperm from the Chaco of Mato Grosso do Sul. Iheringia – Ser Bot 73:22–33. https://doi.org/10.21826/2446-8231201873s22

Silva JSV, Abdon MM (1998) Delimitação do pantanal brasileiro e suas sub-regiões. Pesqui Agropecuária Bras 33:1703–1711

Silva Junior MC, Felfili JM, Nogueira PE, Resende AV (1998) Análise florística das Mata de Galeria no Distrito Federal. In: Ribeiro JF (ed) Cerrado: Matas de Galeria. Embrapa CPAC, Planaltina, pp 53–93

Silva MP, Mauro R, Mourão G, Coutinho M (2000a) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Rev Bras Botânica 23:143–152. https://doi.org/10.1590/S0100-84042000000200004

Silva MP, Pott VJ, Ponzoni FJ, Pott A (2000b) Fitossociologia e estrutura de Cerradão e Mata Semidecidua do Pantanal da Nhecolândia, MS. III Sinmpósio sobre Recur Nat e Sócio-Economicos do Pantanal os desafios do Novo Milênio, pp 1–22

Soares JJ, Oliveira AKM (2009) O paratudal do Pantanal de Miranda, Corumbá-MS, Brasil. Rev Árvore 33:339–347. https://doi.org/10.1590/S0100-67622009000200015

Soares AF, Silva JSV, Ferrari DL (2006) Solos da paisagem do Pantanal brasileiro – adequação para o atual sistema de classificação. In: Anais 1º Simpósio de Geotecnologias no Pantanal, pp 275–284

Souza EB, Damasceno-Junior GA, Pott A (2019) Soil seed bank in Pantanal riparian forest: persistence, abundance, functional diversity and composition. Oecologia Aust 23:891–903

Spera ST, Cardoso EL (2000) Atualização da legenda do levantamento de reconhecimento de alta intensidade dos solos da borda oeste do pantanal: maciço do urucum e adjacências, MS. Embrapa Pantanal

Spichiger R, Calenge C, Bastian B (2005) Discriminant analysis of the spatial distribution of plant species occurrences: II. Distribution of major tree communities in Paraguay. Candollea 60:563–575

Trujillo-Arias N, Dantas GPM, Arbeláez-Cortés E, Naoki K, Gómez MI, Santos FR, Miyaki CY, Aleixo A, Tubaro PL, Cabanne GS (2017) The niche and phylogeography of a passerine reveal the history of biological diversification between the Andean and the Atlantic forests. Mol Phylogenet Evol 112:107–121. https://doi.org/10.1016/j.ympev.2017.03.025

Ussami N, Shiraiwa S, Dominguez JML (1999) Basement reactivation in a sub-Andean foreland flexural bulge: the Pantanal wetland, SW Brazil. Tectonics 18:25–39. https://doi.org/10.1029/1998TC900004

Ward JH (1963) Hierarchical grouping to optimize an objective function. J Am Stat Assoc 58:236–244

Wittmann F, Marques MCM, Damasceno-Junior GA, Budke JC, Piedade MTF, Wittmann AO, Montero JC, Assis RL, Targhetta N, Parolin P, Junk WJ, Householder JE (2017) The Brazilian freshwater wetscape: changes in tree community diversity and composition on climatic and geographic gradients. PLoS One 12. https://doi.org/10.1371/journal.pone.0175003

Zeilhofer P (2006) Soil mapping in the Pantanal of Mato Grosso, Brazil, using multitemporal Landsat TM data. Wetl Ecol Manag 14:445–461. https://doi.org/10.1007/s11273-006-0007-2

Chapter 10
Natural Pastures of the Pantanal: Diversity, Productive Potential and Dynamics

**Sandra Aparecida Santos, Evaldo Luis Cardoso,
José Francisco Montenegro Valls, and Arnildo Pott**

10.1 Introduction

The Pantanal is considered the world's largest tropical floodplain, and it is rich in biodiversity. The region contains complex and dynamic environments ruled by the flood pulse, which interferes with the floristic dynamics (Scremin-Dias et al. 2011). Native pastures are the main renewable resource because they are present in the different landscapes, and this is the basis of the strong natural potential of the Pantanal for the extensive production of beef cattle (Santos et al. 2011).

The Pantanal has a heterogeneity of plant communities forming a mosaic of landscapes that vary spatiotemporally as a function of the edaphoclimatic and anthropic conditions and their interactions (Pott 1994). The first comprehensive inventory of native forage resources of the Pantanal was made by Allem and Valls (1987). Pott and Pott (1999) (see Chap. 3) present an updated list of phanerogams with 2250 species, whose main families are legumes (240 species), grasses (212 species) and sedges (92 species). Cattle feed on all types of vegetation, from aquatic forage to browse plants; therefore, the concept of natural pasture in the Pantanal is very broad (Pott et al. 2011).

Anthropogenic and natural disturbances (e.g. fire, drought, herbivory, flood) have shaped natural grazing ecosystems. Pristine grasslands of the Pantanal were probably dominated by tall grasses such as *Andropogon hypogynus*, but with the

---

S. A. Santos (✉) · E. L. Cardoso
Embrapa Pantanal, Corumbá, MS, Brazil
e-mail: sandra.santos@embrapa.br

J. F. M. Valls
Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF, Brazil

A. Pott
Laboratório de Ecologia Vegetal/Laboratório de Botânica, Instituto de Biociências,
Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_10

cattle ranching activity, they changed to short grasses, such as *Axonopus purpusii* (Pott et al. 2013). Some types of natural grassland have little variations in floristic composition, mainly those located at higher and flood-free areas, while in more flooded areas, the floristic composition is species richer and extremely dynamic (Santos et al. 2011).

The major challenge faced by technicians and ranchers is the management and monitoring of these heterogeneous and dynamic grasslands. Sustainable native pasture management depends upon a good understanding of the main pasture types and their respective availability and quantity in order to estimate the appropriate stocking rate, selection of the proper grazing system (continuous or rotation grazing) for each pasture ecosystem, the need for providing protein, energy and mineral supplementation to grazing cattle and the management strategies/control of woody invaders in pastures.

This chapter focuses on the classification of the main native pasture types of the Pantanal, addressing their diversity, key species, productive potential and dynamics, aiming at developing adaptive and sustainable management strategies.

10.2 Diversity of Native Pastures and Ecological Sites

Biodiversity encompasses various levels: landscape, ecosystem, community, species and genetics, and each of these levels is composed of three factors: compositional, structural and functional, which are interdependent and interconnected. Since the Pantanal landscapes are complex and dynamic, the use of a hierarchical approach in the classification of native pastures and ecological sites seems to be more appropriate (Noss 1990; Santos et al. 2019), considering multiscale spatio-temporal levels.

For the Pantanal, native pastures can be classified based on soil texture (Allem and Valls 1987), substrate moisture (Rodela et al. 2007), habitat (Nunes da Cunha and Junk 2011), phytophysiognomy (Silva et al. 2000), plant formations (Allem and Valls 1987), communities, functional groups and dominant/key forage species (Santos et al. 2013a, 2019). The length of the hydroperiod and the availability of moisture in the soil during the dry season influence plant formations in the Pantanal (Allem and Valls 1987). Variations in soil chemical attributes also influence the species composition of the landscapes of the Pantanal (Cardoso et al. 2016).

In a native pasture, key forage species are those that are dominant and are preferred by the grazing animals. In certain communities, several key species may appear, and their dominance may switch under the effects of anthropic and climatic factors. The diversity of forage species contributes to the maintenance and stability of forage mass cover in space and time. A functional group comprises a set of species that respond similarly to specific environmental conditions (Guretzky et al. 2005) and perform similar functions (Drobnik et al. 2011). In the classification of native pastures proposed here, functional groups were defined according to terms of practical use (Santos et al. 2019).

Table 10.1 presents a proposal for the classification of native pastures, serving as a guide to assist the identification of pasture types or ecological sites to guide management strategies. Figure 10.1 shows some examples of landscapes and Fig. 10.2 some native grassland types found in the Nhecolândia subregion. For example, in usually dry sandy areas, in cerrado grassland, we find perennial short grasses with the C_4 photosynthetic pathway as key forage, such as *Mesosetum chaseae*. This grass can have either a prostrate stoloniferous growth in grazed patches in physiognomies/communities of *Byrsonima cydoniifolia* and *Curatella americana* monodominant savannas (see Chap. 8) or an ascending habit in *Elionurus* grassland. In sandy areas, in usually seasonal, open grassland, we also find mostly perennial, short C_4 grasses, such as *Axonopus purpusii*. Although *A. purpusii* is a perennial species and consumed throughout the year by cattle (Santos et al. 2002), it can disappear or become reduced after consecutive dry years or under grazing exclosure (Santos et al. 2004), being either replaced by non-grazed plants such as *Waltheria*

Fig. 10.1 Landscapes and natural pastures of the Pantanal

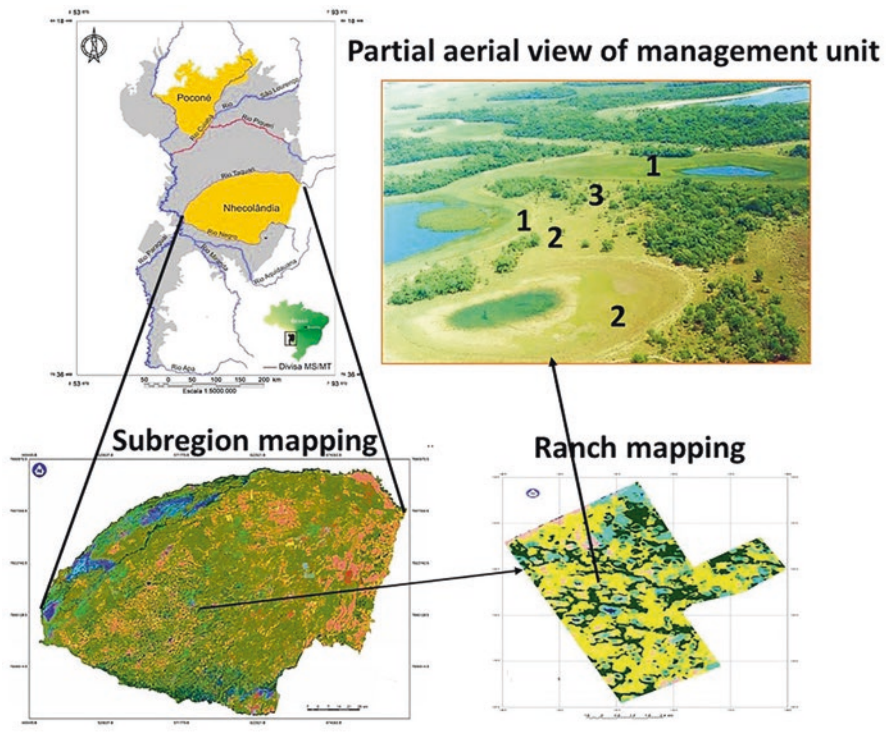


Fig. 10.2 Examples of natural grasslands found within a management unit in the Pantanal subregion of Nhecolândia 1. Wetland vegetation. Usually wet/sandy soil. Phytophysiognomy/community: shore of water bodies. Functional group: perennial C3 grasses. Key forage species: *Hymenachne amplexicaulis*. Productivity: high. Quality: high. Grazing: cattle, horses, capybaras, pampas deer etc. 2. Grassland vegetation. Usually seasonal/sandy soil. Phytophysiognomy/community: open grassland. Functional group: perennial short C4 grasses. Key forage species: *Axonopus purpusii*. Productivity: low. Quality: medium. Grazing: cattle, horses, pampas deer etc. 3. Savanna vegetation. Mostly dry/sandy soil. Phytophysiognomy/community: cerrado grassland. Functional group: perennial short C4 grasses. Key forage species: *Mesosetum chaseae*. Productivity: low. Quality: low to medium. Grazing: cattle, horses, pampas deer etc.

albicans or shaded out by a fast succession to taller grasses. Afterwards, other key forage species may dominate, e.g. *Setaria parviflora* and *Steinchisma laxum*, both pioneer grasses on bare soil and with abundant small seeds. *Axonopus purpusii* can also occur as a key species in other physiognomies/communities (shrubby grassland, seasonal streams and riversides). In areas of usually wet, sandy soil, in the physiognomy of pond shores, we can find perennial C_3 grasses such as *Hymenachne amplexicaulis*. This key grass also occurs in several other physiognomies/communities, such as swamps, riversides and seasonal streams. In some environments, such as pond shores of the Nhecolândia subregion, *H. amplexicaulis* occurs associated with *Luziola subintegra*, another key species. Their dominance depends on climatic conditions. In general, heavy flood leads to a decline of *H. amplexicaulis*.

In the hierarchical classification of native pastures, we can classify a high diversity of pasture types with their patterns of spatiotemporal variation. Such gradients of native pastures in an area can be managed year-round, assuring forage for the animals in different seasons. However, livestock must be removed from deep, long flooded river floodplains, whereas the herds can remain throughout the year in zones that are flooded just by rain, when, during the time of flooding, they are able to graze during the day on wet and moist areas, seeking higher ground at night.

Another important form of classification for rangelands much utilized to define state-transition models refers to the classes of ecological sites and ecological site descriptions (ESDs). Unlike vegetation classification (see Chap. 2), ecological site classification uses climate, soil, geomorphology, hydrology and vegetation information to describe the ecological potential of land areas. Bestelmeyer and Brown (2010) described ecosystem structures, functions and dynamics in the form of an ecological site for rangeland management. They define an ecological site as a basic unit for study, evaluation and management, whose development starts with stratifying the landscape into hierarchical units according to climate, landforms and soils.

In Table 10.2, we display a proposal of an identification key of some of the main ecological sites of the Pantanal. As our basis, we used the classification made by Assine et al. (2015), according to hydro-sedimentological settings characterized by geological and geomorphologic features, hydrological regimes and sedimentological dynamics (Fig. 10.3), determined by the source areas. We also considered the flooding level (duration and depth) and soil chemistry and texture (Couto and Oliveira 2011).

10.3 Productive Potential and Carrying Capacity of the Native Pastures

Regarding productive potential, forage plants can be classified in terms of quantity and quality. Quantity refers to the annual production and availability of dry matter (DM), which is essential information for the estimation of stocking rate and grazing pressure (Santos et al. 2008). For practical purposes, the production of native pastures in the Pantanal is classified as low when the available forage is <1000 kg DM.ha^{-1}; medium when the production is between 1000 and 3000 kg DM.ha^{-1}; and high when the production is >3000 kg DM.ha^{-1}. For example, open grassland with a predominance of *Andropogon hypogynus*, a perennial C_4 bunchgrass, presents a high yield, though of low to medium quality, depending on the proportion of perennial short C_4 species in the composition, such as *Axonopus purpusii* and/or *Steinchisma laxum*. Another critical factor refers to the quality of the ingested forage, as it affects consumption, with a consequence for animal productivity. In general, there are pastures of low, medium and high quality. Grasslands of low quality produce forage with a crude protein (CP) percentage of <7%, the minimum requirement of ruminants. These pastures generally occur in drier savanna areas (cerrado savanna, cerrado grassland, shrubby grassland, etc.), on soils that by nature are of

Table 10.1 Hierarchical levels of the types of landscapes and native pastures of the Pantanal

Vegetation form	Soil moisture/sandy, silty and clayey soil	Phytophysiognomies/communities	Functional group	Dominant species and/or key forages (type of grassland or community)
1. Forest 2. Savanna 3. Grassland 4. Aquatic	1. Mostly dry 2. Mostly seasonal 3. Mostly wet	1. Dry forest (seasonal deciduous forest) 2. Forest (seasonal semideciduous forest)/*Attalea phalerata* palm forest, *A. speciosa* palm forest 3. Riparian/gallery forest 4. *Vochysia divergens* woodland 5. Cerradão (forested savanna) 6. Gallery forest 7. Cerrado (savanna) 8. Cerrado grassland 9. Park savanna/*Tabebuia aurea*/*Handroanthus heptaphyllus*/*Copernicia alba* 10. Freshwater pond shores 11. Brackish ponds and shores 12. Vazantes and baixadas 13. Open grassland/*Axonopus purpusii* grassland, *Paspalum plicatulum* grassland, *Elionurus* grassland 14. Earthmound savanna 15. Shrubby grassland/*Byrsonima cydoniifolia*/*Curatella americana*/*Licania parvifolia*/*Combretum* spp./*Xylopia aromatica* 16. Chaco (Stepic savanna) 17. Swamp/*Ipomoea carnea*/*Cyperus giganteus*/*Thalia geniculata*/Spiny scrub 18. River and riversides 19. Seasonal small river (corixo) and riversides 20. Forest islet 21. Man-made mound forest islet 22. Grassland patch (Campina) 23. Vereda/*Mauritia flexuosa* swamp 24. *Erythrina fusca* stand 25. Swampy woodland (Landizal) Others	1. Perennial C_3 grasses 2. Perennial bunch C_4 grasses 3. Perennial short C_4 grasses 4. Pioneer grasses 5. Annual grasses 6. Exotic perennial C_4 grasses 7. Native invasive shrubs 8. Native herbaceous weeds 9. Weedy C_4 grasses 10. Forage legumes 11. Weedy legumes 12. Herbs 13. Shrubs 14. Trees 15. Amphibious macrophytes 16. Emergent macrophytes 17. “Rooted” floating macrophytes 18. Rooted submerged macrophytes 19. Free-floating macrophytes 20. Lianas Others	List of forage species (Pott & Pott, 1999). E.g.: 1. *Mesosetum chaseae* (grassland with dominance of *M. chaseae*; savanna or cerrado grassland with dominance of *M. chaseae*) 2. *Andropogon hypogynus* 3. *Elionurus muticus* 4. *Hymenachne amplexicaulis* 5. *Reimarochloa* spp. 6. *Axonopus purpusii* 7. *Paspalum lineare*/*P. carinatum* 8. *Luziola subintegra* 9. *Paspalum wrightii* 10. *Paspalum plicatulum* Others

Table 10.2 Proposal of a key of ecological sites of the Pantanal for rangeland management

I. **The Paraguay trunk-river plains**	**Ecological site**
A. High flooding	Clayey grassland with *Paspalum fasciculatum* Clayey grassland with C_3 grasses (*Hymenachne amplexicaulis*, *Luziola* spp., *Oryza* spp.) Clayey grassy-woody savanna with *Vochysia divergens* Clayey marsh with *Ipomoea carnea* Floating aquatic vegetation (floating meadows)
B. Medium flooding	Clayey grassy-woody savanna with *Vochysia divergens* Clayey shrubland with *Mimosa pellita*
C. Low flooding	Clayey riparian forest with *Rugoloa hylaeica*
II. **Fluvial fans sourced by the tablelands catchment area**	
A. Fluvial flooding	Sandy river floodplain with C_3 grasses Sandy floodable grassland with tall grasses (*Axonopus paraguayensis*, etc.) Sandy grassy-woody savanna with *Leptobalanus parvifolius*
B. Pluvial flooding	
B1. Wet	Sandy pond shores with C_3 species Sandy shores with *Andropogon hypogynus*
Sodic soils	Brackish pond shores with *Paspalum vaginatum*
B2. Seasonal	Pond shores with short grasses (*Reimarochloa* spp., *Axonopus purpusii*) Seasonal streams with short grasses (*Reimarochloa* spp., *Leersia hexandra*) Sandy open grassland with *Andropogon hypogynus* Sandy lowland with short grasses Sandy grassy-woody savanna with *Paspalum plicatulum* Sandy open grassland with cultivated *Urochloa humidicola*
Sodic soils	Sandy grassy-woody savanna (*Curatella americana* and *Byrsonima cydoniifolia*/*Andropogon hypogynus*)
B3. Dry	Grassy-woody savanna with *Copernicia alba* Sandy open grassland with *Elionurus muticus* Sandy grass-woody savanna (*Curatella americana* and *Byrsonima cydoniifolia*/*Mesosetum chaseae*) Sandy *Attalea phalerata* forest Sandy *Attalea speciosa* forest Sandy woodland with Cerrado species
III. **Fluvial fans sourced by lowlands** A. High flooding	Clayey marsh with *Canna glauca* Clayey marsh with *Cyperus giganteus* Clayey marsh with *Ipomoea carnea* Clayey marsh grassland with *Schizachyrium sulcatum* Clayey channels covered with riparian trees Clayey grass-woody with *Leptobalanus parvifolius* Clayey grassy-woody with *Combretum* spp. and *Paspalum oteroi* Clayey forest of *Vochysia divergens* Clayey shrubland with *Combretum lanceolatum* and *C. laxum*

(continued)

Table 10.2 (continued)

B. Medium flooding	Clayey grassy-woody of *Tabebuia aurea* Clayey open grassland with *Andropogon hypogynus* Clayey open grassland with *Paspalum wrightii* Clayey grassy-woody with *Paspalum plicatulum* Clayey open grassland with cultivated *Urochloa humidicola* Sandy-clayey grassy-woody earthmound with *Curatella americana* and *Axonopus brasiliensis*/*Paspalum carinatum* Clayey grassy-woody earthmound with *Alchornea discolor* and *Loudetia flammida* Clayey woodland
IV. **Fluvial interfans** A. Medium flooding	Sandy open grassland with cultivated *Urochloa humidicola* Sandy-clayey alkaline grassy-woody of *Copernicia alba* with *Hemarthria altissima*
B. Dry	Sandy shrubland with *Leptochloa uninervia* Sandy open grassland with *Paspalum notatum* and other naturalized grasses

low fertility. The pastures of medium quality, with 7–9% CP, are generally present in seasonally flooded areas and are mostly open grasslands. Those of high quality, with CP levels >9% and In vitro dry matter digestibility (IVDMD) >58% (Santos et al. 2020), generally occur in wetter areas, such as pond shores, with a predominance of C_3 grasses (Santos et al. 2002), plus aquatic legumes such as *Aeschynomene fluminensis* and *Discolobium* spp. subshrubs with nodules that fix nitrogen.

Cattle select these pasture types with preferred forage species of better quality, resulting in different degrees of grazing (Santos et al. 2013a, b). In the continuous grazing system in the Pantanal, in general, cattle have a mosaic of types of native pastures available for grazing. These pasture types contain desirable forage species as well as undesirable coarse grasses. Santos et al. (2003) classified the main forage plants of the Pantanal according to the degree of preference by cattle.

The *Elionurus muticus* and *Paspalum carinatum*/*P. lineare* grasslands, which have a low CP content, except at regrowth immediately after a fire, have been widely replaced by *Urochloa humidicola*. Although environmentalists criticized this introduction of an exotic grass, in fact, it has reduced the traditional use of fire as a management tool and the occurrence of wildfires spread by *E. muticus*, as that species is very flammable because of its oil content. Native grazers also benefit from the sown grass. Nonetheless, both types of native grasslands, especially the low-density sward of *Paspalum* spp., contain quite a rich tiny herb flora that becomes impoverished. The main grass *Elionurus* produces inflorescences a month after a fire (see the Chap. 18 on "Fire"), whereas when it is not burned and not grazed, the second most abundant grass *Trachypogon spicatus* flowers.

To prevent overgrazing in an area of common grazing of wildlife and domestic animals, the carrying capacity should largely be determined by the grazing needs of the large wild herbivores because they graze much less but deer are more selective than the domestic animals. Santos et al. (2013b) developed a system to estimate the carrying capacity taking into consideration the use in common by domestic and

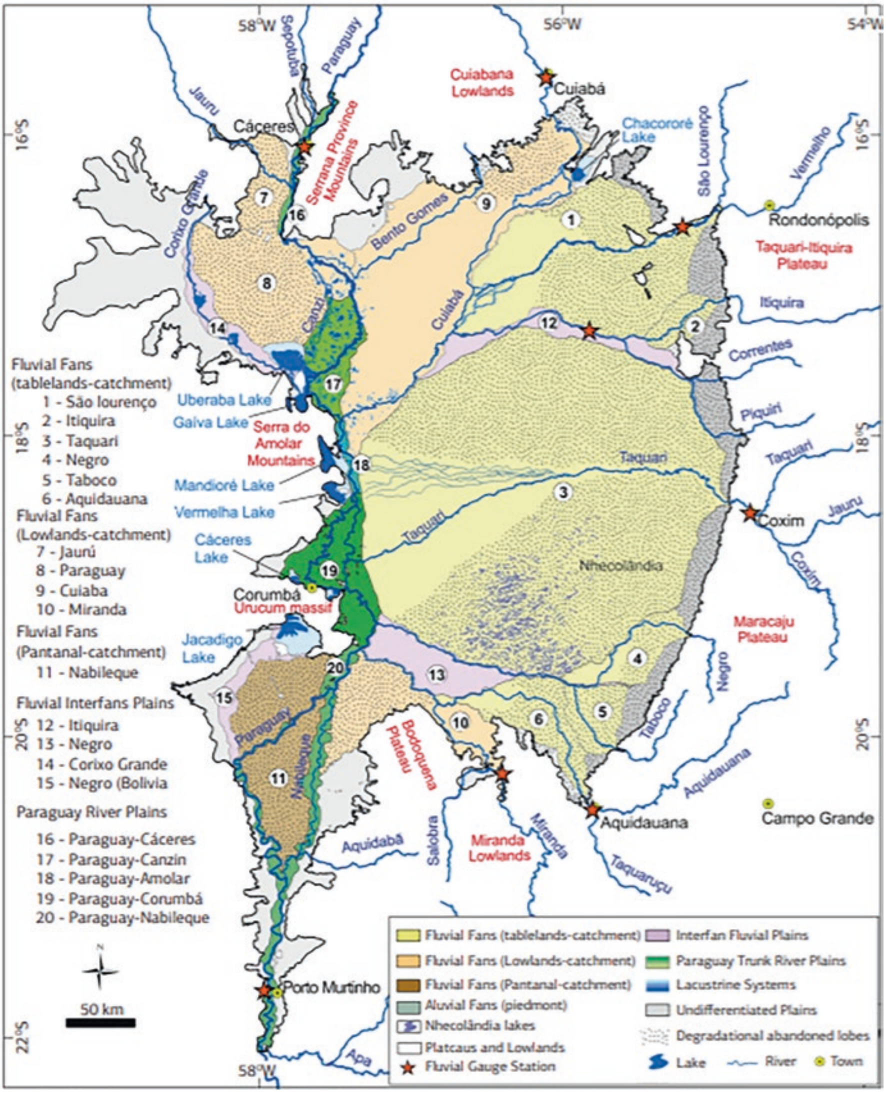


Fig. 10.3 Classification of the Pantanal according to hydro-sedimentological settings. (https://www.scielo.br/j/bjgeo/a/g5nSxCVjLDZKXz5JwBJzyqN/?lang=en&format=pdf; Assine et al. 2015)

wild animals in a continuous grazing system. They classified the pastures according to the degree of utilization and identified by faecal microhistology the key forage species for the different animal species using an management unit. Table 10.3 exhibits the carrying capacity under multiple uses by cattle, pampas deer and capybaras in the Nhecolândia subregion.

Table 10.3 Estimates of carrying capacity of pastures under multiple uses of five categories of pastures

Categories of pastures	Degree of pasture utilization (%)[a]	Key forage species identified in diet[b]	Selected crude protein (%)[c]			Annual forage yield (kg. ha^{-1})	Area (ha)	Carrying capacity (UA/ha)[d]
			B	C	V			
Casual use (savanna area)	10	***Axonopus purpusii*** *(B)*, ***Mesosetum chaseae*** *(B)*, *Microstachys hispida (V)*, ***Byrsonima cydoniifolia*** *(V)*	6.6	–	9.8	3000	6.7	0.8; 0; 4.6
Casual use (tussock grassland)	10	***A. purpusii*** *(B)*, ***M. chaseae*** *(B)*, *M. hispida (V)*, ***B. cydoniifolia*** *(V)*	6.6	–	8.8	6000	28.7	6.7; 0; 39.3
Moderate use (open grassland)	50	***A. purpusii*** *(B, V)*, ***M. chaseae*** *(B)*	7.0	–	7.0	3000	30.6	18.0; 0; 52.4
Intense use (seasonally flooded open grassland)	75	***A. purpusii*** *(B, C, V)*, ***Steinchisma laxum*** *(B, C)*, *Cynodon dactylon (B, C)*	7.0	9.5	7.0	2000	17.4	10.2; 44.7; 19.9
Intense use (wet grassland)	75	***Hymenachne amplexicaulis*** *(B, C, V)*, ***S. laxum*** *(B, C, V)*, ***Eleocharis minima*** *(B, C)* *Aeschynomene fluminensis (V)*, *Melochia simplex (V)*, *Ludwigia* spp. (V)	12.0	12.0	12.6	3000	10.5	9.2; 45.6; 36
Total pasture								**44.9; 90.3; 152.2**

[a] Degree of utilization is the proportion of the annual forage production utilized by a group of animal species

[b] Key species composes up to 2% of the total diet of the studied animals, cattle (B), capybara (C) and pampas deer (V). Key species of the diet in bold

[c] Mean crude protein of the selected diet considering the proportion of key species in each pasture

[d] Animal unit (AU) represents 350 kg/ha, 40 kg/ha and 30 kg/ha for cattle, capybaras and pampas deer, respectively (Santos et al. 2013b)

10.4 Dynamics and Adaptative Management of the Native Pastures – A Multifunctional System

The traditional management system of the native grasslands, basically extensive management in large areas under continuous grazing, is losing sustainability for various reasons, such as degradation, due to overgrazing and brush encroachment (see the Chap. 11 on "Encroachment"). Because of the dynamics and complexity of the landscapes that determine the variability and biodiversity in the Pantanal, the sustainable management strategies should be multifunctional to maintain the richness of landscapes, favouring the diversity of plant species and especially the types of native grasslands, rendering the ecosystems more resilience (Santos et al. 2011) and providing a multitude of ecosystem services. In general, the low efficiency of the extensive cattle rearing systems in the region is due to the use of pre-set rules/management without taking into consideration the dynamics of productivity and quality of the pastures resulting from rainfall and flood level, variable in time and space. The decisions in a Pantanal ranch are made at various scales (Fig. 10.4), because what seems stable at a large scale is extremely dynamic at smaller scales, e.g. shown in the succession of species of wet native grasslands. In the case of native pastures, the main decision occurs at the scale of a management unit ("paddock") that is generally large (around 1000 ha) and heterogeneous, i.e. composed of various landscape units, such as forested areas, cerrado savanna, cerrado grassland, open grassland, ponds, seasonal streams, etc., arranged in a mosaic. Many of these landscapes have dominant forage grasses, thus constituting different "types of pastures" based on the dominant key forage species. The frequency of use of these grasslands is probably related to the presence of more or less surface water in the areas and the

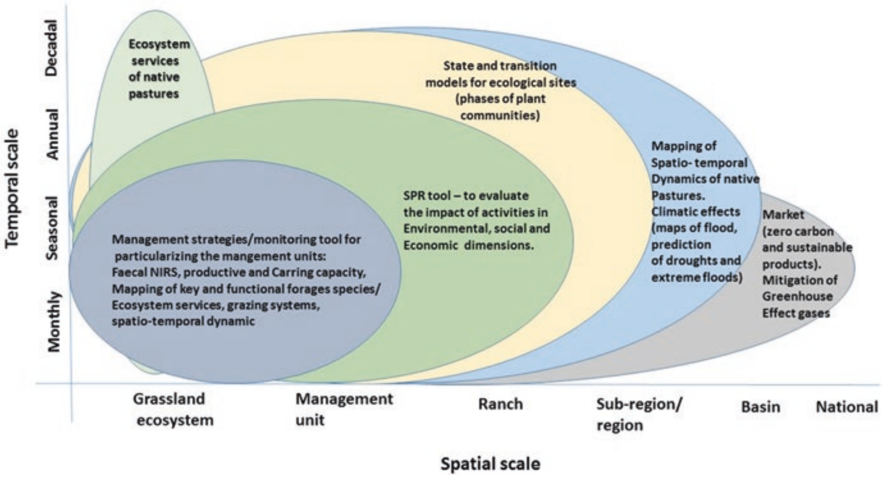


Fig. 10.4 Spatiotemporal scale for decision-making and studies on native pastures of the Pantanal (*NIRS* near-infrared spectroscopy, *SPR* Sustainable Pantanal Ranch tool)

pasture quality/availability. However, not all are grazed at the same intensity by cattle.

Nowadays, one of the main problems faced by the cattle ranchers of the Pantanal is the reduced carrying capacity of the native and exotic grasslands, due to degradation and invasion by shrubby species (see the Chap. 11 on "Encroachment"), caused by climatic and anthropic factors. Management strategies have to be adaptative and variable in response to the degree of conservation or degradation of the native grasslands, as well as their productivity and quality. In an adaptative plan, the management strategies also have to be formulated regarding the level and distribution of rainfall and its variability over the years. A grassland which already lost resilience will need more external inputs for recovery than a grassland undergoing degradation, where simple management practices can be effective. Thus, due to the landscape complexity and the system dynamics, a management decision should, preferably or necessarily, be adaptive according environment conditions.

Native pasture communities can be in different states of condition, dependent on the history of their management and climatic conditions (Mauro et al. 1998). State-transition models are theoretical tools which help in understanding the pasture dynamics and the response mechanisms to disturbances, management and climatic conditions, as well as to support decision-making (Westoby 1989). The response of ecosystems and landscapes to disturbances depends on resistance (capacity to absorb disturbance without alteration), response (amplitude of change), recovery (time of return to the original state), stability (rate of return to the prior state) and resilience (ability of return to the original state). Therefore, knowledge on how the landscape or pasture responds to different disturbances over time and in space is fundamental to manage the structure and function of the ecosystem (Fuhlendorf and Engle 2004), as well as to define management and recovery strategies.

Condition states can be characterized by species abundance and composition, as well as function (Suding and Hobbs 2009). From the ecological point of view, there are no states considered more desirable, opposite to the objective of productive systems, wherein the most desirable state corresponds to that providing the best productivity. Many communities present a predominance of herbaceous plants, especially grasses and sedges, which favour the raising of beef cattle. The wet areas around water bodies and low-lying areas have good quality forage and are more intensely grazed (Santos et al. 2002), but often the green look of those overgrazed pastures can be misleading from afar, when most of the cover may be composed of small sedges (e.g. *Cyperus brevifolius*) and annual herbs (e.g. *Helanthium tenellum*).

In general, the communities are dynamic, particularly the periodically flooded communities. However, these ecosystems can lose that function when their state of condition changes, i.e. from a state dominated by herbaceous plants of forage interest to a state dominated by herbaceous plants with little forage value. Threshold relationships between vegetation structure and functioning can determine the change in states. However, when this happens, the ecosystem may have lost its resilience, i.e. the capacity for recovery to desirable state. Nonetheless, for evaluation of the states of condition, it is necessary to know the functional groups of occurring plants, as aforementioned in Table 10.1. Santos et al. (2014) evaluated the resilience

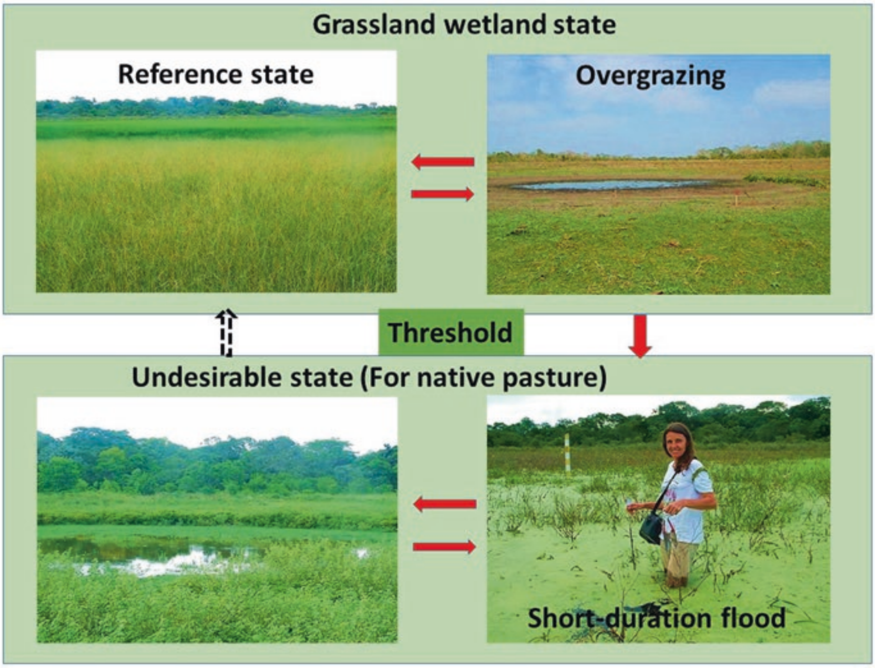


Fig. 10.5 State and transition models of wet areas (pond shores) of the sandy Pantanal after consecutive years of overgrazing, short-duration droughts and floods (which cause a transient dynamic in the ecosystem with the change in dominance of forage species, but an adaptative resilience can be observed)

of a native pasture on a pond shore in the Nhecolândia subregion that was overgrazed for several years of drought and brief floods. Santos et al. (2014) found that the forage species were replaced by invasive native herbaceous species such as *Sida acuta*. Evaluations of the soil seed banks in natural grasslands demonstrated vast and varied storage of species, which can emerge in response to seasonal conditions or after disturbance (Bao et al. 2014; Souza et al. 2016) (see Chap. 15). To unravel the dynamics, state-transition models can help to understand the processes (Fig. 10.5). In general, wet areas show an adaptative resilience which contributes to the conservation of these ecosystems, but many of the states are not desirable for cattle raising. In wet areas, we may observe a drop in resilience when the state deviates from the desirable state, as the new colonizing species are not always desirable for cattle rearing. Treading in these areas may impede the water retention and can hinder other ecosystem services besides the provision of forage. Cardoso et al. (2017) assessed the C and N stocks in the soil under different states of conservation of native grasslands of wet areas in the Pantanal, significantly higher in areas under seasonal flooding regime than the non-flooded ones. Also, the reduction in the conservation status of native pastures, as evaluated by means of indicators of the SPR tool (Santos et al. 2017), showed a significant reduction in C and N stocks. Hence, the monetary value of the service supported by the soil, expressed by the storage of C and N, was higher in better conserved native pastures.

In the case of cattle production systems, the ecosystems where forage species dominate are the most wanted, because their main function is forage production. Biodiversity is important to maintain the resilience and ecosystem services of these native pastures since different species present different functions and/or characteristics of adaptation. Some grass species adapted to wet areas such as *Hymenachne amplexicaulis* may disappear in years of high floods (Fig. 10.3), according to Santos et al. (2002), while, in contrast, some species with more phenotypical plasticity, such as *Paspalum fasciculatum* (Santos et al. 2016), which withstands drought and flood as well as grazing, can become prostrate or form a stratum of sprouts near the flood surface. Probably *H. amplexicaulis* is hindered because it becomes submerged

Table 10.4 Causes and controls of the main weeds of native pastures of the Pantanal, described by cattle ranchers

Plant name	Causes[a, b]	Control[b]
Combretum spp.	Treading (overgrazing), lack of brush control, lack of burning; long periods of flood	Mechanical control (chain) or manual slashing at the beginning of the rainy season, before seed ripening
Vochysia divergens	Lack of burning, lack of brush control, adaptation to new environmental conditions; long periods of flood (seed spread)	Manual or mechanical cut of all plants with diameter at breast height <40 cm
Byrsonima cydoniifolia	Overgrazing, inadequate pasture management at early invasion, lack of brush control, lack of burning, pluri-annual drier cycles	Manual or mechanical cut at the base of plants before the flood; in flood-free areas, use a toothed blade to pull the whole plants out, that can be racked or piled in windrows
Ipomoea carnea ssp. *fistulosa*	Excess of flood with seed spread, inadequate pasture management such as undue burning	Slashing at the beginning of the dry season, variable among sites; repeat at the beginning of flooding; slashed material must dry off
Vachellia farnesiana	Overgrazing, long period of drought, low consumption by animals; herbivores and birds spread seed through their faeces	Maintain the soil totally covered by means of adequate pasture management; prescribed burning
Couepia uiti	Lack of burning, long periods of flood and adaptation to new environmental conditions	Mechanical control with toothed blade; do not remove trees near lakes or streams
Senna alata	Overgrazing, years of long droughts, various factors	Manual or mechanical slashing and if possible incorporate it into the soil as green manure, but before seed set; reduce stocking rate and defer the area
Curatella americana	Overgrazing, inadequate pasture management at early invasion, lack of flood	Use of chain; ring barking

[a] Santos et al. (2006); Santos and Comastri Filho (2012)

[b] Santos and Comastri Filho (2012)

when shortened by grazing. Indeed, this grass is aquatic and, when ungrazed, grows in over 2 m deep water, as can be observed in the cage (without grazing) (in the state of seasonal flood). Understanding these dynamics is fundamental for adaptative management aiming at native pasture resilience. Thus, the resilience of native pastures depends on the physiognomy, on the soil seed bank and soil nutrients, associated with disturbances and climatic conditions. The ideal would be to be able to stimulate the conservation of the native pastures, especially those of wet areas, to maintain several ecosystem services in a multifunctional landscape (see Chap. 21).

Pasture weed control (see Chap. 11) is one of the activities that most encumbers the production system. The choice of the best options for each troublesome species has been a dilemma for Pantanal cattle ranchers. The first decision to be taken in this respect concerns the stocking rate at the level of the management unit, but the possibilities favouring recovery have to be evaluated per type of pasture, i.e. in a particularized way. One of the main strategies to prevent invasion and pasture degradation is the early detection of the problem, i.e. before the pasture loses resilience. Luckily, the Pantanal is so far free from exotic tropical weeds of wetlands, such as the Australian *Melaleuca quinquenervia*. In turn, *Mimosa pigra*, native to Brazil, is a weed in Australian wetlands and *Schinus terebinthifolius* in the Everglades in the USA. Table 10.4 shows the main causes of invasion of unwanted species described by ranchers, of species already mentioned by Pott et al. (2013). Santos and Comastri Filho (2012) reported other weedy species common in the Pantanal, their causes of invasion and ways of control. The use of brush killer herbicides is not allowed in the Pantanal, though it is frequent in the upper basin and some residues are brought in by the rivers.

The species listed in Table 10.4 are all native to the Pantanal and possess mechanisms for persistence and dominance, excluding competitors and shading out heliophytic grasses. *Combretum* spp. have diaspores dispersed by the wind as well as by water, but once the plant is established, its on-site propagation is vegetative, forming an entangling mass. The tree *V. divergens* builds monodominant stands which inhibit even its seedlings, and only later on many forest species move in. The shrub or treelet *B. cydoniifolia* reaches high densities on sandy floodable areas, even hindering cattle access to good grasses (*A. purpusii*, *S. laxum*) underneath. The slender shrub *I. carnea* has floating, hairy seeds which are dispersed over long distances by the water. It has a guerrilla strategy for on-site spreading like a crawling soldier since decumbent stems that touch the ground and any piece of broken off stem roots quickly, whereas flooded stems already develop adventitious roots. This species dominates wetlands under tidal oscillation of the Amazon River in the State of Amapá, due to overgrazing by buffalo. The spiny *V. farnesiana* is a rather flood-free pasture shrub on fertile soil. *C. uiti* occurs localized, but its umbrella-like canopy nearly reaches the ground as it does not have a browse line since it is not browsed by cattle nor by native animals. It can resprout after being chopped. *Senna alata* is a shrub of only 1–2 m tall, alike *S. aculeata*; both increase in degraded pasture such as around salt and water troughs and gates, the last species also inside ponds. Just logging does not control *C. americana* because of its resprouting capacity from old stumps.

Unwanted woody vegetation has taken over large areas of prior grasslands, mainly in the Poconé subregion (see the Chap. 11 on “Encroachment”). Perhaps areas under a flowing flood regime more strongly experience woody invasion than those with standing water. For example, the tree *Vitex cymosa* withstands 4 m of running flood near a river, but not even 0.4 m in the standing water of a pond.

For the rural producer to stay in business, he needs to become updated and modernized, searching for new technologies. However, that does not mean changing to an intensive production system; new landowners sometimes intend to achieve the same productivity as elsewhere, at the expense of conservation. Nevertheless, the adoption of adequate technologies depends on proper farm management, which, in turn, needs appropriate tools for planning and decision-taking with the target of sustainability and multifunctionality. Besides, nowadays, TV, cell phone and Internet have reached the Pantanal, and several new tools are available to gather all sorts of information to assist the farmer. For example, a cell phone photograph of a suspected toxic plant can be sent to be identified within minutes or compared with online pictures. The Brazilian Navy daily records the Paraguay River level and reports a flood alert, already used since 1900 when the fluvial gauge was installed. It is known that El Niño (more rain) and La Niña (less rain), or ENSO (El Niño-Southern Oscillation), influence the weather and the floods in the Pantanal. Thus, the forecast of these phenomena from the satellite NOAA can help to predict their consequences. Other satellites provide images to assess the vegetation, floods, etc.

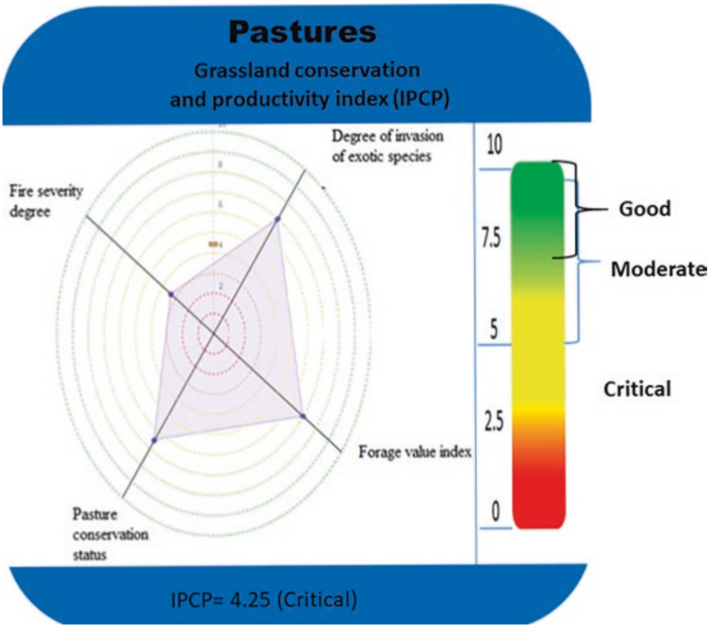


Fig. 10.6 Example of index of pasture conservation and productivity (IPCP) obtained in a ranch of the Pantanal

Aerial photographs and videos obtained with drones can be useful to follow changes in native pastures and surface water or monitor livestock and wildlife.

To assist decision-taking and diagnosis of the production system, the tool Fazenda Pantaneira Sustentável, or Sustainable Pantanal Farm (Santos et al. 2017), allows to evaluate various aspects of the farm by means of practical and straightforward indicators, as in the case of the index of pasture conservation and productivity (IPCP). Four indicators/indexes were selected based on scientific studies and experts meetings: (1) pasture conservation status (PCS), (2) forage value index (FVI), (3) fire severity degree (FSD) and (4) degree of invasion of exotic species (DIES). The PCS indicates if the grassland is conserved, is in degradation, is degraded or is dominated by invading species. FVI indicates the functional forage composition and quality of pastures. FSD indicates the fire intensity in different vegetation communities and DIES the extent and severity of invasion in the natural vegetation of the pastures located in permanent preservation areas (e.g. wetland areas). To perform the inferences and subsequent analysis, the Webfuzzy software and the IPCP, composed of PCS, FVI, FSD and DIES, required 255 decision rules. A fuzzy set was defined for each indicator, expressed in linguistic terms such as "bad", "marginal", "moderate" and "optimal". The results of each index are presented as radar graphs, showing the individual value (0–10) of each indicator or linguistic terms ("good", "moderate" and "critical"). Figure 10.6 shows an example of a ranch with IPCP critic (value of 4.25).

Animal production in unstable systems such as the Pantanal is a great challenge because management strategies cannot be pre-set and have to be holistic and particularized for each farm. That is, a diagnosis should concern the landscapes, the water resources and the native pastures (natural capital) and define management strategies, which in turn have to be adaptative to the intensity, level and duration of floods, variable every year.

Acknowledgments This research was financially supported by Embrapa, FUNDECT (091/2015 SIAFEM 024370), CNPq (474323/2013-7) and CPP/MCT and support of Humberto Perotto-Baldivieso of the Department of Environmental Science and Technology, Cranfield University, UK and Geraldo Alves Damasceno Junior for the assistance in the elaboration of the figures.

References

Allem AC, Valls JFM (1987) Recursos forrageiros nativos do Pantanal Matogrossense. Embrapa-Cenargen, Brasília (Documentos, 8)

Assine M, Merino E, Pupim F, Warren L, Guerreiro R, McGlue M (2015) Geology and geomorphology of the Pantanal Basin. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal wetland in South America. Springer, Berlin/Heidelberg

Bao F, Pott A, Ferreira FA, Arruda R (2014) Soil seed bank of floodable native and cultivated grassland in the Pantanal wetland: effects of flood gradient, season and species invasion. Braz J Bot 37:239–250

Bestelmeyer BT, Brown JR (2010) An introduction to the special issue on ecological sites. Rangelands 32:3–4

Cardoso EL, Santos SA, Urbanetz C, Carvalho Filho A, Naime UJ, Silva MLN, Curi N (2016) Relação entre solos e unidades da paisagem no ecossistema Pantanal. Pesq Agrop Brasileira 51(9):1231–1240

Cardoso EL, Santos SA, Fernandes AHM, Fernandes FA, Oliveira MD, Takahashi F. (2017) Valoração dos estoques de carbono e nitrogênio no solo sob pastagens nativas de áreas úmidas no Pantanal. In: Simpósio Internacional de Microbacias Hidrográficas, 5. Botucatu. Anais.

Couto EG, Oliveira VA (2011) The soil diversity of the Pantanal. In: Junk WJ, Nunes da Cunha C, da Silva CJ, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft Publishers, Sofia, pp 71–102

Drobnik J, Römermann C, Bernhardt-Römermann M, Poschlod P (2011) Adaptation of plant functional group composition to management changes in calcareous grassland. Agric Ecosyst Environ 45:29–37

Fuhlendorf SD, ENGLE DM (2004) Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. J Appl Ecol 41:604–614

Guretzky JA, Moore KJ, Brummer EC, Burras CL (2005) Species diversity and functional composition of pastures that vary in landscape position and grazing management. Crop Sci 45:282–289

Mauro RA, Pott A, Silva MP (1998) La sabana tropical inundable: el Pantanal arenoso. Una propuesta de modelos de estados y transiciones. Ecotropicos 10(2):99–112

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conserv Biol 4:355–364

Nunes da Cunha C, Junk WJ (2011) A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to national and international wetland classification systems. In Junk WJ, da Silva CJ, Nunes da Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia [et al.], pp 127–141

Pott A (1994) Ecossistema Pantanal. In: Puignau JP (ed) Utilización y manejo de pastizales. IICA-PROCISUR, Montevideo, pp 31–44

Pott A, Pott VJ (1999) Flora do Pantanal, listagem atual de Fanerógamas. In: Anais... II Simpósio sobre Recursos Naturais e Socio-econômicos do Pantanal, Corumbá, 1996. Embrapa, Corumbá, pp 297–325

Pott A, Oliveira AKM, Damasceno-Junior GA, Silva JSV (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71(1):265–273

Pott A, Santos AS, Valls JFM (2013) Pantanal. In: Reis RA, Bernardes TF, Siqueira GR (eds) Forragicultura: ciência, tecnologia e gestão dos recursos forrageiros. Maria de Lourdes Brandel, Jaboticabal. Cap.12, pp 173–186

Rodela LG, Queiroz Neto JPd, Santos AS (2007) Classificação das pastagens nativas do Pantanal da Nhecolândia, Mato Grosso do Sul, por meio de imagens de satélite. In: SIMPÓSIO BRASILEIRO DE SENSORIAMENTO REMOTO, 13, 2007, Florianópolis. Anais... São José dos Campos: INPE, 2007. pp 4187–4194

Santos SA, Comastri Filho JA (2012) Práticas de limpeza de campo para o Pantanal. Embrapa Pantanal, Corumbá, 8 p. (Embrapa Pantanal. Comunicado Técnico 92)

Santos SA, Costa C, Souza GS (2002) Qualidade da dieta selecionada por bovinos no Pantanal da sub-região da Nhecolândia. Rev Bras Zootec 31(4):1663–1673

Santos SA, Costa C, Pott A, Crispim SMA, Soriano BM, Alvarez JM (2003) Grau de preferência e índice de valor forrageiro das pastagens nativas consumidas por bovinos no Pantanal. Corumbá: Embrapa Pantanal 53 p. (Embrapa Pantanal. Boletim de Pesquisa e Desenvolvimento 49). Disponível em: https://www.infoteca.cnptia.embrapa.br/bitstream/doc/811099/1/BP49.pdf

Santos SA, Landon A, Comastri Filho JA, Cardoso EL, Soriano BMA, Cheikh N (2004) Potencial da grama-do-Cerrado (Mesosetum chaseae) na Recuperação de Campos Degradados por Malva (Waltheria albicans) no Pantanal Arenoso. In: SIMPÓSIO SOBRE RECURSOS NATURAIS E SÓCIOECONÔMICOS DO PANTANAL, 5, 2004, Corumbá. Anais... Corumbá: Embrapa Pantanal, pp 1–6

Santos SA, Cunha CN, Tomás WM, Abreu UGP, Couto JA (2006) Plantas invasoras no Pantanal: como entender o problema e soluções de manejo por meio de diagnóstico participativo. Embrapa Pantanal, Corumbá 45 p. (Embrapa Pantanal. Boletim de Pesquisa e Desenvolvimento 66)

Santos SA, Desbiez A, Abreu UGP, Crispim SMA (2008) Guia para estimativa da taxa de lotação e pressão de pastejo em pastagens nativas do Pantanal. Embrapa Pantanal, Corumbá, 26p

Santos SA, Abreu UGP, Tomich TR, Comastri-Filho JA (2011) Traditional beef cattle ranching and sustainable production in the Pantanal. In: Junk WJ, Silva CJ, Nunes da Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft Publishers, Sofia, pp 755–774

Santos SA, Lima HP, Perotto Baldiviezo H, Oliveira LO, Tomás WM (2013a) GIS-fuzzy logic approach for building indices: regional feasibility and natural potential of ranching in tropical wetland. J Agric Inf 5(2):26–33

Santos SA, Desbiez ALJ Baldiviezzo-Perotto HL, Pellegrin LA (2013b) Uso de tecnologia de precisão na estimativa da capacidade de suporte em pastagens sob uso múltiplo no Pantanal. Circular Técnica, 107. 6p

Santos SA, Perotto-Baldiviezo H, Young D (2014) Resilience and degradation in a tropical wetland overgrazed by cattle. Trop Grassl – Forrajes Trop 2:138–139

Santos SA, Valls JFM, Pott A, Berselli C (2016) Adaptive phenotypic plasticity of the native forage grass *Paspalum fasciculatum*: a trait relevant to climatic changes in wetlands. In: Simpósio Internacional sobre efeito de gases de efeito estufa na Agropecuária, 2, Campo Grande. Resumos, pp 476–477. Available in: https://ainfo.cnptia.embrapa.br/digital/bitstream/item/153770/1/DOC216.pdf

Santos SA, Lima HP, Massuhá SMFS, Abreu UGP, Tomás WM, Salis SM, Cardoso EL, Oliveira MD, Soares MTS, Santos AJR, Oliveira LOF, Calheiros DF, Crispim SMA, Soriano BM, Nunes AP, Pellegrin LA (2017) A fuzzy logic-based tool to assess beef cattle ranching sustainability in complex environmental systems. J Environ Manag 1(198):95–106.

Santos SA, Pott A, Cardoso EL, Salis SM, Valls JFM, Garcia JB (2019) Guia para identificação de pastagens nativas do Pantanal. Embrapa Pantanal, Corumbá. 222p

Scremin-Dias E, Lorenz-Lemke AP, Oliveira AKM (2011) The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress. Braz J Biol 71(1):275–282

Silva MP, Mauro R, Mourao G, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Rev Bras Bot 23(2):143–152

Souza EB, Ferreira FA, Pott A (2016) Effects of flooding and its temporal variation on seedling recruitment from the soil seed bank of a Neotropical floodplain. Acta Bot Bras 30:1–9

Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. Trends Ecol Evol 24:271–279

Westoby M (1989) Opportunistic management for rangelands not at equilibrium. J Range Manag 42:266–274

Chapter 11
Woody Encroachment and Its Control in Periodically Flooded Grasslands of the Pantanal, a Large Brazilian Wetland

Cátia Nunes da Cunha, Fernando Henrique Barbosa da Silva, Cândida Pereira da Costa, and Wolfgang Johannes Junk

11.1 Introduction

Human colonization by groups of indigenous Tupi-Guarani in the Brazilian Pantanal dates back some 5000 years BP. The arrival of the Europeans occurred as from about 300 years BP. From this period to the present in the Pantanal, the area of non-forest ecosystems as grasslands and savannas decreased when compared to the area of forests (Overbeck et al. 2015).

In the Pantanal, the most frequent non-forest ecosystems are the grassland communities. Colonists and their descendants removed woody plants from grasslands to increase pasture areas for cattle raised in low density, thus influencing the permanence of the contemporary diversity of grasslands in the Pantanal. This resulted in a cultural landscape actively maintained by humans, with a high value for aesthetic and cultural services as ecotourism, scenery, and ranching (Junk and Nunes da Cunha 2012).

C. Nunes da Cunha (✉)
Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas INCT/INAU-UFMT,
Cuiabá, MT, Brazil

Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Instituto de Biociências, Universidade Federal de Mato Grosso, Mato Grosso, Brazil

F. H. Barbosa da Silva
Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Botânica (PPGBOT), Porto Alegre, RS, Brazil

C. P. da Costa
Faculdade de Engenharia Agrícola, Universidade Estadual de Campinas,
Campinas, SP, Brazil

W. J. Junk
Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas INCT/INAU-UFMT,
Cuiabá, MT, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_11

Currently, the human occupation in the Pantanal is more diversified and includes intense grazing regimes on artificial pastures with exotic grasses and the removal of woody plants with machinery. In addition, it is believed that human-induced changes such as reduced water tables, nutrient influxes, and disturbance suppression create favorable conditions for colonization and growth of woody plants (Warren II et al. 2007).

The climate of the Pantanal and the geography of its landscapes originated around 2.5 million years ago. The region's complex paleoclimatic history gave rise to the formation of several plains and megafans with inactive and active compartments leading to a variety of sedimentological patterns (Assine 2010, 2015). The predictable and monomodal flood pulse increased the dynamics of the system by generating a variety of habitats, ranging from permanent terrestrial to permanent aquatic. In the aquatic-terrestrial transition zone (Junk et al. 1989), alternating droughts and floods are a permanent feature affecting plant and animal communities (Nunes da Cunha and Junk 2011). Over time, pluriannual wet and dry periods associated with extreme flood and drought events became common, with the latter associated with higher fire frequencies and intensities. The annual and multiannual variations resulted in disturbances at different scales and thus in a diversification of biota in the Pantanal (Nunes da Cunha and Junk 2015).

In the Pantanal, a large diversity of landscape units associated with unique hydrological and botanical characteristics, denominated by Nunes da Cunha and Junk (2011, 2015) as macrohabitats, has allowed the occurrence of a large variety of plants and animals that differ in their tolerance of periodic flooding and drought. In the Brazilian wetland classification (Junk et al. 2014, 2015), the macrohabitat unit corresponds to the most detailed landscape level and is the scale best suited to understanding and managing not only the Pantanal but also other Neotropical wetlands (Junk et al. 2018). The different macrohabitats form a mosaic, whose individual units are interconnected and interact in complex ways when examined on fine scales. Aquatic and terrestrial animals migrate among the different macrohabitats, in search of food, protection against predators, refuge from flood or drought, and safe places for reproduction. Thus, any management and/or protection plan developed for the Pantanal must consider its diversity of macrohabitats because their protection also ensures the structural and functional integrity of this wetland ecosystem and its biodiversity.

Plant communities in wetlands are often at early developmental stages, due to the impacts of drought, fire, and flood as well as management practices responsible for the destruction or removal of older plants. Ranchers in the Pantanal remove woody plants from floodplains that are occupied by grassland communities covered by C_4 grasses and herbaceous plants during the dry season and by macrophytes during the wet season. In some cases, if not removed at an early stage of development, they can form shrubland or forest stands that are difficult to restore to the typical composition of grasslands (Junk and Nunes da Cunha 2012). This phenomenon, referred to as woody encroachment, represents a fundamental change in habitats and the trophic structure, usually implicating in negative and immediate responses from grassland-obligate plants and animals (Archer et al. 2011). The process continues until disturbances such as droughts, fires, floods, grazing, or mechanical removal eliminate the woody species (Junk and Nunes da Cunha 2012). The restoration of grassland macrohabitats after woody removal is beneficial for herbaceous forage production for the cattle (Clark and Wilson 2001; Angassa 2005; Pozer and Nogueira 2005). It also improves the conservation and sustainable use of plant diversity and its components (GSPC 2002) due to the maintenance of a key habitat for native herbs, grasses, and macrophytes (Schessl 1999) and grassland-obligate fauna (Desbiez et al. 2011; Tomas et al. 2011; Dorado-Rodrigues et al. 2015).

The Pantanal and other large Neotropical floodplains are commonly used on a large scale as natural pastures (Junk et al. 2015). At local scale, cattle exclusion leads to the accumulation of dead herbaceous biomass (Pozer and Nogueira 2005) and the encroachment of woody species (Nunes da Cunha and Junk 2004). On the other hand, overgrazing by cattle can selectively reduce the abundance of herbaceous plants, making the area more susceptible to the abiotic and biotic disturbances, including the entrance of encroaching species. In addition to grazing exclusion and overgrazing, woody encroachment in the Pantanal is driven by multiannual dry and wet cycles related to excessive floods, droughts, and fire events (Nunes da Cunha and Junk 2004) that favor the expansion of different groups of woody species over grasslands. Savanna species are favored by dry periods with intense wildfires, while forest species are favored by wet periods with pronounced floods. The responses of ecosystem variables to woody encroachment are context dependent and will depend on the factors and species involved (Archer et al. 2011; Eldridge et al. 2011; Maestre et al. 2016). In the Pantanal, ranchers perceive the woody encroachment as negative due to the diminished value of forage production (Santos et al. 2006). The authors perceive it as negative as well because long-term woody encroachment eliminates a large diversity of herbaceous species, and in some cases, the removal of woody plants does not result in the restoration of the herbaceous communities.

In the Pantanal, traditional ranchers have asserted their right to pasture clearing, including the removal of woody plants from grassland macrohabitats, in order to maintain the economic viability of traditional low-density cattle ranching (Junk and Nunes da Cunha 2012). By limiting the support capacity of grasslands, woody encroachment hinders cattle management and reduces productivity (Van Auken 2009). The ranchers also argue that traditional ranching maintains grassland diversity, because the removal of encroaching woody species implies that the habitat for native herbaceous species increases. In the following, we present current knowledge about the grassland macrohabitats in the Pantanal that are vulnerable to woody encroachment. We discuss the impact of the encroaching woody species on the diversity of herbaceous plants and animals and evaluate the possibilities for restoration as well as the sustainable management of the landscape.

11.2 Pantanal Grassland Macrohabitats Under Woody Encroachment

Three distinct major types of flooded grassland macrohabitats (i.e., hyperseasonal savannas) are recognized in the northern region (Schessl 1999). These grasslands on the floodplains are subjected to a period of weeks to up to 6 months of submergence (Nunes da Cunha and Junk 2015). They are rich in species, mostly composed of C_4 graminoids during the dry season and C_3 macrophytes during the wet season (Table 11.1). The water regime and soil properties in the macrohabitats correspond with differences in the species composition of the various types of grasslands (Zeilhofer and Schessl 2000). Various combinations of types of grasslands and kind of encroaching species each may differ in specific features (Archer et al. 2011; Eldridge et al. 2011), but as grasslands that are vulnerable to woody encroachment and experience an equivalent hydrological regime (i.e., seasonally flooded), they share important similarities for management and conservation strategies.

*11.2.1 Shortgrass-Floodplain Community (*Campo de Mimosinho*, Sensu Schessl 1999 and Nunes da Cunha and Junk 2015)*

As suggested by its name, this macrohabitat is formed by a community of short and prostrated grasses and herbaceous plants (Schessl 1999). In the *campo de mimosinho*, key forage species are abundant (Desbiez et al. 2011), mostly with prostrate growth form that is associated with high grazing pressure (Pérez-Harguindeguy et al. 2013; Pott et al. 1989). The community occurs in areas subject to a flooding regime that lasts for up to 6 months (Nunes da Cunha and Junk 2015), in which water levels may rise between 0.5 and 1 m, but with clearly distinct drought and flood periods (Zeilhofer and Schessl 2000). During the dry season, the C_4 grasses *Reimarochloa brasiliensis* and *Setaria parviflora* are dominant, whereas C_3 graminoids such as *Eleocharis acutangula*, *Hymenachne amplexicaulis*, and *Steinchisma laxum* become abundant during the wet season (Table 11.1) (see also the chapter on “Natural Grasslands” Chap. 10). The significance of this macrohabitat as a natural pasture is related to its supply of high-quality forage resources preferred by herbivorous animals, such as *Hydrochoerus hydrochaeris* Linnaeus, 1766 (capybara), *Blastocerus dichotomus* Illiger, 1815 (marsh deer), *Ozotoceros bezoarticus* Linnaeus, 1758 (pampas deer), and *Tapirus terrestris* Linnaeus, 1758 (tapir), as well as by cattle (Desbiez et al. 2011).

During the dry season, the herbaceous cover is in the range of 50–97%, of which up to 91% may be composed of species belonging to the family Poaceae. Plant biomass increases with the onset of the rains, from October to December, and reaches a maximum in January, when macrohabitat flooding favors the development of macrophytes, among them the Pontederiaceae species *Eichhornia crassipes* and

Table 11.1 Species and photosynthetic pathways (C_3 and C_4) occurring in the grassland macrohabitats covered by hyperseasonal savannas during the dry and wet seasons of the northern Pantanal wetland. Species names validated by Flora of Brazil 2020

Family	Species	Season	Photosynthetic pathway
Alismataceae	*Echinodorus lanceolatus* Rataj	Dry, wet	C_3
Boraginaceae	*Euploca filiformis* (Lehm.) J.I.M.Melo & Semir	Dry	C_3
Commelinaceae	*Murdannia semifoliata* (C.B.Clarke) G. Brückn.	Dry, wet	C_3
Convolvulaceae	*Ipomoea carnea* Jacq.	Dry, wet	C_3
Cyperaceae	*Cyperus haspan* L.	Dry, wet	C_3
	Cyperus surinamensis Rottb.	Dry, wet	C_3
	Eleocharis minima Kunth	Dry, wet	C_4
	Rhynchospora barbata (Vahl) Kunth	Dry, wet	C_4
	Scleria gaertneri Raddi	Dry, wet	C_3
Euphorbiaceae	*Caperonia castaneifolia* (L.) A.St.-Hil.	Dry, wet	C_3
	Croton glandulosus L.	Dry	C_3
	Euphorbia hyssopifolia L.	Dry	CAM
Fabaceae	*Aeschynomene fluminensis* Vell.	Dry, wet	C_3
	Desmodium incanum (Sw.) DC.	Dry	C_3
	Discolobium psoraleaefolium Benth.	Dry, wet	C_3
Hydroleaceae	*Hydrolea spinosa* L.	Dry, wet	C_3
Lamiaceae	*Hyptis lorentziana* O.Hoffm.	Dry, wet	C_3
Lentibulariaceae	*Utricularia foliosa* L.	Wet	C_3
	Utricularia meyeri Pilg.	Wet	C_3
Malvaceae	*Melochia arenosa* Benth.	Dry, wet	C_3
Marantaceae	*Thalia geniculata* L.	Wet	C_3
Menyanthaceae	*Nymphoides grayana* (Griseb.) Kuntze	Dry, wet	C_3
Nymphaeaceae	*Nymphaea gardneriana* planch.	Wet	C_3
Onagraceae	*Ludwigia inclinata* (L.f.) M.Gómez	Dry, wet	C_3

(continued)

Table 11.1 (continued)

Family	Species	Season	Photosynthetic pathway
Phyllanthaceae	*Phyllanthus stipulatus* (Raf.) G.L.Webster	Dry, wet	C_3
Poaceae	*Andropogon bicornis* L.	Dry, wet	C_4
	Andropogon hypogynus hack.	Dry, wet	C_4
	Axonopus leptostachyus (Flüggé) Hitchc.	Dry, wet	C_4
	Axonopus purpusii (Mez) chase	Dry	C_4
	Hymenachne amplexicaulis (Rudge) Nees	Wet	C_3
	Leersia hexandra Sw.	Wet	C_3
	Paspalum lineare Trin.	Dry	C_4
	Paspalum plicatulum Michx.	Dry	C_4
	Paspalum wrightii Hitchc. & chase	Wet	C_4
	Reimarochloa brasiliensis (Spreng.) Hitchc.	Dry	C_4
	Setaria parviflora (Poir.) Kerguélen	Dry	C_4
	Steinchisma laxum (Sw.) Zuloaga	Dry, wet	C_3
Polygalaceae	*Polygala molluginifolia* A.St.-Hil. & Moq.	Dry	C_3
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	Wet	C_3
	Pontederia parviflora Alexander	Wet	C_3
Rubiaceae	*Diodia kuntzei* K.Schum.	Dry, wet	C_3
	Richardia grandiflora (Cham. & Schltdl.) Steud	Dry	C_3
Sapindaceae	*Serjania caracasana* (Jacq.) Willd.	Dry, wet	C_3
Turneraceae	*Piriqueta corumbensis* Moura	Dry	C_3
Vitaceae	*Cissus spinosa* Cambess.	Dry, wet	C_3

Pontederia parviflora (Table 11.1) and a variety of species from the Alismataceae, Lentibulariaceae, and Nymphaeaceae families. The increased biomass of hydrophytic grasses, such as *H. amplexicaulis*, *Leersia hexandra*, and *S. laxum*, makes them significant in the consumption by wild herbivores and cattle (Schessl 1999; Desbiez et al. 2011). At the end of the rainy season, the water level begins to decrease and the macrophytes decompose (Schessl 1999; Rebellato et al. 2012). The decomposition of macrophytes provides a nutrient enrichment resulting in a high productivity of grasslands during the dry season (Pozer and Nogueira 2005).

*11.2.2 Small Tussock Grassland (*Campos de Murundus, *Sensu Schessl 1999, Nunes da Cunha and Junk 2015)*

This macrohabitat typically is a small tussock grassland community interspersed with earth mounds formed by termite nests, popularly known as *murundus*. In the *murundus* area, woody vegetation establishes away from the flood reach and has a herbaceous layer with *Bromelia balansae* (Schessl 1999). The species composition of the small tussock grassland established on the floodplain, outside the *murundus*, is dominated by perennial and tussock grasses (i.e., bunchgrasses) with sclerophyllous leaves. It comprises a savanna that is shallowly flooded during 3–12 weeks of the year, with water levels of up to 0.3 m. During the dry season, dominant C_4 graminoids such as *Axonopus purpusii*, *Paspalum lineare*, and *Rhynchospora barbata* are abundant (Table 11.1). During the wet season, annual species such as *Eleocharis minima*, *Syngonanthus cuyabensis*, *S. gracilis*, *Utricularia hydrocarpa*, and *U. simulans* appear for short periods (Schessl 1999; Rebellato et al. 2012). The *murundus* are 0.3–1 m higher than the ground level of the surrounding herbaceous community and host a variety of shrubs and trees typical of the Cerrado biome, including *Andira cujabensis*, *Annona aurantiaca*, *Annona dioica*, *Astronium fraxinifolium*, and *Hyptis crenata*. In addition to these woody species, *Byrsonima cydoniifolia* and *Curatella americana* are found at high abundance and frequency in the *murundus* (Schessl 1999). They are able to colonize adjacent grassland macrohabitats in the Pantanal (Santos et al. 2006; Junk and Nunes da Cunha 2012). The small tussock grasslands are managed by the presence of livestock and pasture clearing, the latter consisting of the removal of undesirable woody species from the herbaceous community while avoiding their removal on the earth mounds.

*11.2.3 Tall Tussock Grasslands (*Campos de Rabo de Burro, *Sensu Schessl 1999, Nunes da Cunha and Junk 2015)*

This macrohabitat occurs in areas subject to flooding depths of 0.5–1 m that persist for about 3 months. It is dominated by tall C_4 bunchgrasses such as *Andropogon bicornis*, *Andropogon hypogynus*, and *Axonopus leptostachyus* (Table 11.1). The popular names given to this macrohabitat, *campo de rabo de burro* (donkey tail grassland) and *campo de capim vermelho* (red grass grassland), refer, respectively, to the plumose synflorescence associated with *Andropogon* species such as *A. bicornis* and to the reddish color of *A. hypogynus*. These grasslands are also referred to as *macega*. Its tall tussock grasses become fibrous when mature and are largely shunned by cattle, such that ranchers use fire to promote regrowth. During the aquatic season, *L. hexandra* may occur between the tussocks.

11.3 Encroaching Woody Species in the Pantanal

Among the 756 woody plants estimated to comprise the Pantanal flora (Pott and Pott 1999), the following (Table 11.2) are considered by traditional ranchers to be potentially invasive of grassland macrohabitats: *Byrsonima cydoniifolia* (*canjiqueira*), *Combretum lanceolatum* and *Combretum laxum* (*pombeiro*), *Curatella americana* (*lixeira*), and *Vochysia divergens* (*cambará*).

The effects of the woody encroachment of *B. cydoniifolia*, *C. americana*, *C. laxum*, and *V. divergens* on herbaceous communities of the Pantanal wetland have been investigated by Nascimento and Nunes da Cunha (1989), Nunes da Cunha and Junk (2004), Arieira and Nunes da Cunha (2006), Costa (2013), and Barbosa da Silva et al. (2016). In the first stage, the grasslands under cattle grazing develop a great abundance of small woody stands (Nascimento and Nunes da Cunha 1989). Later, the spread and retraction of the woody, encroaching species appears related to wet and dry multiannual periods in the Pantanal (Nunes da Cunha and Junk 2004). Also, encroaching species of fluvial forests may form monodominant stands under more pronounced flooding regimes (Arieira and Nunes da Cunha 2006), while encroaching species typical of savannas occupy grasslands under shallow flooding (Costa 2013). Moreover, it was noticed that intermediate levels of encroachment may be favorable to herbaceous diversity, although the cover and richness of herbaceous species ultimately decrease (Barbosa da Silva et al. 2016). These results are summarized in Table 11.2.

11.3.1 **Byrsonima cydoniifolia** *A. Juss. (Malpighiaceae)*

This shrub species occurs in the flooded grasslands of Amazonia, Bolivia, and Central Brazil (Pott and Pott 1994). In the Pantanal, it colonizes roadsides, deforested areas, and the grasslands forming the *canjiqueiral* (Pott and Pott 1994; Silva et al. 2000; Marimon and Lima 2001; Marchesan et al. 2006; Silvério and Fernandes-Bulhão 2009; see also Chap. 8 on “Monodominant Stands” Chap. 8). It can reach heights of 1–5 m, occurring frequently in macrohabitats under shallow floods or that are dry. The species is tolerant to fire except when young. Based on field observations and phenological classifications of *Byrsonima* species

Table 11.2 Potentially invasive woody species of grassland macrohabitats in the Pantanal according to traditional ranchers

Family	Species	Common name	Growth form
Malpighiaceae	*Byrsonima cydoniifolia* A. Juss.	*Canjiqueira*	Shrub
Dilleniaceae	*Curatella americana* L.	*Lixeira*	Tree
Combretaceae	*Combretum lanceolatum* Pohl ex Eichler *C. laxum* Jacq.	*Pombeiro*	Shrub
Vochysiaceae	*Vochysia divergens* Pohl	*Cambará*	Tree

(Pirani et al. 2009), *B. cydoniifolia* is brevideciduous, carrying a leaf drop during the dry season (July–September), while the budding of young leaves is in September–October.

According to Silvério and Fernandes-Bulhão (2009), *B. cydoniifolia* produces flowers during the dry season and early rains (June–October), while peak flowering occurs in September, followed by a fruiting period that begins during the rainy season (October–March) and peaks in December. The wood density of this species is estimated to be 0.51 g cm^{-3} (Marchesan et al. 2006).

11.3.2 **Combretum lanceolatum** ***Pohl ex Eichler and*** **C. laxum** ***Jacq. (Combretaceae)***

Both species are climbing shrubs. *C. lanceolatum* flowers between April and July, during the end of the flooding season, and *C. laxum* between June and October, during the beginning of the dry season when temperatures are lower. The fruiting of *C. lanceolatum* occurs with the increase in temperature that characterizes the dry season, and its fruits disperse in October, at the beginning of the rainy season (Fig. 11.1a). The fruiting of *C. laxum* takes place from December to February, during the higher rainfall of the rainy season (Fig. 11.1b). Dispersal of the winged fruits of both *C. lanceolatum* and *C. laxum* is by wind (anemochory). A study of the buoyancy of the two species showed that the latter could float for >70 days. The fruiting phenology and buoyancy of *C. laxum* strongly indicate the importance of water as an agent for seed dispersal (hydrochory). Germination of *C. lanceolatum* and *C. laxum* is cryptocotyledonar hypogean and unipolar, with a lateral axis of the cotyledons. The optimal temperature range for germination, defined as the highest germination percentage during the shortest time interval, is 25–30 °C. Thus, the reproductive phenology and mode of fruit dispersal of *C. lanceolatum* and *C. laxum* are compatible with the annual flood cycle in the Pantanal. The encroachment behavior of these two species is similar even though occurring under different conditions.

11.3.3 **Curatella americana** ***L. (Dilleniaceae)***

This tree is found from Central America to Bolivia and in almost all Brazilian savannas (Cerrado biome), until the southern boundary to São Paulo State (Bruniera and Groppo 2010). In the Pantanal, it occurs frequently in *capões*, *cordilheiras*, *campo cerrados*, and *murundus* and has a wide distribution in the flooding gradient (Oliveira-Filho 1984, Nunes da Cunha and Junk 1999, 2001; Costa et al. 2010). Classified as brevideciduous (Pirani et al. 2009), *C. americana* trees drop their leaves during the dry season (June–September) peaking in August,

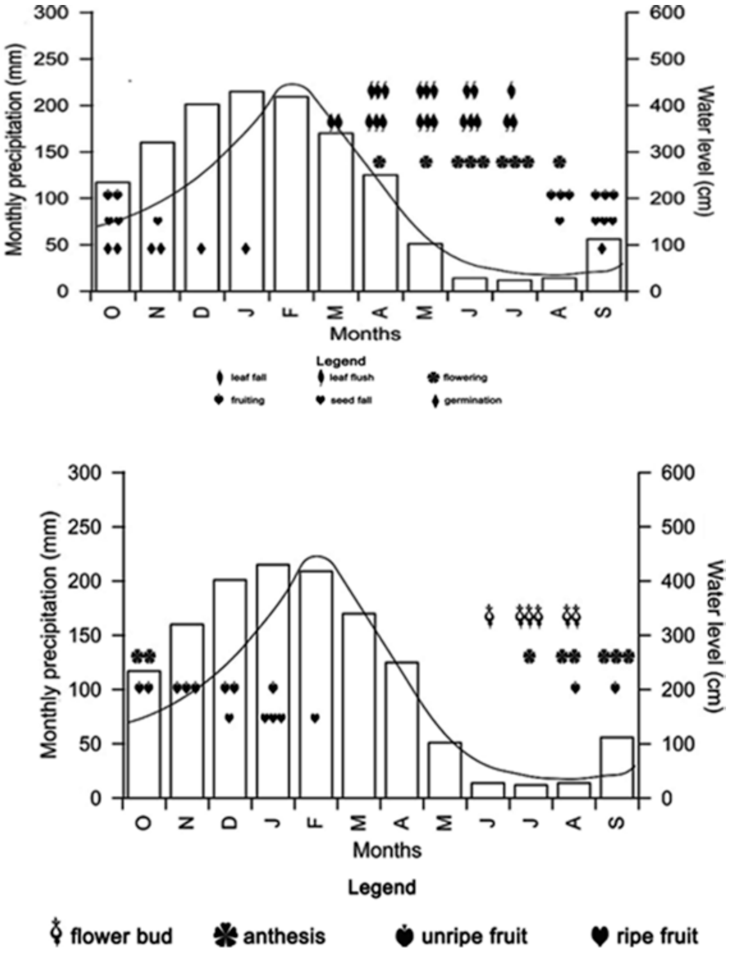


Fig. 11.1 Phenological aspects of **(1.1)** *Combretum lanceolatum* and **(1.2)** *C. laxum* showing phenophases: flower bud, anthesis, unripe fruit, and ripe fruit in relation to the monthly pattern of precipitation and the river's water level, as proxies to the terrestrial and aquatic phases of the Pantanal

and the budding of new leaves begins during the drought period and lasts until the start of the rainy season (August–November). Flowering occurs during the dry season (June–August) and peaks in August, while fruits develop during the dry and into the rainy season (July–January), with an indistinct peak (Pirani et al. 2009). The species is fire resistant and is regarded as a species fire climax (Barbosa and Fearnside 2004; Barbosa et al. 2005). Its estimated wood density is 0.41 g cm^{-3} (Barbosa and Fearnside 2004).

11.3.4 Vochysia divergens *Pohl (Vochysiaceae)*

This pioneer tree forms monodominant forests called *cambarazais* (Arieira and Nunes da Cunha 2006; see also Chap. 8 on "Monodominant Stands" Chap. 8). The specie is a component of riparian forest communities found on the banks of the Cuiabá and São Lourenço Rivers, from where *V. divergens* has gradually spread throughout the Pantanal, forming stands in areas previously occupied by grassland macrohabitats (Nascimento and Nunes da Cunha 1989). Its height varies from 7 to 20 m, and it forms a leafy canopy. Phenological studies in the northern Pantanal showed that the main leaf-shedding period for *V. divergens* is from April to June, at the end of the rainy season. As the flush of new leaves occurs at the same time, the tree always bears leaves. Flowering begins as the water level subsides and continues until July. During that time, the trees dominate the landscape of the Pantanal with their impressive yellow flowers.

11.4 The Colonization of Grassland Macrohabitats by Encroaching Woody Plants

11.4.1 General Considerations

Woody encroachment in tropical grasslands can be due to different factors and have different consequences, though in general there are a decrease in grass cover and, often, an increase in soil carbon and nitrogen stocks. Dominant grasses in the Pantanal grasslands, as in other tropical savannas, are C_4 grasses, which are shade intolerant. Gradually, as the abundance of woody C_3 plants increases, the cover, biomass, and richness of herbaceous species decrease (Scholes and Archer 1997; Angassa 2005; Eldridge et al. 2011; Ratajczak et al. 2012; Belay et al. 2013).

The effects of woody encroachment by *B. cydoniifolia* and *C. americana* in *campos de murundus* were described by Costa (2013), by *C. laxum* in *campo de mimosinho* in that of Barbosa da Silva et al. (2016), and by *V. divergens* in *campo de rabo de burro* in Avelar (2018) and Santos et al. (2006). These authors compared ecological variables during three stages of woody encroachment. The first stage comprises the native grassland communities without a cover of woody species in the herbaceous stratum. The second stage comprises the coexistence of woody and grassland species, normally with the woody plants at low abundance. And, the advanced third stage is a dominated by woody species with a low diversity of herbaceous plants. During multiannual dry periods, the encroachment by the trees *B. cydoniifolia* and *C. americana* is favored, whereas during wet periods, these species decline in the murundus and in the small tussock grasslands (Costa 2013). Nunes da Cunha and Junk (2004) found that encroaching species from savanna vegetation were favored by a series of dry years. A period of wet years with high flooding has started in 1974 favoring the encroachment of flood-tolerant species such as *V. divergens*. The *campo de mimosinho*, usually favored by periods of wet years, occurs in areas under long-lasting flooding and heavy grazing and can shift to monospecific shrublands dominated by *C. laxum* and with a poor cover of herbaceous species (see below).

11.4.2 The Colonization of Campo de Mimosinho *by* Combretum laxum

Barbosa da Silva et al. (2016) also described three stages in the progressive colonization of *C. laxum* of the *campo de mimosinho*: (1) a grassland stage, in which the shortgrass-herbaceous layer is dominant and encroaching plants are absent; (2) an intermediate stage, named shrub islands, due to sparse individuals or small groups of *C. laxum* being interspaced in the grassland community; and (3) a shrubland stage, when the woody plant has become dominant and the grassland community mostly eliminated.

The species composition and structure of the original community were described in Sect. 2.1. During the end of dry season, the cover in point samples in the *campo de mimosinho* community indicated the abundance of *R. brasiliensis* (66%) and *A. leptostachyus* (8%). This species composition is desired by ranchers due to the high nutritional value of these grasses for livestock production (Santos et al. 2002; Desbiez et al. 2011) (see also the chapter on “Natural Grasslands” Chap. 10). The largest variability in vegetation structure and plant species composition occurs when the *C. laxum* cover is between 20% and 60%. During this intermediate stage, *C. laxum* individuals are mostly arranged on islands of up to 3 m high and formed by their extensive and circular canopies that prostrate near to the soil surface. The combination of an intermediate shrub cover and a herbaceous community increases the environmental heterogeneity and results in a higher number of herbaceous species at stand scale. Samples from the intermediate stage are more dissimilar among themselves than are samples from the initial and final stages. From the initial to the intermediate stage, an increase occurs in the mean cover of many ruderal species such as *Euphorbia hyssopifolia* (3–31%), *H. spinosa* (4–11%), and *Hyptis lorentziana* (4–21%).

The final and most advanced stage named shrubland is a nearly monospecific, impenetrable thicket of up to 3 m in height, with a closed canopy and a mean cover by *C. laxum* of 89%. The shift from a grassland to a shrubland vegetation resulted in the displacement of the 31 species recorded in the grassland and shrub island stages (Barbosa da Silva et al. 2016). In the final shrubland stage, only three climber species were recorded, namely, *Cissus spinosa*, *Scleria gaertneri*, and *Serjania caracasana*, probably favored by the tangled woody cover as a support, improving their light acquisition (Ibarra-Manriquez and Martínez-Ramos 2002). Despite being a community with a low number of species, the shrubland stage of *C. laxum* encroachment has its own ecological value. The *C. laxum* shrubland may be beneficial for other biodiversity groups such as birds and bees, as well as other plant-associated processes, such as water and carbon cycling and productivity (Maestre et al. 2016).

11.5 Woody Encroachment and Fauna

Few studies have examined the impact of woody encroachment on the fauna of the Pantanal. The response of anurans to the progressive increase of *C. laxum* cover was recorded for the same sites studied by Barbosa da Silva et al. (2016). Anurans responded in a similar way as the herbaceous plants, with an increase in the number of species and in abundance in stands with low to medium cover by *C. laxum*, but a quantitative decrease thereafter (Fig. 11.2; Dorado-Rodrigues et al. 2015). While anurans and herbaceous plants may have been jeopardized by habitat homogenization, bees, birds, and monkeys are attracted by the nectar of the flowers of *Combretum lanceolatum* and *C. laxum* (Pott and Pott 1994). The importance of *C. lanceolatum* as a food resource was determined at first for 28 bird species belonging to eight families (Sazima et al. 2001) and later for 38 species (Silva and Rubio 2007). Thus, although the anuran and herbaceous diversity may display negative responses, other biodiversity components may benefit from the shift from *campo de mimosinho* to *Combretum* shrublands.

Species richness and abundance of small mammals were recorded in samples of grasslands with a *C. lanceolatum* cover of up to 80% and under cattle grazing.

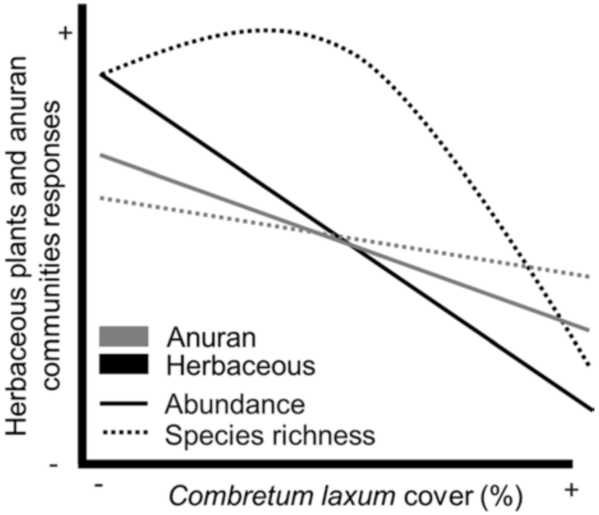


Fig. 11.2 Community-level (i.e., abundance and richness) responses of herbaceous plants and anurans in *campo de mimosinho* under *Combretum laxum* encroachment in the Pantanal (from Dorado-Rodrigues et al. 2015, and Barbosa da Silva et al. 2016)

Seven species, two marsupials and five rodents, were recorded. Three rodent species, namely, *Holochilus sciureus* (Wagner, 1842), *Calomys* cf. *callosus* (Rengger, 1830), and *Necromys lasiurus* (Lund, 1840), made up >90% of the detections (Layme et al. 2012). In a comparison among grasslands and forests, *Necromys lasiurus* was recorded only in sites covered by savanna dry forest. The species *H. sciureus* was recorded only in *cambarazal*, a flooded forest associated with encroachment in the Pantanal, and *Calomys* cf. *callosus* in all habitats (Aragona 2008). Most abundant rodents are generalists in their use of habitats (Tomas et al. 2011; Weksler et al. 2016), so the combination of grassland community, termite mounds, and forests and shrublands derived from woody encroachment may favor the overall number of species. Another important aspect, especially to *Holochilus sciureus*, is the distance from rivers and water bodies (Aragona 2008; Layme et al. 2012). The Pantanal is located at the southern limits of the distribution of *Holochilus sciureus* (Weksler et al. 2016) where the species can be locally abundant (Tomas et al. 2011).

The *V. divergens* forests typically contain a rich bird fauna. Pinho and Marini (2012) compared four forest types and found the highest nesting success in *cambarazais*. The spotted species included the band-tailed antbird *Hypocnemoides maculicauda* (Pelzeln, 1868) and the antbird *Cercomacra melanaria* (Ménétriès, 1835), some of the few species endemic to the Pantanal (Pinho et al. 2016). Aragona and Pinho (2012) found that small mammals and birds, including rare species, benefit from habitats resulting from wood encroachment in the Pantanal. They compared these groups in stands of *V. divergens* of different ages and recorded the highest number of species in the oldest stands.

Grassland communities are important to many fauna components such as anurans, mammals, and cattle (Desbiez et al. 2011; Tomas et al. 2011). Woody stands at the intermediate development stage have a species composition similar to the grasslands and the final stages of woody encroachment. The relatively high number of anurans and small mammals may be favored by the increased complexity of the vegetation structure (Layme et al. 2012; Dorado-Rodrigues et al. 2015). However, the final stages of encroachment are very dissimilar from the grasslands in terms of species composition. Animals that use flooded grasslands as their main habitat, such as the marsh deer and the pampas deer, will most likely experience declines in their populations in the high cover of encroaching woody species. It should be stressed, however, that not only woody encroachment but also disease transmission by cattle has negative impacts on the populations of these emblematic grassland mammals (Tomas et al. 2011).

11.6 Control of Woody Encroachment: Vegetation States, Costs, History, Legal Aspects, and Current Perspectives

The encroachment of woody plants into natural or cultural grasslands has economic consequences for cattle ranchers and usually negative ecological consequences for the grassland flora and fauna, in addition to altering the aesthetic appearance of the landscape (Augustine and Mcnaughton 2004; Junk and Nunes da Cunha 2012). Under natural conditions, the balance between woody species and grasslands was maintained by long-lasting floods, droughts, and wildfires. With the introduction of cattle grazing, traditional ranchers began to remove woody plants from pasture lands, initially by using axes, machetes, hoes, and fire on areas around farmhouses. Further, cattle grazing helped to control the growth of woody plants in the grassland macrohabitats. However, the introduction of mechanical techniques for the large-scale removal of woody plants may disturb the soil in addition to increased runoff and erosion (Archer et al. 2011), and this is a potential problem in the Pantanal where there is river overflow.

Nunes da Cunha and Junk (2017) analyzed the trajectory in shortgrass-floodplain macrohabitats in which pasture was created by clearing heavy encroachment by *Combretum lanceolatum*. Although mechanical machinery was used for brush removal, after 8 years, the initial shrub vegetation returned, instead of the expected recovery of the grassland communities. The grasses, especially forage species such as *Paspalum wrightii* (*capim macega branca*), *Oryza latifolia* (*arroz do brejo*), and *Paspalum plicatulum* (*felpudo*) did not reestablish independent of the machine type used for shrub removal and despite the use of fire. As noted by Archer et al. (2011), the removal of woody plants without managing the factors promoting their abundance may not be enough to curtail or reverse encroachment.

In shortgrass-floodplain macrohabitats under encroachment by *C. laxum*, the use of mechanical techniques during the early stages allowed the restoration of the flora of the reference grassland community (Nunes da Cunha and Junk 2017). However, the removal of woody plants at advanced stages of encroachment is linked to high costs and uncertain success in attempts to recover the earlier, desirable species composition of the grasslands (Clark and Wilson 2001; Archer et al. 2011). In a cost-benefit analysis of *C. laxum* removal from grasslands, using the best data available regarding cattle cost, management operation, and area size, the results showed that the improved livestock production may not compensate for the costs of pasture clearing. Moreover, Archer et al. (2011) found that the increased forage availability achieved by the removal of encroaching woody plants does not warrant an increase in livestock capacity since in some cases the stocking rates are already near capacity. For the management plan of the Pantanal, we suggest that pasture clearing be conducted only during the first stages of woody encroachment and in small areas in grassland macrohabitats, where the restoration of herbaceous communities is feasible. Nearby grassland matrices contribute seeds, while the formation of seed banks provides a source of propagules allowing natural regeneration and therefore low-cost grassland restoration following pasture clearing.

Today, forest and pasture clearing are regulated by different laws, for example, in the states of Mato Grosso and Mato Grosso do Sul, that in some cases are contradictory. In Mato Grosso, the state's Environmental Secretariat (SEMA/MT) is responsible for environmental control and, after a technical analysis has been conducted, for authorizing deforestation. The aim is the maintenance of the Legal Reserve and the Areas of Permanent Protection (APP), according to the requirements of the forest legislation of the State and the National Forest Code. The landowner has to comply with the requirements of the *Cadastro Ambiental Rural* (CAR) before starting the process of applying for forest removal. The law of the State of Mato Grosso, n. 8.830/2008 Art. 11, allows pasture clearing of *Combretum lanceolatum* and *C. laxum* (*pombeiro*), *Byrsonima cydoniifolia* (*canjiqueira*), *Couepia uiti* (*pateiro*), *Leptobalanus parvifolius* (*pimenteira*), *Vochysia divergens* (*cambará*), *Ipomoea carnea* (*algodoeiro*), *Senna aculeata* (*mata pasto amarelo*), *Hydrolea spinosa* (*amoroso*), and *Sphinctanthus microphyllus* (*arrebenta laço*), but prohibits pasture clearing on paleo-levees (*capões* and *cordilheiras*), recent natural levees, and in riparian forests. In Mato Grosso do Sul, resolution SEMAC n° 18 of 05/08/2008 regulates pasture management in the Pantanal, but Art. 2° of SEMAC n° 21 of 2011 freed pasture clearing from the list of activities requiring the permission of the environmental authorities.

The maintenance of the diversity of habitats and species while ensuring the livelihoods of the Pantanal's ranchers, who are also the owners of most of this unique region, can only be achieved through modern management plans that include total protection in some macrohabitats and pasture management in exchange for forest protection in others (Junk and Nunes da Cunha 2012). The preliminary habitat classification provided by Nunes da Cunha and Junk (2011, 2015, 2017) can be used to determine key habitats for permanent protection and others for low- to medium-impact management.

11.7 Discussion

From its initial 56 units described by Nunes da Cunha and Junk (2015), macrohabitat diversity in the Pantanal has increased and is now represented by 74 units, with the inclusion of those specific to Mato Grosso do Sul (see Chap. 7 on "Macrohabitats" Chap. 7). Thus, more macrohabitats can be distinguished in the Pantanal than in other large Brazilian floodplains, such as the *várzeas* (36 units) and *igapós* (25 units) in the Amazon biome. In addition, in many areas of the Pantanal, the macrohabitats are relatively small and densely packed, which leads to a complex structure of the landscape. This allows the coexistence of many plant and animal species and accounts for the Pantanal's popularity as a tourist destination.

The high macrohabitat diversity is the result of a complex hydromorphological structure that formed in response to paleoclimatic changes (Assine 2010, 2015). Recent hydrological processes have led to sedimentation and erosion along the river channels, while the annual flood pulse, multiannual dry and wet periods, and wildfires have rapidly modified the vegetation (see also the chapter on "Fire" Chap. 18). Furthermore, anthropogenic hydrological and sedimentological changes as well as modifications in vegetation cover have strongly impacted macrohabitat diversity and distribution, such that many vegetation units have to be considered as successional stages. This means that native encroaching woody species occupy only those areas suitable for their growth and remain there until natural driving forces, such as prolonged floods, droughts, wildfires, or human activities, cause their elimination.

A trend of an increasing abundance of woody plants in ecosystems historically dominated by grasses and herbaceous plants, such as the grasslands and savannas in terrestrial and wetland ecosystems, has been observed in recent years (Eldridge et al. 2011; Saintilan and Rogers 2015). In those reports, woody encroachment was associated with both global and local drivers. The former includes contemporary climate change and atmospheric processes, and the latter land-use practices (Van Auken 2009; Ravi and D'Odorico 2008; Archer et al. 2011). In the Pantanal, the alternation between wet and dry periods, occurrence of fires, overgrazing, and grazing exclusion were identified as drivers of the woody encroachment (Nunes da Cunha and Junk 2004). Consequently, woody encroachment and its effects have to be analyzed on a case-by-case basis, i.e., considering the specific local natural and socioeconomic conditions.

In addition to the studies of Costa (2013) and Barbosa da Silva et al. (2016), other records in the literature have described the gradual conversion of grasslands to woody physiognomies. These are related to reductions in the cover of important herbaceous plants, the amount of forage, and the size of the area available for grazing (Scholes and Archer 1997; Angassa 2005; Price and Morgan 2008; Eldridge et al. 2011; Ratajczak et al. 2012; Belay et al. 2013). However, a woody plant cover of up to 60% may trigger improvements in local biodiversity (Dorado-Rodrigues et al. 2015; Barbosa da Silva et al. 2016), soil fertility, microclimate, and other ecosystem functions, such as the provision of shelter for drought, in addition to alleviating grazing stress (Soliveres et al. 2014; Eldridge and Soliveres 2014; Maestre et al. 2016).

The faunal responses to woody encroachment vary between taxa and functional groups. In C_4 grasslands under arid climate in North America, the number of ant species increases in stands with encroaching woody species (Bestelmeyer 2005), and rodents can play a keystone role by limiting the recruitment and abundance of grasses through direct graminivory, and may favor the persistence of shrublands (Kerley and Whitford 2009). In African C_4 grasslands, mammal herbivores of various sizes, including small bovids, elephants, and giraffes, can control the cover of woody plants (Augustine and Mcnaughton 2004). In the Pantanal wetland, anurans and small mammals may profit from a mosaic of grasses, encroaching species, and water bodies in the grassland habitats (Layme et al. 2012; Dorado-Rodrigues et al. 2015). Pampas deer, capybaras, and cattle are the mammals mainly found in the open grasslands of the Pantanal (Desbiez et al. 2011; Tomas et al. 2011). They can be impacted by reductions in standing green biomass and herbaceous cover that follows the development into shrublands and forests (Pozer and Nogueira 2005; Barbosa da Silva et al. 2016) and decrease in the accessibility and movement within areas under encroachment, especially in *Combretum* shrublands (Santos et al. 2006).

For many environmentalists, pasture clearing is a Trojan horse that will finally lead to deforestation of the Pantanal, destruction of its habitat diversity, the introduction of exotic grasses, and thus a loss of its multiple ecosystem functions and natural species diversity. The available data show that the heavy encroachment of woody plants into pasture areas leads to reductions in herbaceous cover and in the number of species at stand scale. Although we do not have estimates of alterations in the cover of herbaceous and woody plants at wider temporal and spatial scales, for example, at the landscape level, from the physiognomic perspective, the woody encroachment is transformative. If the registered reductions of herbaceous communities occur frequently over time and space, this could lead to the loss of characteristic grassland communities, species, and consequently the occurrence of emblematic large mammals. Thus, while advocating for the benefits of maintaining livestock production, we are supporting the perspective of grassland diversity conservation and the sustainable use of its components as proposed by the contemporary conservation agenda (GSPC 2002). Although highly modified to croplands and artificial pastures, the conservation of grasslands does not receive equivalent attention in legislation as given to the forests (Overbeck et al. 2015).

The natural encroachment of woody vegetation into grasslands counteracts the efforts of the Pantanal's ranchers to maintain higher covers of herbaceous plants in the grasslands for their livestock. Traditional low-density cattle ranching and mechanical removal of woody plants are cultural management tools that can prevent forest advance by maintaining the macrohabitats and their associated biodiversity (Nunes da Cunha and Junk 2004). Thus, they interfered in the contemporary proportion of area between natural and man-made vegetation units in the Pantanal. Uncontrolled woody encroachment places this new equilibrium at risk such that a plan that involves the ranchers is necessary. Only 5% of the Pantanal is protected as conservation units or private reserves (Junk 2002). Thus, landowner participation is fundamental to defend grassland macrohabitats against encroaching woody species, without destroying valuable forested macrohabitats. A possible strategy is to adjust the traditional knowledge on pasture clearing in the Pantanal to more aims than increasing forage production and the economic viability of its grasslands (Junk and Nunes da Cunha 2012), to include the maintenance of scenic value and wildlife habitats, the control of invasive species, and the reduction of wildfires.

References

Angassa A (2005) The ecological impact of bush encroachment on the yield of grasses in Borana rangeland ecosystem. Afr J Ecol 43:14–20

Aragona M (2008) História natural, biologia reprodutiva, parâmetros populacionais e comunidades de pequenos mamíferos não-voadores em três habitats florestados do Pantanal de Poconé, MT. Dissertation, Universidade de Brasília

Aragona M, Pinho JB (2012) Richness and abundance of birds and terrestrial small mammals in Cambarazal forests of different ages. In: 49th annual meeting of the association for tropical biology and conservation, 1st edn. Bonito/MS

Archer SR, Davies KW, Fulbright TE, McDaniel KC, Wilcox BP, Predick KI (2011) Brush management as a rangeland conservation strategy: a critical evaluation. In: Briske DD (ed) Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps, 1st edn. USDA, Natural Resources Conservation Service, Lawrence, pp 105–170

Arieira J, Nunes da Cunha C (2006) Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae), no Pantanal Norte, MT, Brasil. Acta Bot Bras 20:569–580

Assine ML (2010) Pantanal Mato-grossense: uma paisagem de exceção. In: Modenesi-Gauttieri MC, Bartorelli A, Mantesso-Neto V, Carneiro CDR, Lisboa MBAL (eds) A obra de Aziz Nacib Ab'Saber, 1st edn. Beca-BALL Edições, Sao Paulo, pp 464–489

Assine ML (2015) Brazilian Pantanal: a large pristine tropical wetland. In: Vieira B, Salgado A, Santos L (eds) Landscapes and landforms of Brazil. World Geomorphological Landscapes. Springer, Dordrecht, pp 135–146

Augustine DJ, Mcnaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on east African rangeland. J Appl Ecol 41:45–58

Avelar TC (2018) Sequestro e estoque de carbono na biomassa aérea em Floresta Sempre Verde Sazonalmente Inundada (Cambarazal) no Pantanal. Dissertation, Universidade Federal de Mato Grosso

Barbosa da Silva FH, Arieira J, Parolin P, Nunes da Cunha C, Junk WJ (2016) Shrub encroachment influences herbaceous communities in flooded grasslands of a neotropical savanna wetland. Appl Veg Sci 19:391–400

Barbosa RI, Fearnside PM (2004) Wood density of trees in open savannas of the Brazilian Amazon. For Ecol Manag 199:115–123

Barbosa, RI, Mourão M Jr, Casadio, GML, Silva, SJR (2005) Bioecologia do caimbé [*Curatella americana* L. (Dilleniaceae)]~II: Estudos fenológicos. EMBRAPA, Roraima

Belay TA, Totland Ø, Moe SR (2013) Ecosystem responses to woody plant encroachment in a semiarid savanna rangeland. Plant Ecol 214:1211–1222

Bestelmeyer BT (2005) Does desertification diminish biodiversity? Enhancement of ant diversity by shrub invasion in south- western USA. Divers Distrib 11:45–55

Bruniera CP, Groppo M (2010) Flora da Serra do Cipó, Minas Gerais: Dilleniaceae. Boletim de Botânica 28:59–67

Clark DL, Wilson MV (2001) Fire, mowing, and hand- removal of woody species in restoring a native wetland prairie in the Willamette Valley of Oregon. Wetlands 21:135–144

Costa CP (2013) Padrões da Distribuição de Plantas Arbóreo-Arbustivas em Meso-escala no Pantanal de Mato Grosso. Dissertation, Universidade de Brasília

Costa CP, Nunes da Cunha C, Costa SC (2010) Caracterização da flora e estrutura do estrato arbustivo-arbóreo de um cerrado no Pantanal de Poconé, MT. Biota Neotropica 10:61–73

Desbiez ALJ, Santos SA, Alvarez JM, Tomas WM (2011) Forage use in domestic cattle (*Bos indicus*), capybara (*Hydrochoerus hydrochaeris*) and pampas deer (*Ozotoceros bezoarticus*) in a seasonal Neotropical wetland. Mamm Biol 76:351–357

Dorado-Rodrigues TF, Layme VMG, Silva FHB, Nunes da Cunha C, Strüssmann C (2015) Effects of shrub encroachment on the anuran community in periodically flooded grasslands of the largest Neotropical wetland. Austral Ecol 40:547–557

Eldridge DJ, Soliveres S (2014) Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia. Aust J Bot 62:594–608

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol Lett 14:709–722

Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro, Rio de Janeiro. http://floradobrasil.jbrj.gov.br. Accessed 21 Jul 2019

Global Strategy for Plant Conservation (2002) Report of the convention on biological diversity. Available via Convention on Biological Diversity. https://www.cbd.int/doc/meetings/cop/cop-06/information/cop-06-inf-21-en.pdf. Accessed 29 Jul 2019

Ibarra-Manriquez G, Martínez-Ramos M (2002) Landscape variation of liana communities in a Neotropical rain forest. Plant Ecol 160:91–112

Junk WJ (2002) Long-term environmental trends and the future of tropical wetlands. Environ Conserv 29:414–435

Junk WJ, Nunes da Cunha C (2012) Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction? Wetl Ecol Manag 20:111–122

Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. Can Spec Publ Fish Aquat Sci 106:110–127

Junk WJ, Piedade MTF, Lourival R, Wittmann F, Kandus P, Lacerda LD, Bozelli RL, Esteves FA, Nunes da Cunha C, Maltchick L, Schöngart J, Schaeffer-Novelli Y, Agostinho AA (2014) Brazilian wetlands: definition, delineation, and classification for research, sustainable management, and protection. Aquat Conserv Marine Freshw Environm 24:5–22

Junk WJ, Piedade MTF, Nunes da Cunha C, Wittmann F, Schöngart J, Parolin P et al (2015) Definição e Classificação das Áreas Úmidas (AUs) Brasileiras: Base Científica para uma Nova Política de Proteção e Manejo Sustentável. In: Nunes da Cunha C, Piedade MTF, Wolfgang JJ (eds) Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus macrohabitats, 1st edn. EdUFMT, Cuiabá, pp 13–82

Junk WJ, Piedade MTF, Nunes da Cunha C, Wittmann F, Schöngart J (2018) Macrohabitat studies in large Brazilian floodplains to support sustainable development in the face of climate change. Ecohydrol Hydrobiol 18:334–344

Kerley GIH, Whitford WG (2009) Can kangaroo rat graminivory contribute to the persistence of desertified shrublands? J Arid Environ 73:651–657

Layme VMG, Candelária LP, Santos APM, Alcantara PB (2012) Estrutura da Comunidade de Pequenos Mamíferos Não Voadores em Campos Nativos do Pantanal de Poconé. Oecologia Australis 16:949–957

Maestre FT, Eldridge DJ, Soliveres S (2016) A multifaceted view on the impacts of shrub encroachment. Appl Veg Sci 19:369–370

Marchesan R, Mattos PP, Savares GK, Salis SM (2006) Caracterização Física, Química e Anatômica da madeira de *Byrsonima cydoniifolia*. Embrapa Florestas. Available via EMBRAPA. https://ainfo.cnptia.embrapa.br/digital/bitstream/item/99684/1/2006-RAC-CaracterizacaoFisica.pdf. Accessed 18 Jul 2019

Marimon BS, Lima ES (2001) Caracterização fitofisionômica e levantamento florístico preliminar no Pantanal dos Rios Mortes – Araguaia, Cocalinho, Mato Grosso, Brasil. Acta Bot Bras 15:213–229

Nascimento MT, Nunes da Cunha C (1989) Composição Florística e Estrutural de um Cambarazal no Pantanal de Poconé-MT. Acta Bot Bras 3:3–23

Nunes da Cunha C, Junk WJ (1999) Composição florística de Capões e Cordilheiras. Localização das espécies lenhosas quanto ao gradiente de inundação no Pantanal de Poconé, MT, Brasil. In: Anais do Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, Manejo e Conservação 2, 1st edn. Embrapa Pantanal, Corumbá, pp 387–406

Nunes da Cunha C, Junk WJ (2001) Distribution of wood plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. Int J Ecol Environ Sci 27:63–70

Nunes da Cunha C, Junk WJ (2004) Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. Appl Veg Sci 7:103–110

Nunes da Cunha C, Junk WJ (2011) A preliminary classification of habitats of the Pantanal of Mato Grosso and Mato Grosso do Sul, and its relation to national and international wetland classification systems. In: Junk WJ, da Silva CJ, Nunes da Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland, 1st edn. Pensoft, Sofia, pp 127–141

Nunes da Cunha C, Junk WJ (2015) A Classificação dos Macrohabitats do Pantanal Mato-grossense. In: Nunes da Cunha C, MTF P, Junk WJ (eds) Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats, 1st edn. EdUFMT, Cuiabá, pp 83–130

Nunes da Cunha C, Junk WJ (2017) Drivers of the tree encroachment and establishment of criteria for macrohabitats restoration. In: Annual meeting of the National Institute of science and technology on wetlands, 1st edn. INAU-CNPq/UFMT

Oliveira Filho AT (1984) Estudo florístico e fitossociológico em um cerrado na Chapada dos Guimarães – Mato Grosso uma análise de gradientes. Dissertation, Universidade Estadual de Campinas

Overbeck GE, Vélez-Martin E, Scarano FR, Lewinsohn TM, Fonseca CR, Meyer et al (2015) Conservation in Brazil needs to include non-forest ecosystems. Divers Distrib 21:1455–1460

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorte H et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167–234

Pinho JB, Marini MÂ (2012) Using birds to set conservation priorities for Pantanal wetland forests, Brazil. Bird Conserv Int 22:155–169

Pinho JB, Lopes LE, Marini MÂ (2016) Birds from the Pirizal region, Pantanal of Poconé, Mato Grosso, Brazil. Revista Brasileira de Ornitologia 24:267–285

Pirani FR, Sanchez M, Pedroni F (2009) Fenologia de uma comunidade arbórea em cerrado sentido restrito, Barra do Garças, MT, Brasil. Acta Bot Bras 23:1096–1109

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa-CPAP, Corumbá

Pott A, Pott VJ (1999) Flora do Pantanal – listagem atual de Fanerógamas. In: Anais do Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal, Manejo e Conservação 2, 1st edn. Embrapa Pantanal, Corumbá, pp 234–325

Pott EB, Pott A, Boock A (1989) Reconhecimento florístico e avaliação nutritiva preliminares de espécies forrageiras das sub-regiões de Miranda e Nabileque, no Pantanal Mato-grossense. Pesq Agrop Brasileira 4:623–629

Pozer CG, Nogueira F (2005) Flooded native pastures of the northern region of the Pantanal of Mato Grosso: biomass and primary productivity variations. Braz J Biol 64:859–866

Price JN, Morgan JW (2008) Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia. Austral Ecol 33:278–289

Ratajczak Z, Nippert JB, Collins S (2012) Woody encroachment decreases diversity across north American grasslands and savannas. Ecology 93:697–703

Ravi S, D'Odorico P (2008) Post-fire resource redistribution and fertility island dynamics in shrub encroached desert grasslands: a modeling approach. Landsc Ecol 24:325–335

Rebellato L, Nunes da Cunha C, Figueira JEC (2012) Respostas da comunidade herbácea ao pulso de inundação no Pantanal de Poconé, Mato Grosso. Oecologia Australis 16:797–818

Saintilan N, Rogers K (2015) Woody plant encroachment of grasslands: a comparison of terrestrial and wetland settings. New Phytol 205:1062–1070

Santos SA, Costa C, Souza GS, Moraes AS, Arrigoni MB (2002) Qualidade da Dieta Selecionada por Bovinos na Sub-Região da Nhecolândia, Pantanal. Rev Bras Zootec 31:1663–1673

Santos SA, Cunha CN, Tomás W, Abreu UGP, Arieira J (2006) Plantas Invasoras no Pantanal: Como Entender o Problema e Soluções de Manejo por Meio de Diagnóstico Participativo. Empresa Brasileira de Pesquisa Agropecuária. Available via Embrapa Pantanal. https://www.embrapa.br/pantanal/busca-de-publicacoes/-/publicacao/812197/plantas-invasoras-no-pantanal-como-entender-o-problema-e-solucoes-de-manejo-por-meio-de-diagnostico-participativo. Accessed 28 Jul 2019

Sazima M, Vogel S, Prado LA, Oliveira MD, Franz G, Sazima I (2001) The sweet jelly of *Combretum lanceolatum* flowers (Combretaceae): a cornucopia resource for bird pollinators in the Pantanal, western Brazil. Plant Syst Evol 227:195–208

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

Scholes RJ, Archer SR (1997) Tree–grass interactions in savannas. Annu Rev Ecol Evol Syst 28:517–544

Silva JF, Rubio T (2007) *Combretum lanceolatum* como recurso alimentar para aves no Pantanal. Revista Brasileira de Ornitologia 15:459–460

Silva MP, Mauro R, Mourão GE, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Rev Bras Bot 23:143–152

Silvério DV, Fernandes-Bulhão C (2009) Fenologia reprodutiva e biometria de frutos e sementes de três espécies de *Byrsonima* Rich. Ex Kunth (Malpighiaceae) no Parque do Bacaba, Nova Xavantina – Mato Grosso. Revista Brasileira Neotropical 6:55–73

Soliveres S, Maestre FT, Eldridge DJ, Delgado-Baquerizo M, Quero JL, Bowker MA, Gallardo A (2014) Plant diversity and ecosystem multifunctionality peak at intermediate levels of woody cover in global drylands. Glob Ecol Biogeogr 23:1408–1416

Tomas WM, Cáceres NC, Nunes AP, Fisher E, Mourão G (2011) Mammals in the Pantanal wetland, Brazil. In: Junk WJ, Da Silva CJ, Nunes da Cunha C, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland, 1st edn. Pensoft, Sofia, pp 565–597

Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. J Environ Manag 90:2931–2942

Warren RJW II, Rossell IM, Moorhead KK, Dan Pittillo J (2007) The influence of woody encroachment upon herbaceous vegetation in a Southern Appalachian Wetland Complex. Am Midl Nat 157:39–51

Weksler M, Queirolo D, Brito D (2016) *Holochilus sciureus*. The IUCN red list of threatened species. https://www.iucnredlist.org/species/10220/115096276. Accessed 29 Jul 2019

Zeilhofer P, Schessl M (2000) Relationship between vegetation and environmental conditions in the northern Pantanal of Mato Grosso, Brazil. J Biogeogr 27:159–168

Chapter 12
Paleovegetation Inferences and Landscape Evolution in the Pantanal Basin

Carlos D'Apolito, Mariza Gomes Rodrigues, Barbara Fernandes Becker, and Silane Aparecida Ferreira Silva-Caminha

12.1 Introduction

The Pantanal Basin is a depression in central South America belonging to the Upper Paraguay River drainage and acting as an active sediment trap (Assine 2015). The basin has ca. 150,000 km^2 of extension and is located mostly in mid-western Brazil, but also in Paraguay and Bolivia, where it neighbours the Chaco Basin. Elevations throughout the Pantanal alluvial plain are lower than 200 m. The surrounding areas are highlands where rivers are born; they are composed of older Palaeozoic/Precambrian rocks. The origins of the Pantanal Basin are linked to the Andean foreland system (Almeida 1959; Horton and DeCelles 1997; Shiraiwa 1994; Ussami et al. 1999) and to regional epeirogenic uplifts (Ab'Sáber 1988; Almeida and Carneiro 1998). These processes would have compressed the interior of the South American continent, created water divides between the Paraná and Chaco areas and consequently led to subsidence of the central part where the Pantanal Basin developed (Assine 2015). Although the basin is believed to have opened in the lower Cenozoic, an age for the initial sedimentation phase has not been offered yet. This is due to a lack of chronological data from sediments drilled in the deepest part of the basin, which is located in central areas; there, holes have been drilled in over 400 m of sediments without reaching the basement (Ussami et al. 1999; Assine et al. 2015). One possibility is that the basin opened because of the late Andean uplift around 3 million years ago (Clapperton 1993).

C. D'Apolito (✉) · B. F. Becker · S. A. F. Silva-Caminha
Faculdade de Geociências, Universidade Federal de Mato Grosso, Cuiabá, MT, Brazil

M. G. Rodrigues
Faculdade de Geociências, Universidade Federal de Mato Grosso, Cuiabá, MT, Brazil

Departamento de Geologia, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, SP, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_12

Rivers, floodplains and associated lakes dominate the landscapes of the Pantanal. Fluvial courses born in highland catchment areas are confined and flow downstream quickly carrying significant amounts of sediment. When they reach the alluvial plains, these rivers are no longer confined and run slower and sedimentation develops in a low-gradient avulsive system (Assine et al. 2016). The low topographical gradient is a key feature in producing the geomorphologies seen in the Pantanal Basin. Another essential aspect of the wetland dynamics is seasonality of flood pulses that occur basin-wide. During the austral summer (Dec–Jan–Feb), heavy rainfall originating from the South American Summer Monsoon system (SASM) in the basin and catchment is retained, leading to extensive floods that last for 5–6 months (Zhou and Lau 1998). During winter (Jun-Jul-Aug), there is a marked dry season. Precipitation decreases from NE to SW with annual means from 1,200 to 1,300 mm, and as low as 800 mm in some areas near the border between Brazil and Bolivia. Temperature varies from 10 °C to 40 °C with a mean around 25 °C (Alvares et al. 2014). Climate classification is almost entirely savannah climate (Aw in Köppen's scheme; Alvares et al. 2014). Differences in topography, climate and flood dynamics constrain vegetation types in the Pantanal Basin (Nunes da Cunha and Junk 2001; Nunes da Cunha et al. 2007). Permanently flooded areas develop aquatic vegetation; seasonally inundated areas develop fringe vegetation alongside rivers and savannahs on floodplains; above the level of inundation, seasonally dry tropical forests (SDTFs) grow. The Pantanal flora is constituted by elements from open, wooded and flooded savannahs, linked to the Cerrado biome; in lower proportions, elements from Amazonian and Atlantic Forests can be found contributing to the plant pool in the basin. According to Pott and Silva (2016), the recent geological age (Quaternary) explains the low level of endemism of the Pantanal flora.

The evolution of the Pantanal vegetation in historical time is a subject still under study. So far, only a few records have provided direct data on plant communities for the upper Pleistocene and Holocene, encompassing the last ca. 42,000 years before present. During this period of time, South American climate experienced drastic changes in precipitation regimes with drier and wetter phases varying in space and time (e.g. Baker et al. 2001; Cruz et al. 2005, 2009; Wang et al. 2017), with direct implications on biome distribution (e.g. Bonaccorso et al. 2006; Leite et al. 2016). In the Pantanal region, pieces of evidence point to dry climates during the late Pleistocene and wetter conditions in the Holocene (Whitney et al. 2011), leading to the establishment of wetlands (Assine and Soares 2004). This climatic evolution and its direct influence on landforms shape vegetation patterns in the Pantanal today and in the past. This chapter reviews the pollen records available and makes an attempt to synthesize them in a coherent vegetation reconstruction and to compare paleo-histories of surrounding regions.

12.2 Pollen Records in the Pantanal

12.2.1 Pantanal Vegetation Types and Pollen Rain

Plant diversity and vegetation types were summarized in Pott et al. (2011) and are also the aim of the current book (Chap. 3). It is pivotal to identify the different floristic components and plant associations in order to calibrate pollen-based interpretations. The Pantanal flora has over 2,000 species (Chap. 3), most of which belong to broad-distribution groups (Cerrado, SDTFs, Chaco, Amazonia and Atlantic Forest) and nearly no endemics. Main vegetation types can be divided in cerrados that are savannahs of varying degrees of openness and inundation – some can be wooded, unflooded and contain *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae), *Caryocar brasiliense* Cambess. (Caryocaraceae), *Eriotheca gracilipes* (K. Schum.) A. Robyns (Malvaceae), *Annona dioica* A. St.-Hil. (Annonaceae), *Curatella americana* L. (Dilleniaceae), *Vochysia* Aubl. and *Qualea* Aubl. species (Vochysiaceae), among others (Chap. 9). Floodable cerrados will exhibit open fields rich in Poaceae, Cyperaceae and other herbaceous and shrubby groups; sometimes these formations have sparse or monodominant stands of tree species. Unflooded fields also occur with a thick grassy stratum and sparse trees. Aquatic vegetation develops in lakes, rivers and flooded plains and contains aquatic plants like macrophytes (Chap. 4), e.g. *Eichhornia* Kunth. (Pontederiaceae), *Cyperus blepharoleptos* Steud. (Cyperaceae), *Alternanthera* Forssk. (Amaranthaceae), *Echinodorus* Rich. (Alismataceae), *Hyptis* Jacq. (Lamiaceae), *Ludwigia* L. (Onagraceae), *Myriophyllum* L. (Haloragaceae), *Polygonum* L. (Polygonaceae), *Pontederia* Kunth (Pontederiaceae) and *Eleocharis plicarhachis* (Griseb.) Svens. (Cyperaceae), as well as aquatic ferns like *Salvinia* Ség. (Salviniaceae) and *Pityrogramma* Link (Pteridaceae). These ferns, as well as *C. blepharoleptos* and *Eleocharis*, can form thick floating mats, or floating meadows, that develop in deeper waters. Aquatic vegetation also includes large and dominant stands of *Oryza* L. (Poaceae) species (wild rice).

Along water bodies like rivers and lakes, riparian vegetation can develop. They are commonly found along the Paraguay River and are characterized by flood-tolerant species like *Albizia inundata* (Mart.) Barneby & J.W. Grimes (Fabaceae), *Cassia grandis* L.f. (Fabaceae), *Vitex cymosa* Bertero (Lamiaceae), *Andira inermis* Kunth (Fabaceae), *Inga vera* (DC.) T.D. Penn. (Fabaceae), *Sapium obovatum* Klotzsch ex Müll. (Euphorbiaceae), *Alchornea castaneifolia* (Willd.) A. Juss. (Euphorbiaceae), *Piranhea trifoliata* Baill. (Picrodendraceae) and *Symmeria paniculata* Benth. (Polygonaceae) (Nunes da Cunha and Junk 2001; Damasceno-Júnior et al. 2005; Pott et al. 2011; Flora do Brasil 2020; GBIF). Finally, there occur SDTFs, though at a lower proportion when compared to cerrados and aquatic vegetation; they are non-flooded and tend to be more prevalent in hills than on plains. A large SDTF is found in the northwestern region of the Pantanal in the Bolivian Chiquitano area and lower proportions elsewhere in the basin. Important floristic elements are *Anadenanthera colubrina* (Vell.) Brenan (Fabaceae), *Astronium fraxinifolium* Schott (Anacardiaceae), *Attalea phalerata* Mart. ex Spreng. (Arecaceae), *Copernicia alba* Morong ex Morong & Britton (Arecaceae), *Tabebuia* Gomes ex DC. species (Bignoniaceae) and many Moraceae like *Ficus* L. and *Maclura* Nutt. species, among others (Prado and Gibbs 1993; Jardim et al. 2003; Pott et al. 2011). Some examples of the complex pollen and spore morphologies from the Pantanal flora are given in Fig. 12.1.

The imprint that these vegetation types leave on modern sediments, i.e. their pollen rain, reveals the vegetation-pollen relationships. Unfortunately, such information is largely lacking in the Pantanal Basin. One study (Whitney et al. 2011) analysed six modern surface sediment samples from the La Gaiba Lake (see topic 12.2.2). The shallow parts of the lake contained higher proportions of Poaceae and Cyperaceae and less trees, which was interpreted by the authors as indicative of the proximal Pantanal flooded savannahs (Whitney et al. 2011). Deeper parts reflected a nearby SDTF with more abundant Moraceae/Urticaceae, *Anadenanthera* and *Astronium* and also captured riparian vegetation (*Alchornea*, *S. paniculata* and *Piranhea*). This survey showed that modern pollen rain in the Pantanal captures mostly the local aquatic diversity, but also dry and flooded forests can be identifiable with confidence due to the presence of indicator taxa. Another important pollen rain study was performed outside the Pantanal in northeastern Bolivia (Gosling et al. 2009) but included SDTFs and savannahs. Gosling et al. (2009) revealed a hierarchy in pollen production with denser forests (e.g. rainforests and SDTFs) producing and dispersing more pollen than savannahs. They also pointed out that higher Moraceae proportions indicate more closed canopies and that SDTFs can be safely indicated by *Anadenanthera* pollen. Moreover, there are silent taxa (indicators of vegetation not seen in pollen spectra) and Poaceae may not be very abundant in wooded savannahs (cerradão), especially when compared to lake environments, in line with Pantanal surface samples demonstrating the aquatic vegetation (Whitney et al. 2011). Pollen rain from the cerrados in central Brazil (summarized in Ledru 2002) also indicates the importance of Poaceae but cautions that it can be in lower abundances than expected in cerradão. Ledru (2002) also found underrepresented taxa like *Qualea*, *Curatella* and *Caryocar*. Altogether, these contrasts in vegetation-pollen rain relationships can sometimes mask the local to regional occurrence of certain vegetation types (Jones et al. 2011; D'Apolito et al. 2018).

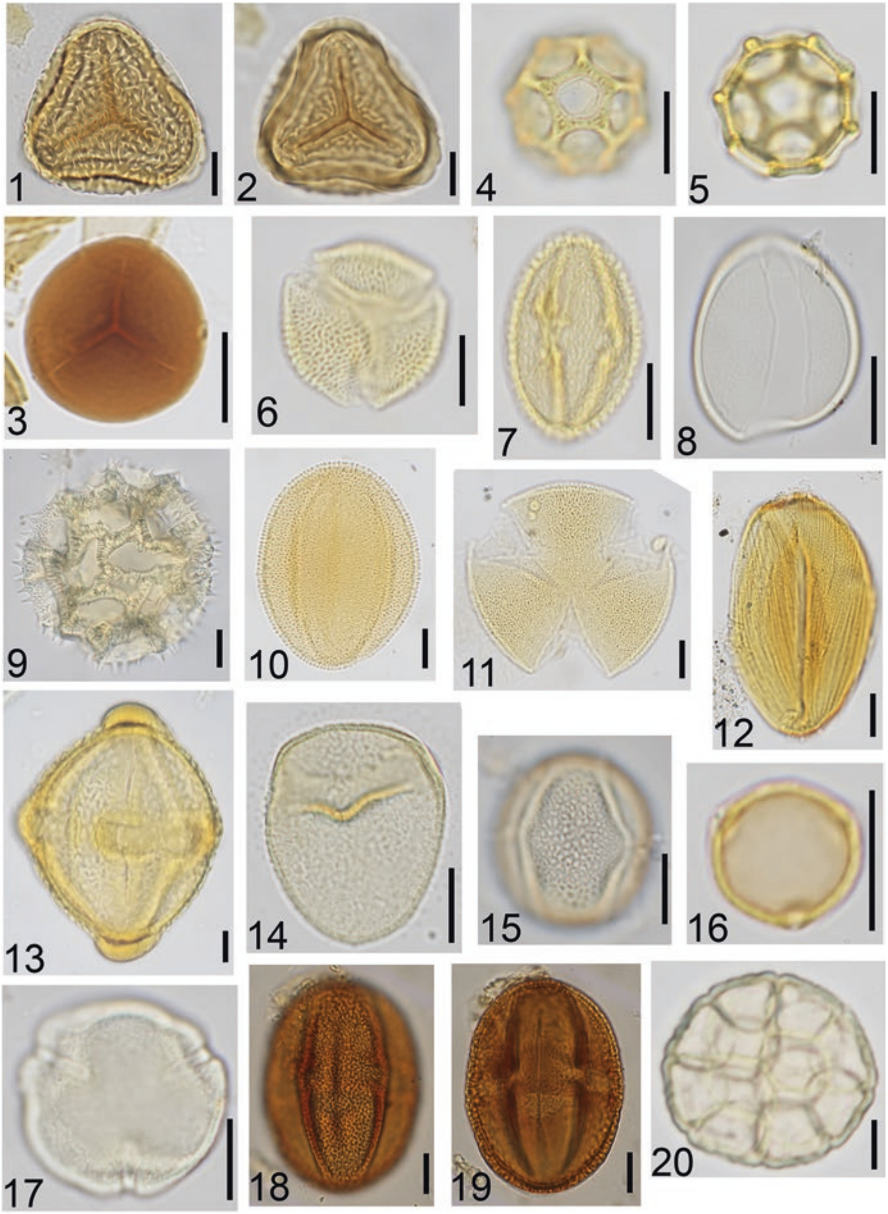


Fig. 12.1 Examples of the morphological diversity of pollen and spores from the Pantanal Basin cited in the text. Taxa illustrated belong to the pollen reference collection from the Paleontology and Palynology Laboratory, Universidade Federal de Mato Grosso (UFMT). Pteridophytes, Pteridaceae: (1–2) *Pityrogramma calomelanos* (L.) Link (1, distal face focus; 2, proximal face focus); Salviniaceae: (3) *Salvinia minima* Baker. Angiosperms, Amaranthaceae: (4–5) *Alternanthera aquatica* (D. Parodi) Chodat; Anacardiaceae: (6–7) *Astronium fraxinifolium* Schott (6, polar view; 7, equatorial view); Arecaceae: (8) *Copernicia alba* Morong; Asteraceae: (9) *Chrysolaena obovata* (Less.) M. Dematt.; Bignoniaceae: (10–11) *Tabebuia aurea* (Silva Manso) Benth. & Hook. f. ex S. Moore (10, equatorial view; 11, polar view); Cabombaceae: (12) *Cabomba furcata* Schult. & Schult. f.; Caryocaraceae: (13) *Caryocar brasiliense* A.St.-Hil.: (14) *Cyperus blepharoleptos* Steud.; Dilleniaceae: (15) *Curatella americana* L.; Euphorbiaceae: (16) *Acalypha communis* Müll. Arg.; (17) *Alchornea castaneifolia* (Humb. & Bonpl. ex Willd.) A. Juss.; (18–19) *Sapium haematospermum* Müll. Arg.; Fabaceae: (20) *Anadenanthera colubrina* (Vell.) Brenan;

(continued)

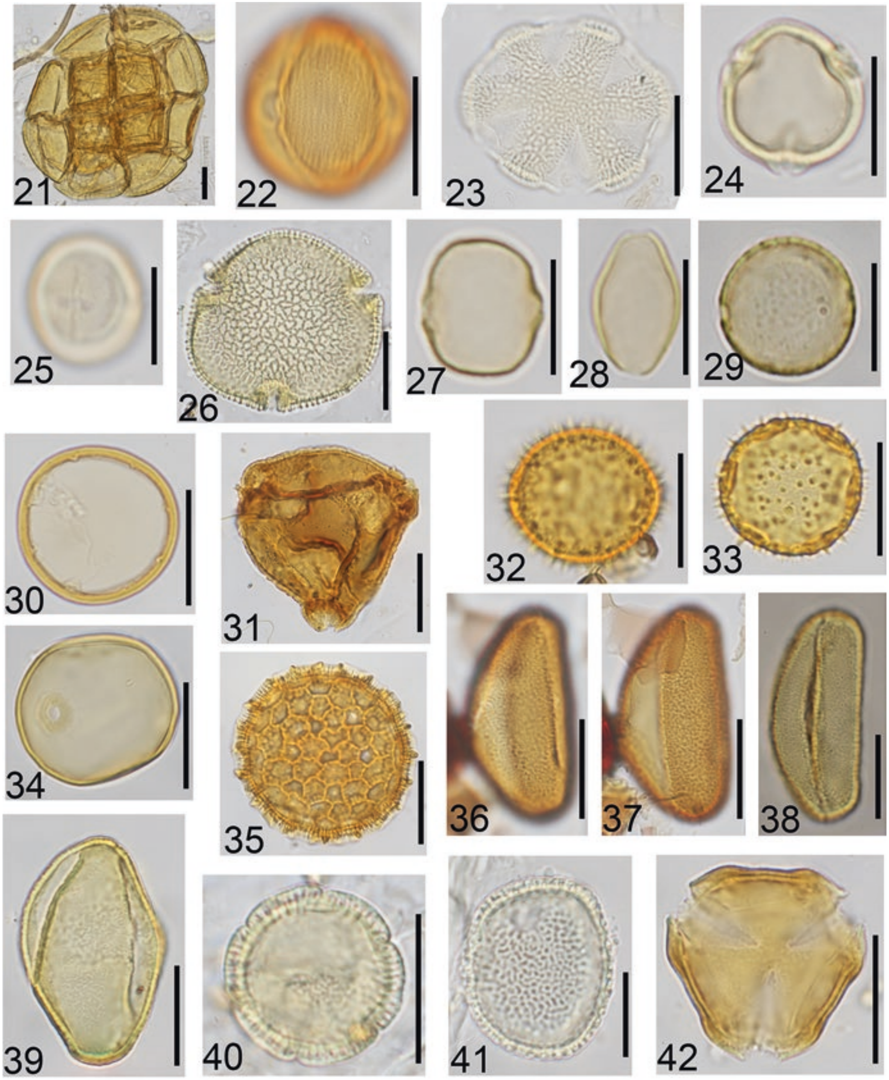


Fig. 12.1 (continued) (21) *Inga vera* Willd.; (22) *Macrolobium* cf. *campestre* Huber; Lamiaceae: (23) *Hyptis hirsuta* Kunth; Malpighiaceae: (24–25) *Byrsonima crassifolia* (L.) Kunth (24, polar view; 25 equatorial view); Malvaceae: (26) *Eriotheca gracilipes* (K. Schum.) A. Robyns; Moraceae: (27) *Brosimum gaudichaudii* Trécul; (28) *Ficus citrifolia* Mill.; (29) *Maclura tinctoria* (L.) D. Don ex Steud.; Nymphaeaceae: (30) *Nymphaea amazonum* Mart. & Zucc.; Onagraceae: (31) *Ludwigia octovalvis* (Jacq.) P.H. Raven; Picrodendraceae: (32–33) *Piranhea trifoliata* Baill. (32, equatorial view; 33, polar view); Poaceae: (34) *Elionurus muticus* (Spreng.) Kuntze; Polygonaceae: (35) *Polygonum hydropiperoides* Michx.; Pontederiaceae: (36–37) *Eichhornia crassipes* (Mart.) Solms; (38–39) *Pontederia subovata* (Seub.) Lowden; Rubiaceae: (40) *Spermacoce quadrifaria* (E.L. Cabral) Govaerts; Typhaceae: (41) *Typha domingensis* Pers.; Vochysiaceae: (42) *Vochysia divergens* Pohl. All scale bars = 10 μm

12.2.2 Lake Gaiva (17°45′S, 57°35′W)

The Gaiva (or La Gaiba, in Spanish) Lake is located in northern Pantanal and is directly associated with the Upper Paraguay River drainage (Fig. 12.2). Gaiva is a shallow lake (4–6 m deep) surrounded by vast portions of aquatic vegetation (aquatic grasses, *Eichhornia* spp., among others), SDTF, Cerrado savannahs on summits and

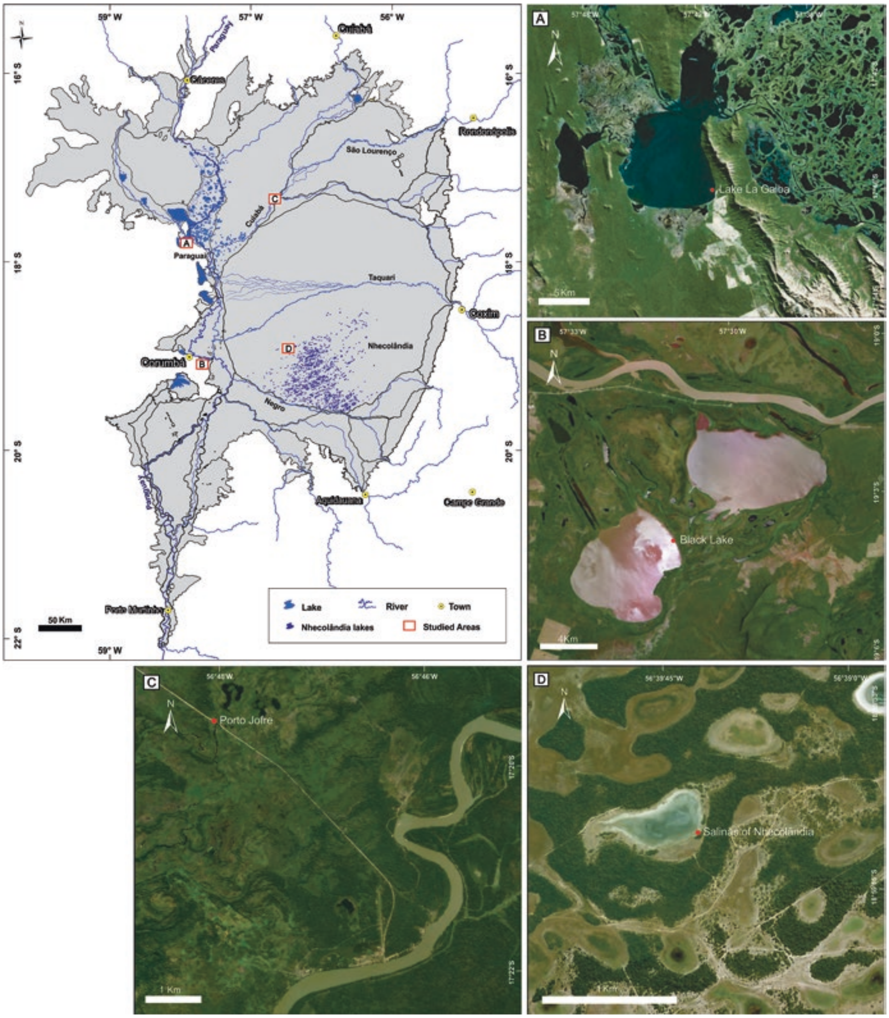


Fig. 12.2 Map of the Pantanal Basin (top left) with main rivers and lakes. (Adapted from Assine et al. 2015) and pollen sites discussed in the text (**a**–**d**). (**a**) Lake Gaiva and (**b**) Lagoa Negra, both in the Paraguay trunk river plain; (**c**) Porto Jofre area on the Cuiabá River fluvial fan; (**d**) Salina Lake in Nhecolândia on the south lobe of the Taquari River megafan. (Images **a**–**d** from Google Earth™)

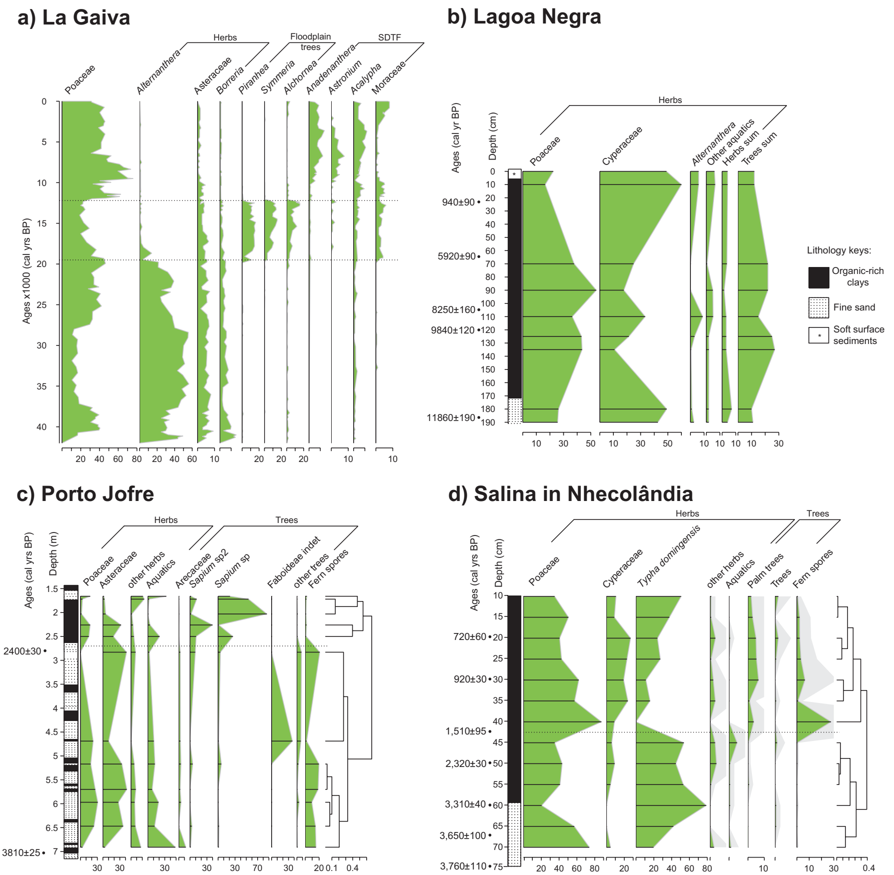


Fig. 12.3 Pollen diagrams from Pantanal Basin localities discussed in the text. (**a**) La Gaiva Lake (Whitney et al. 2011); (**b**) Black Lake (Bezerra 1999; de Oliveira et al. 1999); (**c**) Porto Jofre (unpublished data); and (**d**) Saline Lake (Becker et al. 2018). Data from authors or from diagrams in original publications (Op. cit.); selected taxa are shown. Horizontal axes are relative abundances (%). Clusters in (**c**) and (**d**) are CONISS cluster of sum of squares performed on full pollen matrices. Dotted horizontal lines are pollen zones from original publications. All diagrams and clusters produced with the R language using package `rioja` (Juggins 2015). Radiocarbon dates of (**b**), (**c**) and (**d**) were recalibrated using the SHcal13 curve (Hogg et al. 2013) with R package `Bchron` (Parnell 2016). SDTF, seasonally dry tropical forest

in lower proportions by riparian forest and palm swamps composed mainly of *Copernicia alba* (Whitney et al. 2011; Power et al. 2016). Sediment cores from the lake were integrated and had basal radiocarbon ages starting from ca. 42 ka. Abundant pollen was recovered from 94 samples that altogether permitted the reconstruction of three main vegetation phases in the area with a resolution of ~445 years/sample or ~4 cm/sample (Fig. 12.3a; Whitney et al. 2011). From ca. 42 to 19.5 ka, the pollen content is heavily dominated by the herbs (Fig. 12.3a)

Alternanthera (Amaranthaceae), Poaceae, Cyperaceae, *Borreria* G. Mey./*Spermacoce* Bercht. & J. Presl (Rubiaceae) and Asteraceae and a minor component of trees and shrubs: Mimosoideae, Myrtaceae, Urticaceae and *Acalypha* Juss. ex Menge (Euphorbiaceae). From 19.5 to 12.2 ka, there is a marked increase in trees (Fig. 12.3a) – *Symmeria paniculata* (Polygonaceae), *Piranhea*, *Alchornea*, Combretaceae/Melastomataceae and Moraceae (mainly *Maclura*) – and a concomitant decline in the previously dominant herbs. From 12.2 ka to present, the pollen content reflects a reduction in floodplain habitat owing to rising lake levels and is represented by *Anadenanthera*, *Astronium*, *Acalypha* and Moraceae, as well as an initial peak in Poaceae and Cyperaceae (Fig. 12.3a). The Moraceae during this period are represented by *Brosimum* Sw. and later on after ~3 ka by types related to *Helicostylis* Trécul, *Pseudolmedia* Trécul, *Maquira* Aubl. and *Ficus*.

The cited authors have interpreted these data as showing the evolution from an open savannah from ca. 42 to 19.5 ka, dominated by herbaceous communities and with few trees, to the establishment of an inundation-tolerant forest in the low-lying terrain around the lake from 19.5 to 12.2 ka. This change is also supported by a diatom assemblage that indicates shallow waters after 19.5 ka. The arboreal pollen plus planktonic diatoms from 19.5 to 12.2 ka point to an increase in moisture that led to the growth of two forest formations, the inundated forest on floodplains and adjacent SDTFs. Two key plant taxa indicate the flooded vegetation during this period of time, *S. paniculata* and *Piranhea*. The first of these is a monospecific genus common in Pantanal flooded forests (Melo 2015). SDTFs are detectable after 19.5 ka by the presence of *Maclura*, *Acalypha*, *Celtis* L. and especially *Astronium*. That is typical of dry forests in South American biomes (Prado and Gibbs 1993). However, the absence of *Anadenanthera*, which is currently dominant in SDTFs of the region and elsewhere (Whitney et al. 2011; Prado and Gibbs 1993), was interpreted as evidence for late-glacial SDTFs compositionally different from today's (Whitney et al. 2011). At 12.2 ka, the rapid decline in inundated forest pollen provides evidence for a higher lake level that terminated the local inundated forest and gave room to more prevalent lake conditions. More widespread SDTF is also evident by higher percentages of *Anadenanthera* and *Astronium*. These taxa rise in dominance from 10 to 6.4 ka, which was interpreted as a drier or more seasonal early to middle Holocene period. During this same time, a minimum of Moraceae (*Brosimum* and *Ficus*) also points to a lesser extent of evergreen forests and riparian vegetation. This impoverished early to middle Holocene SDTF can be also in part explained by the effect of fire that is recorded with charcoal remains (Power et al. 2016). The modern flora at the Gaiva Lake was probably attained at ca. 3 ka with a rise in evergreen forest Moraceae pollen types indicated by the genera *Brosimum*, *Helicostylis*, *Pseudolmedia* and *Maquira*, as well as a return of *Alchornea*, a pioneer Euphorbiaceae which is typical of floodplains and riparian forests of the Pantanal (Damasceno-Junior et al. 2005).

The pollen data of Whitney et al. (2011) were also used to model quantitative temperature estimates (Punyasena 2008; Punyasena et al. 2008). The estimates obtained by the authors are of a 4 °C cooler full-glacial period (<20 ka) with mean annual temperatures around 22 °C, compared with the late glacial and Holocene

(>16 ka) with temperatures centred around 26 °C. Today, in the Pantanal, the lowest temperatures recorded are 1–3 °C (Alho 2005; INMET), but normally above 10 °C during winter. The polar cold air masses that cause such cooling events were likely intensified during most of the last glacial period from ca. 42 to 19.5 ka, with more often frosts. This climatic regime explains the lack of tropical trees during the dry and cold full-glacial period as they tend to be frost sensitive (Whitney et al. 2011). Low temperatures and particularly frosts are important factors controlling tropical biomes (Box and Fujiwara 2005; Oliveira-Filho et al. 2015). An open vegetation dominated by C_4 grasses and C_3 herbs was also confirmed by the carbon isotopic content ($\delta^{13}C$) of leaf waxes from the same sediments (Fornace et al. 2016).

12.2.3 Lagoa Negra (Black Lake) (19°04′S, 57°31′W)

The Lagoa Negra is a lake in the floodplain system of the Paraguay River near the town of Corumbá (Fig. 12.2). The lake is ca. 2–3 m deep during its low stand and is periodically flooded by the Paraguay River. Vegetation types in the area are of deciduous and semi-deciduous forest in uplands, riparian forests in floodable areas as well as flooded grasslands (Bortolotto et al. 1999; Damasceno-Junior et al. 2005). A core from the bottom of Lagoa Negra reached 272 cm and had a basal calibrated age near 20 ka (Bezerra and Mozeto 2008). The bottommost sediment layers were sandier and did not contain pollen. The upper ca. 200 cm, however, yielded abundant pollen that was studied by De Oliveira et al. (1999) and also reported in Bezerra (1999). Although in low sampling resolution (nine samples; ~1320 years/sample, or ~21 cm/sample) and only the main pollen and ecological groups reported, some interesting observations of the data were made by the authors. First, a similar-to-recent pollen flora was obtained since ca. 12 ka (Fig. 12.3b), with Poaceae and Cyperaceae heavily dominating the pollen counts, what reflects the establishment of floodplain aquatic vegetation (De Oliveira et al. 1999; Bezerra and Mozeto 2008). Other typical aquatic plants identified in the pollen spectra were *Alternanthera*, *Echinodorus*, *Eichhornia*, *Hyptis*, *Ludwigia*, *Myriophyllum*, *Polygonum* and *Pontederia*. Second, from around 9.8 ka, arboreal taxa increase and are represented by *Alchornea*, *Macrolobium* Schreb. (Fabaceae), Mimosoideae, *Tapirira* Aubl. (Anacardiaceae) and Moraceae/Urticaceae. This was interpreted by the authors as the local development of evergreen and riparian forests on marginal levees. Higher humidity after the Pleistocene-Holocene transition led to enhanced fluvial activity, sediment transport and therefore marginal sediment accumulation, later on stabilized by riparian vegetation. *Astronium* is also reported by Bezerra (1999) but without an associated age or stratigraphical range; therefore, the establishment of SDTF cannot be concluded from the data, but its presence can be expected. The early to middle Holocene in the Lagoa Negra record (ca. 8.3 to 6 ka) shows a minor decrease in arboreal pollen sum and a peak in Poaceae. This was discussed to be an increase of aquatic grasses in a shallowing lake, evidence of lower moisture availability (De Oliveira et al. 2005). In general, despite some fluctuations, the pollen data of Lagoa

Negra show stability of the local aquatic and riparian vegetation throughout the Holocene.

12.2.4 Porto Jofre (17°19′ S, 56°48′ W)

Porto Jofre is an area in the middle Cuiabá River drainage (Fig. 12.2). This river forms a megafan of ca. 15,000 km^2 with a distal position at the Paraguay River (Assine 2003; Pupim et al. 2017). The area is known as Pantanal de Poconé, and its vegetation is primarily defined by savannahs, with Cerrado physiognomies and both wooded and open grasslands; there are also patches of SDTF and aquatic vegetation in lakes/flooded river margins (Nunes da Cunha et al. 2010; Brandão et al. 2011). A 14.5 m core was drilled near the Transpantaneira road in the Cuiabá River alluvial plain, around 3.5 km from the riverbed (Fig. 12.2; unpublished data). The fining upwards succession had pollen recovery in 12 samples from 1.5 m to ca. 7 m and barren sands in the remaining bottom of the core. Two radiocarbon dates constrain the chronology that starts from ca. 3.8 ka at 7 m. The analyses had an average resolution of ~320 years/sample, or 58 cm/samples (Fig. 12.3c; unpublished data). From 3.8 to 2.4 ka, the pollen spectrum is dominated by the herbaceous and aquatic communities rich in Poaceae, Asteraceae, *Ludwigia*, *Polygonum*, *Alternanthera*, Cyperaceae, *Borreria* and Bromeliaceae (Fig. 12.3c). Ferns are also well represented in this phase with high abundances of *Pityrogramma* (Pteridaceae) and *Ceratopteris* Brongn. (Parkeriaceae) – both are pioneer herbs and colonize recently flooded areas where the original vegetation was destroyed, as well as nutrient-rich lakes (Pott and Pott 2000). *Pityrogramma*, in particular, has common species in 'baceiros' (floating meadows) that indicate a higher water column (Pivari et al. 2008; Cunha et al. 2012). *Eriotheca* and *Anadenanthera*, although in negligible percentages, provide evidence of dry forests in the region since 3.8 ka. After ca. 2.4 ka, the pollen data point to a more restricted aquatic environment due to the disappearance of aquatic ferns (Fig. 12.3c) and growth of arboreal vegetation represented by two species of *Sapium*. *Sapium* includes pioneer trees of broad distribution and has species adapted to gallery or inundated forest conditions (Pott and Pott 1997; Damasceno-Junior et al. 2005).

The Porto Jofre pollen record can be interpreted as an initial migrating channel that caused the abandonment of meanders in the Cuiabá alluvial plain. The lowest ca. 7 m of the core, before 3.8 ka, are composed of unconsolidated sands from a more active channel. From 3.8 to 2.4 ka, there was a stronger influence from the river into the plain in this area, creating inundated areas that supported an aquatic vegetation. This is seen in the pollen data and also in the higher frequency of alternating sands and clays (Fig. 12.3c). Later on, from 2.4 ka onwards, the establishment of local arboreal vegetation points to a weaker extension and lower level of inundation in the area. These events are typical in meandering rivers; therefore, the pollen data can be translated into a sequence of vegetation adapting to the local avulsive dynamics.

12.2.5 Salinas of Nhecolândia (18°59′ S, 56°39′ W)

Nhecolândia is a geographical subdivision of the Pantanal in the southern lobe of the Taquari River megafan (Assine 2005). This subregion is ca. 24,000 km^2 and covered by ca. 10,000 small lakes, of which 10% are saline, known locally as *salinas* (Barbiéro et al. 2002). *Salinas* are bounded by 2–5 m high sandy ridges (*cordilheiras*) where inundation-free Cerrado and SDTF vegetation grows. The subregion is drained by wide and shallow waterways (*vazantes*) that are characterized by open and humid savannahs rich in grasses and sedges, among other herbs and few trees. A 170 cm core from Lake Salina da Ponta was studied by Becker et al. (2018) who managed to retrieve abundant and well-preserved palynomorphs despite alkaline waters, potentially leading to poor preservation of organic materials in these *salinas*. Pollen data was obtained in the top 75 cm of the core, with an age starting from 3.7 ka, and with an average analytical resolution of ~240 years/sample, or ~4.7 cm/sample. Two main phases of vegetation development could be reconstructed (Fig. 12.3d). From 3.7 to 1.5 ka, the lake was shallow and supported an herbaceous community dominated by Poaceae and cattail (*Typha domingensis* Pers., Typhaceae); few other herbs and aquatics are also seen, like *Nymphaea* L. (Nymphaeaceae) and *Cabomba* Aubl. (Cabombaceae). The poor herbaceous community is accompanied by a poor freshwater algae community and a lack of fern spores. From 1.5 ka onwards, there is an increment in the herbaceous community, especially in the Cyperaceae, the appearance of fern spores, diverse algae, and trees become more abundant, mainly palms like *Attalea phalerata* and *Copernicia alba* that are indicators of *cordilheira* and *salina* border vegetation.

The poorer pollen diversity and restricted herbaceous taxa from 3.7 to 1.5 ka coincide with lower organic carbon preservation and less negative δ^{13}C values (indicative of the C_4 photosynthetic pathway) in Salina da Ponta sediments studied by McGlue et al. (2017). Altogether, the palynological and geochemical evidences reconstruct a more open, herbaceous-dominated landscape in that period. After 1.5 ka, on the other hand, the data point to the *cordilheira* vegetation establishment, higher carbon preservation and more negative δ^{13}C values that, although still in the range of C_4 plants, indicate admixture of C_3 plants, in agreement with the fringe vegetation suggested by the pollen data. This evolution from a shallow, herb-dominated lake to a higher water table with surrounding vegetation was interpreted as a climatic shift to higher humidity.

12.3 Discussion

12.3.1 Potential and Obstacles of Pollen Studies in the Pantanal Basin

To date, paleovegetation data from the Pantanal Basin are restricted to the late glacial and mostly to the Holocene periods. No findings have been reported from deeper timescales, which could be at least Pliocene to early Quaternary in the upper part of the basin (Clapperton 1993; Ussami et al. 1999). We are still just starting to accumulate pollen data from sedimentary sections in the Pantanal, and this paucity of studied localities relates to a lack of closed basins (like isolated lakes that accumulate organic-rich sediments slowly), which along with the Caatinga semi-arid thorn woodlands makes the Pantanal the least understood biogeographic domain in terms of past vegetation in Brazil (De Oliveira et al. 2005).

Pollen data from the studies reviewed here have two main aspects that cannot be dissociated from each other: climatic and landscape signals. Precipitation regimes and extremes of temperature constrain vegetation; thus, changing climate can be observed from pollen data. This is clearer in closed basins that are not affected by river processes, like the *salinas* of Nhecolândia (Becker et al. 2018). Because *salinas* are sourced with rain and groundwater only and because of a negative water balance (evaporation outweighs precipitation), the change in pollen data to higher arboreal and fern abundances plus diverse and abundant algae can be more reliably associated with an ameliorating climate (increased rainfall). All other sites are more directly influenced by inundation dynamics, and hence river processes like avulsion can mask climatic signals. For instance, it is not clear whether the pollen sequence from Porto Jofre (unpublished data) recorded an increase in rainfall that favoured arboreal vegetation, or whether it recorded fluvial migration. Channel migration leading to meander abandonment could create an oxbow lake hydrologically linked to the river (more prevalent inundated conditions) and later isolated from the river (less prevalent to no connection to the river). This interpretation is preferred given the regional geomorphological context of the Cuiabá alluvial plain (Pupim et al. 2017). Critically, however, is that channel aggradation and avulsion could be related to an increase in rainfall, what in turn is reflected indirectly in the pollen record. Both interpretation possibilities can be exploited and converge to an integrated environmental-climatic reconstruction. The pollen records from the main drainage in the Paraguay River plains (De Oliveira et al. 1999; Whitney et al. 2011) are more suitable for lake and base level reconstructions. They respond more directly to inundation dynamics, so the extent of aquatic and riparian vegetation, for instance, can be measured.

Another aspect of relevance is the over-dominance of herbaceous pollen in all studied sites, attaining ca. 50% to >90% of nearly all samples (Fig. 12.3). Depositional environments in the Pantanal are related to inundation of vast areas, where different hydrosere vegetation stages occur. Hydroseral herbs can form fibrous root systems (e.g. Poaceae, Cyperaceae, *Typha*, *Pityrogramma*) like floating meadows in high water stands, or they can be floating macrophytes (e.g. Nymphaeaceae, *Pistia* L. (Araceae), Cabombaceae, *Ceratopteris*). They occur on all parts of floodable areas, from permanently inundated lakes and plains to periodically inundated fringe forests, palm swamps and open humid grasslands. Above the inundation limit, open grasslands (e.g. *Elionurus* Humb. & Bonpl. ex Willd.) can also occur. All of these harbour herbaceous plant communities rich in Poaceae, Cyperaceae, Asteraceae and *Alternanthera*, among others, that can inhabit dry or waterlogged substrates (Pott and Pott 2000), and are well represented in pollen spectra (Fig. 12.3). Diverse and abundant herbaceous fractions of pollen counts are, therefore, a product of the proximity of depositional environments with these surrounding vegetation, following expected rules of pollen transport, deposition and representation (Prentice 1985; Sugita 1994). These relationships restrict interpretations of fossil pollen floras to the local scale, so regional interpretations and correlations should be done very carefully. Another issue with herbs is that many of the identified taxa can inhabit both inundated and dry substrates. Differentiating them is difficult but possible with detailed pollen rain studies (e.g. Absy et al. 2014). Poaceae predominate in all pollen data from the Pantanal. Much has been discussed about this pollen type, and its significance is considered ambiguous (Bush 2002; Absy et al. 2014), meaning it can indicate humid or dry grasslands. It is pivotal, then, to identify other indicators in the whole assemblage to inform on paleoecologies, not to mention coupling palynology with other proxies like stable isotopes, sedimentology, phytoliths and algal remains, among others.

Regional scale interpretations can be made with pollen from parent vegetation of non-inundated sources like the SDTF identified by Whitney et al. (2011) in the Gaiva Lake. In such a context, key pollen like *Astronium* and *Anadenanthera* are essential and have proven useful in identifying specific forests even when in low abundances (Gosling et al. 2009; Whitney et al. 2011). Another valuable information is differentiating between Moraceae genera. It usually is not done by palynologists, but it can resolve parent vegetation for this family, differentiating between riparian and dry forests (Burn and Mayle 2008; Whitney et al. 2011). A focus on arboreal pollen has been seen to be more informative in reconstructing habitat openness of central Brazilian savannahs, what may sometimes lead to in higher pollen counts, so rare arboreal pollen become better represented (Cassino et al. 2015). Increasing arboreal pollen counts is desired and should be given special attention in the Pantanal Basin due to extensive open habitats near depositional settings. Probably the more detailed forest story told in the Gaiva record from Whitney et al. (2011) is partly due to the fact that aquatic pollen was not included in the main pollen sum of 300 grains, in contrast with the other sites.

In general, pollen data from the Pantanal exhibit great potential as paleovegetation archives. Key aspects of the Pantanal pollen sequences include (1) overdominance of herbs, (2) ambiguous signals between 'dry vs. wet substrate' herbaceous groups (e.g. Poaceae, Cyperaceae, *Alternanthera*), (3) low abundances of important arboreal taxa and (4) difficulties in telling apart local vs. regional pollen sources and closed vs. open depositional settings. Overcoming these issues requires (1) detailed pollen rain studies (telling apart floating aquatic from other plants is desired), (2) pollen counts high enough to include as much arboreal pollen as possible and (3) an integrated understanding of the sedimentary history in a regional geomorphological context with the pollen data. These and other aspects will improve our ability of interpreting pollen records and reconstructing paleovegetation more precisely.

Finally, an effort towards more ancient pollen data is a necessity; it will probably come from central parts of the Pantanal drainage, like the plains and associated lakes of the Paraguay River, where sedimentation is more likely to have continued even despite lowering base levels during past dry phases. Studying older pollen sequences will require deep coring, the expertise of multidisciplinary fields and large funding schemes. These goals will only be achieved with international cooperation since large lakes in the central Paraguay River areas lie on international borders.

12.3.2 Late-Glacial Vegetation

Pollen data from the Gaiva Lake is so far the only direct evidence of late-glacial vegetation in the Pantanal area. Whitney et al. (2011) reconstructed an open landscape with few trees from ca. 42 to 19.5 ka, responding strongly to drier and colder climatic conditions of the last glacial cycle. According to these authors, the surrounding vegetation was herbaceous, with the absence of tropical forest elements. This scenario was probably the result of low pCO_2 concentrations, more frequent and stronger frosts as well as lower precipitation. Seasonally dry tropical forests (SDTFs) either had a limited expansion or did not exist in the area during this period (Whitney et al. 2014). This drier scenario is in agreement with paleorecords from neighbouring regions, for instance, the retreat of evergreen forest in the Amazon-savannah boundary in northern Bolivia (Mayle et al. 2000; Burbridge et al. 2004) and southern Amazonia (Pará state) (Fontes et al. 2017) and stronger seasonality in the Chaco Basin (Latrubesse et al. 2012). All of these records point to stronger drier and seasonal conditions during the Last Glacial Maximum (LGM) at ca. 21 ka, as is also confirmed from the Gaiva isotopic record (Fornace et al. 2016). After 20 ka and until the onset of the Holocene, the northern Pantanal gradually became more humid and warmer, supporting riparian forests and SDTFs that were probably compositionally different from today's due to the rarity of *Anadenanthera* Speg. This late-glacial period was not as cold as the full glacial and probably frost-free given the presence of tropical tree taxa like *Symmeria paniculata* and *Piranhea* (Whitney et al. 2011, 2014).

The fact that the Pantanal climate is controlled by the monsoonal system that acts over South America, plus that the basin lies in the heart of the continent, makes it an important and potential paleo-archive to be explored. The dryer and colder settings during the glacial part of the record, ~20 to >40 ka, including the LGM in northern Pantanal, are well correlated with drying in Amazonia (the main source of moisture to the Pantanal Basin). In Amazonia, speleothem isotopic records show up to 42% less rain fell in its eastern part during the last glacial period (Wang et al. 2017), what is in concert with forest retraction in southern Amazonia (Op. cit.). This dry and cold phase in the Pantanal and Amazonia contrasts with moist climates around cerrado localities >25 ka (Ferraz-Vicentini and Salgado-Labouriau 1996; Ledru 2002) and south-southeastern Brazil (Cruz et al. 2005). After 25 ka, however, and especially around the LGM, the cerrado localities are dry and cold, in line with the Pantanal and Amazonian records. In contrast, south-southeastern areas (Cruz et al. 2005) and mid-western Brazil just south of the Pantanal Basin (Novello et al. 2017) have speleothem records showing moist phases. Could the Pantanal have undergone differing climatic regimes in the past? This is an open question that needs to be answered. One observation in this regard is that climatic zones south of the Pantanal in Mato Grosso do Sul have large areas of Am climate (1,300–1,600 mm/year; Alvares et al. 2014), which is significantly more humid than most of Pantanal's Aw zone (1,000–1,300 mm/year).

12.3.3 Holocene Vegetation

From ca. 12 ka to the present, the Pantanal vegetation was very close to its modern climatic and vegetation patterns. In the main drainage, aquatic vegetation was dominant (De Oliveira et al. 1999; Bezerra 1999); riparian evergreen and SDTF establish in the NW portion in Bolivia (Whitney et al. 2011, 2014), which is more evident in the late Holocene after ca. 3 ka. During the early and middle Holocene, an enhanced rainfall seasonality can still be detected in Gaiva and neighbouring regions (Burbridge et al. 2004; Latrubesse et al. 2012). This seasonality is reflected in drought-tolerant taxa and a lower plant diversity interpreted from lower palynological richness (Whitney et al. 2014), which is also explained by fire activity and its impact on SDTF diversity (Power et al. 2016). A drier climate is also detected in Nhecolândia in the early Holocene by the formation of aeolian dunes (McGlue et al. 2017). After ca. 3.7 ka in this region, there is a humid grassland signal that around 1.5 ka changes to a mixture of humid grassland and *cordilheira* formation like presently (Becker et al. 2018). This humid phase after 1.5 ka is also detected in the Chaco Basin (Latrubesse et al. 2012) and the Gaiva Lake level record (Whitney and Mayle 2012). A similar trend from predominantly herbaceous-aquatic from after ca. 3.8 ka is seen in Porto Jofre but with a more forested phase after ca. 2.4 ka (unpublished data); however, this could be a geomorphological signal only (see Sect. 12.2.3). Overall, after 4 to 3 ka and mainly after 1.5 ka, vegetation in the Pantanal seems to be undifferentiated from today's vegetation.

12.3.4 Final Considerations and Perspectives

Despite still an understudied biogeographic region, pollen sequences from the Pantanal are growing in number and showing great potential in telling the vegetation history of this wetland system. This history points to similar responses to climatic forcing by the Pantanal vegetation as in other areas like the Amazon and Chaco, and an opposite response to areas in central and southeastern Brazil. A summarized trend in vegetation change would be open savannahs in the full glacial (>40 to 20 ka) and increased tropical tree coverage including SDTF in the late glacial (20 to ca. 12 ka), both phases covering at least the northern part of the basin. Thereafter, to a broader geographical extension, near modern conditions were attained during the early Holocene and modern vegetation after ca. 4 ka and especially 1.5 ka.

More localities are needed to confirm these reconstructed vegetation patterns. In particular, it would be key to have full- and late-glacial sequences from central and southern locations in order to test the open savannah and impoverished tropical forest reconstructions from northern Pantanal (Whitney et al. 2011, 2014). These have direct impacts on Pleistocene biogeographic hypotheses (e.g. Prado and Gibbs 1993) and central South American precipitation regime reconstructions (e.g. Novello et al. 2017). Moreover, understanding the responses of plant communities to periods of known drier climates in the past can improve our ability to predict future scenarios of biodiversity change in the Pantanal Basin and elsewhere.

We also highlighted the potential of pollen data in geomorphological studies and in late Holocene successions from saline lakes (Becker et al. 2018). Knowledge on all sites and the whole Pantanal will improve immensely from studies of modern pollen rain spectra, their associated parental vegetation and the environments of deposition.

Acknowledgements This chapter benefited from reviews by Danilo Neves and two anonymous reviewers to whom the authors are thankful. We also thank Arnildo Pott and Geraldo A. Damasceno Júnior for comments on an earlier version of this work and Bruno Scudeiro for making photomicrographs. The authors are grateful for funding from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) [DCR grant number 568838/2017 to C.D.; FAPEMAT grant number 401809/2010-2 to S.S.C.; and CNPq grant number 476020/2013-1 to S.S.C.].

References

Ab'Sáber AN (1988) O Pantanal Mato-Grossense e a teoria dos refúgios. Rev Bras Geogr 50:9–57

Absy ML, Cleef AM, D'Apolito C, Silva MFF (2014) Palynological differentiation of savanna types in Carajás, Brazil (southeastern Amazonia). Palynology 38(1):78–89. https://doi.org/10.1080/01916122.2013.842189

Alho CJR (2005) The Pantanal. In: Fraser LH, Keddy PA (eds) The World's largest wetlands: ecology and conservation. Cambridge University Press, Cambridge, pp 203–271

Almeida FFM (1959) Traços gerais da geomorfologia do centro-oeste brasileiro. In: Almeida FFM, Lima MA (eds) Planalto centro-ocidental e Pantanal matogrossense, Guia de Excursão, XVIII Congresso Internacional de Geografia, Rio de Janeiro, pp 7–65

Almeida FFM, Carneiro CDR (1998) Origem e evolução da Serra do Mar. Revista Bras Geociências 28:135–150

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2014) Köppen's climate classification map for Brazil. Meteorol Z 22(6):711–728. https://doi.org/10.1127/0941-2948/2013/0507

Assine ML (2003) Sedimentação na Bacia do Pantanal Mato-Grossense, Centro-Oeste do Brasil. Tese de Livre-Docência, Universidade Estadual Paulista (UNESP)

Assine ML (2005) River avulsions on the Taquari megafan, Pantanal wetland, Brazil. Geomorphology 70:357–371. https://doi.org/10.1016/j.geomorph.2005.02.013

Assine ML (2015) Brazilian Pantanal: a large pristine tropical wetland. In: Vieira BC, Salgado AAR, dos Santos LJC (eds) Landscapes and landforms of Brazil. Springer, Dordrecht, pp 135–146

Assine ML, Soares PC (2004) Quaternary of the Pantanal, west-central Brazil. Quat Int 114:23–34. https://doi.org/10.1016/S1040-6182(03)00039-9

Assine ML, Merino ER, Pupim FN, Macedo HA, Santos MGM (2015) The Quaternary alluvial systems tract of the Pantanal Basin, Brazil. Braz J Geol 45(3):475–489. https://doi.org/10.1590/2317-4889201520150014

Assine ML, Macedo HA, Stevaux JC, Bergier I, Padovani CR, Silva A (2016) Avulsive rivers in the hydrology of the Pantanal wetland. In: Bergier I. Assine ML (eds.) Dynamics of the Pantanal wetland in South America, Springer, pp 83–110

Barbiéro L, Queiroz-Neto JP, Ciornei G, Sakamoto AY, Capellari B, Fernandes E, Valles V (2002) Geochemistry of water and ground water In the Nhecolândia, Pantanal of Mato Grosso, Brazil: variability and associated processes. Wetlands 22:528–540

Becker BF, Silva-Caminha SAF, Guerreiro RL, Oliveira EJ, D'Apolito C, Assine ML (2018) Late Holocene palynology of a saline lake in the Pantanal of Nhecolândia, Brazil. Palynology. https://doi.org/10.1080/01916122.2017.1386843

Baker PA, Seltzer GO, Fritz SC, Dunbar RB, Grove MJ, Tapia PM, Cross SL, Rowe HD, Broda JP (2001) The history of South American tropical precipitation for the past 25,000 years. Science 291:640–643

Bezerra MAO (1999) Uso de multi-traçadores na reconstrução do Holoceno no Pantanal Mato-grossense, Corumbá, MS. Universidade Federal de São Carlos, Tese de Doutorado

Bezerra MAO, Mozeto AA (2008) Deposição de carbono orgânico na planície de inundação do Rio Paraguai durante o Holoceno médio. Oecologia Brasiliensis 12(1):155–171

Bonaccorso E, Koch I, Peterson AT (2006) Pleistocene fragmentation of Amazon species' ranges. Divers Distrib 12:157–164

Bortolotto IM, Damasceno-Júnior GA, Isquierdo SWG (1999) Caracterização das unidades fitofisionômicas da bacia da lagoa Negra – Ladário – MS. In: Anais do II simpósio sobre recursos naturais e sócio-econômicos do Pantanal - Manejo e Consevação. CPAP Embrapa & UFMS, Corumbá, pp 283–289

Box EO, Fujiwara K (2005) Vegetation types and their broad-scale distribution. In: van der Maarel E (ed) Vegetation ecology. Blackwell Science, pp 107–128

Brandão LG, Aantas PTZ, Oliveira LFB, Jorge-Pádua MT, Pereira NC, Valutky WW (2011) Plano de Manejo da Reserva Particular de Patrimônio Natural do SESC Pantanal, vol 3. SESC Departamento Nacional, Rio de Janeiro, 148 p

Burbridge RE, Mayle FE, Killeen T (2004) Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. Quat Res 61:215–230. https://doi.org/10.1016/j.yqres.2003.12.004

Burn MJ, Mayle FE (2008) Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. Rev Palaeobot Palynol 149:187–201. https://doi.org/10.1016/j.revpalbo.2007.12.003

Bush MB (2002) On the interpretation of fossil Poaceae pollen in the lowland humid neotropics. Palaeogeogr Palaeoclimatol Palaeoecol 177:5–17. https://doi.org/10.1016/S0031-0182(01)00348-0

Cassino RF, Martinho CT, Silva-Caminha SAF (2015) Modern pollen spectra of the Cerrado vegetation in two national parks of Central Brazil, and implications for interpreting fossil pollen records. Rev Palaeobot Palynol 223:71–86. https://doi.org/10.1016/j.revpalbo.2015.09.002

Clapperton C (1993) Quaternary geology and geomorphology of South America. Elsevier, Dordrecht

Cruz FW, Burns SJ, Karmann I, Sharp WD, Vuille M, Cardoso AO, Ferrari JA, Dias PLS, Viana O (2005) Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. Nature 434:63–66

Cruz FW, Vuille M, Burns SJ, Wang XF, Cheng H, Werner M, Edwards RL, Karmann I, Auler AS, Nguyen H (2009) Orbitally driven east-west antiphasing of South American precipitation. Nature Geoscience 2:210–214

Cunha NL, Delatorre N, Rodrigues RB, Vidotto C, Gonçalvez F, Scremin-Dias E, Damasceno-Júnior GA, Pott VJ, Pott A (2012) Structure of aquatic vegetation of a large lake, western border of the Brazilian Pantanal. Braz J Biol 72(3):519–531

D'Apolito C, Latrubesse EM, Absy ML (2018) Results confirm a relatively dry setting during the last glacial (MIS 3 and LGM) in Carajás, Amazonia: a comment on Guimarães et al. The Holocene 28(2):330–331

Damasceno-Junior GA, Semir J, Santos FAM, Leitão-Filho HF (2005) Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200:119–135. https://doi.org/10.1016/j.flora.2004.09.002

De Oliveira PE, Bezerra MAO, Mozeto A, Aravena R (1999) Vegetação e clima do Quaternário Tardio do Pantanal Sul-Matogrossense: Palinologia da Lagoa Negra, Corumbá, MS. In: Anais do 7° Congresso da Abequa, Porto Seguro, Bahia

De Oliveira PE, Behling H, Ledru M-P, Barberi M, Bush M, Salgado-Labouriau ML, Garcia MJ, Medeanic S, Barth OM, Barros MA, Sheel-Ybert R (2005) Paleovegetação e Paleoclimas do Quaternário do Brasil. In: Souza CRG, Suguio K, Oliveira AMS, De Oliveira PE (eds) Quaternário do Brasil. Holos Editora, Ribeirão Preto, pp 52–69

Ferraz-Vicentini KR, Salgado-Labouriau ML (1996) Palynological analysis of a palm swamp in central Brazil. J S Am Earth Sci 9(3-4):207–219. https://doi.org/10.1016/0895-9811(96)00007-7

Flora do Brasil 2020 under construction. Jardim Botânico do Rio de Janeiro. Available at: http://floradobrasil.jbrj.gov.br/. Accessed on 16 Aug 2018

Fontes D, Cordeiro RC, Martins GS, Behling H, Turcq B, Sifeddine A, Seoane JCS, Moreira LS, Rodrigues RA (2017) Paleoenvironmental dynamics in South Amazonia, Brazil, during the last 35,000 years inferred from pollen and geochemical records of Lago do Saci. Quat Sci Rev 173:161–180. https://doi.org/10.1016/j.quascirev.2017.08.021

Fornace KL, Whitney BS, Galy V, Hughen KA, Mayle FE (2016) Late Quaternary environmental change in the interior South American tropics: new insight from leaf wax stable isotopes. Earth Planet Sci 438:75–85

GBIF.org (2018) GBIF Occurrence Download. https://doi.org/10.15468/dl.fpwlzt

Gosling WD, Mayle FE, Tate NJ, Killeen TJ (2009) Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. Rev Palaeobot Palynol 153:70–85. https://doi.org/10.1016/j.revpalbo.2008.06.007

Hogg A, Hua Q, Blackwell PG, Niu M, Buck CE, Guilderson TP, Heaton TJ, Palmer JG, Reimer PJ, Reimer RW (2013) SHCal13 Southern Hemisphere calibration, 0–50,000 years cal BP. Radiocarbon 55(4):1889–1903. https://doi.org/10.2458/azu_js_rc.55.16783

Horton BK, DeCelles PG (1997) The modern foreland basin system adjacent to the Central Andes. Geology 25:895–898

Jardim A, Killeen TJ, Fuentes A (2003) Guía de los Árboles y Arbustos del Bosque Seco Chiquitano, Bolivia, Fundacíon Amigos de la Naturaleza Noel Kempff (FAN), Santa Cruz

Jones HT, Mayle FE, Pennington RT et al (2011) Characterisation of Bolivian savanna ecosystems by their modern pollen rain and implications for fossil pollen records. Rev Palaeobot Palynol 164:223–237

Juggins S (2015) Rioja: Analysis of Quaternary Science Data, R package version (0.9-9). http://cran.r-project.org/package=rioja

Latrubesse EM, Stevaux JC, Cremon EH, May J-H, Tatumi SH, Hurtado MA, Bezada M, Argollo JB (2012) Late Quaternary megafans, fans and fluvio-aeolian interactions in the Bolivian Chaco, Tropical South America. Palaeogeogr Palaeoclimatol Palaeoecol 356–357:75–88. https://doi.org/10.1016/j.palaeo.2012.04.003

Ledru M-P (2002) Late quaternary history and evolution of the cerrados as revealed by palynological records. In: Oliveria PS, Marquis RJ (eds) The Cerrados of Brazil. Columbia University Press, New York, pp 33–51

Leite YLR, Costa LP, Loss AN, Rocha RG, Batalha-Filho H, Bastos AC, Quaresma VS, Fagundes V, Paresque R, Passamani M, Pardini R (2016) Neotropical forest expansion during the last glacial period challenges refuge hypothesis. Proc Natl Acad Sci 113(4):1008–1013

Mayle FE, Burbridge R, Killeen TJ (2000) Millennial-scale dynamics of Southern Amazonian rain forests. Science 290:2291–2294. https://doi.org/10.1126/science.290.5500.2291

McGlue MM, Guerreiro RL, Bergier I, Silva A, Pupim FN, Oberc V, Assine ML (2017) Holocene stratigraphic evolution of saline lakes in Nhecolândia, southern Pantanal wetlands (Brazil). Quat Res 88(3):472–490. https://doi.org/10.1017/qua.2017.57

Melo E (2015) Polygonaceae in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. Available at http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB24337

Novello VF, Cruz FW, Vuille M, Stríkis NM, Edwards RL, Cheng H, Emerick S, de Paula MS, Li X, Barreto ES, Karmann I, Santos RV (2017) A high-resolution history of the South American monsoon from last glacial maximum to the holocene. Sci Rep 7:44267. https://doi.org/10.1038/srep44267

Nunes da Cunha C, Junk W (2001) Distribution of wood plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. Int J Ecol Environ Sci 27:63–70

Nunes da Cunha C, Junk W, Leitão-Filho JHF (2007) Woody vegetation in the Pantanal of Mato Grosso, Brazil: a preliminary typology. Amazoniana 19:159–184

Nunes da Cunha C, Rebellato L, Costa CP (2010) Vegetação e Flora: experiência pantaneira no sistema de grade. In: Fernandes IM, Signor CA, Penha J (eds) Biodiversidade no Pantanal de Poconé. Cuiabá, Centro de Pesquisa do Pantanal, pp 37–57

Oliveira-Filho AT, Budke JC, Jarenkow JA, Eisenlohr PV, Neves DRM (2015) Delving into the variations in tree species composition and richness across south American subtropical Atlantic and Pampean forests. J Plant Ecol 8(3):242–260. https://doi.org/10.1093/jpe/rtt058

Parnell A (2016) Bchron: radiocarbon dating, age-depth modelling, relative sea level rate estimation, and non-parametric phase modelling. R package version 4.2.6. https://CRAN.R-project.org/package=Bchron

Pivari MOD, Pott VJ, POTT A (2008) Macrófitas aquáticas de ilhas flutuantes (baceiros) nas sub-regiões do Abobral e Miranda, Pantanal, MS, Brasil. Acta Bot Bras 22(2):563–571

Pott VJ, Pott A (1997) Plants of Pantanal. Embrapa, Centro de Pesquisa Agropecuária do Pantanal. Embrapa, Corumbá

Pott VJ, Pott A (2000) Plantas aquáticas do Pantanal. Embrapa, Centro de Pesquisa Agropecuária do Pantanal. Embrapa, Corumbá

Pott A, Oliveira AKM, Damasceno-Junior GA, Silva JSV (2011). Plant diversity of the Pantanal wetland. Braz J Biol 71(1):265–273

Pott A, Silva JSV (2016) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I. Assine ML (eds) Dynamics of the Pantanal wetland in South America, Springer, pp 111–131.

Power MJ, Whitney BS, Mayle FE, Neves DM, de Boer EJ, Maclean KS (2016) Fire, climate and vegetation linkages in the Bolivian Chiquitano seasonally dry tropical forest. Philos Trans R Soc B 371:20150165. https://doi.org/10.1098/rstb.2015.0165

Prado DE, Gibbs PE (1993) Patterns of species distributions in the dry seasonal forests of South America. Ann Mo Bot Gard 80(4):902–927

Prentice IC (1985) Pollen representation, source area and basin size: towards a unified theory of pollen analysis. Quat Res 23:76–86

Punyasena SW (2008) Estimating Neotropical palaeotemperature and palaeoprecipitation using plant family climatic optima. Palaeogeogr Palaeoclimatol Palaeoecol 265:226–237. https://doi.org/10.1016/j.palaeo.2008.04.025

Punyasena SW, Mayle FE, McElwain JC (2008) Quantitative estimates of glacial and Holocene temperature and precipitation change in lowland Amazonian Bolivia. Geology 36:667–670. https://doi.org/10.1130/G24784A.1

Pupim FN, Assine ML, Sawakuchi AO (2017) Late Quaternary Cuiabá megafan, Brazilian Pantanal: channel patterns and paleoenvironmental changes. Quat Int 438:108–125

Sapium in Flora do Brasil 2020 under construction. Jardim Botânico do Rio de Janeiro. Available at: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB17662. Accessed 21 Feb 2018

Shiraiwa S (1994) Flexura da litosfera continental sob os Andes Centrais e a origem da Bacia do Pantanal. PhD thesis, Universidade de São Paulo

Sugita S (1994) Pollen representation of vegetation in quaternary sediments: Theory and method in patchy vegetation. J Ecol 82(4):881–897

Ussami N, Shiraiwa S, Dominguez JML (1999) Basement reactivation in a sub-Andean foreland flexural bulge: the Pantanal wetland, SW Brazil. Tectonics 18:25–39

Wang X, Edwards RL, Auler AS, Cheng H, Kong X, Wang Y, Cruz FW, Dorale JA, Chiang H-W (2017) Hydroclimate changes across the Amazon lowlands over the past 45,000 years. Nature 541:204–207. https://doi.org/10.1038/nature20787

Whitney BS, Mayle FE (2012) *Pediastrum* species as potential indicators of lake-level change in tropical South America. J Paleolimnol 47(4):601–615. https://doi.org/10.1007/s10933-012-9583-8

Whitney BS, Mayle FE, Punyasena SW, Fitzpatrick KA, Burn MJ, Guillen R, Chavez E, Mann D, Pennington RT, Metcalfe SE (2011) A 45 kyr palaeoclimate record from the lowland interior of tropical South America. Palaeogeogr Palaeoclimatol Palaeoecol 307:177–192. https://doi.org/10.1016/j.palaeo.2011.05.012

Whitney BS, Mayle FE, Burn MJ, Guillen R, Chavez E, Pennington RT, Metcalfe SE (2014) Sensitivity of Bolivian seasonally-dry tropical forest to precipitation and temperature changes over glacial–interglacial timescales. Veg Hist Archaeobotany 23(1):1–14. https://doi.org/10.1007/s00334-013-0395-1

Zhou JY, Lau KM (1998) Does a monsoon climate exist over South America? J Clim 11:1020–1040

Chapter 13
Synthesis of the Present Knowledge on Plant Phenology of the Pantanal

Camila Aoki, Rogério Rodrigues Faria, Geraldo Alves Damasceno-Junior, and Arnildo Pott

13.1 Introduction

Phenology is the study of the life cycle of organisms (Rathcke and Lacey 1985; van Schaik et al. 1993). In plant communities, the great variety of phenological patterns found in a given habitat can reflect the actions of different biotic and abiotic selective pressures (Fenner 1998). The time, period and intensity of the phases, or phenophases, of the life cycle of plants affect their fitness from pollination onwards including seed development, dispersal and germination (Sarmiento and Monasterio 1983). Hence, primary consumers (e.g. pollinators, dispersers and herbivores) are important agents of natural selection which influence phenological patterns (van Schaik et al. 1993). But apart from biotic and abiotic factors, phylogeny was also suggested to affect phenological patterns (Munguía-Rosas et al. 2011). Related species share characteristics from a common ancestor, and subsequent differentiation in the evolutive course in flowering periods may be driven by selective processes causing changes in genetic, physiological and ecological traits (Wright and Calderon 1995).

C. Aoki (✉)
Universidade Federal de Mato Grosso do Sul, Campus de Aquidauana, Grupo de Estudos Integrados em Biodiversidade do Cerrado e Pantanal, Aquidauana MS, Brasil

Universidade Federal de Mato Grosso do Sul, Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biociências (INBIO), Campo Grande MS, Brasil

Universidade Federal de Mato Grosso do Sul, Programa de Pós-Graduação em Recursos Naturais, Faculdade de Engenharias, Arquitetura e Urbanismo e Geografia (FAENG), Campo Grande MS, Brasil
e-mail: camila.aoki@ufms.br

R. R. Faria
Universidade Federal de Mato Grosso do Sul, Campus de Aquidauana, Grupo de Estudos Integrados em Biodiversidade do Cerrado e Pantanal, Aquidauana MS, Brasil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_13

Overall, phenology is a well-delimited scientific field, with a series of reviews and syntheses (e.g. Rathcke and Lacey 1985; van Schaik et al. 1993; Fenner 1998; Sakai 2001; Visser et al. 2010; Rodriguez et al. 2014; Tang et al. 2016; Chuine and Régnière 2017; Abernethy et al. 2018) and comprehensive bibliographic works (e.g. Hudson and Keatley 2010; Schwartz 2013). Besides being a valuable descriptive tool of plant life-history patterns, phenology is of great utility in predictive models of ecosystem dynamics and as an environmental monitoring tool (Morellato et al. 2016; Bush et al. 2018). Despite their relevance for tropical species, there are relatively few phenological studies given the huge plant diversity (Abernethy et al. 2018). A survey on phenological studies for Central and South America indicated a total of 145 published articles for the entire Neotropical zone (Morellato et al. 2013). This low number already indicates that certain areas have been little explored on plant phenology, and one of them is the Pantanal. In the same review, the Pantanal was grouped with another seven ecosystems in the vegetation type "open grassy savanna", and this group scored a total of only 12 records.

The Pantanal is one of the world's largest continuous wetlands. The Pantanal floodplain has a very gentle slope varying between 50 and 30 cm/km in east-west direction and 3 to 1.5 cm/km in north-south direction (Alvarenga et al. 1982). The most striking characteristic of the Pantanal is its dynamics in annual droughts and floods that determine the ecological interactions and the patterns of biological diversity (Junk et al. 2006). The climatic and hydrological processes between the surrounding highland and the floodplain are fundamental for the maintenance of the water regimes in this complex ecosystem. The depth and duration of flooding can vary from year to year and can show a huge multi-annual fluctuation, from a minimum of 11,000 km^2 to a maximum flooded area reaching 110,000 km^2 (Hamilton et al. 1996). The flood periods vary from shallow and short floods of 2–3 months to deep floods of 9 months, and there are also some permanently flooded areas (Hamilton et al. 1996). The soils vary from very sandy to eutrophic clays, besides alluvial soils (Oliveira et al. 2006) that receive seasonal inputs of nutrients and have a high water availability. Nonetheless, eutrophication and flood also can act as constraints, for example, causing anoxia, whereas drier and more sandy zones may undergo a shortage of water and nutrients (Scremin-Dias et al. 2011) within the

---

Universidade Federal de Mato Grosso do Sul, Programa de Pós-Graduação em Recursos Naturais, Faculdade de Engenharias, Arquitetura e Urbanismo e Geografia (FAENG), Campo Grande MS, Brasil

G. A. Damasceno-Junior
Universidade Federal de Mato Grosso do Sul, Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biociências (INBIO), Campo Grande MS, Brasil

A. Pott
Universidade Federal de Mato Grosso do Sul, Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biociências (INBIO), Campo Grande MS, Brasil

Universidade Federal de Mato Grosso do Sul, Programa de Pós-Graduação em Recursos Naturais, Faculdade de Engenharias, Arquitetura e Urbanismo e Geografia (FAENG), Campo Grande MS, Brasil

mosaic of landforms and habitats (see the Chap. 7 on "Macrohabitats"). Many aquatic macrophytes tend to flower when the flood recedes, a process that generally occurs in a shifting zonation over the topographic gradient; but others already start flowering at the rise of the water (see the Chap. 4 on "Aquatic Plants").

Climatologically, the Pantanal falls in climate type Aw, characterized by two distinct periods of temperature and rain regimes (Pell et al. 2007): a drier period with milder temperatures (May–September) and a rainy period with higher mean temperatures (between October and April). The mean temperatures range between 21 and 27 °C, and the mean annual rainfall varies in space and time, from 800 to 1400 mm. Another differentiation is the photoperiod, as in the dry season the days are on average shorter than in the rainy season. Seasons are considered the central unit for the understanding of phenological events since the variations in the phenophases help in the understanding of the rhythm and amplitude of the seasons (Jeanneret and Rutishauser 2010).

The Pantanal represents a convergence area of plant associations typically linked to Amazonia, the Cerrado, the Atlantic Forest and the Chaco (Pott and Pott 2009). The adjacent Cerrado is the domain that has most influence on the Pantanal in terms of flora, and in some biodiversity studies, the Cerrado and Pantanal are often simplified into one unit (e.g. MMA 2002). Considering the influence in floristic composition from the Cerrado, as well as the similarity in climate, we might suppose that the phenology of the plants in the Pantanal would be strongly correlated to that of the plants in the Cerrado. The starting point to check such a correlation was shown by Oliveira (2008), based on the model of Sarmiento and Monasterio (1983) concerning life forms and phenology of tropical savanna plants. According to Oliveira (2008), in the Cerrado, the phenological variation can be explained when the dry season is regarded as a reference and not as a determinant: the soil dries up during the dry season, which can last up to 6 months. This drying-up can affect the soil until 2 m deep, and it acts as a rigorous environmental filter. Thus, the same author claims that cerrado species synchronize the seed germination and seedling establishment to the beginning of the rainy season. Thus, species that release their seeds at the end of the wet season or during the dry season keep them dormant until the beginning of the next rainy season, and this adjustment maximizes the survival of the seedling (Oliveira 2008). Therefore, in Cerrado areas, it is common to find the different phenophases of species with various strategies of fruit dispersal and different pollination syndromes year-round (Oliveira 2008).

In a morpho-anatomical approach, which is a useful proxy for ecophysiological performance, Scremin-Dias et al. (2011) classified the plants of the Pantanal according to their habitats: Pantanal *sensu lato* (*s.l.*), zones not affected by the periodical flood, and Pantanal *sensu stricto* (*s.s.*) with species living in zones strongly affected by the flood. Hence, the dry season would exert a strong influence on the morpho-anatomical species of the Pantanal *s.l.*, while the flood would act as an essential environmental filter for the establishment of the morpho-anatomical species of the Pantanal *s.s.* Besides, the species of Pantanal *s.s.* group would differ considerably along a gradient, reflecting the large variation in flooding time between the different zones of the Pantanal.

As the Pantanal presents unique temporal dynamics in abiotic factors, which involve the climate and the flood regime, the analysis of temporal series suscitates further studies regarding the adaptations of plants, as well as evolutive approaches. The objective of this review is to establish the state of the art of phenological studies on plant species in the Pantanal, as well as to detect relations between phenological patterns and the main drivers.

13.2 Methods

To establish the state of the art of the phenological studies for the Pantanal, we performed searches in the main available scientific bases: platform CAPES-PERIÓDICOS (www.periodicos-capes-gov-br); Scopus (Elsevier); Science Citation Index Expanded (Web of Science); OneFile (GALE); Technology Research Database; Engineering Research Database; Aquatic Science Journals; ASFA: Aquatic Sciences and Fisheries Abstracts; Springer (CrossRef); SpringerLink; MEDLINE/PubMed (NLM); Materials Science & Engineering Database; Directory of Open Access Journals (DOAJ); AGRIS (United Nations, Food and Agriculture Organization); JSTOR Archival Journals; SciELO (CrossRef); ProQuest Advanced Technologies & Aerospace Collection; Advanced Technologies & Aerospace Database; BioOne; ScienceDirect Journals (Elsevier); and Elsevier (CrossRef).

We did searches only for peer-reviewed articles, with the terms related to phenological studies and utilizing the term "Pantanal" as filter: "Pantanal-pollination"; "Pantanal-phenology"; "Pantanal-frugivory"; "Pantanal-florivory"; "Pantanal-seasonality"; "Pantanal-senescence"; "Pantanal-sprouting"; "Pantanal-remote sensing"; "Pantanal-litterfall"; "Pantanal-herbivory".

Next, we inspected each article for the presence of data of some plant phenophase (flowering, fructification, leaf sprouting and leaf fall). The information on taxonomy, locality, plant phenophase and period of activity were obtained from each article and organized into electronic spreadsheets. We updated plant names according to Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br).

13.3 Results and Discussion

The search returned a total of 1940 articles, and after exclusion of duplicities and removal of those without data on plant phenophases, the result was 17 studies. The selected articles were published between 2002 and 2015, and their number increased during the last years. In the tropics, studies on phenology began to grow during the 1990s (Chambers et al. 2013; Morellato et al. 2013). Most studies covered 1 year (52%), and none is of long term. Long-term data sets on individual phenology are critical to understand how the recurrent cycles vary within a population and change during plant life (Abernethy et al. 2018). Recent studies point to variation in the production of leaves and fruits over the years as a result of climatic variations (Camargo et al. 2018; Dunham et al. 2018; Mendoza et al. 2018).

Although the phenological information covers more than a decade, the existing phenological data on the Pantanal are still insufficient, as most studies were conducted on just one or a few species (Ragusa-Netto 2002; Nunes-da-Cunha and Junk 2004; Salis and Matos 2009; Domene et al. 2010; Bertazzoni and Damasceno-Junior 2011; Fava et al. 2011; Machado et al. 2015) and utilized different methods and foci. Studies with a focus on the community (or assemblages) are rare (Araújo and Sazima 2003; Ragusa-Netto and Fecchio 2006; Boff et al. 2013; Freitas et al. 2013; Neves and Damasceno-Junior 2011) (also see the Chap. 14 on "Temporal Patterns of Pollination and Seed Dispersal in Capões of the Southern Pantanal"). Most studies investigated only the reproductive phenology (flowering and/or fructification), while only four studies included vegetative phenophases.

Considerable part of the information on plant phenology of the Pantanal involves pollination (Araújo and Sazima 2003; Boff et al. 2013) or frugivory (Ragusa-Netto 2002, 2004, 2007, 2015; Ragusa-Netto and Fecchio 2006; França et al. 2009; Paiva et al. 2013). Reproductive phenology (flower and fruit production) still is the key to understand the reach of the individual responses and the potential of climatic changes to start trophic changes within ecosystems (Abernethy et al. 2018 and cited literature).

We observed that the phenological studies are geographically unevenly distributed, with only two in the northern part of the Pantanal (Fig. 13.1). That is in line with Mendoza et al. (2017) who point to Mato Grosso as a state deficient in

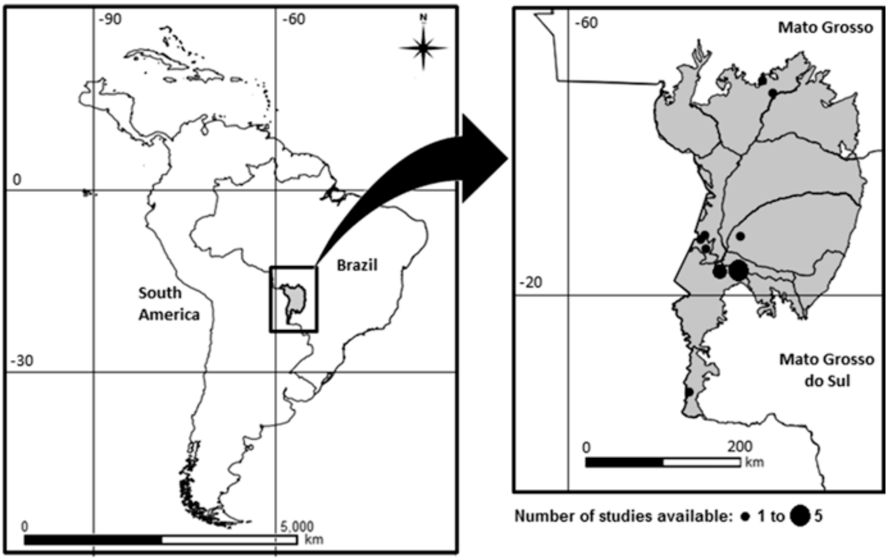


Fig. 13.1 Location of the Brazilian Pantanal wetland in South America; the study areas are represented by circles (circle diameter represents the number of articles)

phenological data. Considering the 11 subregions proposed by Silva and Abdon (1998), there is a concentration of studies in the Miranda-Abobral (5) and Nabileque (4) subregions, both adding up to 53% of the publications. To our knowledge, there is no information about four subregions (Aquidauana, Barão de Melgaço, Cáceres and Paiaguás). Given that the subregions vary in flood, topography/elevation, soil and vegetation, we can conclude that more studies are necessary to verify how the phenophases are affected by such characteristics.

Twenty-nine per cent of the publications included arboreal species in their samplings; around 41% included three or more life forms. Circa 37% of the studied species are arboreal; 36% are herbaceous or subshrubs (Tables 1–4). Among the recorded articles, 15 specified the period of occurrence of the phenophases for the studied species. In our analysis, we did not include the reports of Neves and Damasceno-Junior (2011) and Freitas et al. (2013) because they did not allow to extract the necessary information about the period of occurrence of each phenophase.

The reviewed studies provide phenological information on 78 plant species, belonging to 70 genera and 36 families (Tables 1–4). Considering that there are 2250 species of phanerogams with confirmed occurrence in the Pantanal (see the Chap. 3 on "Flora"), our data include less than 4% of the flora. The family with the highest number of information is Fabaceae (14 species), followed by Malvaceae (8 species), Rubiaceae (5 species) and Arecaceae (4 species). Except for Arecaceae, the others are among the richest families in the Pantanal, together with Poaceae, Cyperaceae and Asteraceae, for which there is scarce or no information.

Only two publications included palustrine and/or aquatic plants in the sampling, totalling five species, four of which have data only on flowering: *Bacopa australis* V.C.Souza, *Echinodorus paniculatus* Micheli, *Helanthium tenellum* (Mart.) Britton and *Ludwigia octovalvis* (Jacq.) P.H.Raven (Boff et al. 2013). The fifth species, *Oryza latifolia* Desv., has data on vegetative and reproductive phenology (Bertazzoni and Damasceno-Junior 2011). For the aquatic macrophyte flora of the floodplain of ca. 280 species (Pott et al. 2011), there are available data for less than 2% of the species, or less, considering the updated number of 534 (see the Chap. 4), which makes this a neglected group not only in the Pantanal but in phenological studies in general.

The time defined as rainy season varied little between articles and is generally between October and March. According to that, the pattern arising for leaf sprouting (Table 13.1) and leaf fall (Table 13.2) is of occurrence of these phenophases throughout the year for practically all studied species; however, the results show a bias for

Table 13.1 Data on leaf flush of plant species of the Pantanal over the year. Grey areas represent the rainy season

Family	Species (Reference)	J	F	M	A	M	J	J	A	S	O	N	D
Arecaceae	*Attalea phalerata* Mart. ex Spreng.(1)	•	•	•	•	•	•	•	•	•	•	•	•
Arecaceae	*Bactris glaucescens* Drude (1)	•	•	•	•	•	•	•	•	•	•	•	•
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand(2)	•	•	•	•	•	•	•	•	•	•	•	•
Vochysiaceae	*Vochysia divergens* Pohl(3)			•	•	•	•	•					

(1)Fava et al. (2011), (2)Domene et al. (2010), (3)Nunes-da-Cunha and Junk (2004)

Table 13.2 Data on leaf fall of plant species of the Pantanal over the year. Grey areas represent the rainy season

Family	Species $^{(Reference)}$	J	F	M	A	M	J	J	A	S	O	N	D
Arecaceae	*Attalea phalerata* Mart. ex Spreng.(1)	•	•	•	•	•	•	•	•	•	•	•	•
Arecaceae	*Bactris glaucescens* Drude (1)	•	•	•	•	•	•	•	•	•	•	•	•
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand(2)	•	•	•	•	•	•	•	•	•	•	•	•
Vochysiaceae	*Vochysia divergens* Pohl(3, 4)	•	•	•	•	•	•	•	•	•	•	•	•

(1)Fava et al. (2011), (2)Domene et al. (2010), (3)Nunes-da-Cunha and Junk (2004), (4)Machado et al. (2015)

Table 13.3 Data on flowering of plant species of the Pantanal over the year. Grey areas represent the rainy season

Family	Species $^{(Reference)}$	J	F	M	A	M	J	J	A	S	O	N	D
Alismataceae	*Echinodorus paniculatus* Micheli(1)		•										
Alismataceae	*Helanthium tenellum* (Mart.) Britton(1)				•								
Amaryllidaceae	*Hippeastrum puniceum* (Lam.) Kuntze(2)										•		
Apocynaceae	*Aspidosperma australe* Müll.Arg.(3)									•			
Apocynaceae	*Prestonia coalita* (Vell.) Woodson(2)			•								•	•
Apocynaceae	*Thevetia bicornuta* Müll.Arg.(2)	•		•									
Arecaceae	*Acrocomia aculeata* (Jacq.) Lodd. ex Mart.(4)	•	•	•							•	•	•
Arecaceae	*Attalea phalerata* Mart. ex Spreng.(5)	•	•	•	•	•	•	•	•	•	•	•	•
Arecaceae	*Bactris glaucescens* Drude(5)	•	•	•	•						•	•	•
Arecaceae	*Copernicia alba* Morong ex Morong & Britton(4, 6)							•	•	•	•	•	•
Asteraceae	*Centratherum punctatum* Cass.(1)	•										•	
Asteraceae	*Sphagneticola brachycarpa* (Baker) Pruski(1)	•									•	•	•
Bignoniaceae	*Fridericia pubescens* (L.) L.G.Lohmann(2)						•	•	•	•	•		

(1)Boff et al. (2013), (2)Araújo e Sazima (2003), (3)Ragusa-Netto (2015), (4)Salis and Matos (2009), (5)Fava et al. (2011), (6)Ragusa-Netto and Fecchio (2006), (7)Ragusa-Netto (2004), (8)Ragusa-Netto (2007), (9)Paiva et al. (2013), (10)Domene et al. (2010), (11)Bertazzoni and Damasceno-Junior (2011), (12)Nunes-da-Cunha and Junk (2004), (13)Machado et al. (2015)

palms, which represents 50% of the species known to have information about these phenophases.

For reproductive phenology, there are data on flowering for 66 species (Table 13.3) and fructification for 33 species (Table 13.4). There are records of flowers and fruits year-round, vital for the maintenance of the fauna depending on these resources (e.g. flower visitors and frugivores). That probably is a reflex of different reproductive strategies of the plants developed in response to the most varied biotic and abiotic factors.

In the herbaceous-subshrubby component, as well as lianas and palms, the peak of flowering occurs during the rainy season, with a marked reduction during the dry

Table 13.4 Data on fructification of plant species of the Pantanal over the year. Grey areas represent the rainy season

Family	**Species (Reference)**			**M**	**A**	**M**	**J**	**J**	**A**	**S**			**D**
Apocynaceae	*Aspidosperma australe* Müll.Arg.(1, 2)			•	•	•	•	•					
Arecaceae	*Acrocomia aculeata* (Jacq.) Lodd. ex Mart. (3)	•	•	•	•	•	•	•	•	•	•	•	•
Arecaceae	*Attalea phalerata* Mart. ex Spreng. (1, 2, 4, 5)	•	•	•	•	•	•	•	•	•	•	•	•
Arecaceae	*Bactris glaucescens* Drude(5)	•	•	•	•						•	•	•
Arecaceae	*Copernicia alba* Morong ex Morong & Britton(1, 2, 3, 4, 6, 7)	•	•	•	•	•	•					•	•
Bignoniaceae	*Handroanthus heptaphyllus* (Vell.) Mattos(1)							•	•	•			
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand(8)	•	•								•	•	•
Capparaceae	*Crateva tapia* L. (1, 2, 7)	•	•	•					•			•	•
Euphorbiaceae	*Sapium obovatum* Klotzsch ex Müll.Arg. (1, 2)		•	•	•	•							
Fabaceae	*Albizia inundata* (Mart.) Barneby & J.W.Grimes(1, 2)								•	•	•	•	•
Fabaceae	*Albizia niopoides* (Spruce ex Benth.) Burkart(1, 2)						•	•	•	•	•		
Fabaceae	*Andira inermis* (W.Wright) DC.(7)	•											
Fabaceae	*Cassia grandis* L.f. (1)							•	•	•	•		
Fabaceae	*Enterolobium contortisiliquum* (Vell.) Morong(1, 2)						•	•	•	•	•		
Fabaceae	*Inga vera* Willd. (1, 2, 4, 6)	•	•	•	•	•	•	•	•				
Fabaceae	*Lonchocarpus pluvialis* Rusby (1)					•							
Lamiaceae	*Vitex cymosa* Bertero ex Spreng. (1, 2, 4, 7)	•	•									•	•
Lauraceae	*Ocotea diospyrifolia* (Meisn.) Mez(1, 2)	•	•									•	•
Malpighiaceae	*Byrsonima cydoniifolia* A.Juss. (7)		•	•									
Malvaceae	*Guazuma ulmifolia* Lam. (1, 2)	•		•	•	•	•	•	•				
Moraceae	*Ficus calyptroceras* (Miq.) Miq. (8)	•	•	•	•	•	•	•	•	•	•	•	•
Moraceae	*Ficus luschnathiana* (Miq.) Miq.(1, 2, 4, 6, 7)	•	•	•	•		•	•		•	•	•	•
Myrtaceae	*Eugenia chiquitensis* O.Berg(7)											•	
Myrtaceae	*Myrcia egensis* (O.Berg) McVaugh(7)											•	
Poaceae	*Oryza latifolia* Desv.					•	•	•	•	•	•	•	
Polygonaceae	*Coccoloba cujabensis* Wedd. (7)										•		
Polygonaceae	*Triplaris americana* L. (1, 2)									•	•	•	
Rubiaceae	*Genipa americana* L. (6, 7, 10)					•	•	•	•	•	•		
Salicaceae	*Banara arguta* Briq. (1, 2, 4, 7, 10)		•	•	•	•	•						
Santalaceae	*Phoradendron quadrangulare* (Kunth) Griseb. (4)					•							
Smilacaceae	*Smilax fluminensis* Steud. (7)					•							
Urticaceae	*Cecropia pachystachya* Trécul(1, 2, 4, 6, 7, 10)	•	•	•	•	•	•	•	•	•	•	•	•
Vochysiaceae	*Vochysia divergens* Pohl(11)								•	•	•		

(1)Ragusa-Netto and Fecchio (2006), (2)Ragusa-Netto (2007), (3)Salis and Matos (2009), (4)Ragusa-Netto (2004), (5)Fava et al. (2011), (6)França et al. (2009), (7)Ragusa-Netto (2015), (8)Domene et al. (2010), (9)Bertazzoni and Damasceno-Junior (2011), (10)Paiva et al. (2013), (11)Nunes-da-Cunha and Junk (2004)

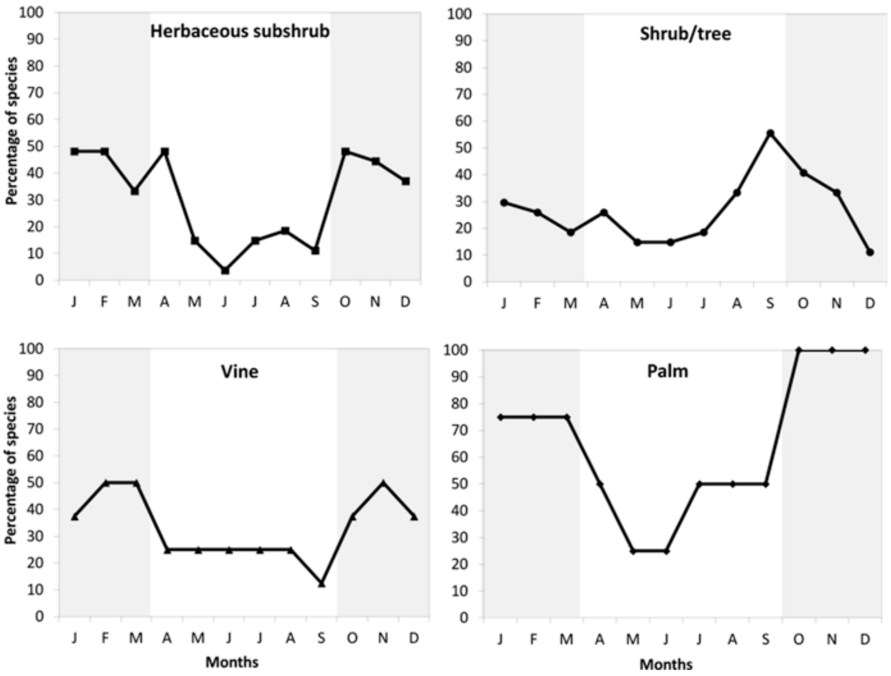


Fig. 13.2 Percentage of species belonging to different vegetation components flowering in the Pantanal over the dry and the rainy season (in grey)

season (Fig. 13.2). In the shrubby-arboreal component, the peak of flowering occurs at the end of the dry season (Fig. 13.2). The literature shows such a distinct behaviour of the herbaceous-subshrubby component compared with the shrubby-arboreal stratum for the Cerrado, also under a seasonal climatic domain (Mantovani and Martins 1988; Batalha et al. 1997; Batalha and Mantovani 2000; Batalha and Martins 2004). That probably results, among other factors, from differences in the stratification of the root systems and of different responses to water shortage in the driest period (Barbosa and Sazima 2008). In seasonal environments, the herbaceous component generally shows its best development in the rainy season (Sarmiento 1983; Cianciaruso et al. 2005) once the roots exploit the upper soil layers with available moisture (Sarmiento 1983).

Regarding fructification, most available information is for arboreal (75%) and zoochoric species (72%), because most of the studies containing these data focused on frugivory. Anemochoric species (N = 5) showed the peak of fructification at the end of the dry season, whereas autochoric (N = 3) and barochoric (N = 1) extended it to the beginning of the rainy season. In contrast, zoochoric species (N = 24) presented the peak of fructification during the rainy season (Fig. 13.3).

Similar results were recorded in seasonal environments of the Cerrado (Mantovani and Martins 1988; Batalha et al. 1997). This pattern was also found in a Chaco community in the southernmost subregion of the Pantanal (Porto Murtinho) (Freitas

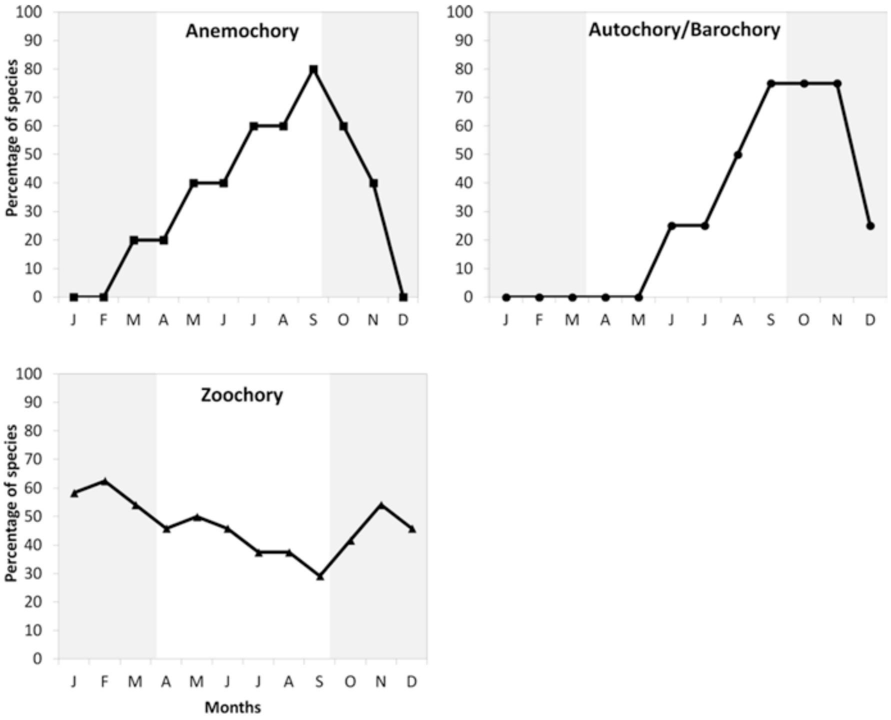


Fig. 13.3 Percentage of species of different dispersal syndromes at fructification in the Pantanal over the dry and the rainy season (in grey)

et al. 2013) and in forest islets (see the Chap. 14 on "Temporal Patterns of Pollination and Seed Dispersal in Capões of the Southern Pantanal"). In seasonal climates, anemochory is more efficient in the dry season. This is suggested as an adaptation to enhance dispersal, as deciduous species typically lose their leaves during water shortage periods, thus reducing obstacles to dispersal units (Morellato and Leitão Filho 1996; Griz and Machado 2001). For seed dispersal, the fruits are generally dry or dehydrate to free their seeds (Batalha and Mantovani 2000). Fleshy fruits are usually common during the rainy season since the pulp requires a high water content for ripening (Chen et al. 2016).

There are records of species that fructify throughout the year. Fruit set and seed dispersal during the dry or in the wet season are often associated with the best time for seedling establishment (Oliveira 2008). This requires different strategies of dormancy to maximally use the ideal time for germination, and that typically is at the onset of the rainy season (Garwwood 1983).

Among the studied variables to explain the phenological behaviour of the species are, in order of frequency, rainfall (Araújo and Sazima 2003; Nunes-da-Cunha and Junk 2004; Ragusa-Netto and Fecchio 2006; Domene et al. 2010; Fava et al. 2011; Neves and Damasceno-Junior 2011; Freitas et al. 2013; Ragusa-Netto 2015), water level (Nunes-da-Cunha and Junk 2004; Ragusa-Netto and Fecchio 2006; Bertazzoni and Damasceno-Junior 2011; Fava et al. 2011), temperature (Bertazzoni and Damasceno-Junior 2011; Fava et al. 2011; Dalmolin et al. 2015), photoperiod (Bertazzoni and Damasceno-Junior 2011; Dalmolin et al. 2015), relative humidity (Dalmolin et al. 2015) and vapour pressure deficit (Dalmolin et al. 2015). Seven articles did not relate the phenophases to the predictive variables. Regarding the influence received from different biomes and the unique soil-climate conditions, the Pantanal provides an opportunity to study genotype-environment effects, as well as phylogenetic restrictions on phenology, given that the plain region is continuously colonized by species from the surrounding biomes with different biotic and abiotic conditions.

In the Pantanal, the characteristics of soil, relief, hydrological regime, vegetation and climate denote obvious differences between subregions, and therefore these are also called "pantanals" and therefore each one is also called "pantanais" by the local people, even in publications (Faria et al. 2013). We may interpret such characteristics as drivers of the phenological patterns of the plants of the Pantanal.

Fire is another factor interfering with phenology (see the **Chap. 18** on "Fire"). For example, we observed that the monodominant grass *Elionurus muticus* sets inflorescences a month after a fire, or a few weeks later if heavily grazed, whereas the associated *Trachypogon polymorphus* flowers only 1 year after burning. Fire events also help to synchronize the flowering of *Tabebuia aurea* and cause leaf drop followed by leaf flush in many other species, as well as top kill and basal resprouting.

Studies in other wetlands point out the critical role of the flood as a synchronizer of phenological patterns in plants. In one study, some species showed a fourfold higher growth in diameter when planted in soils with a sufficient water retention capacity (Cardoso et al. 2012). Tree species of floodplains can synchronize their fructification during the flood period (Haugaasen and Peres 2005), deciduous species of floodable areas can synchronize their leaf fall in the flood period (Parolin 2000), and submersion and drought can cause a state of dormancy in seedlings (Parolin 2001). In the Pantanal, where the flood period is well pronounced, we can expect a strong influence of flood on phenological patterns. The study on the phenology of *Oryza latifolia* in the Paraguay River (Bertazzoni and Damasceno-Junior 2011) is an example. It shows that the percentage of cover of this species increases with the increasing water level, varying from 30% cover in the lower level of inundation until 80% cover during the highest level. It also shows that flowering is synchronizing to increased water level and diminishing day length. A case of response to day length is *Bidens gardneri* Baker, which flowers and fructifies year-round in the Pantanal, while in the Cerrado of São Paulo, the species is responsive to photoperiod, according to Klein (1994).

Concerning the biotic influences on the phenology of plants, it is worth to mention that the majority of animal species of the Pantanal have a wide geographic distribution and few are endemic (Brown-Junior 1984; Junk and Cunha 2005; Junk et al. 2006). The species distribution varies within and between the different habitats over the flood gradient (Silva et al. 2001; Alho 2008). Moreover, the behaviour of primary consumers under the influence of flood in the Pantanal may differ from the behaviour they exhibit in their respective adjacent biomes, a factor that would induce phenological adjustments in the plants.

The scarcity of phenological information hinders detailed and robust analyses of the triggering factors of the phenophases. The short time of data sampling on phenology in the Pantanal is still an obstacle to the understanding of the interannual variations in the phenology of individuals, populations and communities. The systematic collection of such information, the standardization of the sampling protocols (to solve the challenges of comparisons between localities, continental and global), long-term sampling and investment of resources for phenological research are among the main challenges and recommendations to enhance the understanding of these ecological processes in the Pantanal.

Acknowledgements This study was funded in part by the Universidade Federal de Mato Grosso do Sul (UFMS/MEC-Brazil), Coordination for the Improvement of Higher Education Personnel – Brazil (CAPES) – Finance Code 001; and Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia de MS (FUNDECT) for financial support through the project “Reprodução de Angiospermas no Pantanal: Fenologia e Redes Ecológicas” (Process No. 59/300.048/2015) and CNPq for the research grant to G. A. Damasceno-Junior (process n° 307429/2019-9). We would like to thank the three anonymous reviewers for their suggestions and comments.

References

Abernethy K, Bush ER, Forget PM, Mendoza I, Morellato LPC (2018) Current issues in tropical phenology: a synthesis. Biotropica 50(3):477–482

Alho CJR (2008) Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. Braz J Biol 68(4):957–966

Alvarenga SM, Brasil AE, Del’Arco DM (1982) Geomorfologia. In: BRASIL. Ministério das Minas e Energia. Projeto RADAMBRASIL. Rio de Janeiro-RJ, Brasil, pp. 125–184

Araújo AC, Sazima M (2003) The assemblage of flowers visited by hummingbirds in the “capões” of Southern Pantanal, Mato Grosso do Sul, Brazil. Flora 198:427–435

Barbosa AAA, Sazima M (2008) Biologia reprodutiva de plantas herbáceo-arbustivas de uma área de Campo Sujo de Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: Ecologia e Flora. Embrapa Cerrados, Brasília, pp 291–307

Batalha MA, Mantovani W (2000) Reproductive phenological patterns of cerrado plant species at the Pé-de-Gigante reserve (Santa Rita do Passa Quatro, SP, Brazil): a comparison between the herbaceous and woody floras. Rev Bras Biol 60:129–145

Batalha MA, Martins FR (2004) Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). Aust J Bot 52:140–161

Batalha MA, Aragaki S, Mantovani W (1997) Variações fenológicas das espécies do Cerrado em Emas (Pirassununga, SP). Acta Bot Bras 11:61–78

Bertazzoni EC, Damasceno-Junior GA (2011) Aspectos da biologia e fenologia de *Oryza latifolia* Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Bot Bras 2:476–786

Boff S, Araujo AC, Pott A (2013) Bees (Hymenoptera: Apoidea) and flowers of natural forest patches of southern Pantanal. Biota Neotropica 13(4):46–56

Brown-Junior K (1984) Zoogeografia da região do Pantanal Mato-grossense. In: Anais do simpósio sobre os Recursos Naturais e Sócio-Econômicos do Pantanal. Corumbá. EMBRAPA, Brasília, pp 137–78

Bush ER, Bunnefeld N, Dimoto E, Dikangadissi JT, Jeffery K, Tutin C, White L, Abernethy KA (2018) Towards effective monitoring of tropical phenology: maximizing returns and reducing uncertainty in long-term studies. Biotropica 50(3):455–464

Camargo G, Alberton B, De Carvalho GH, Pays Magalhães PAN, Morellato LPC (2018) Leafing patterns and leaf exchange strategies of a cerrado woody community. Biotropica 50:442–454

Cardoso FCG, Marques R, Botosso PC, Marques MCM (2012) Stem growth and phenology of two tropical trees in contrasting soil conditions. Plant Soil 354:269–281

Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont LJ, Crawford RJM, Durant JM, Hughes L, Keatley MR, Low M, Morellato LPC, Poloczanska ES, Ruoppolo V, Vanstreels RET, Woehler EJ, Wolfaardt AC (2013) Phenological changes in the Southern Hemisphere. PLoS ONE 8:e75514

Chen SC, Cornwell WK, Zhang HX, Moles AT (2016) Plants show more flesh in the tropics: variation in fruit type along latitudinal and climatic gradients. Ecography 40:531–538

Chuine I, Régnière J (2017) Process-based models of phenology for plants and animals. Annu Rev Ecol Evol Syst 48:159–182

Cianciaruso MV, Batalha MA, Silva IA (2005) Seasonal variation of a hyperseasonal cerrado in Emas National Park, central Brazil. Flora 200(4):345–353

Dalmolin AC, Lobo FA, Vourlitis GL, Silva PR, Dalmagro HJ, Antunes MZ Jr, Ortíz CER (2015) Is the dry season an important driver of phenology and growth for two Brazilian savanna tree species with contrasting leaf habits? Plant Ecol 216:406–417

Domene VD, Mattos PP, Salis SM (2010) Fenologia e crescimento de Almécega no Pantanal da Nhecolândia, Mato Grosso do Sul. Corumbá, Embrapa Pantanal. Comunicado Técnico 263(83):1–5

Dunham AE, Razafindratsima OH, Rakotonirina P, Wright PC (2018) Fruiting phenology is linked to rainfall variability in a tropical rain forest. Biotropica 50:396–404

Faria RR, Braga RT, Mioto C, Paranhos-Filho AC, Souza FL, Bini LM (2013) Correspondências entre classificações fisiográficas e padrões espaciais de assembleias de aves e mamíferos no Pantanal Brasileiro. Ecol Aust 23:08–17

Fava WS, Covre WS, Sigrist MR (2011) *Attalea phalerata* and *Bactris glaucescens* (Arecaceae, Arecoideae): Phenology and pollination ecology in the Pantanal, Brazil. Flora 206:575–584

Fenner M (1998) The phenology of growth and reproduction in plants. Perspect Plant Ecol Evol Syst 1:78–91

França LF, Ragusa-Netto J, Paiva LV (2009) Consumo de frutos e abundância de Tucano Toco (*Ramphastos toco*) em dois hábitats do Pantanal Sul. Biota Neotropica 9:125–130

Freitas TG, Souza CS, Aoki C, Arakaki LMM, Stefanello TH, Sartori ALB, Sigrist MR (2013) Flora of Brazilian humid Chaco: Composition and reproductive phenology. Check List 9(5):973–979

Garwwod NC (1983) Seed germination in a seasonal tropical forest in Panama: a community study. Ecol Monogr 53:159–181

Griz LMS, Machado ICS (2001) Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. J Trop Ecol 17:303–321

Hamilton SK, Zippel S, Melak JM (1996) Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. Arch Hydrobiol 37(1):1–23

Haugaasen T, Peres CA (2005) Tree phenology in adjacent Amazonian flooded and unflooded forests. Biotropica 37(4):620–630

Hudson IL, Keatley MR (eds) (2010) Phenological research: methods for environmental and climate change analysis. Springer, Dordrecht, 525p

Jeanneret F, Rutishauser T (2010) Seasonality as a core business of phenology. In: Hudson IL, Keatley MR (eds) Phenological research: methods for environmental and climate change analysis. Springer, Dordrecht, pp 63–74

Junk WJ, Cunha CN (2005) Pantanal: a large South American wetland at a crossroads. Ecol Eng 24:391–401

Junk WJ, Cunha CN, Wantzen KM, Petermann P, Strüssmann C, Marques MI, Adis J (2006) Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquat Sci 69(3):278–309

Klein AL (1994) Fenologia e desenvolvimento de diferentes populações de *Bidens gardneri* Baker (Asteraceae). In: Anais do VI Congresso de Iniciação Científica da UNESP, Guaratinguetá

Machado NG, Sanches L, Aquino AM, Silva LB, Novais JWZ, Biudes MS (2015) Growth rhythm of *Vochysia divergens* Pohl (Vochysiaceae) in the Northern Pantanal. Acta Sci 37(1):81–90

Mantovani W, Martins FR (1988) Variações fenológicas das espécies do cerrado da Reserva Biológica de Moji Guaçu, Estado de São Paulo. Rev Bras Bot 11:101–112

Mendoza I, Peres CA, Morellato LPC (2017) Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. Glob Planet Chang 148:227–241

Mendoza I, Condit R, Wright SJ, Caubere A, Châtelet P, Hardy I, Forget PM (2018) Inter-annual variability of fruit timing and quantity in Nouragues (French Guiana): insights from hierarchical Bayesian analyses. Biotropica 50:431–441

MMA (2002) Avaliação e identificação de áreas e ações prioritárias para a conservação, utilização sustentável e repartição dos benefícios da biodiversidade nos biomas brasileiros. MMA/SBF, Brasília, 404 p

Morellato LPC, Leitão-Filho H (1996) Reproductive phenology of climbers in a Southeastern Brazilian forest. Biotropica 28(2):180–191

Morellato LPC, Camargo MGG, Gressler E (2013) A review of plant phenology in South and Central America 91-113p. In: Schartz MD (ed) Phenology: an integrative environmental science, 2nd edn. Springer, Dordrecht, 610p

Morellato LPC, Alberton B, Alvarado ST, Borges B, Buisson E, Camargo MGG, Cancian LF, Carstensena DW, Escobar DFE, Leite PTP, Mendoza I, Rocha NMWB, Soares NC, Silva TSF, Staggemeier VG, Streher AS, Vargas BC, Peres CA (2016) Linking plant phenology to conservation biology. Biol Conserv 195:60–72

Munguía-Rosas MA, Ollerton J, Parra-Tabla V, De-Nova JA (2011) Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. Ecol Lett 14:511–521

Neves DRM, Damasceno-Junior GA (2011) Post-fire phenology in a campo sujo vegetation in the Urucum plateau, Mato Grosso do Sul, Brazil. Braz J Biol 71(4):881–888

Nunes-da-Cunha C, Junk WJ (2004) Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. Appl Veg Sci 7:103–110

Oliveira PE (2008) Fenologia e biologia reprodutiva das espécies do Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: ecologia e flora. Embrapa-CPAC, Planaltina, pp 275–286

Oliveira H, Carvalho-Filho A, Schaefer CE, Reynaud G, Cardoso EL (2006) Soils of the Pantanal. In: Dekker M (ed) Encyclopedia of soil science. Taylor & Francis, pp 1–6

Paiva LV, Ragusa-Netto J, França LF (2013) Disponibilidade de alimento e abundância de *Ortalis canicollis* durante a estação seca em matas no Pantanal Sul, Brasil. Neotropical Biol Conserv 8(1):31–40

Parolin P (2000) Phenology and CO2-assimilation of trees in Central Amazonian floodplains. J Trop Ecol 16:465–473

Parolin P (2001) Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. Oecologia 128:326–335

Pell MC, Finlayson BL, Mcahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Aust Hydrol Earth Syst Sci 11:1633–1644

Pott A, Pott VJ (2009) Vegetação do Pantanal: fitogeografia e dinâmica. Anais 2° Simpósio de Geotecnologias no Pantanal, Corumbá-MS, Embrapa Informática Agropecuária/INPE, pp 1065–1076

Pott VJ, Pott A, Lima LCP, Moreira SN, Oliveira AKM (2011) Aquatic macrophyte diversity of the Pantanal wetland and upper basin. Braz J Biol 71(1):255–263

Ragusa-Netto J (2002) Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). Braz J Biol 62(2):339–346

Ragusa-Netto J (2004) Flowers, fruits, and the abundance of the Yellow-chevroned Parakeet (*Brotogeris chiriri*) at a gallery forest in the south Pantanal (Brazil). Braz J Biol 64:867–877

Ragusa-Netto J (2007) Nectar, fleshy fruits and the abundance of parrots at a gallery forest in the southern Pantanal (Brazil). Stud Neotropical Fauna Environ 42(2):93–99

Ragusa-Netto J (2015) Chaco Chachalaca (*Ortalis canicollis*, Wagler, 1830) feeding ecology in a gallery forest in the South Pantanal (Brazil). Braz J Biol 75(1):49–57

Ragusa-Netto J, Fecchio A (2006) Plant food resources and the diet of a parrot community in a gallery forest of the southern Pantanal (Brazil). Braz J Biol 66(4):1021–1032

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Annu Rev Ecol Syst 16:179–214

Rodriguez HG, Maiti R, Sarkar NC (2014) Phenology of woody species: a review. Int J Bio-resour Stress Manag 5(3):436–443

Sakai S (2001) Phenological diversity in tropical forests. Popul Ecol 43:77–86

Salis SM, Matos PP (2009) Floração e Frutificação da Bocaiúva (*Acrocomia aculeata*) e do Carandá (*Copernicia alba*) no Pantanal. Comunicado Técnico da Embrapa 78:1–6

Sarmiento G (1983) The savannas of tropical America. In: Goodall DW (ed) Ecosystems of the world: tropical savannas. Elsevier, Amsterdam, pp 245–288

Sarmiento G, Monasterio M (1983) Life forms and phenology. In: Bouliere F (ed) Ecosystems of the world: tropical savannas. Elsevier, Amsterdam, pp 79–108

Schwartz MD (ed) (2013) Phenology: an integrative environmental science, 2nd edn. Springer. 610p

Scremin-Dias E, Lorenz-Lemke AP, Oliveira AKM (2011) The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress. Braz J Biol 71(1):275–282

Silva JSV, Abdon MM (1998) Delimitação do Pantanal Brasileiro e suas sub-regiões. Pesqui. Agropecu. Bras. 33:1703–1711

Silva CJ, Watzen KM, Nunes-da-Cunha C, Machado FA (2001) Biodiversity in the Pantanal wetland, Brasil. In: Gopal B, Junk WJ, Davis JA (eds) Biodiversity in wetlands: assessment, function and conservation, vol 2. Backhuys Publishers, Leiden, pp 187–215

Tang J, Körner C, Muraoka H, Piao S, Shen M, Thackeray SJ, Yang X (2016) Emerging opportunities and challenges in phenology: a review. Ecosphere 7(8):117

van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptative significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377

Visser ME, Caro SP, van Oers K, Schaper SV, Helm B (2010) Phenology, seasonal timing and circannual rhythms: towards a unified framework. Philos Trans R Soc B 365:3113–3127

Wright SJ, Calderon O (1995) Phylogenetic patterns among tropical flowering phenologies. J Ecol 83:937–948

Chapter 14
Temporal Patterns of Pollination and Seed Dispersal in *Capões* of the Southern Pantanal

Vanessa Gabrielle Nóbrega Gomes, Marlies Sazima, Rafael Arruda, Erich Fischer, and Andréa Cardoso Araujo

14.1 Introduction

Reproductive phenology involves temporal patterns of resource availability throughout the year, these patterns being regulated by both environmental and biotic factors, including herbivores, pollinators and seed dispersers (Rathcke and Lacey 1985; Morellato et al. 2016; see also the chapter on "Synthesis of the Present Knowledge on Plant Phenology of the Pantanal" Chap. 13). Pollination and seed dispersal are two key processes in the reproductive ecology of most plants, which depend on a myriad of different pollen and seed vectors (Hansen and Muller 2009). The concept of syndromes comprises a set of characteristics of plant species commonly adjusted to a particular biotic group or abiotic agent as a result of providing pollination and seed dispersal services (Faegri and van der Pijl 1979; van der Pijl 1982). Floral attributes, such as shape, size, colour of corolla, period of anthesis and presence and type of odour, as well as offered resources, frequently vary among types of pollen vectors. Similarly, fruit traits like shape, size, weight, consistency, colour, dehiscence, pulp composition and seed size are variable according to different seed vectors.

V. G. N. Gomes
Instituto Nacional do Semiárido, Campina Grande, PB, Brazil

M. Sazima
Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil

R. Arruda
Instituto de Ciências Naturais, Humanas e Sociais, Universidade Federal de Mato Grosso, Sinop, MT, Brazil

E. Fischer · A. C. Araujo (✉)
Instituto de Biologia, Universidade Federal de Mato Grosso do Sul,
Campo Grande, MS, Brazil
e-mail: andrea.araujo@ufms.br

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_14

Most tropical plant species greatly depend on biotic vectors for reproduction, being invertebrates the commonest pollinators (van der Pijl 1982; Bawa 1990; Fleming and Kress 2013; Rech et al. 2016). Bees represent the most important group of pollinators, since they pollinate a vast number of Neotropical species (Bawa 1990; Aoki and Sigrist 2006; Lopes et al. 2007; Souza et al. 2016). Birds and bats pollinate ca. 15% to 28% of the plant species in a given community, being the most important groups of pollen vectors among vertebrates (Borges 2000; Oliveira and Gibbs 2000; Machado and Lopes 2004; Fischer et al. 2014; Quirino and Machado 2014). Likewise, animal-mediated seed dispersal is the main strategy among tropical plants, representing 50–90% of the species in local forest communities (Howe and Smallwood 1982; Jordano 2000; Tabarelli and Peres 2002). In wet forests, many plants produce fleshy fruits adapted to animal consumption, whereas anemochoric species or those dispersed by other abiotic modes prevail in dry environments with marked seasonality (Machado et al. 1997; Griz and Machado 2001; Jara-Guerrero et al. 2011; Carvalho and Sartori 2014).

Different groups of pollinators and seed dispersers can present seasonal variation in the use of flower and fruit resources (Koptur et al. 1988; Fischer et al. 2018). In addition, these groups may use different strata of the forests, as each stratum presents microclimatic conditions and availability of resources associated with a specific fauna (Bawa et al. 1985; Almeida-Neto et al. 2008). Since animal communities are stratified and seasonally variable in relation to their requirements and to their frequency of occurrence, the vertical distribution in the vegetation and seasonality are expected to affect plant-animal interactions (Koptur et al. 1988; Bawa 1990; Araujo and Sazima 2003; Souza et al. 2018).

The concept of pollination syndrome by Faegri and van der Pijl (1979) has been controversial because it assumes specialization of animal-plant interactions though specialized pollination systems are uncommon (Waser et al. 1996; Ollerton et al. 2009; Jordano 2010). Nonetheless, the concept of syndrome allows to objectively classify plant species according to their main pollinator types, being useful for addressing plant reproductive ecology at the community level and for comparisons among vegetation types (Machado and Lopes 2004). Results on seed dispersal syndromes are likewise useful in the same contexts, and they have indeed been used for such studies (Griz and Machado 2001). Overall, results of pollination and seed dispersal syndromes can raise broad ecological issues and provide valuable information for finer studies on plant reproductive biology (Dafni and O'Toole 1994; Parra-Tabla and Bullock 2002; Muchhala and Jarrín 2002).

Studies on pollination in the Pantanal have mainly focused on particular plant species in open physiognomies and riparian forests (e.g. Sazima et al. 2001; Longo and Fischer 2006; Paulino-Neto 2007; Fava et al. 2011; Silva et al. 2013; Cunha et al. 2014; Fadini et al. 2018), likewise studies on seed dispersal, which are notably related to mammals or fishes (Teixeira et al. 2009; Costa-Pereira et al. 2011; Donatti et al. 2011; Wang et al. 2011; Munin et al. 2012; Correa et al. 2016; Correa and

Fischer 2017; Fischer et al. 2018). Araujo and Sazima (2003) evaluated the year-round flower availability for hummingbirds and the species pollinated by them in the capões of the Pantanal, i.e. natural semideciduous forest patches (0.5 to 5 ha) surrounded by seasonally floodable grasslands. Since the capões form a patchy-forested landscape, the knowledge on phenology, pollination and dispersal modes in this physiognomy can offer a comparative basis and provide guidelines for understanding plant reproductive biology in fragmented forests.

In this chapter, we provide an overview on flowering and fruiting phenology, as well as on the pollination and seed dispersal syndromes of species occurring in capões. In addition, we describe patterns of occurrence of syndromes among microhabitats and the seasonal occurrence of syndromes throughout the year, thus also assessing resource availability for flower visitors and fruit eaters. Overall, this study reports how the pollination and seed dispersal syndromes of the plant community are arranged in time and in the vertical space in capões of the southern Pantanal.

14.2 Methods

14.2.1 Study Site

Fieldwork was carried out in 52 capões ranging from 0.2 to 3.8 ha (0.99 ± 0.75 ha) in the Miranda subregion, southern Pantanal (14° to 22° S and 53° to 66° W), yielding a total sample area of about 51.6 ha. These forest patches are commonly circular or elliptical in shape and 1–3 m more elevated than the natural grasslands surrounding them (Fig. 14.1). They are important elements of the landscape by sheltering flood-intolerant plant species and terrestrial animals during the flood pulses. Their origin has been attributed to abiotic and biotic factors associated with local geomorphology and differential erosion. Floristically, the interior of capões is mainly composed of species typical of semideciduous alluvial forests and their edges composed of plants characteristic of gallery forests and Chaco (Prance and Schaller 1982; Damasceno-Junior et al. 1999).

The climate in the southern Pantanal is tropical and markedly seasonal, with hot and wet summers and dry winters with cold fronts. The average annual rainfall ranges between 800 and 1400 mm, 80% being concentrated from November to March (Silva et al. 2000). During the period of data collection (1999–2000), the average annual rainfall and temperature were 1058 mm and 24.9 °C, respectively (data obtained from a local station, available in CEMTEC, the Monitoring Center for Weather, Climate and Water Resources of the State of Mato Grosso do Sul, Brazil).

Fig. 14.1 Overview of a capão in the southern Pantanal, Mato Grosso do Sul state, Brazil

14.2.2 Reproductive Phenology

Flowering and fruiting phenology were studied for all plant species in the 52 capões between May 1999 and May 2000. Each forest patch was entirely sampled for flowering and fruiting individuals once during the study period, and we haphazardly selected three to five different patches each month (at least 1 km apart from each other). We recorded all reproductive individuals for habit and numbers of open flowers, unripe and ripe fruits. Data, including all plants' life-forms (tree, shrub, herb, hemiparasite and climber), were noted in the field and confirmed in the literature (Pott and Pott 1994; Damasceno-Junior et al. 1999; Pott et al. 2011). The duration of flowering and fruiting periods was calculated for each syndrome, and the phenological patterns were classified as brief (1 month), intermediate (2–5 months) or extended (more than 5 months) (sensu Newstrom et al. 1994).

14.2.3 Pollination and Seed Dispersal Syndromes

Plants were classified into pollination and seed dispersal syndromes according to their flower and fruit characteristics, respectively (sensu Faegri and van der Pijl 1979; van der Pijl 1982). We collected flowers and fruits from different individual plants and preserved them in ethanol 70% for complementary morphological measurements in the laboratory. For flowers, we recorded colour, presence of odour, period of anthesis and floral rewards. Flower types were classified as open, tube, gullet, flag, bell, brush or inconspicuous (Faegri and van der Pijl 1979). We occasionally recorded flower visitors for 87 plant species and systematically recorded the visitors of 44 species, summing 131 species (53%) with records of floral visitors. Focal observations lasted 1–15 h ($\bar{x}$ = 3.7 ± 3.35 h) for each plant species and summed 151 h 29 min (143 h 19 min during daylight and 8 h 10 min at night). Data on flower visitors and the literature helped to check for species pollination syndromes, inferred based on floral biology and morphological attributes. Pollination syndrome classes were melittophily (bees), sphingophily (moths), cantharophily (beetles), myophily (flies), psychophily (butterflies), ornithophily (birds), chiropterophily (bats) and anemophily (wind) (sensu Faegri and van der Pijl 1979). Species whose flowers appeared to be pollinated by more than one group of insects were classified as generalist-entomophilous. Six species were classified as undetermined pollination syndromes, and they were not included in the analyses. Seed dispersal syndromes were classified based on the evaluation of morphological attributes of fruits or infructescences, as well as on the literature. We considered colour, size, weight, consistence (dry, fleshy), dehiscence, seed size and number. Fruit types followed the classification of Spjut (1994). Seed dispersal syndromes were then classified as zoochory, either when diaspores presented tissues consumed by animals or adhesive structures as hooks or viscous substances to adhere to animals' bodies (epizoochory); anemochory, when diaspores were winged or plumed; and autochory, when diaspores primarily depend on the parent plant for dispersal through explosion or dropping by gravity (van der Pijl 1982).

14.3 Results

We recorded 284 plant species belonging to 65 families in the 52 capões of the Miranda subregion. The richest family was Fabaceae (N = 51 species), followed by Malvaceae (N = 26), Asteraceae (N = 14), Rubiaceae (N = 14) and Euphorbiaceae (N = 12). The other families contributed with one to nine species (Table 14.1). We recorded 248 flowering species and 111 fruiting species in the capões. Based on pollination and seed dispersal syndromes, most plant species were associated with animal vectors (Table 14.1; Fig. 14.2).

Pollination syndromes ranked as follows: melittophilous (47.2%), generalist-entomophilous (34.7%), myophilous (6.1%), psychophilous (3.1%), ornithophilous (2.4%), sphingophilous (1.4%), cantharophilous and chiropterophilous (both with 1%). Anemophily was recorded for 3.1% of the species (Fig. 14.2a). Concerning seed dispersal syndromes, zoochory was predominant (63.7%), followed by anemochory (19.1%) and autochory (17.2%) (Fig. 14.2b). Diaspores with tissues consumed by animals prevailed among zoochoric species (95%; N = 67), whereas epizoochory was recorded for only 5% of them (N = 4).

Table 14.1 Pollination and seed dispersal syndromes (sensu Faegri and van der Pijl 1979 and van der Pijl 1982, respectively) of 248 flowering species and 111 fruiting species recorded in 52 capões of the southern Pantanal, Miranda subregion. Nomenclature follows REFLORA (http://floradobrasil.jbrj.gov.br)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Acanthaceae			
Ruellia erythropus (Nees) Lindau	Shrub	Melittophily	–
Ruellia geminiflora Kunth	Herb	Melittophily	–
Ruellia simplex Wright	Herb	Melittophily	–
Alismataceae			
Echinodorus grandiflorus (Cham. & Schltr.) Micheli	Herb	Melittophily	–
Echinodorus lanceolatus Rataj	Herb	Melittophily	–
Echinodorus macrophyllus (Kunth) Micheli	Herb	Melittophily	–
Amaranthaceae			
Pfaffia glomerata (Spreng.) Pedersen	Herb	Entomophily	–
Amaryllidaceae			
Hippeastrum puniceum (Lam.) Kuntze	Herb	Ornithophily	–
Anacardiaceae			
Astronium fraxinifolium Schott	Tree	Melittophily	Anemochory
Astronium urundeuva (M. Allemão) Engl.	Tree	–	Anemochory
Mangifera indica L.	Tree	Entomophily	Zoochory
Annonaceae			
Annona cornifolia A.St.-Hil.	Shrub	Cantharophily	Zoochory
Annona emarginata (Schltdl.) H.Rainer	Tree	Cantharophily	Zoochory
Unonopsis guatterioides (A.DC.) R.E.Fr.	Tree	Melittophily	Zoochory
Apiaceae			
Eryngium elegans Cham. & Schltdl.	Herb	Psychophily	–
Apocynaceae			
Aspidosperma australe Müll. Arg.	Tree	Myophily	Anemochory
Forsteronia pubescens A. DC.	Climber	Melittophily	–
Funastrum clausum (Jacq.) Schltr.	Climber	–	Anemochory
Prestonia quinquangularis (Jacq.) Spreng.	Climber	Melittophily	–
Prestonia coalita (Vell.) Woodson	Climber	Melittophily	–
Rauvolfia ligustrina Willd.	Shrub	Melittophily	–
Rhabdadenia madida (Vell.) Miers	Climber	Melittophily	Anemochory
Tabernaemontana siphilitica (L.f.) Leeuwenb.	Shrub	Psychophily	–
Thevetia bicornuta Müll. Arg.	Shrub	Melittophily	–
Arecaceae			

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	Tree	–	Zoochory
Attalea phalerata Mart. ex Spreng.	Tree	Melittophily	Zoochory
Bactris glaucescens Drude	Shrub	Entomophily	–
Copernicia alba Morong ex Morong & Britton	Tree	Entomophily	Zoochory
Desmoncus horridus subsp. *prostratus* (Lindman) Henderson	Tree	–	Zoochory
Praxelis diffusa (Rich.) Pruski	Herb	Entomophily	–
Aristolochiaceae			
Aristolochia esperanzae Kuntze	Climber	Myophily	Anemochory
Asteraceae			
Ageratum conyzoides L.	Herb	Entomophily	–
Aspilia latissima Malme	Herb	Entomophily	–
Baccharis glutinosa Pers.	Shrub	Entomophily	–
Bidens gardneri Baker	Shrub	Entomophily	Epizoochory
Centratherum punctatum Cass.	Shrub	Melittophily	–
Chromolaena maximilianii (Schrad. ex DC.) R.M.King & H. Rob.	Shrub	Entomophily	–
Chromolaena odorata (L.) R.M. King & H. Rob.	Shrub	Entomophily	Anemochory
Lessingianthus rubricaulis (Humb. & Bonpl.) H. Rob.	Shrub	Entomophily	–
Mikania capricorni B.L. Rob.	Climber	Entomophily	Anemochory
Mikania micrantha Kunth	Climber	Entomophily	–
Mikania sp.1	Climber	Entomophily	–
Orthopappus angustifolius (Sw.) Gleason	Herb	Entomophily	–
Sphagneticola brachycarpa (Baker) Pruski	Herb	Entomophily	–
Stilpnopappus pantanalensis H. Rob.	Herb	Entomophily	–
Vernonia sp.1	Shrub	Entomophily	Anemochory
Bignoniaceae			
Amphilophium crucigerum (L.) L.G. Lohmann	Climber	Melittophily	–
Bignoniaceae sp.1	Climber	Melittophily	–
Cuspidaria lateriflora (Mart.) DC.	Climber	–	Anemochory
Dolichandra uncata (Andrews) L.G. Lohmann	Climber	Melittophily	–
Fridericia pubescens (L.) L.G. Lohmann	Climber	Melittophily	Anemochory
Handroanthus heptaphyllus (Vell.) Mattos	Tree	–	Anemochory

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S. Moore	Tree	Melittophily	Anemochory
Tanaecium neobrasiliense L.G. Lohmann	Climber	Melittophily	–
Tanaecium pyramidatum (Rich.) L.G. Lohmann	Climber	Melittophily	Anemochory
Boraginaceae			
Cordia glabrata (Mart.) A. DC.	Tree	Melittophily	Anemochory
Euploca filiformis (Lehm.) J.I.M.Melo & Semir	Shrub	Melittophily	–
Heliotropium indicum L.	Shrub	Melittophily	–
Varronia curassavica Jacq.	Shrub	Melittophily	–
Bromeliaceae			
Bromelia balansae Mez	Herb	Ornithophily	–
Cannabaceae			
Celtis iguanaea (Jacq.) Sarg.	Shrub	–	Zoochory
Trema micrantha (L.) Blume	Tree	Anemophily	Zoochory
Celastraceae			
Hippocratea volubilis L.	Climber	Entomophily	Anemochory
Salacia elliptica (Mart. ex Schult.) G. Don	Tree	Entomophily	Zoochory
Chrysobalanaceae			
Couepia uiti (Mart. & Zucc.) Benth. ex Hook.f.	Tree	Melittophily	Zoochory
Leptobalanus parvifolius (Huber) Sothers & Prance	Shrub	Melittophily	–
Combretaceae			
Combretum lanceolatum Pohl ex Eichler	Shrub	–	Anemochory
Combretum laxum Jacq.	Shrub	Entomophily	Anemochory
Combretum leprosum Mart.	Tree	Melittophily	–
Commelinaceae			
Murdannia nudiflora (L.) Brenan	Herb	Melittophily	–
Convolvulaceae			
Aniseia martinicensis (Jacq.) Choisy	Climber	Melittophily	–
Camonea umbellata (L.) A.R.Simões & Staples.	Climber	Melittophily	Autochory
Ipomoea rubens Choisy	Climber	Melittophily	–
Ipomoea subtomentosa (Chodat & Hassl.) O'Donell	Climber	Melittophily	–
Ipomoea sp.	Climber	–	Autochory
Jacquemontia densiflora (Meisn.) Hallier f.	Climber	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Cucurbitaceae			
Cayaponia podantha Cogn.	Climber	–	Zoochory
Momordica charantia L.	Climber	Melittophily	–
Dilleniaceae			
Doliocarpus dentatus (Aubl.) Standl.	Shrub	–	Zoochory
Ebenaceae			
Diospyros sp.1	Tree	–	Zoochory
Erythroxylaceae			
Erythroxylum anguifugum Mart.	Shrub	Melittophily	Zoochory
Euphorbiaceae			
Acalypha communis Müll. Arg.	Shrub	Anemophily	–
Alchornea discolor Poepp.	Shrub	Melittophily	–
Astraea lobata (L.) Klotzsch	Herb	Entomophily	–
Croton corumbensis S. Moore	Shrub	Entomophily	Zoochory
Croton glandulosus L.	Shrub	Melittophily	–
Croton montevidensis Spreng.	Shrub	Melittophily	–
Croton sarcopetaloides S. Moore	Shrub	Entomophily	–
Croton urucurana Baill.	Shrub	Entomophily	–
Manihot carthagenensis (Jacq.) Müll. Arg.	Shrub	Melittophily	–
Microstachys hispida (Mart. & Zucc.) Govaerts	Shrub	Myophily	–
Sapium haematospermum Müll. Arg.	Tree	Entomophily	Zoochory
Sebastiania sp.1	Shrub	Myophily	–
Fabaceae			
Anadenanthera colubrina (Vell.) Brenan	Shrub	Melittophily	–
Ancistrotropis peduncularis (Kunth) A. Delgado	Climber	Melittophily	–
Andira inermis (W.Wright) DC.	Tree	–	Zoochory
Bauhinia mollis (Bong.) Dietr.	Shrub	Sphingophily	Autochory
Bauhinia pentandra (Bong.) D. Dietr.	Shrub	–	Autochory
Calopogonium caeruleum (Benth.) C.Wright	Climber	–	Autochory
Camptosema ellipticum (Desv.) Burk.	Shrub	Ornithophily	Autochory
Canavalia mattogrossensis (Barb. Rodr.) Malme	Climber	Melittophily	–
Canavalia piperi Killip & J.F. Macbr.	Climber	Melittophily	–
Canavalia rosea (Sw.) DC.	Climber	Melittophily	–
Canavalia sp.1	Climber	–	Autochory
Centrosema brasilianum (L.) Benth.	Climber	Melittophily	Autochory
Centrosema vexillatum Benth.	Climber	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Chaetocalyx brasiliensis (Vogel) Benth.	Climber	Melittophily	Epizoochory
Chamaecrista nictitans (L.) Moench	Shrub	Melittophily	–
Crotalaria incana L.	Shrub	Melittophily	–
Crotalaria micans Link	Shrub	Melittophily	–
Crotalaria stipularia Desv.	Shrub	Melittophily	–
Ctenodon histrix (Poir.) D.B.O.S. Cardoso, P.L.R. Morales	Shrub	Entomophily	Epizoochory
Desmodium barbatum (L.) Benth.	Shrub	Entomophily	–
Desmodium cuneatum Hook. & Arn.	Shrub	Melittophily	–
Desmodium incanum (Sw.) DC.	Shrub	Melittophily	–
Desmodium tortuosum (Sw.) DC.	Shrub	Melittophily	–
Dioclea burkartii R. H. Maxwell	Climber	–	Autochory
Dioclea glabra Benth.	Climber	–	Autochory
Discolobium pulchellum Benth.	Shrub	Melittophily	–
Enterolobium contortisiliquum (Vell.) Morong	Tree	Melittophily	Zoochory
Eriosema platycarpon Micheli	Shrub	Entomophily	–
Indigofera lespedezioides Kunth	Climber	Melittophily	Autochory
Indigofera suffruticosa Mill.	Shrub	–	Autochory
Indigofera sabulicola Benth.	Herb	Melittophily	–
Inga vera Willd.	Tree	–	Zoochory
Inga vera subsp. *affinis* (DC.) T.D.Penn.	Tree	Entomophily	–
Lachesiodendronviridiflorum (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow	Tree	–	Autochory
Machaerium amplum Benth.	Shrub	Melittophily	–
Macroptilium lathyroides (L.) Urb.	Climber	Melittophily	–
Mimosa debilis Humb. & Bonpl. ex Willd.	Shrub	Entomophily	–
Mimosa pellita Humb. & Bonpl. ex Willd.	Shrub	Entomophily	–
Mimosa polycarpa Kunth	Shrub	Entomophily	–
Mimosa pudica L.	Shrub	–	Autochory
Mimosa sp.1	Shrub	–	Autochory
Senegalia tenuifolia (L.) Britton & Rose	Tree	Melittophily	Autochory
Senna aculeata (Pohl ex Benth.) H.S.Irwin & Barneby	Shrub	Melittophily	–
Senna occidentalis (L.) Link	Shrub	Melittophily	–
Senna pilifera (Vogel) H.S.Irwin & Barneby	Shrub	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Senna splendida (Vogel) H.S.Irwin & Barneby	Shrub	Melittophily	–
Sesbania virgata (Cav.) Pers.	Shrub	Melittophily	Autochory
Stylosanthes acuminata M.B.Ferreira & Sousa Costa	Shrub	Melittophily	–
Vigna longifolia (Benth.) Verdc.	Climber	Melittophily	–
Zornia crinita (Mohlenbr.) Vanni	Shrub	Entomophily	–
Gentianaceae			
Coutoubea ramosa Aubl.	Shrub	Entomophily	–
Iridaceae			
Cipura paludosa Aubl.	Herb	Melittophily	–
Lamiaceae			
Aegiphila vitelliniflora Walp.	Shrub	Psychophily	Zoochory
Hyptis campestris Harley & J.F.B. Pastore	Herb	Melittophily	–
Hyptis sp.1	Herb	Melittophily	–
Hyptis sp.2	Herb	Melittophily	–
Mesosphaerum suaveolens (L.) Kuntze	Shrub	Melittophily	–
Vitex cymosa Bertero ex Spreng.	Tree	Melittophily	Zoochory
Lauraceae			
Ocotea diospyrifolia (Meisn.) Mez	Tree	Melittophily	Zoochory
Loranthaceae			
Psittacanthus acinarius (Mart.) Mart.	Hemiparasite	Chiropterophily	Zoochory
Psittacanthus cordatus (Hoffmanns.) G. Don	Hemiparasite	Ornithophily	Zoochory
Lythraceae			
Adenaria floribunda Kunth	Shrub	Melittophily	Zoochory
Cuphea antisyphilitica Kunth	Shrub	Melittophily	–
Cuphea melvilla Lindl.	Shrub	Ornithophily	–
Malpighiaceae			
Amorimia pubiflora (A.Juss.) W.R. Anderson	Climber	Melittophily	–
Byrsonima cydoniifolia A. Juss.	Shrub	Melittophily	Zoochory
Heteropterys hypericifolia A. Juss.	Climber	Melittophily	Anemochory
Mascagnia sepium (A. Juss.) Griseb.	Climber	Melittophily	–
Malvaceae			
Abutilon sp. 1	Herb	Entomophily	–
Abutilon sp. 2	Herb	Entomophily	–
Byttneria rhamnifolia Benth.	Tree	Myophily	–
Corchorus hirtus L.	Shrub	Melittophily	–
Corchorus argutus Kunth	Shrub	Melittophily	–
Guazuma ulmifolia Lam.	Tree	Entomophily	Zoochory

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Helicteres guazumifolia Kunth	Shrub	Ornithophily	Autochory
Helicteres lhotzkyana (Schott & Endl.) K.Schum.	Shrub	Chiropterophily	Autochory
Herissantia nemoralis (A.St.-Hil.) Brizicky	Herb	Entomophily	–
Malvaceae sp.1	Herb	Entomophily	–
Malvaceae sp.2	Shrub	Entomophily	–
Malvastrum americanum (L.) Torr.	Shrub	Entomophily	–
Melochia parvifolia Kunth	Shrub	Entomophily	–
Melochia pyramidata L.	Herb	Entomophily	–
Melochia simplex A.St.-Hil.	Shrub	Entomophily	–
Melochia villosa (Mill.) Fawc. & Rendle	Shrub	Entomophily	–
Pavonia sidifolia Kunth	Shrub	Entomophily	–
Pseudabutilon aristulosum (K. Schum.) Krapov.	Shrub	Entomophily	–
Sterculia apetala (Jacq.) H. Karst.	Tree	Entomophily	Zoochory
Sida cerradoensis Krapov.	Shrub	Entomophily	–
Sida linifolia Cav.	Shrub	Entomophily	–
Sida rhombifolia L.	Herb	Entomophily	–
Sida santaremensis Mont.	Shrub	Entomophily	–
Waltheria indica L.	Shrub	Melittophily	–
Wissadula amplissima (L.) R.E.Fr.	Shrub	–	Autochory
Wissadula hernandioides (L.Hér.) Garcke	Shrub	Entomophily	–
Meliaceae			
Trichilia elegans A. Juss.	Tree	Melittophily	–
Menispermaceae			
Cissampelos pareira L.	Climber	Myophily	Zoochory
Cissampelos sp.1	Climber	Myophily	–
Hyperbaena hassleri Diels	Climber	Myophily	–
Odontocarya tamoides (DC.) Miers	Climber	Myophily	Zoochory
Moraceae			
Ficus insipida Willd.	Tree	–	Zoochory
Ficus luschnathiana (Miq.) Miq.	Tree	Melittophily	–
Ficus obtusifolia Kunth	Tree	–	Zoochory
Ficus pertusa L.F.	Tree	–	Zoochory
Molluginaceae			
Mollugo verticillata L.	Herb	Entomophily	–
Myrtaceae			
Eugenia egensis DC.	Shrub	Melittophily	Zoochory
Eugenia florida DC.	Tree	Melittophily	–

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Eugenia sp.1	Shrub	–	Zoochory
Eugenia sp.2	Shrub	–	Zoochory
Myrtaceae sp.1	Shrub	Melittophily	–
Psidium guajava L.	Shrub	Melittophily	Zoochory
Psidium guineense Sw.	Shrub	Melittophily	Zoochory
Psidium nutans O. Berg	Shrub	Melittophily	–
Nyctaginaceae			
Neea hermaphrodita S. Moore	Shrub	Entomophily	Zoochory
Ochnaceae			
Ouratea purpuripes S. Moore	Tree	Melittophily	–
Sauvagesia erecta L.	Herb	Melittophily	–
Onagraceae			
Ludwigia grandiflora (Michx.) Greuter & Burdet	Herb	Melittophily	–
Ludwigia irwinii Ramamoorthy	Shrub	Melittophily	–
Ludwigia octovalvis (Jacq.) P.H. Raven	Shrub	Melittophily	–
Ludwigia sp.1	Herb	Melittophily	–
Orobanchaceae			
Buchnera longifolia Kunth	Shrub	Melittophily	–
Passifloraceae			
Passiflora foetida L.	Climber	Melittophily	Zoochory
Passiflora pohlii Mast.	Climber	Melittophily	Zoochory
Phyllanthaceae			
Phyllanthus orbiculatus Rich.	Shrub	Entomophily	–
Piperaceae			
Piper aduncum L.	Shrub	Myophily	Zoochory
Piper tuberculatum Jacq.	Tree	Myophily	–
Plantaginaceae			
Angelonia salicariifolia Bonpl.	Shrub	Melittophily	–
Bacopa scabra (Benth.) Descole & Borsini	Herb	Melittophily	–
Scoparia montevidensis (Spreng.) R.E.Fr.	Herb	Melittophily	–
Poaceae			
Axonopus leptostachyus (Flüggé) Hitchc.	Herb	Anemophily	–
Panicum sp.1	Herb	Anemophily	–
Setaria vulpiseta (Lam.) Roem. & Schult.	Herb	Anemophily	–
Sorghastrum setosum (Griseb.) Hitchc.	Herb	Anemophily	–
Trachypogon spicatus (L.f.) Kuntze	Herb	Anemophily	Epizoochory
Polygalaceae			

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Asemeia violacea (Aubl.) J.F.B.Pastore & J.R.Abbott	Herb	Melittophily	–
Polygala timoutoides Chodat	Herb	Melittophily	–
Polygonaceae			
Coccoloba cujabensis Wedd.	Shrub	–	Zoochory
Coccoloba parimensis Benth.	Shrub	Entomophily	Zoochory
Portulacaceae			
Portulaca fluvialis D. Legrand	Herb	Melittophily	–
Rhamnaceae			
Gouania lupuloides (L.) Urb.	Climber	Myophily	Anemochory
Rhamnidium elaeocarpum Reissek	Tree	Myophily	Zoochory
Rubiaceae			
Borreria quadrifaria E.L.Cabral	Herb	Entomophily	–
Borreria verticillata (L.) G.Mey.	Herb	Entomophily	–
Borreria sp.1	Herb	Entomophily	–
Cordiera sessilis (Vell.) Kuntze	Shrub	–	Zoochory
Genipa americana L.	Tree	Entomophily	Zoochory
Guettarda sp.	Shrub	–	Zoochory
Psychotria carthagenensis Jacq.	Shrub	Entomophily	Zoochory
Randia armata (Sw.) DC.	Shrub	–	Zoochory
Richardia grandiflora (Cham. & Schltdl.) Steud.	Shrub	Entomophily	–
Sabicea aspera Aubl.	Climber	Melittophily	–
Spermacoce eryngioides (Cham. & Schltdl.) Kuntze	Shrub	Entomophily	–
Spermacoce exilis (L.O.Williams) C.D. Adams	Herb	Entomophily	–
Staelia thymoides Cham. & Schltdl.	Shrub	Entomophily	–
Tocoyena formosa (Cham. & Schltdl.) K. Schum.	Shrub	Sphingophily	Zoochory
Rutaceae			
Zanthoxylum rigidum Humb. & Bonpl. ex Willd.	Tree	Entomophily	Zoochory
Salicaceae			Zoochory
Casearia aculeata Jacq.	Shrub	Entomophily	Zoochory
Casearia sylvestris Sw.	Tree	–	Zoochory
Xylosma venosa N.E.Br.	Shrub	Entomophily	Zoochory
Sapindaceae			
Cardiospermum grandiflorum Sw.	Climber	Entomophily	Anemochory
Cardiospermum halicacabum L.	Climber	–	Anemochory
Dilodendron bipinnatum Radlk.	Tree	Entomophily	–
Melicoccus lepidopetalus Radlk.	Tree	Entomophily	Zoochory

(continued)

Table 14.1 (continued)

Family Species	Life-form	Pollination syndrome	Seed dispersal syndrome
Paullinia elegans Cambess	Climber	Entomophily	Zoochory
Paullinia pinnata L.	Climber	Entomophily	Zoochory
Sapindus saponaria L.	Tree	Entomophily	Zoochory
Serjania caracasana (Jacq.) Willd.	Climber	Entomophily	Anemochory
Serjania erecta Radlk.	Shrub	Entomophily	Anemochory
Smilacaceae			
Smilax campestris Griseb.	Climber	Myophily	–
Smilax sp.1	Climber	Myophily	–
Solanaceae			
Cestrum obovatum Sendtn.	Shrub	Sphingophily	Zoochory
Cestrum strigilatum Ruiz & Pav.	Shrub	Sphingophily	–
Nicotiana plumbaginifolia Viv.	Herb	Entomophily	–
Solanum aculeatissimum Jacq.	Shrub	Melittophily	–
Solanum americanum Mill.	Shrub	–	Zoochory
Solanum viarum Dunal	Shrub	Melittophily	–
Solanum sp.1	Herb	Melittophily	–
Talinaceae			
Talinum fruticosum (L.) Juss.	Herb	Melittophily	–
Turneraceae			
Turnera melochioides Cambess.	Shrub	Melittophily	–
Urticaceae			
Cecropia pachystachya Trécul	Tree	Myophily	Zoochory
Verbenaceae			
Lantana camara L.	Shrub	Psychophily	–
Lantana canescens Kunth	Shrub	Psychophily	–
Lantana trifolia L.	Shrub	Psychophily	–
Lippia alba (Mill.) N.E.Br. ex P. Wilson	Shrub	Psychophily	–
Stachytarpheta cayennensis (Rich.) Vahl	Shrub	Psychophily	–
Violaceae			
Pombalia communis (A.St.-Hil.) Paula-Souza	Shrub	Melittophily	–
Vitaceae			
Cissus erosa Rich.	Climber	Entomophily	Zoochory
Cissus spinosa Cambess.	Climber	Entomophily	Zoochory
Cissus verticillata (L.) Nicolson & Jarvis	Climber	Entomophily	Zoochory
Vochysiaceae			
Vochysia divergens Pohl	Shrub	Melittophily	–

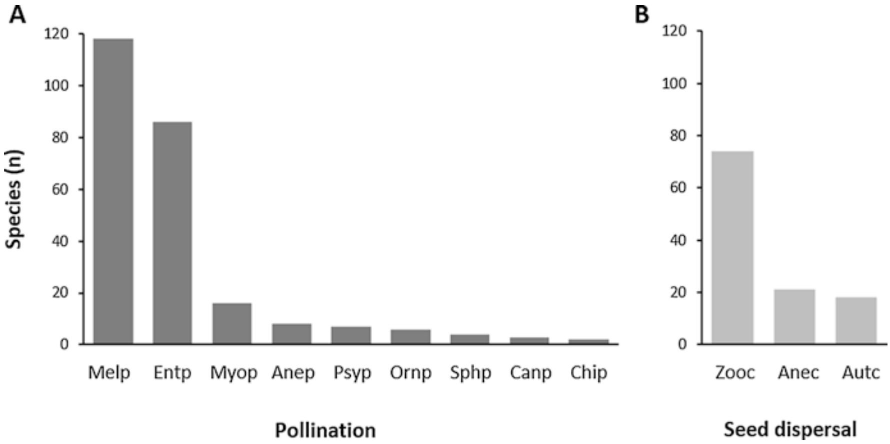


Fig. 14.2 Number of species within pollination (**a**) and seed dispersal (**b**) syndromes recorded in 52 capões in the southern Pantanal, Miranda subregion. Melp, melittophily; Entp, entomophily; Myop, myophily; Anep, anemophily; Psyp, psychophily; Ornp, ornithophily; Sphp, sphingophily; Canp, cantharophily; Chip, chiropterophily; Zooc, zoochory; Anec, anemochory; Autc, autochory

We recorded predominance of white and yellow-coloured flowers. Among different floral types reported, open or tube flowers were related to different pollination syndromes, whereas gullet flowers predominated among melittophilous species. On the other hand, inconspicuous flowers were mainly anemophilous, whereas flag and brush flowers were related to pollination by bees, bats or hummingbirds (Fig. 14.3). Fleshy fruits were found in 64% of the fruiting species, and 36% presented dry fruits. Berries were the most abundant fruit type, followed by legumes, drupes, capsules and samaras (Fig. 14.3).

The pollination syndromes had representatives among all different life-forms. Melittophily, generalist-entomophily and ornithophily occurred in the greatest variety of life-forms, whereas sphingophily exclusively occurred in shrub species (Fig. 14.4a). Myophilous and anemophilous species were predominantly climbers and herbs, respectively (Fig. 14.4a). Regarding seed dispersal syndromes, zoochoric species showed the greater variety of life-forms, with a predominance of trees and shrubs. Autochory predominated among shrub species and anemochory among herbs (Fig. 14.4b).

Flower and fruit sources peaked during the rainy season (December to March), although they were available for pollinators and seed dispersers throughout the year. The richness of blooming species in each pollination syndrome varied monthly during the study, and it peaked during the rainy season (Fig. 14.5). All pollination syndromes were represented in March, and at least four of them were represented in the other months. Melittophily and generalist-entomophily were the syndromes with more species blooming each month (Fig. 14.5).

Duration of flowering seasons was intermediate or brief for most species. Generalist-entomophilous, psychophilous, ornithophilous and cantarophilous

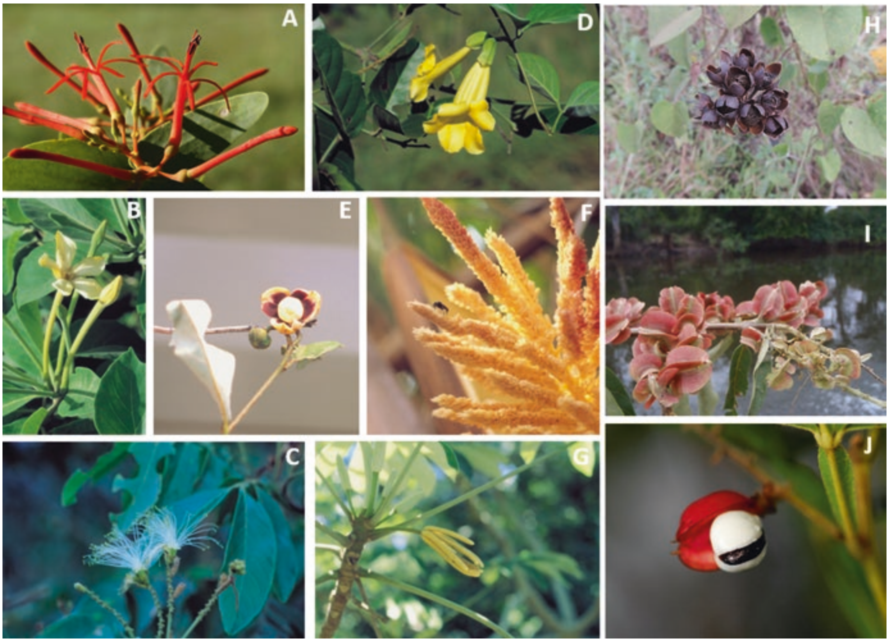


Fig. 14.3 Flowers and fruits of species recorded in capões of the southern Pantanal, Miranda subregion. (**a**) *Psittacanthus cordatus* (Loranthaceae) – ornithophily; (**b**) *Tocoyena formosa* (Rubiaceae) – sphingophily; (**c**) *Inga vera* subsp. *affinis* (Fabaceae) – generalist-entomophily; (**d**) *Dolichandra uncata* (Bignoniaceae) – melittophily; (**e**) *Annona cornifolia* (Annonaceae) – cantharophily; (**f**) *Attalea phalerata* (Arecaceae) – melittophily; (**g**) *Cecropia pachystachya* (Urticaceae) – myophily; (**h**) *Merremia umbellata* (Convolvulaceae) – autochory; (**i**) *Combretum lanceolatum* (Combretaceae) – anemochory; (**j**) *Paullinia pinnata* (Sapindaceae) – zoochory. Credits for images: (**h**) Camila Silveira Souza; (**i** and **j**) Paulo Robson de Souza

species frequently presented flowering seasons of intermediate duration; anemophilous species showed mainly brief flowering periods; whereas flowering seasons of myophilous, chiropterophilous, sphingophilous and melittophilous species were brief or intermediate. Extended flowering seasons occurred for melittophilous, generalist-entomophilous, myophilous and ornithophilous species. Ornithophilous species were those with longer flowering seasons.

The density of flowering individuals was also greater in the rainy season, between November and March, for most pollination syndromes (Fig. 14.6). Generalist-entomophilous species presented the highest density of individuals peaking in February. Sphingophilous species presented two flowering peaks, one in the dry season (August) and another one in the rainy season (January) (Fig. 14.6). Melittophilous species presented greater density of flowering individuals in February, and anemophilous species peaked in October, both in the rainy season. On the other hand, the highest density of chiropterophilous flowers was recorded in April, during the dry period (Fig. 14.6).

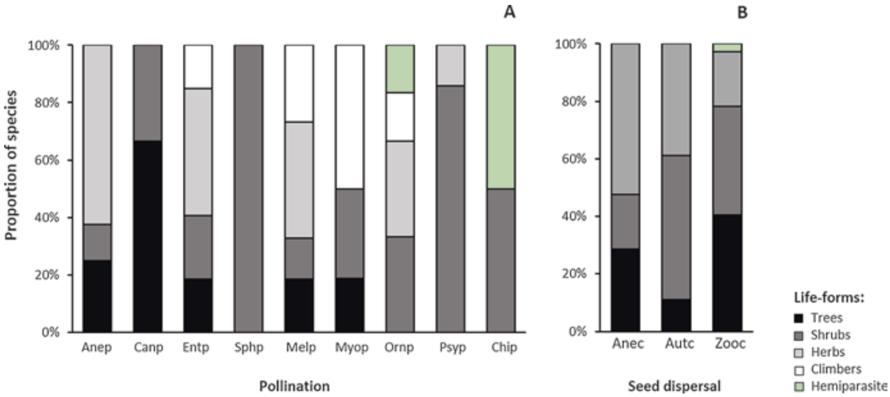


Fig. 14.4 Pollination (**a**) and seed dispersal (**b**) syndromes recorded for different life-forms in capões of the southern Pantanal, Miranda subregion. Melp, melittophily; Entp, entomophily; Myop, myophily; Anep, anemophily; Psyp, psychophily; Ornp, ornithophily; Sphp, sphingophily; Canp, cantharophily; Chip, chiropterophily; Zooc, zoochory; Anec, anemochory; Autc, autochory

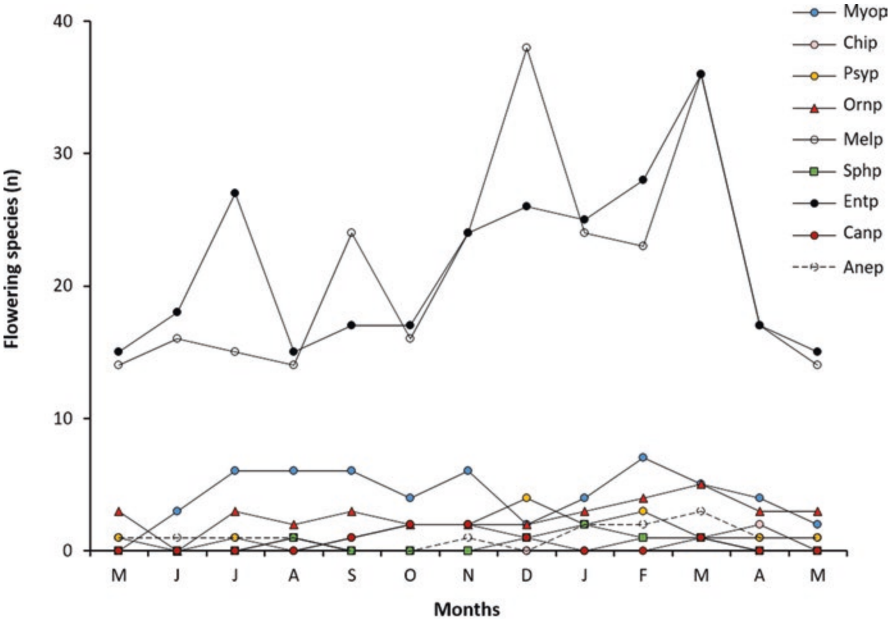


Fig. 14.5 Number of flowering species bearing different pollination syndromes throughout the year in 52 capões of the southern Pantanal, Miranda subregion. Melp, melittophily; Entp, entomophily; Myop, myophily; Anep, anemophily; Psyp, psychophily; Ornp, ornithophily; Sphp, sphingophily; Canp, cantharophily; Chip, chiropterophily

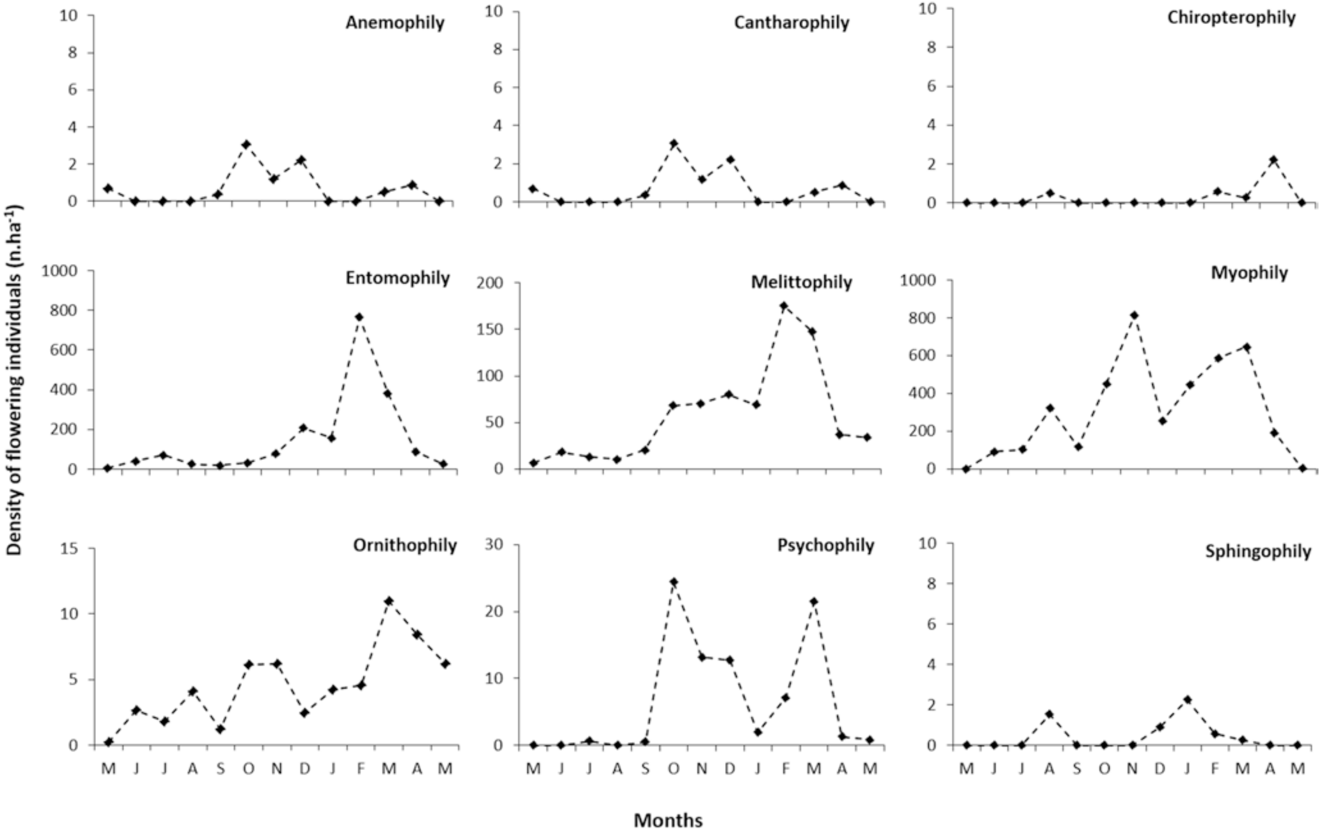


Fig. 14.6 Density of flowering individuals bearing different pollination syndromes throughout the year in 52 capões of the southern Pantanal, Miranda subregion

Fruiting of the different syndromes in the capões varied throughout the year with different patterns. Most zoochoric species fruited during the rainy season, between November and January, whereas the highest diversity of autochoric and anemochoric species occurred in the dry season, in July–August and August–September, respectively (Fig. 14.7a). The duration of fruiting periods for most of the species was intermediate. Zoochoric species presented periods of intermediate and extended fruiting duration, whereas autochoric and anemochoric species showed mainly brief fruiting seasons.

The highest density of fruiting individuals was recorded among zoochoric species, followed by anemochoric and autochoric. Zoochoric fruits were available throughout the year with a peak in January, in the rainy season (Fig. 14.7b). Anemochoric fruits peaked from September to November, corresponding to the

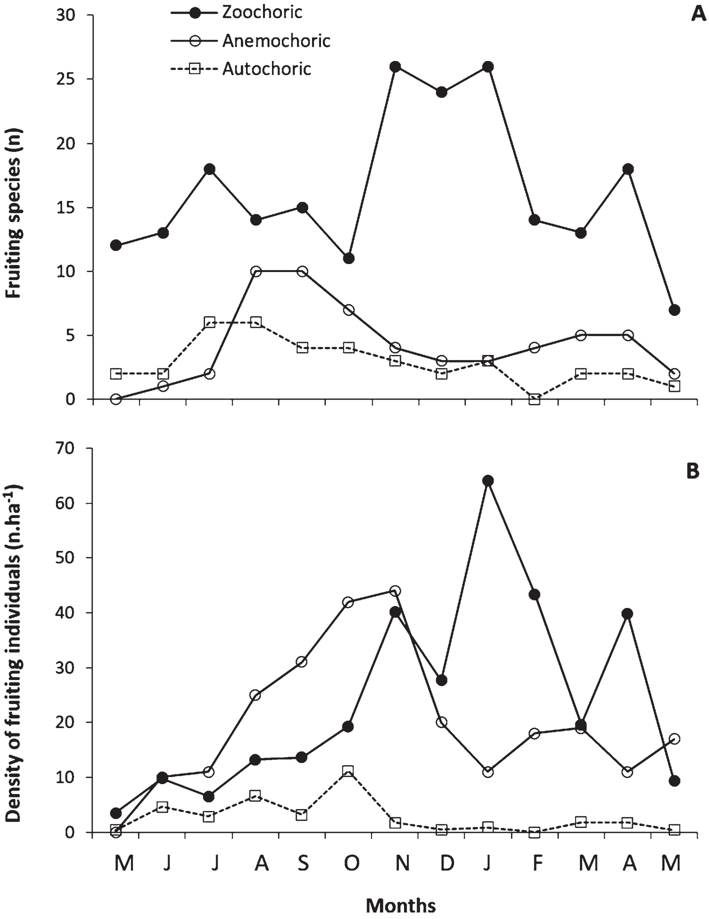


Fig. 14.7 Number of fruiting species and density of fruiting individuals in each seed dispersal syndrome throughout the year in 52 capões of the southern Pantanal, Miranda subregion

transition from the dry to the wet season (Fig. 14.7b). Autochoric species presented greater density of fruiting individuals between June and October, corresponding to the dry period, with few fruiting individuals in the rainy season (Fig. 14.7b).

14.4 Discussion

Our results show that animals, rather than wind or gravity, greatly mediate pollination and seed dispersal throughout the year in capões of the southern Pantanal, as expected for Neotropical forests in general (Griz and Machado 2001; Machado and Lopes 2004; Ramírez 2004; Quirino and Machado 2014; Carvalho and Sartori 2014; Souza et al. 2016; Rech et al. 2016). The high resource availability for pollinators and seed dispersers in the capões throughout the year highlights the importance of these forested patches in providing resources to local fauna. A total of 97% of the species are zoophilous, 93% are pollinated by invertebrates and 4% by vertebrates, whereas the abiotic syndrome was recorded for only 3% of the species. Likewise, 60.4% of the fruiting species offer resources for fruit-eating animals, while 39.6% are epizoochoric or depend on abiotic agents for seed dispersal. The predominance of plant species that rely upon animals for pollen and diaspore dispersion, and the dependence of these animals on floral and fruit sources, makes tropical forests the setting for complex interactions that influence species distributions and the structure and diversity of local communities (Jordano et al. 2006; Fleming and Kress 2013; Rech et al. 2016). In the capões of the Pantanal, though most plant species are associated with mutualist animals, their pollination and seed dispersal systems appear to be rather generalists, a situation likely related with the severe and markedly seasonal floods and droughts.

Melittophily and generalist-entomophily were the most frequent pollination syndromes in the capões (81% of species). This result is similar to those recorded in other tropical environments, including humid and dry forests (Silberbauer-Gottsberger and Gottsberger 1988; Oliveira and Gibbs 2000; Machado and Lopes 2004; Quirino and Machado 2014; Souza et al. 2016). Most melittophilous and generalist-entomophilous flowers were the open type and offered nectar and pollen as reward to flower visitors, what indicates a high predominance of generalist pollination systems because resources from such flowers are easily accessible by different visitors varying in time and space (Ollerton et al. 2007). Furthermore, several melittophilous and generalist-entomophilous species are also important sources of nectar for hummingbirds inhabiting the capões of the Pantanal (Araujo and Sazima 2003).

The proportions of ornithophilous and chiropterophilous species in the capões (2.4% and 1%, respectively) were similar to those reported in sites in the Cerrado (Silberbauer-Gottsberger and Gottsberger 1988; Oliveira and Gibbs 2000) and lower than those in the Brazilian Caatinga (Machado and Lopes 2004; Quirino and Machado 2014). The marked seasonality with a severe dry season and the patchy distribution of capões in a vast matrix of open grasslands are both factors likely to contribute to a low richness and abundance of hummingbirds and hummingbird-pollinated flowers (Araujo and Sazima 2003).

Chiropterophily is still rarer than ornithophily in the capões of the southern Pantanal, and it does not occur among tree species (but just for one shrub and one hemiparasite), contrasting with other Neotropical forests where bat-pollinated trees are relatively common (Atlantic Forest, Sazima et al. 1999; Caatinga, Machado and Lopes 2004; Quirino and Machado 2014; Nhecolândia subregion of the Pantanal, Munin et al. 2012). When compared with the Caatinga's community, these values are contrasting, since Machado and Lopes (2004) and Quirino and Machado (2014) reported a high proportion of chiropterophilous species, corresponding to 13.1% and 11%, respectively. In the Caatinga, there is an elevated diversity of trees and columnar cacti that are bat-pollinated (Queiroz 2014). Additionally, the low proportion of pollination by bats compared with the other pollination syndromes in the capões seems to be related with the low representativity of specialized nectarivorous bats in the Pantanal (Fischer et al. 2018). Moreover, the same features that limit the richness of hummingbirds may be associated with the low diversity of nectarivorous bats, as both are long-lived vertebrates.

The percentage (3%) of anemophily in the capões was close to that reported for tropical humid forests and the semiarid Caatinga. Approximately 2.5% of the flora of tropical forests and 3–4% of the Caatinga flora have been reported to be wind-pollinated (Bawa et al. 1985; Kress and Beach 1994; Machado and Lopes 2004; Quirino and Machado 2014). In the Cerrado, however, anemophily can reach 14% of species in the local flora, mainly represented by grasses (Silberbauer-Gottsberger and Gottsberger 1988; but see Oliveira and Gibbs 2000).

Melittophilous, generalist-entomophilous, myophilous and ornithophilous flowers occurred in all vertical strata of the vegetation, anemophilous species occurred mostly in the herbaceous stratum, and cantharophilous, psychophilous and sphingophilous species occurred only in the lowest stratum (herbaceous and shrubby) of the capões (Fig. 14.4a). The stratification of the pollination syndromes recorded in the capões was similar to those found in other studied communities and should be related to the vertical distribution of the anthophilous fauna (Machado and Lopes 2004; Quirino and Machado 2014; Souza et al. 2016).

Zoochory has been reported as the predominant seed dispersal syndrome in tropical regions, where it may reach more than 80% of the local species in humid forests, with a decreasing frequency towards less humid or dry environments (Gentry 1983; Carvalho and Sartori 2014). Seed dispersal by animals is a determinant step for plant reproductive success, since it increases the probability of colonization of new areas and reduces the density of dispersed seeds, thus decreasing predation on seeds and intraspecific competition among seedlings in the vicinity of the mother plants (Jordano 2017). Therefore, zoochory seems to be especially important for plants inhabiting small forest patches such as the capões of the Pantanal.

We observed that zoochory was predominant among tree and shrub species, as reported by Griz and Machado (2001) in the Brazilian Caatinga and by Freitas et al. (2013) and Carvalho and Sartori (2014) in the Brazilian Chaco. On the other hand, for the herbaceous species prevailed anemochory followed by autochory syndromes.

Stratification of the vegetation may affect the distribution of resources to dispersers (Morellato and Leitão-Filho 1992). Generally, zoochory is well represented along the vertical strata among trees, shrubs and climbers, and their seed dispersers can move both horizontally and vertically, thus increasing the efficiency of seed dispersal (Fenner 1985; Jordano 2000). Therefore, the different proportions of fleshy fruits produced by plants with different life-forms (and therefore occupying different strata) in the capões (Fig. 14.4b) can reduce the overlap of niches among animals that depend on these resources.

Most species and individuals flowered in the rainy season in the capões, similarly to those recorded in other tropical environments, especially in communities with a pronounced dry season (Machado and Lopes 2004; Quirino and Machado 2014; Souza et al. 2016; see also the chapter on "Synthesis of the Present Knowledge on Plant Phenology of the Pantanal" Chap. 13). Zoochorous species showed a fruiting peak during the rainy season, whereas anemochoric species peaked in the transition between the dry and the rainy periods, and autochoric species in the dry period. These results follow a general pattern among tropical forests (Machado et al. 1997; Griz and Machado 2001; Freitas et al. 2013; Carvalho and Sartori 2014).

Our study highlights that animal-mediated pollination and seed dispersal are common and crucial for the dynamics of the capões in the southern Pantanal. The disruption of pollination and seed dispersal interactions, together with their benefits, directly results in the impairment of the reproductive success of the partnership and reduction of the likelihood of individuals remaining in the habitat (Bascompte and Jordano 2014). The loss of ecological interactions may occur before species disappearance, affecting species functionality and ecosystems services at a faster rate than species extinctions (Valiente-Banuet et al. 2015). Therefore, conserving pollination and seed dispersal, including the animals that provide these services to plants, should become a priority in forest conservation efforts globally (Neuschulz et al. 2016).

As the capões of the Pantanal are small and sparse forest patches in an open landscape, local plant population genetic structures depend upon the ability of pollinators or seed dispersers to move between them. The presence of scattered shrubs and trees in the grassland matrix likely provides additional resources for flower visitors and seed dispersers (Silveira et al. 2018), thus stimulating movements of animal vectors among different capões. Therefore, detailed field studies addressing mechanisms of pollen and seed dispersal by different animal groups (invertebrates and vertebrates) are necessary for a better understanding of how their foraging activities across the landscape may affect gene flow among these forested patches in the southern Pantanal. These natural forest patches and their plant and animal assemblages were established throughout long-term ecological processes of successful colonization and establishment, rather than by contemporaneous disturbances caused by forest fragmentation and land modifications for human use. In this sense, further studies on pollination and seed dispersal dynamics in the capões of the Pantanal, and on the composition of the surrounding open matrix, can raise important issues on the species assembly and sustainability in situations of forest loss and fragmentation.

Acknowledgements We thank A. Brun (in memoriam), P.A.A. Cara and L. Ramos for field assistance; G. Damasceno-Júnior and U. Rezende for plant identification; and the staff of the Base de Estudos do Pantanal (UFMS) for logistical support. Funds were provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) fellowship grant to VGNG; Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia de MS (FUNDECT), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support through the project "Padrões de diversidade da fauna e flora no Pantanal Sul Matogrossense" (521746/97); CNPq also provided research productivity fellowships to ACA (310999/2018-9), EF (484808/2013-3) and MS (302781/2016-1).

References

Almeida-Neto M, Campassi F, Galetti M, Jordano P, Oliveira-Filho A (2008) Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. Glob Ecol Biogeogr 17:503–513

Aoki C, Sigrist MR (2006) Inventário dos visitantes florais no Complexo Aporé-Sucuriú. In: Pagoto TCS, Souza PR (eds) Biodiversidade do Complexo Aporé-Sucuriú. Subsídios à conservação e ao manejo do Cerrado. Editora da Universidade Federal de Mato Grosso do Sul, Campo Grande, pp 143–162

Araujo AC, Sazima M (2003) The assemblage of flowers visited by hummingbirds in the "capões" of Southern Pantanal, Mato Grosso do Sul, Brazil. Flora 198:427–435

Bascompte J, Jordano P (2014) Mutualistic networks. Monographs in population biology. Princeton University Press, Princeton, p 208

Bawa KS (1990) Plant-pollinator interactions in tropical rain forest. Annu Rev Ecol Evol Syst 21:399–422

Bawa KS, Bullock SH, Perry DR, Coville RE, Grayum MH (1985) Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. Am J Bot 72:346–356

Borges HBN (2000) Biologia reprodutiva e conservação do estrato lenhoso numa comunidade do cerrado, Ph.D. thesis, Universidade de Campinas, Campinas

Carvalho FS, Sartori AL (2014) Reproductive phenology and seed dispersal syndromes of woody species in the Brazilian Chaco. J Veg Sci 26:302–311

Corrêa CE, Fischer E (2017) Bizarre *Cecropia pachystachya* (Urticaceae) hemiepiphytic growth on palms in the "Pantanal" wetland. Braz J Bot 40:215–223

Correa SB, Arujo JK, Penha J, Nunes da Cunha C, Bobier KE, Anderson JT (2016) Stability and generalization in seed dispersal networks: a case study of frugivorous fish in Neotropical wetlands. Proc R Soc B 283:20161267

Costa-Pereira R, Severo-Neto F, Yule TS, Pereira APT (2011) Fruit-eating fishes of *Banara arguta* (Salicaceae) in the Miranda River floodplain, Pantanal wetland. Biota Neotrop 11:373–376

Cunha NL, Fischer E, Lorenz-Lemke AP, Barrett SCH (2014) Floral variation and environmental heterogeneity in a tristylous clonal aquatic of the Pantanal wetlands of Brazil. Ann Bot 114:1637–1649

Dafni A, O'Toole C (1994) Pollination syndromes in the Mediterranean: generalizations and peculiarities. In: Arianoutsou M, Groves RH (eds) Plant–animal interactions in Mediterranean-type ecosystems. Kluwer, Dordrecht, pp 125–135

Damasceno-Junior GA, Bezerra MAO, Bortolotto IM, Pott A (1999) Aspectos florísticos e fitofisionômicos dos capões do Pantanal do Abobral. In: Anais do II Simpósio sobre recursos naturais e sócio econômicos do Pantanal – Manejo e Conservação. CPAP Embrapa and UFMS, Corumbá, pp 203–214

Donatti CI, Guimarães PR, Galetti M, Pizo MA, Marquitti FMD, Dirzo R (2011) Analysis of a hyperdiverse seed dispersal network: modularity and underlying mechanisms. Ecol Lett 14:773–781

Fadini RF, Fischer E, Castro SJ, Araujo AC, Ornelas JF, Souza PR (2018) Bat and bee pollination in *Psittacanthus* mistletoes, a genus regarded as exclusively hummingbird-pollinated. Ecology 99:1–3

Faegri K, van der Pijl L (1979) The principles of pollination ecology. Pergamon Press, New York, p 244

Fava WS, Covre WS, Sigrist MR (2011) *Attalea phalerata* and *Bactris glaucescens* (Arecaceae, Arecoideae): phenology and pollination ecology in the Pantanal, Brazil. Flora 206:575–584

Fenner M (1985) Seed ecology. Chapman and Hall, London, p 151

Fischer E, Araujo AC, Gonçalves F (2014) Polinização por vertebrados. In: Rech AR, Agostini K, Oliveira PE, Machado IC (eds) Biologia da polinização. Editora Projeto Cultural, Rio de Janeiro, pp 311–326

Fischer E, Silveira M, Munin RL, Camargo G, Santos CF, Ramos Pereira MJ, Fischer W, Eriksson A (2018) Bats in the dry and wet Pantanal. Hystrix It J Mamm 29:11–17

Fleming TH, Kress WJ (2013) The ornaments of life: coevolution and conservation in the tropics. University of Chicago Press, Chicago, p 616

Freitas TG, Souza CS, Aoki C, Arakaki LMM, Stefanello TH, Sartori ALB, Sigrist MR (2013) Flora of Brazilian humid Chaco: composition and reproductive phenology. Checklist 9:973–979

Gentry A (1983) Dispersal ecology and diversity in neotropical forest communities. Sonderb Naturwiss Vereins Hamburg 7:303–314

Griz L, Machado I (2001) Fruiting phenology and seed dispersal syndromes in Caatinga, a tropical dry forest in the northeast of Brazil. J Trop Ecol 17:303–321

Hansen DM, Muller CB (2009) Reproductive ecology of the endangered enigmatic Mauritian endemic *Roussea simplex* (Rousseaceae). Int J Plant Sci 170:42–52

Howe H, Smallwood J (1982) Ecology of seed dispersal. Annu Rev Ecol Evol Syst 13:201–228

Jara-Guerrero A, De la Cruz M, Mendez M (2011) Seed dispersal spectrum of woody species in south Ecuadorian dry forests: environmental correlates and the effect of considering species abundance. Biotropica 43:722–730

Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CABI Publishing, Wallingford, pp 125–166

Jordano P (2010) Coevolution in multispecific interactions among free-living species. Evol Ed Outreach 3:40–46

Jordano P, Galetti M, Pizo MA, Silva WR (2006) Ligando frugivoria e dispersão de sementes à Biologia da Conservação. In: Rocha CFD, Bergallo HG, Alves MS (eds) Biologia da Conservação: Essências. Editora RIMA, São Carlos, pp 411–436

Jordano P (2017) What is long-distance dispersal? And a taxonomy of dispersal events. J Ecol 105:75–84

Koptur S, Haber WA, Frankie GW, Baker HG (1988) Phenological studies of shrub and treelet species in tropical cloud forest of Costa Rica. J Trop Ecol 4:323–346

Kress WJ, Beach JH (1994) Flowering plant reproductive system. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) La selva, ecology and natural history of a Neotropical rain forest. University of Chicago Press, Chicago, pp 161–182

Longo JM, Fischer E (2006) Efeito da taxa de secreção de néctar sobre a polinização e a produção desementes em flores de *Passiflora speciosa* Gardn. (Passifloraceae) no Pantanal. Rev Brasil Bot 29:481–488

Lopes LA, Blochtein B, Ott AP (2007) Diversidade de insetos antófilos em áreas de reflorestamento de eucalipto, Município de Triunfo, Rio Grande do Sul, Brasil. Iheringia Ser Zool 97:181–193

Machado IC, Lopes AV (2004) Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry Forest. Ann Bot 94:365–376

Machado I, Barros L, Sampaio E (1997) Phenology of caatinga species at Serra Talhada, PE, northeastern Brazil. Biotropica 29:57–68

Morellato LPC, Leitão-Filho HF (1992) Padrões de frutificação e dispersão na Serra do Japi. In: Morellato LPC (ed) História Natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil. Editora da Unicamp, Campinas, pp 112–140

Morellato LPC, Alberton B, Alvarado ST, Borges B, Buisson B, Camargo MGG, Cancian LF, Carstensen DW, Escobar DFE, Leite PTP, Mendoza I, Rocha NMWB, Soares NC, Silva TSF, Staggemeier VG, Streher AS, Vargas BC, Peres CA (2016) Linking plant phenology to conservation biology. Biol Conserv 195:60–72

Muchhala N, Jarrin VP (2002) Flower visitation by bats in cloud forests of Western Ecuador. Biotropica 34:387–395

Munin RL, Fischer E, Gonçalves F (2012) Food habits and dietary overlap in a phyllostomid bat assemblage in the Pantanal of Brazil. Acta Chiropterol 14:195–204

Neuschulz EL, Muller T, Schleuning M, Bohning-Gaese K (2016) Pollination and seed dispersal are the most threatened processes of plant regeneration. Sci Rep 6:29839

Newstrom LE, Frankie GW, Baker HG, Cowell RK (1994) Diversity of long-term flowering patterns. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) La Selva, ecology and natural history of a Neotropical rain forest. Chicago University Press, Chicago, pp 142–160

Oliveira PE, Gibbs PE (2000) Reproductive biology of woody plants in a cerrado community of Central Brazil. Flora 195:311–329

Ollerton J, Killick A, Lamborn E, Watts S, Whiston M (2007) Multiple meaning and modes: on the many ways to be a generalist flower. Taxon 56:717–728

Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, Cranmer L, Hingston A, Peter CI, Rotenberry J (2009) A global test of the pollination syndrome hypothesis. Ann Bot 103:1471–1480

Parra-Tabla V, Bullock SH (2002) La polinización en la selva tropical de Chamela. In: Nogueira FA, Vega Rivera JHA, Garcia Aldrete N, Quesada Avendaño M (eds) História Natural de Chamela. UNAM – Instítuto de Biologia, México, pp 499–515

Paulino-Neto HF (2007) Pollination and breeding system of *Couepia uiti* (Mart. and Zucc.) Benth (Chrysobalanaceae) in the Pantanal da Nhecolândia. Braz J Biol 67:715–719

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa, Brasília, p 320

Pott A, Oliveira AKM, Damasceno GA Jr, Silva JSV (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71:265–273

Prance GT, Schaller GB (1982) Preliminary study of some vegetation types of the Pantanal. Mato Grosso, Brazil. Brittonia 34:228–251

Queiroz JA (2014) Flores de antese noturna e seus polinizadores em área de Caatinga: redes e sistemas mistos de polinização. Ph.D. Universidade Federal de Pernambuco, Recife

Quirino ZGM, Machado IC (2014) Pollination syndromes in a Caatinga plant community in northeastern Brazil: seasonal availability of floral resources in different plant growth habits. Braz J Biol 74:62–71

Ramírez N (2004) Pollination specialization and time of pollination on a tropical Venezuelan plain: variations in time and space. Bot J Linn Soc 145:1–16

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Annu Rev Ecol Evol Syst 16:179–214

Rech AR, Dalsgaard B, Sandel B, Sonne J, Svenning J, Holmes N, Ollerton J (2016) The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. Plant Ecol Divers 9:253–262

Sazima M, Buzato S, Sazima I (1999) Bat-pollinated flower assemblages and bat visitors at two Atlantic forest sites in Brazil. Ann Bot 83:705–712

Sazima M, Vogel S, Prado AL, Oliveira DM, Franz G, Sazima I (2001) The sweet jelly of *Combretum lanceolatum* flowers (Combretaceae): a cornucopia resource for bird pollinators in the Pantanal, western Brazil. Plant Syst Evol 227:195–208

Silberbauer-Gottsberger I, Gottsberger G (1988) A polinização de plantas do Cerrado. Rev Bras Biol 48:651–663

Silva MP, Mauro R, Mourão G, Coutinho M (2000) Distribuição e quantificação de classes de vegetação do Pantanal através de levantamento aéreo. Braz J Bot 23:143–152

Silva LAC, Pagliarini MS, Santos AS, Valle CB (2013) Stigma receptivity, mode of reproduction, and mating system in *Mesosetum chaseae* Luces (Poaceae), a native grass of the Brazilian Pantanal. Genet Mol Res 12:5038–5045

Silveira M, Tomas WM, Fischer E, Bordignon MO (2018) Habitat occupancy by *Artibeus planirostris* bats in the Pantanal wetland, Brazil. Mammal Biol 91:1–6

Souza CS, Aoki C, Alcantara DMC, Laroca S, Sazima M, Pott A, Sigrist MR (2016) Diurnal anthophilous fauna in Brazilian Chaco vegetation: phenology and interaction with flora. Braz J Bot 4:1–11

Souza CS, Maruyama PK, Aoki C, Sigrist MR, Raizer J, Gross CL, Araujo AC (2018) Temporal variation in plant–pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. J Ecol 106:2409–2420

Spjut RW (1994) A systematic treatment of fruit types. Mem N Y Bot Gard 70:70–93

Tabarelli M, Peres CA (2002) Abiotic and vertebrate seed dispersal in Brazilian Atlantic Forest: implications for forest regeneration. Biol Conserv 106:165–176

Teixeira RC, Corrêa CE, Fischer E (2009) Frugivory by *Artibeus jamaicensis* (Phyllostomidae) bats in the Pantanal, Brazil. Stud Neotrop Fauna Environ 44:7–15

Valiente-Banuet A, Aizen MA, Alcantara JM, Arroyo J, Cocucci A, Galetti M, Garcia MB, Garcia D, Gomez JM, Jordano P, Medel R, Navarro L, Obeso JR, Oviedo R, Ramirez N, Rey PJ, Traveset A, Verdú M, Zamora R (2015) Beyond species loss: the extinction of ecological interactions in a changing world. Funct Ecol 29:299–307

van der Pijl L (1982) Principles of dispersal in higher plants. Springer, Berlin, p 218

Wang E, Donatti CI, Ferreira VL, Raizer J, Himmelstein J (2011) Food habits and notes on the biology of *Chelonoidis carbonaria* (Spix 1824) (Testudinidae, Chelonia) in the southern Pantanal, Brazil. South Am J Herpetol 6:11–19

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060

Chapter 15
Soil Seed Banks in the Pantanal Wetland

Arnildo Pott, Francielli Bao, and Evaldo Benedito de Souza

15.1 Introduction

Plant regeneration depends on persistence mechanisms, either by seed or vegetative propagation, and many species utilize both (Harper 1977). The soil seed bank is a reserve of buried seeds, and those on the soil surface or in the submerged sediments in ponds and lakes can also be considered seed banks. The soil seed bank is part of the local flora and can indicate which species can appear in plant succession to recompose the natural vegetation after disturbances, since it represents the main regeneration potential (Bakker et al. 1996, Cronk and Fennessy 2001). It can be transient or persistent; the transient soil seed reservoir tends to fill seasonal gaps, while the persistent bank allows the regeneration after unpredictable disturbance (Thompson and Grime 1979). A persistent seed bank is associated with small, compact, smooth seeds with exact requirements for germination; species without seed banks are bigger, are frequently long or flat, and often have hairs or awns and lack requirements for germination (Thompson 1987). The species pool and abundance of the soil seed bank is determined by a set of physical and biological factors that influence the input and output of seeds, including seed production, seed rain (dispersal), germination requirements, predation, burial depth, physiological death, and pathogens (Simpson et al. 1989). The soil seed bank contains genotypes selected over a long time (Fenner 1995), with a key role in the maintenance and regeneration of plant species (Harper 1977) and succession (Grime 1989). It is the memory of plant communities in the soil (Thompson 1992) that replaces plants damaged by

---

A. Pott (✉) · E. B. de Souza
Laboratório de Ecologia Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

F. Bao
Universidade Estadual Paulista Julio de Mesquita Filho, Departamento de Biodiversidade, Instituto de Biociências, Rio Claro, SP, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_15

pathogens, herbivores, or other disturbances (Baker 1989), besides resprouting (Cronk and Fennessy 2001). Thompson (1992) described the role of soil seed banks after disturbance in several vegetation types, such as grasslands, wetlands, and forests, concluding that the seed bank function in vegetation dynamics in general is well defined and is closely linked with disturbances. A classification of the seed bank types was suggested for herbaceous vegetation in England, where the transient soil seed reservoir tends to fill seasonal gaps, while the persistent bank allows the regeneration after unpredictable disturbance (Thompson and Grime 1979). Such a classification has not been proposed for the Pantanal wetland yet.

The soil seed bank is particularly relevant in seasonal vegetation, and it is vital under pluriannual oscillations of flood and drought. Plants in freshwater marshes with drawdowns, predominantly annuals, produce high numbers of seeds (Mitsch and Gosselink 1993). Many wetland species, mainly annuals, produce persistent seed banks with a large number of seeds with high longevity (Middleton 2003). The ability of seeds to survive extended drought and periods of drying and wetting that do not lead to seed production will determine the potential species pool for re-establishment of future plant communities of temporary wetlands (Brock 2011). In wetlands, the seed storage is also called sediment seed bank (Mitsch and Gosselink 1993), although in the Pantanal, only the areas flooded by rivers are under ongoing sedimentation. The soil seed bank is a regeneration strategy for most plant species in seasonal wetlands such as the Pantanal (Souza et al. 2019).

15.2 Soil Seed Bank Studies in the Pantanal

The climate of the Pantanal wetland shows a rainy season in October-March and a dry one in April-September (see the Chap. 1 on General Aspects). The flooding regime depends on which location in the Pantanal is being considered, if under direct river overflow or just local rain (Pott and Silva 2015). Besides the annual seasonality, there are pluriannual wetter or drier cycles. Soils also vary greatly, from very poor, almost pure sand far from rivers, to very fertile heavy clays in riverine zones (Pott and Silva 2015). The vegetation is a mosaic of woody, grassland, and aquatic types, described in the chapters on Mapping (Chap. 2), Flora (Chap. 3), Aquatic Plants (Chap. 4), Woody Vegetation (Chap. 9), and Monodominants (Chap. 8). The primary drivers of the vegetation in the Pantanal are fire and flood (Oliveira et al. 2015; Arruda et al. 2016), opening gaps in grasslands or forests. In consequence, perennial plants growing on flood-prone sites are flood-tolerant and/or drought-resistant, and annuals store persistent seeds in the soil for a following favorable condition. Each species overcomes obstacles of seed dispersal, seed burial, and disturbances until germination, to become established, and each particularity is strongly linked to the type of habitat and not only to the disturbance event. The Pantanal is considered one of the main tropical floodplains and includes heterogeneous environments under different influences, including the river-floodplain interaction, as well as of distinct types of surrounding vegetation and hydric seasonality (Pott and Silva 2015). Therefore, the study of the soil seed bank can contribute to explaining many phytogeographic peculiarities of the plain since the distribution and the ecological preferences of the species are determined by the germination during or after undergoing inundation and fire (Souza et al. 2019).

We present a review of a set of studies that present the seed bank as a source of regeneration in 15 environments/habitats of the Brazilian Pantanal. We reviewed the few available studies on soil seed banks in the Pantanal wetland. Plotting the study sites on the Pantanal map, it becomes quite evident how little has been sampled so far (Fig. 15.1). Nonetheless, the existing studies encompass a range of habitats, from ponds to dry forest, and regarding influences such as fire and flood. A few studies were not included for containing insufficient data (e.g., Lima Junior et al. 2007).

There are two main techniques to evaluate the soil seed bank: seedling emergence and seed separation with direct counting (Simpson et al. 1989, Thompson 1992, Mcfarland and Shafer 2011). Both methods have advantages and limitations; it is possible to combine them (Bao et al. 2020b). In wetlands, an additional approach is to test seedling emergence in drained and submerged soil samples and to test inundated trays back to drained conditions (Bao et al. 2018a). The emergence technique does not assess dormant seeds, relevant in long-term persistence. The conditions of moist soil for germination tests are not the same as in the field, neither the simulated flood in tanks nor the ambient temperature and sun radiation in a

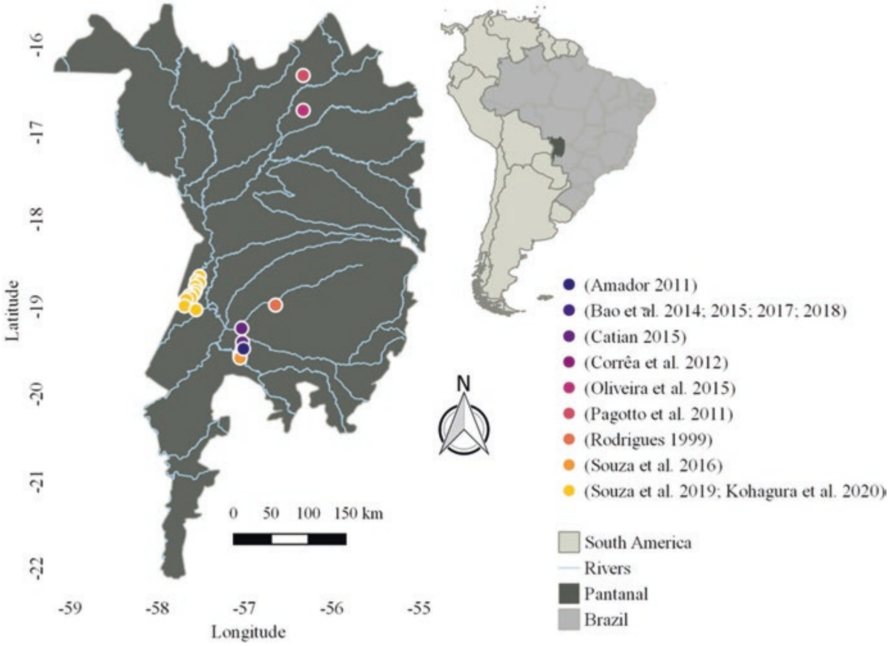


Fig. 15.1 Map of the Pantanal wetland with the sampling points of soil seed banks

greenhouse. Sieving soil includes dead seeds. Seed viability tests with tetrazolium are difficult on tiny seeds, or a germination test can be applied. The seed screening method tends to predict a much higher density of forest seeds (Brown 1992). Seed identification requires knowledge, and a comprehensive seed collection precedes it. Similarly, seedling identification also depends on expertise, but herbarium specimens of seedlings tend to be little useful as they almost disappear after dehydration. When seedlings start to emerge from the Pantanal soil samples, their high density and the high number of species are quite frightening, and identification and removal shall be quick to not hinder the sequential germination. Seeds can be sorted and stored for gradual identification, while seedlings wilt rapidly. Both maintain their shape in alcohol. Also, photographs and drawings help for later check.

Control trays with a sterile substrate verify contamination by incoming diaspores, mainly ferns, in screened greenhouses, or shared with other experiments. Watch for insects since grasshopper nymphs or harvesting ants remove seedlings within hours. A sealed roof prevents heavy rain to unbury seeds or seedlings. Automatic sprinklers need maintenance since the soil quickly dries in the trays. Seedlings are best surveyed in the early morning. Unidentified seedlings can be transplanted to grow or even flower. Tanks with submerged soil samples may have algae blooms, readily removed using a stick. Identification manuals are handy, though not yet available for the Pantanal flora, as most are for weeds (Lorenzi 1994; Kissmann 1997; Kissmann and Groth 1999, 2000). When diaspores are fruits, at least the family can be determined, as well as seeds (Barroso et al. 1999). Only one identification guide of seeds and seedlings is available for some aquatic plant species of the Pantanal (Tirintan et al. 2018, Catian et al. 2021).

Sampling soil seed banks is relatively simple after the design is established. The tools vary from spade to corers. The corer is not adequate for flooded soil since the sampled soil core tends to slip out. A small dredge is better. It is important to relate the sample area to express the results as seeds or seedlings/m^2. The samples should be shaded and not be stored for long in plastic bags; otherwise, the seeds can start to germinate or die. Soil drying may also affect seed viability and/or dormancy. Storing samples under refrigeration may also interfere with seed dormancy or viability. Soil sampling can be stratified; it is recommendable in sedimentation areas such as riverbanks (Souza et al. 2019) and ponds. How deep to sample has to be decided according to the sedimentation dynamics and based on previous surveys or preliminary tests. For example, in Central Amazon, the seed bank samplings were standardized using a template (PVC pipe) of 20 cm diameter and 5 cm high to collect topsoil free from the thick litter (Bordon et al. 2019).

15.3 Synthesis of Soil Seed Bank Studies in the Pantanal

The studies on soil seeds have been concentrated in specific parts of the Pantanal, as shown in Fig. 15.1.

The most frequent and abundant species, found in five or more study sites, were *Eleocharis minima*, *Lippia alba*, *Ludwigia octovalvis*, *Rotala ramosior*, *Hyptis brevipes*, *Cecropia pachystachya*, *Helanthium tenellum*, and *Scoparia montevidensis*. The only tree is *C. pachystachya*, present even in the seed bank of floodable grasslands and ponds, where it is absent in the standing vegetation, though occurring in nearby forest islets (see summary of the species found in most of the different studied sites in Table 15.1). The cited authors applied the seedling emergence technique, except for Catian (2015), who utilized direct diaspore counting, and Bao et al. (2018a, 2020c), who used both separation and seedling emergence. The data were obtained with various soil sample areas and depths, different total sampled areas, and duration of the germination experiment. Therefore, the reports are not straightly comparable but allow an overview of the main species and the floristic diversity of seed banks in the Pantanal (Table 15.1). Also, comparisons should not be drawn between results from the seed extraction and seedling emergence methods (Brown 1992).

The first conclusion from Table 15.1 is that seed banks differ among habitats; the aquatic and the forest habitats share the lowest number of species. Seed banks of different grasslands also vary. Differences between habitats have also been found for the Paraná River floodplain (Schneider et al. 2020) and in other wetlands. In Figs. 15.2 and 15.3, some of the frequent seeds and seedlings detected in floodable grassland soil seed banks in the Pantanal are shown (Bao et al. 2014, 2018a, 2020c).

The first study on soil seed banks in the Pantanal was made on *Elionurus* grassland (Rodrigues 1999). The reviewed existing reports encompass from aquatic habitats (Catian 2015) to dry forest (Amaral 2011), and the seed bank composition differs much according to the flood gradient and according to the corresponding vegetation type, from aquatic to woody. However, all seed banks do not reflect entirely the standing vegetation. That also has been observed in other studies. The highest similarity found in the Pantanal was 34% in ponds compared with very low in most other habitats, or the richness of the vegetation was not given. The seed densities varied from 196/m^2 in riparian forest (Kohagura et al. 2020) to 226.000/m^2 in ponds (Catian 2015). The species richness of seed banks varied from 26 in a floodable grassland (Oliveira et al. 2015) to 124 in *Tabebuia aurea* savanna (Souza et al. 2016). The factors influencing seed bank size and longevity are yet little known in the Pantanal.

The seed bank of 20 ponds was examined washing soil in a set of sieves and sorting and counting the diaspores (Catian 2015). Two studies compared the seed banks of burned and unburned riparian forests of the Paraguay River (Ferreira et al. 2013, Kohagura et al. 2020). In the same riparian forest, an evaluation of the seed bank at four soil depths (0–5, 5–10, 10–15, and 15–20 cm) detected viable seeds in all layers (e.g., *Oryza latifolia* at 5–10 cm and *Cecropia pachystachya* at 15–20 cm deep) (Souza et al. 2019). Those authors observed that in deposition zones of the Paraguay River riparian forests, significant differences in richness and abundance of viable seeds occur between soil layers of at least 10 cm. They used the soil depth as an indicator of seed bank persistence and concluded that species such as *C. pachystachya* and *Cyperus haspan* have persistent soil seed banks and that the soil seed

Table 15.1 Summary of the species composition of soil seed banks of 15 habitats in the Pantanal wetland, indicating sampling depth, total seedling density (m^{-2}), species richness, and main plant species detected (X = presence). Catian (2015) and Bao et al. (2020c) did sieving and direct counting, and all other authors applied the seedling emergence technique. 1, Catian (2015); 2, Ferreira et al. (2013); 3, Kohagura et al. (2020); 4, Souza et al. 2019; 5, Souza et al. (2016); 6, Couto et al. (2006); 7, Bao et al. (2014); 8, Bao et al. (2018a); 9 and 10, Bao et al. (2020c); 11, Pagotto et al. (2011); 12, Oliveira et al. (2015, 2019b); 13, Rodrigues (1999); 14 and 15, Amaral (2011). N.i. = not informed

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Gradient (G) or number of flood levels (1–5)	2	G	G	G	G	5	3	3	3	3	G	G	1	1	1
Sampling depth (cm)	20	5	5	5–20	3	10	3	3	3	3	5	10	5	3	3
Sample area (cm^2)	100	400	400	400	400	400	400	400	400	400	189	576	25.6	225	225
Total sampled area (m^2)	0.8	2	4	0.4	4	0.6	1.2	1.2	1.2		2.6	0.86	5.6	2.5	2.5
Days of seedling emergence experiment	n.i.	90	196	90	n.i.	90	n.i.	n.i.	90 + 90	90 + 90	270	300	547	99	99
Seeds or seedlings m^{-2}	226, 000	X	196	2960	n.i.	0–210	n.i.	n.i.	n.i.	n.i.	1781	6353	997	778	541
Number of species in the soil seed bank	81	44	61	44	124	(0-9)	91	n.i.	70	70	26	44	85	66	61

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Similarity with standing vegetation (% or qualitative)	43%	Very low	Very low	Very low	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	Very low	n.i.	Very low	Very low
Number of species in the vegetation	106	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.
Main families and species															
Alismataceae															
Echinodorus spp.	X									X					
Helanthium tenellum (Mart.) Britton	X						X	X	X	X	X				
Hydrocleys nymphoides (Willd.) Buchenau										X					
Sagittaria guayanensis Kunth									X	X	X	X			
Asteraceae															
Conyza bonariensis Cronq.				X											
Mikania micrantha Kunth		X	X												

(continued)

Table 15.1 (continued)

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Boraginaceae															
Euploca filiformis (Lehm.) J.I.M. Melo & Semir	X				X		X	X							
E. procumbens (Mill.) Diane & Hilger					X										
Burmanniaceae															
Burmannia flava Mart.													X		
Cabombaceae															
Cabomba furcata Schult. & Schult.f.							X	X	X						
Cyperaceae															
Cyperus gardneri Nees				X											
C. haspan L.		X	X	X	X										
C. odoratus L.	X	X													
C. surinamensis Rottb.					X		X							X	X

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Eleocharis minima Kunth	X						X	X	X	X	X	X		X	X
Eleocharis spp.	X											X			
Cyperus sellowianus (Kunth) T.Koyama (*Lipocarpha humboldtiana* Nees)													X		
Cyperus blepharoleptos Steud. (*Oxycaryum* cubense (Poepp. & Kunth) lye)	X														
Fimbristylis dichotoma (L.) Vahl							X	X	X						
Schoenoplectiella supina (L.) lye (*Scirpus supinus*)					X		X								
Eriocaulaceae															

(continued)

Table 15.1 (continued)

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Paepalanthus lamarckii Kunth													X		
Euphorbiaceae															
Croton trinitatis Millsp.					X		X	X	X						
Euphorbia spp.					X										
Fabaceae															
Canavalia mattogrossensis (Barb. Rodr.) Malme			X												
Rhynchosia minima (L.) DC.			X												
Hydroleaceae															
Hydrolea spinosa L.							X	X	X						
Isoetaceae															
Isoetes pedersenii H.P. Fuchs ex E.I.Meza & Macluf								X	X	X		X			
Lamiaceae															

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Hyptis brevipes Poit.	X	X			X		X	X			X		X		
Limnocharitaceae															
Limnocharis flava (L.) Buchenau									X	X					
Lythraceae															
Rotala mexicana Cham. & Schltdl.											X	X			
R. ramosior (L.) Koehne				X	X		X	X	X	X	X			X	
Malvaceae															
Melochia simplex A.St.-Hil.					X		X	X	X						
Sida cerradoensis Krapov.					X		X	X							
Melastomataceae															
Rhynchanthera novemnervia DC.		X													
Nymphaeaceae															
Nymphaea spp.	X										X				X
Onagraceae															

(continued)

Table 15.1 (continued)

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Ludwigia decurrens Walt.		X	X	X											
L. grandiflora (Michx.) Greuter & Burdet		X													
L. inclinata (L.f.) P.H raven		X													
L. leptocarpa (Nutt.) H. Hara	X											X			
L. nervosa (Poir.) H. Hara				X											
L. octovalvis (Jacq.) P.H raven	X				X		X	X		X	X		X	X	
Orobanchaceae															
Buchnera longifolia Kunth					X		X	X	X						
Parkeriaceae															
Ceratopteris pteridoides (hook.) Hieron.		X													

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Pityrogramma pteridoides (L.) link		X													
Poaceae															
Digitaria ciliaris (Retz.) Koel.					X				X						
D. fuscescens (Presl) Henr.	X						X	X	X						
Eragrostis bahiensis Schrad. Ex Schult.							X	X	X						
Eriochloa punctata (L.) Desv.		X		X											
Hymenachne amplexicaulis (Rudge) Nees			X												
Oplismenus hirtus (L.) Desv.				X											

(continued)

Table 15.1 (continued)

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Paspalidium geminatum (Forssk.) Stapf (*P. paludivagum* (Hitchc. & chase) Parodi											X				
Paspalum repens Berg.		X													
Paspalum sp.	X										X				
Setaria parviflora (Poir.) Kerguélen					X				X	X					
Steinchisma laxum (Sw.) Zuloaga		X										X			
Phyllanthaceae															
Phyllanthus stipulatus (Raf.) Webster											X				
Plantaginaceae															
Angelonia salicariifolia Bonpl.							X	X	X						
Bacopa australis V.C. Souza									X	X					

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
B. salzmannii (Benth.) Wettst. & Edwall													X	X	
Stemodia verticillata (Mill.) Hassl.				X											
Scoparia dulcis L.				X											
S. montevidensis (Spreng.) R.E. Fr.					X		X	X					X	X	
Polygalaceae															
Polygala molluginifolia A.St.-Hil.					X		X	X	X						
Polygonaceae															
Polygonum punctatum Elliot							X	X	X						
Pontederiaceae															
Eichhornia azurea (Sw.) Kunth	X										X				
E. crassipes (Mart.) Solm		X													

(continued)

Table 15.1 (continued)

	Pond (1)	Flood plain (2)	Riparian vegetation (3)	Riparian vegetation (4)	*Tabebuia* savanna (5)	Forest, cerrado, grassland, spine scrub (6)	Natural floodable grassland (7)	*Urochloa* floodable grassland (8)	Flood and post-flood (9)	*Urochloa* flooded (10)	Floodable grassland (11)	Floodable grassland (12)	*Elionurus* grassland (13)	Forest islet (14)	Forest islet (15)
Heteranthera limosa (Sw.) Willd.							X	X	X						
Pontederia reflexa D. Sousa									X						
P. subovata (Seub.) Solms										X					
Portulacaceae															
Portulaca pilosa L.							X	X	X						
Rubiaceae											X				
Borreria sp.		X	X										X		
Diodia kuntzei K. Schum.							X	X							
Randia heteromera Judkevich & R.M.Salas.			X												
Richardia grandiflora (Cham. & Schltdl.) Steud.					X		X	X							
Spermacoce glabra Michx.				X											
Urticaceae															
Cecropia pachystachya Tréc.		X	X	X		X								X	X
Verbenaceae															
Lippia alba N.E. Br.					X		X	X	X	X	X		X		

bank is a regeneration strategy for most plant species in wetlands such as the Pantanal (Souza et al. 2019).

An investigation of the soil seed bank along a 5 km transect line across a gradient of five flood levels and respective vegetation types (*Tabebuia aurea* and *Byrsonima cydoniifolia* savanna, paleo-dike with seasonal semideciduous forest, and spiny scrub of *Mimosa pigra* and *Bauhinia bauhinioides*), in consequence of the diversity of habitats, found the highest richness (124 species) of all reviewed studies (Souza et al. 2016). They concluded that the flood is a trigger that helps to hold the recovery of several species in the vegetation after water drawdown (Souza et al. 2016). A survey of the seed bank of seasonally flooded grassland, with three flood levels, compared with that under introduced *Urochloa humidicola*, concluded that the seed bank is persistent under the seasonally flooded cultivated grassland (Bao et al. 2014, 2015, 2018a). Bao et al. (2018a) emphasized the resilience of the seed bank under the introduction of *U. humidicola*, by simulated flooding in an experimental microcosmos and contrasting the species composition of seedlings with a non-flooded treatment, observing that from the submerged soil arose aquatic plants, in contrast with nonaquatic species when the same soil was switched back to a condition of drained soil in the greenhouse.

The first study on soil seed banks in the Pantanal was made on grazed vs ungrazed and burned vs unburned *Elionurus* grassland (Rodrigues 1999). The dominant *Elionurus muticus* did not germinate in the experiment (Rodrigues 1999). In the field occurred more species than detected in the soil seed bank; probably it was undersampled, or the experiment was too short. Another study assessed the seed bank of seasonally flooded grassland under three flooding durations, detecting higher richness and abundance in areas under long periods of flooding (Pagotto et al. 2011). A similar study also monitored seedling emergence from seasonally flooded grassland soil, considering three ground levels (Oliveira et al. 2015). They took 2-cm-stratified soil samples to 10 cm, plus litter, and found an emerged seedling density of 7404 seeds/m^2 of 49 morphospecies, mostly aquatic (63%). In both areas occurred hydrochory to more floodable patches, where both abundance and species richness were highest, and showed a much higher seedling density than other seed bank studies in the Pantanal because spores of *Isoetes pedersenii* greatly outnumbered the angiosperms (Oliveira et al. 2015). This pteridophyte had also been found in a modified grassland a few hundred kilometers south of the cited one (Bao et al. 2014). Its dispersal occurs directly into the soil bank, due to its underground sporocarps, which seems to favor its abundance in the soil bank. Soil disturbance by plowing, harrowing, and grass sowing probably enhanced the spread of spores. The tiny spores are difficult to count when using the diaspore separation technique (Bao et al. 2019, 2020b, c).

A very low floristic similarity was observed between the seed bank and the standing riparian forest of the Paraguay River (Ferreira et al. 2013). A similar pattern was found in forest islets (comparing edge and top) of the Abobral subregion (Amaral 2011). The soil seed bank of the floodable edge and the flood-free center top of forest islets in the Abobral subregion was contrasted, pointing out that few tree seedlings emerge from the soil seed bank, and most species are herbaceous and

Fig. 15.2 Frequent seeds detected in grassland soil seed banks in floodable grassland in the Pantanal wetland by Bao et al. (2018a). Families are mentioned in Table1. (Pictures by F. Bao)

anemochorous (Amaral 2011). One reason may be that in large-seeded trees, seed banks are almost unknown (Thompson 1987). However, even most small-seeded trees are scarcely stored in the soil. Perhaps the seed bank is mainly transient since many deciduous trees have short-lived seeds (e.g., *Astronium urundeuva*, *Handroanthus*, spp. and *Tabebuia aurea*), while zoochorous seeds reach the ground after scarification (e.g., *Cecropia pachystachya*, *Psychotria carthagenensis*), or

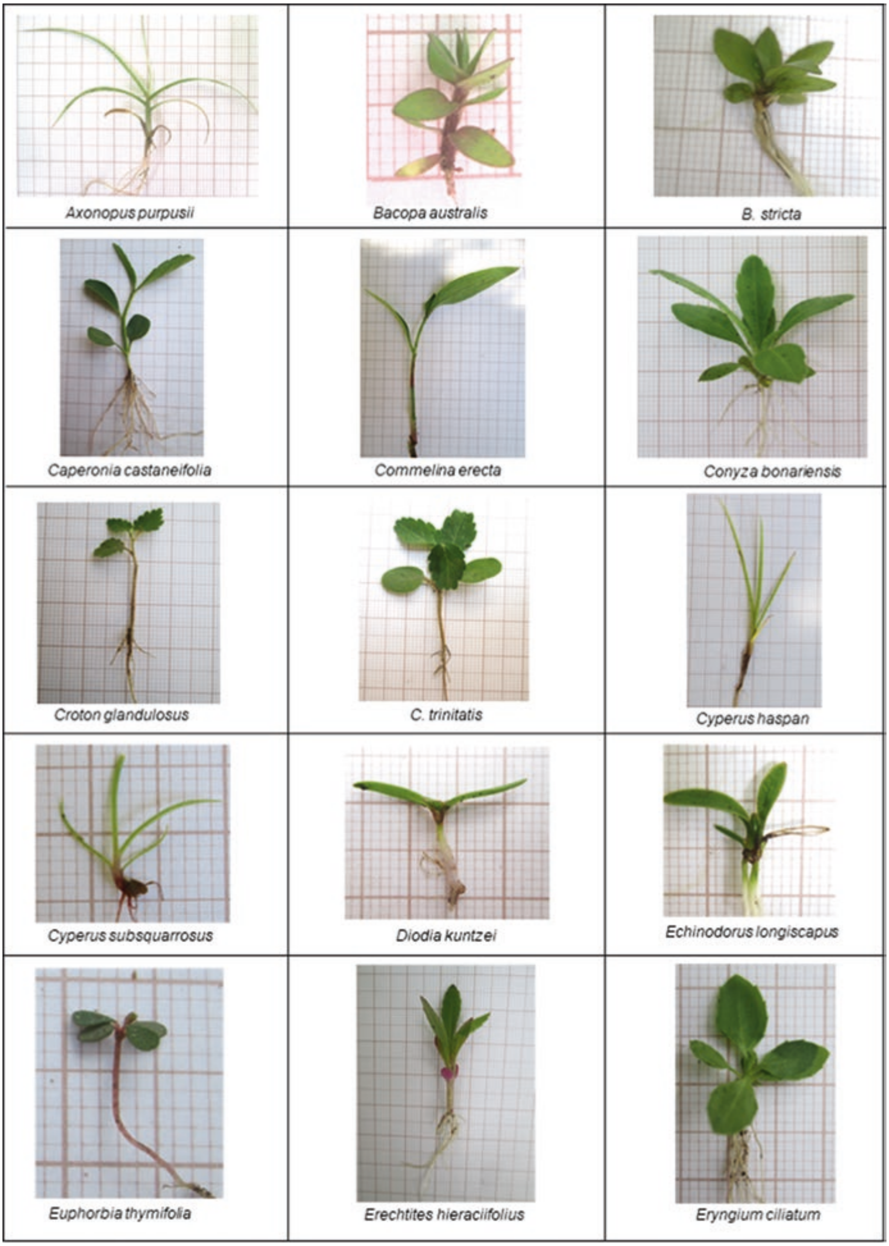


Fig. 15.3 Frequent seedlings detected emerging from floodable grassland soil seed banks in the Pantanal wetland by Bao et al. (2014, 2015, 2018a, 2020c). (Pictures by F. Bao)

there are dormant or hard seeds (e.g., *Attalea phalerata*), and the experiment should last longer. Large diaspores such as those of palms are predated by agouti and parrots. The main species in the seed rain in forest islets are *Ficus* spp. and *Cecropia* (Ferreira 2008). In the seed bank, in addition to the seeds from the standing vegetation, also occur some plants from outside the forest islet (Amaral 2011). A special type of seed bank, quite rich, was found on stems of *Attalea phalerata* in the Pantanal in forest islets, though not an ordinary soil bank, with 75 species; the most abundant are *Cecropia pachystachya* and *Ficus pertusa*, growing in the decomposing organic debris accumulated on the remaining sheaths of dropped palm leaves (Corrêa et al. 2012). In forests elsewhere, no woody species were found with the seedling emergence method, while the seed screening detected a few (Brown 1992). The lowest similarity between seed bank and standing vegetation has been found in forests, while in wetlands it was intermediate, and in grasslands it was the most similar (Hopfensperger 2007).

Diaspores tend to accumulate in low-lying parts of grasslands (Pagotto et al. 2011). Probably due to a similar drift, there is a concentration of seeds in pond beds, not only of aquatic plants but also of terrestrial species, e.g., *Heliotropium indicum* and *Mimosa* spp. Stagnant warm remaining puddles may soften hard seeds, and even kill some. The seed bank does not vary much between the edge and center of permanent and temporary ponds and seasonal streams, neither between these water bodies (Catian 2015). The seed bank of ponds, sampled inside and on the littoral, has only 43% similarity with the vegetation, attributed to seed income by floods (Catian 2015), including many species from drier habitats that do not succeed establishing in ponds, except in very dry years. That is attributed to the homogenizing effect of flood.

Both seed bank assessment techniques can give a better outcome (Bao et al. 2020b). Furthermore, comparisons should not be drawn between results from the seed extraction and seedling emergence methods (Brown 1992). The seed separation and direct counting technique is very laborious and requires experience, seed collection, photographic guides, and help from botanists for identification; otherwise, it can be very time consuming and frustrating. We have yet few illustrated identification guides for seeds, mostly restricted to weeds (e.g., Lorenzi 1994, Kissmann 1997, Kissmann and Groth 1999, 2000) or general taxonomy (e.g., Barroso et al. 1999). A seed display or collection can be quite easily organized, collecting them from known adult plants of the study area and possible external sources, as done by Catian (2015), or eventually from herbarium duplicates. Yet, after sorting in morphotypes, to investigate viability requires further tests, either by germination or tetrazolium, but it is difficult to apply on small seeds as those of most herbs. On the other hand, the seedling emergence method has some limitations as well, e.g., dormant seeds are not detected, and the homogenized soil moisture under glasshouse conditions can favor some species and hinder others. Oliveira et al. (2015) discussed that the artificial conditions provided for germination are not the same as in the field. One advantage is that an unidentified seedling can be left or may be transplanted to develop until it shows enough characteristics, or even to flower. It would be worthwhile to invest in printed and online illustrations, such as the examples shown (Fig. 15.3), to ease the identification of seeds and seedlings of the Pantanal flora.

15.4 Effects of Flood and Fire

Flooding of grassland soil determines the emergence of aquatic plants (Bao et al. 2018a). Floods affect seed survival: while some tree species of the Pantanal are tolerant and can germinate during or after the flood, e.g., *Curatella americana* and *Vochysia divergens*, others do not survive submersion, e.g., *Qualea grandiflora* (Oliveira et al. 2019a). Other species, e.g., *Tabebuia aurea*, produce a larger bunch of seeds that are wind-dispersed after water drawdown providing a transient seed bank. The seedlings colonize the open grassland soon after the end of flooding, but most will die until the next flooding event, and only those seedlings that colonize termite mounds survive. If a fire occurs in the same year, most of the seedlings surviving the flood can be killed by fire, which demonstrates a high dependence of this species on the interaction of flood and fire events (Manrique-Pineda et al. 2021).

A discrepancy was found between the dry season grass community dominated by species from the *Andropogon*, *Imperata*, and *Paspalum* genera and the aquatic species emerging from the soil seed bank which did not include the dominant species from the terrestrial phase (except for *P. lenticulare*, with three seedlings) (Oliveira et al. 2015). That may be related to the maintenance of only a transient bank of grasses and the strong seasonality of the vegetation (Thompson et al. 1997), only detectable by repeated sampling in time (Baskin and Baskin 2014). Brock (2011) investigated characteristics of the seed banks through germination from sediment from five Australian temporary wetlands, with various water regimes, examining two sources of seed bank depletion: (i) length of time dry (longevity up to 12 years) and (ii) successive annual wetting and germination events (up to seven) with intervening periods dry (leaving a residual seed bank), both without seed bank replenishment. She found species-rich, long-lived seed banks that were not exhausted by successive germination events; after 3 years of dry storage, 90% of the original seed bank species germinated, after 6 years 75%, and after 12 years 20%. After seven successive wetting and drying events without seed bank replenishment, 48% of the original species still germinated. The survival time dry for seed bank species, 7.4 years, lasted longer than the recent droughts. Seed bank composition varied among wetlands and over time; most species were not shared by all wetlands, and many occurred in only one. The germination patterns of different species tended to survive long dry periods and several wetting and drying events, though experimental drought diminished species richness and abundance, indicating limits to seed bank persistence. Such long-term studies of seed bank persistence should allow prediction of the species richness and composition of the germinating communities in a wetland with changing water regime, particularly critical under climate change and future wetland conditions.

Post-flood debris in Pantanal grasslands and seasonal ponds hinder seedling emergence from the soil seed bank (Bao et al. 2018b). In a study on seed banks of riparian forests, litter removal did not affect the abundance and diversity of seedlings emerging from bare soil and soil with litter; however, litter removal reduced the richness in a wet year compared with the dry year (Kohagura et al. 2020). Large seeds may have critical importance in seedling emergence through litter (Thompson 1987), but seed size was not measured in the Pantanal (Amaral 2011; Kohagura et al. 2020). The submerged bank contains somewhat large seeds, which is an advantage to emerge through debris and for fast growth before flooding, e.g., *Ipomoea* spp., *Mimosa* spp., *Senna* spp., and *Sesbania virgata*.

Only a few studies compared soil seed banks of burned and unburned vegetation in the Pantanal (Ferreira et al. 2013, Couto et al. 2006, Oliveira et al. 2019b, Kohagura et al. 2020). However, long-term effects are diluted because rarely any spot in the Pantanal never had fires. In floodable savanna grasslands, the species richness and composition did not change under one fire event, except for the top 2 cm layer; both abundance and richness decreased with soil depth, leading to the conclusion that fire tolerance of the soil seed bank needs long-term studies (Oliveira et al. 2019b). Studying the postfire regeneration is a way to estimate the effect of fire on the seed bank (Oliveira et al. 2019b). As a positive effect, besides creating gaps, fire improves germination of some species, e.g., *Copernicia alba* (Fabri 2018), *Microstachys hispida*, *Mimosa* spp., and *Solanum viarum* (Pott and Pott 1994) (see the Chap. 18 on Fire). On sandy soils, *Elionurus muticus* grassland is a transition from seasonally flooded grassland to Cerrado woodland; it is monodominant, with other grasses and herbs growing intermingled; when unburned, the taller tussock grass *Trachypogon polymorphus* increases. The seed bank exhibited 85 species, the main ones being *Digitaria fuscescens* and *Axonopus purpusii*. Large areas have been planted with *Urochloa humidicola* for being mostly flood-free and because *Elionurus* is rejected by cattle, except fresh regrowth after burning, and this well-grazed exotic grass has reduced the use of fire and, consequently, the occurrence of wildfires. However, the remaining seed bank has not been evaluated, as in a modified floodable grassland (Bao et al. 2018a).

A study of the soil seed bank, with and without fire, of *Vochysia divergens* forest, deciduous forest, grassland, and swampy spine scrub, in the SESC Pantanal preserve, showed that fire reduced seedling density, mostly in *V. divergens* stands and spine scrub, not in grassland, and probably had a deleterious effect under denser vegetation, where the topsoil has more litter and organic matter (Couto et al. 2006). They collected soil samples at 0–5 and 5–10 cm, and followed seedling emergence for 3 months in the greenhouse; *Cecropia* was abundant in forest soil (Couto et al. 2006). The immediate effect of fire on riparian herbaceous vegetation was a reduction of the seed number and an abundant germination of Convolvulaceae vines (Ferreira et al. 2013). Old-burn riparian forest presented higher seedling abundance than recent burn, and the interaction between fire and flood did not affect richness, abundance, and diversity of the seed bank (Kohagura et al. 2020). The drier year presented higher abundance, richness, and diversity than a flood year, and strikingly, from the soil seed bank samples of riparian vegetation emerged only two tree species, *Cecropia pachystachya* and *Triplaris americana*, besides the seedling abundance of herbaceous species (Kohagura et al. (2020). Both tree species are pioneers; *C. pachystachya* is dispersed by birds, bats, and monkeys; and *T. americana* is wind-spread. Despite the low similarity expected between the seed bank and the standing vegetation in forests (Hopfensperger 2007), those two species also are some of the most common trees in the Pantanal riparian forests. However, in the field, regeneration from seed in flooded and burned riparian forest areas revealed 50 species, excluding herbs (Oliveira et al. 2014).

The highest soil temperatures under fires are obviously reached in the top layer, exactly where most seeds are stored and, thus, more killed, although many grasslands in the Pantanal show quick surface fires, unless ungrazed. The soil surface also has combustible litter, full of seeds. However, in riparian forests, viable seeds can occur down to 10 cm (Souza et al. 2019). That may explain how, after a fire in dry years, *Oryza* spp. regenerate when those low riverine areas become again flooded. In flammable vegetation types with species originating from the Cerrado, where most plants have the capacity to resprout, seed recruitment occurs in a much smaller quantity (135 ± 38 seeds.m^{-2}; Dairel and Fidelis 2020), when compared with flooded areas of the Pantanal (2806 ± 3105 seeds.m^{-2}; Bao et al. 2014) and the Amazon Forest (1690 ± 2530 seeds.m^{-2}, Souza et al. 2019) that present persistent seed banks as the main source of vegetation maintenance. The severe wildfire in the Pantanal in 2020 probably burned most soil seed banks trapped in histosol in the "corridor of fire and flood" described in the chapter on Fire (Chap. 18). Those areas need an assessment of the seed banks and bud banks to understand the regeneration of the vegetation. Probably the lowest areas had the most abundant seed stock and also highest seed mortality, and that could be verified comparing burned and unburned nearby sites. We expect that the remaining seed bank will trigger regeneration of the vegetation, grasslands first, followed by a secondary succession of woody species, as must have occurred since ancient times.

Finally, an interaction between fire and flood can occur. An evaluation of the germination of *Copernicia alba* palm seeds in a controlled fire and flood experiment, with seed, buried in 3 and 5 cm, and submerged after 60, 120, and 180 days, found a stronger effect of fire than flood on germination (Fabri 2018). When seeds are buried at 5 cm, germination is ameliorated by fire, mainly when fire preceded flood; on the other hand, when the fire was applied with the seed on the surface, the subsequent flooding in the three duration times harmed germination; also, both fire and flood when isolated appear to have little effect on germination (Fabri 2018). Effects of fire and flood and their interactions on seeds in the soil need deeper investigation in the Pantanal.

15.5 Dispersal

Soil seed banks are associated with seed dispersal since its syndromes influence directly seed distribution. In the Pantanal, dispersal has been studied mainly for some plant and animal species (Donatti et al. 2011), and dispersal syndromes in the vegetation such as Chaco (Carvalho & Sartori 2014) and dry forest (Lima & Damasceno Junior 2020). Soil seed banks can have concentrations in some spots because of spread by animals, so-called zoochory. Both exo- and endozoochory can occur. Birds, mammals (bats, tapir, coatimundi, monkeys, armadillos, crab-eating fox, peccaries, feral pig), and fish are seed spreaders, and even ants. In the *Tabebuia aurea* savanna, the earth mounds receive ornithochorous diaspores, e.g., *Paullinia pinnata* and *Erythroxylum anguifugum*, and the trees growing on the mounds work as colonization nuclei. Similarly, everywhere fence lines are pearches and also function as a niche for bird-spread vines (e.g., *Cissus spinosa*, *Odontocarya tamoides*, *Passiflora misera*), shrubs (e.g., *Eugenia egensis*, *Psidium* spp.), and trees (e.g., *Sapium haematospermum*). In riparian vegetation, also a high proportion of seeds comes in from elsewhere. Cattle can have a direct effect on soil seeds, e.g., with cattle 893 seedlings.m^{-2} were recorded compared with slightly more without cows (1137 seedling.m^{-2}) (Rodrigues 1999). Grazing modifies mainly the herbaceous vegetation and can reduce seed yield of some species, while increasing others. Nonetheless, some species are spread by cattle, such as *Acrocomia totai*, *Attalea phalerata*, *Desmodium* spp., *Prosopis ruscifolia*, *Samanea tubulosa*, *Solanum viarum*, and *Vachellia farnesiana* (Pott & Pott 1994), and well-grazed grasses such as *Paspalum* spp. Horses are one of the dispersers of *Psidium guajava*. Sheep and other animals spread hooked or spiny diaspores of *Achyranthes aspera*, *Amaranthus spinosus*, *Pisonia zapallo* (Pott & Pott 1994), *Acanthospermum* spp. (*A. australe* is even called *carrapicho-de-carneiro*, meaning sheep-bur), *Cenchrus echinatus*, and *Triumfetta* spp. People also spread fruit plants (*Acrocomia totai*), as well as burs and sticky diaspores (*Boerhavia diffusa*, *Desmodium* spp., *Priva lappulacea*) (Pott & Pott 1994).

Seed burial reduces predation by invertebrates and facilitates seedling anchorage (Thompson 1987). Earthworms ingest small grassland seeds, burying them and subsequently returning them to the surface in casts (Thompson 1987). Dung beetles can bury seeds attached to animal feces and in them. Digging by pigs, armadillos, and ants all contribute to cover and uncover seeds. Many other animal activities can influence seed burial, such as cattle trampling, feral pig and armadillo digging, also activity of ants and birds, as well as bringing some seeds back to the soil surface. Cattle treading also presses seeds into the ground. Burial is a mechanism to store seeds in the soil, sometimes favored in cracking clays (Thompson 1987). The role of these processes has not been studied in the Pantanal, e.g., in soils with expansive clays that occur in *T. aurea* savanna and Chaco. However, some cracks are deep and seal at wetting, where seeds fail, unless they can float. Some diaspores in the Pantanal have an active burial mechanism, such as *Aristida* spp. and *Trachypogon* spp., with sharp hooked points and awns with back and forth torsion movements under moistening/drying conditions.

Summary of relevant findings:

1. The plant species composition shows high variation among seed banks of different vegetation types.
2. Seeds in pond sediments are homogenized by flooding (Catian 2015).
3. Annual and short-perennial herbs are the species-richest and most abundant group of plants to emerge from all tested seed banks in the Pantanal (Bao et al. 2014, Souza et al. 2016).
4. Seed banks have the lowest similarity with the standing vegetation in forest islets (Amaral 2011), riparian forest (Arruda et al. 2016; Souza et al. 2019, Kohagura et al. 2020), and *Vochysia divergens* monodominant forest (Silva 2011), for little presence of seeds of trees, as well as under *Combretum laxum* thickets (Silva 2011). The seed bank of forest islets is richer in the flood-prone edge than in the flood-free middle zone, and both show low stocks of tree species. The soil seed bank in seasonally flooded grasslands has some similarity with the standing vegetation (Oliveira et al. 2015), except for perennial grasses (Souza et al. 2016) that rely mostly on rhizomes to persist.
5. The soil seed bank in seasonally flooded grasslands is persistent, which helps to explain the apparent resilience of the plant community after the introduction of exotic grasses, flood/drought, grazing, and fire (Bao et al. 2018a).
6. The species-richest and most abundant seed banks occur in the 0–5 cm topsoil (Pagotto et al. 2011, Souza et al. 2019) and in low-lying longer-flooded forest microsites where seeds are carried to (Pagotto et al. 2011, Oliveira et al. 2015).
7. Fire little affects *Elionurus muticus* grassland (Rodrigues 1999) and riparian forest seed banks (Kohagura et al. 2020), but reduces its density under *Vochysia divergens* forest (Couto et al. 2006). However, effects of severe wildfires, as occurred in 2020, on seed banks in histosols are yet unknown.
8. The seed bank functions as a flexible reserve for regeneration, ready to respond to the forthcoming conditions of either flooded or drained soil (Bao et al. 2018a).

15.6 Research Needs

More studies on the soil seed bank are needed to better understand the regeneration dynamics of plant communities of the Pantanal; many types of habitats have not been sampled yet. There is a lack of information on soil seed banks in accumulated organic material (histosols) of floating meadows and deep-flooded habitats, spiny scrub, *Copernicia alba* palm monodominant savanna, and the Brazilian Chaco, as well as long-term studies of seed bank persistence and effects of fire (e.g., wildfire in 2020). Also, studies are needed on plant demography, such as seed production of plant species, dispersal and seed rain, effects of seed size on seed predation and storage, seedling recruitment and death rates, and seed dormancy and longevity. Identification guides and herbarium collections of seeds and seedlings of Pantanal plants shall be welcome.

15.7 Conclusions

The soil seed banks in the Pantanal tend to be rich in annual and short-perennial herbs and subshrubs, predominantly of the pioneer type, even under seasonal and riparian forest. There is some similarity between seed bank composition among vegetation types. The seed bank of forests includes few species and low abundances of trees. Fire does not reduce richness and abundance of most seed banks, except *Vochysia divergens* monodominant forest. Under flooding, seedling emergence shows aquatic species, while on drained soil emerge mainly nonaquatic plants, what we can call a flexible seed bank, i.e., ready for whatever weather.

Acknowledgments To the Brazilian agencies CAPES for scholarships to E.B. Souza and F. Bao and CNPq for a researcher grant to A. Pott. To UFMS for support.

References

Amaral TS (2011) Banco de sementes e estabelecimento de plântulas e jovens em capões do Pantanal Sul. Dissertation, Universidade Federal de Mato Grosso do Sul. https://posgraduacao.ufms.br/portal/trabalho-arquivos/download/432

Arruda WDS, Oldeland J, Paranhos Filho AC, Pott A, Cunha NL, Ishii IH, Damasceno-Junior GA (2016) Inundation and fire shape the structure of riparian forests in the Pantanal, Brazil. PLoS One 11:e0156825

Baker HG (1989) Some aspects of the natural history of seed banks. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. London, Academic Press, p. 5–19

Bakker JP, Poschlod P, Strykstra RJ, Bekker RM, Thompson K (1996) Seed banks and seed dispersal: important topics in restoration ecology. Acta Bot Neerl 45:461–490

Bao F, Pott A, Ferreira FA, Arruda R (2014) Soil seed bank of floodable native and cultivated grassland in the Pantanal wetland: effects of flood gradient, season and species invasion. Braz J Bot 37:239–250. http://link.springer.com/article/10.1007/s40415-014-0076-z4

Bao F, Assis MA, Arruda R, Pott A (2015) Effects of *Urochloa humidicola* on plant diversity in native grasslands in a Neotropical wetland. Wetlands 35(5):841–850. http://link.springer.com/article/10.1007/s13157-015-0673-z

Bao F, Elsey-Quirk T, Assis MA, Pott A (2018a) Seed bank of seasonally flooded grasslands: experimental simulation of flood and post-flood. Aquatic Ecol 52(1):93–105. https://doi.org/10.1007/s10452-017-9647-y

Bao F, Elsey-Quirk T, Assis MA, Arruda R, Pott A (2018b) Seasonal flooding, topography, and organic debris interact to influence the emergence and distribution of seedlings in a tropical grassland. Biotropica 1:1. https://doi.org/10.1111/btp.12550

Bao F, Elsey-Quirk T, Assis MA, Souza EB, Pott A (2019) Do aquatic macrophytes limit the invasion of exotic species in Pantanal grasslands? Wetlands 40:135–142. https://doi.org/10.1007/s13157-019-01168-5

Bao F, Elsey-Quirk T, Assis MA, Souza EB, Pott A (2020a) Do aquatic macrophytes limit the invasion of exotic species in Pantanal grasslands? Wetlands 40:135–142. https://doi.org/10.1007/s13157-019-01168-5

Bao F, Assis MA, Pott A (2020b) Applicability of seed bank assessment methods in wetlands: advantages and disadvantages. Oecol Austr 24(3) https://revistas.ufrj.br/index.php/oa/issue/view/1109/showToc

Bao F, Assis MA, Pott A (2020c) Maintenance of the plant community in wetlands: efficient role of the seed bank in regeneration of native plants. Acta Bot Bras 34(4). https://doi.org/10.1590/0102-33062020abb0112

Barroso GM, Morim MP, Peixoto AL, Ichaso CLF (1999) Frutos e sementes: morfologia aplicada à Sistemática de Dicotiledôneas. Editora UFV, Viçosa

Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and evolution of dormancy and germination, 2nd edn. Academic Press, San Diego

Bordon NG, Nogueira A, Leal Filho N, Higuchi N (2019) Blowdown disturbance effect on the density, richness and species composition of the seed bank in Central Amazonia. For Ecol Mgt 453:117633

Brock M (2011) Persistence of seed banks in Australian temporary wetlands. Freshw Biol 56:1312–1327. https://doi.org/10.1111/j.1365-2427.2010.02570.x

Brown D (1992) Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. Can J Bot 70(8):1603–1612

Carvalho FS, Sartori ALB (2014) Reproductive phenology and seed dispersal syndromes of woody species in the Brazilian Chaco. J Veg Sci 26(2):302–311. https://doi.org/10.1111/jvs.122227

Catian G (2015) Efeitos da dinâmica de inundação nas estratégias reprodutivas, na estrutura do banco de sementes e na diversidade funcional de comunidades de macrófitas aquáticas em lagoas do Pantanal. Dissertation, Universidade Federal de Mato Grosso do Sul. In: https://posgraduacao.ufms.br/portal/trabalho-arquivos/download/4533

Catian G, Lima GT, Fabiano VS, Gonçalves VM, Scremin-Dias E (2021) A guide to the identification of diaspores of the main macrophytes in the Pantanal. Phytotaxa 487(3):2015–2232

Cerezoli CCJ (2018) Banco e chuva de sementes em uma área de pastagem cultivada na região do Cerrado. Dissertation, Universidade Federal de Mato Grosso do Sul

Cerezoli CCJ, Damasceno-Junior GA, Faria RR (2017) Seed Bank in an abandoned pasture of a Cerrado-Pantanal ecotone area. In: SER 2017 - VII Conferência Mundial sobre Restauração Ecológica/V Congreso Iberoamericano y del Caribe de Restauración Ecológica/I Conferência Brasileira de Restauração Ecológica, 2017, Foz do Iguaçu. Linking Science and practice for a better world - Book of Abstracts p351

Corrêa CE, Fischer EA, Santos FAM (2012) Seed banks on *Attalea phalerata* (Arecaceae) stems in the Pantanal wetland, Brazil. Annals Bot 109(4):729–734. https://doi.org/10.1093/aob/mcr317

Couto EG, Chig LA, Nunes da Cunha C, Loureiro MF (2006) Estudo sobre o impacto do fogo na disponibilidade de nutrientes, no banco de sementes e na biota de solos da RPPN SESC Pantanal. Rio de Janeiro, SESC, Departamento Nacional (Conhecendo o Pantanal, 2). https://www.sescpantanal.com.br/arquivos/cadastro.../file-635877032567777339.pdf

Cronk JK, Fennessy MS (2001) Wetland plants: biology and ecology. Lewis Publ, Boca Raton

Dairel M, Fidelis AT (2020) How does fire affect germination of grasses in the Cerrado?. Seed Science Research 30(4):275–283

Donatti CI, Guimarães PR, Galetti M, Pizzo MA, Marquitti FMD, Dirzo R (2011) Analysis of a hyperdiverse seed dispersal network: modularity and underlying mechanisms. Ecol Lett 14:773–781. https://doi.org/10.1111/j.1461-0248-20011.01639.x

Fabri J (2018) Efeitos de inundação e fogo na germinação de sementes de *Copernicia alba* Morong ex Morong & Britton (Arecaceae). Universidade Brasil, Mestrado Profissional em Ciências Ambientais, São Paulo

Fenner M (1995) The ecology of seed banks. In: Kigel J, Galili G (Ed) Seed development and germination. New York: Dekker. p. 507–528

Ferreira S (2008) Efeitos de isolamento e tamanho de capões sobre a diversidade da chuva de sementes no Pantanal do Miranda-Abobral. Dissertation, Universidade Federal de Mato Grosso do Sul. In: livros01.livrosgratis.com.br/cp075143.pdf

Ferreira FA, Pott A, Damasceno Junior GA (2013) Efeito imediato do fogo no banco de sementes em florestas alagáveis, XI Congresso de Ecologia do Brasil, I Congresso Internacional, Porto Seguro, 2013. Sociedade de Ecologia do Brasil, resumos. seb-ecologia.org.br

Ferreira FA, Catian G, Pott A (2016) Diaspore bank of aquatic macrophytes maintaining species diversity in a Neotropical pond. Acta Scient Biol Sci (Online) 38:419–427

Grime JP (1989) Seed banks in ecological perspective. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, London, pp p15–p22

Harper JL (1977) Population biology of plants. Academic Press, London

Hopfensperger KN (2007) A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116:1438–1448

Kissmann KG (1997) Plantas infestantes e nocivas. BASF, São Paulo. Tomo I

Kissmann KG, Groth D (1999) Plantas infestantes e nocivas. BASF, São Paulo. Tomo 3

Kissmann KG, Groth D (2000) Plantas infestantes e nocivas. BASF, São Paulo. Tomo 2

Kohagura TC, Souza EB, Bao F, Ferreira FA, Pott A (2020) Flood and fire affect the soil seed bank of riparian forest in the Pantanal wetland. Rodriguésia 71:e00052018. http://www.scielo.br/scielo.php?script=sci_arttextandpid=S2175-78602020000100200andlng=enandnrm=iso. https://doi.org/10.1590/2175-7860202071013

Lima MS, Damasceno Junior GA (2020) Phenology and dispersal syndromes of woody species in deciduous forest fragments of the Pantanal in Mato Grosso do Sul State, Brazil. Act Bot Bras 34(2). https://doi.org/10.1590/33062019abb0353

Lima Júnior GA, Silva MF, Nunes da Cunha C (2007) Similaridade florística entre banco de sementes de solo de campo e brejo do Pantanal de Poconé, MT. Congresso Brasileiro de Ecologia VII, Caxambu.

Lorenzi H (1994) Manual de identificação e controle de plantas daninhas: plantio direto e convencional. 7. ed. Plantarum, Nova Odessa

Manrique-Pineda DA, de Souza EB, Filho ACP, Encina CCC, Damasceno-Junior GA (2021) Fire, flood and monodominance of Tabebuia aurea in Pantanal. Forest Ecology and Management 479:118599

Mcfarland DG, Shafer DJ (2011) Protocol considerations for aquatic plant seed bank assessment. J Aquatic Plant Mgt 49(1):9–19

Middleton BA (2003) Soil seed banks and the potential restoration of forested wetlands after farming. J Appl Ecol 40:1025–1034

Mitsch WJ, Gosselink JG (1993) Wetlands. Van Nostrand Reinold, New York, 2nd ed.

Oliveira PC, Nunes da Cunha C, Silva TS, Silva FHB (2009) Espectro Biológico do banco de sementes do solo em três campos savânicos sazonalmente inundáveis no Pantanal de Mato Grosso, Brasil. Anais do III Congresso Latino Americano de Ecologia, São Lourenço, 2009

Oliveira MT, Damasceno-Junior GA, Pott A, Paranhos Filho AC, Suarez YR, Parolin P (2014) Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence. Forest Ecol Mgt 331:256–263

Oliveira PC, Nunes da Cunha C, Torrezan JMD (2015) Effects of flooding on the spatial distribution of soil seed and spore banks of native grasslands of the Pantanal wetland. Acta Bot Bras 29(3):400–407. https://doi.org/10.1590/0102-33062015abb0027

Oliveira PC, Parolin P, Borghetti F (2019a) Can germination explain the distribution of tree species in a savanna wetland? Austral Ecol 44:1373–1383. https://doi.org/10.1111/aec.12811

Oliveira PC, Silva FHB, Nunes da Cunha C (2019b) Effect of fire on the soil seed bank of neotropical grasslands in the Pantanal wetland. Oecol Austr 23(4):904–916. https://doi.org/10.4257/oeco.2019.2304.14

Pagotto MA, Silveira RML, Cunha CN, Fantin-Cruz I (2011) Distribution of herbaceous species in the soil seed bank of a flood seasonality area, northern Pantanal, Brazil. Intern Rev Hydrobiol 96(2):149–163. https://doi.org/10.1002/iroh.201111315

Pott VJ, Pott A (2003) Dinâmica da vegetação aquática do Pantanal. In: Thomaz SM, Bini MB (eds.) Ecologia e manejo de macrófitas aquáticas. Eduem, Maringá p 143-162. In: www.eduem.uem.br/livros/ebook/ebook_eemdma.pdf

Pott VJ, Pott A (2011) Species diversity, distribution, and biomass of aquatic macrophytes of the Pantanal. In: Junk WJ, Da Silva CJ, Nunes da Cunha CN, Wantzen KM (eds.). The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia p 257–279

Pott A, Ratter JA (2011) Species diversity of terrestrial plants and human impacts on the vegetation of the Pantanal. In: Junk WJ, Da Silva CJ, Nunes da Cunha CN, Wantzen KM (eds.). The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft, Sofia p 281–300

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa-SPI, Corumbá

Pott A, Silva JSV (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I, Assine ML (eds.) Dynamics of the Pantanal wetland in South America. Chapter 3 (The handbook of environmental chemistry 37:111-132) Springer International Publishing, Switzerland. https://doi.org/10.1007/698_2015_352

Rodrigues CAG (1999) Efeitos do fogo e da presença animal sobre a biomassa aérea e radicular, nutrientes do solo, composição florística, fenologia e dinâmica de um campo de capim-carona (*Elyonurus muticus* (Spreng.) O. Ktze.) no Pantanal (sub-região de Nhecolândia). Dissertation, Universidade Estadual de Campinas. In: http://repositorio.unicamp.br/handle/REPOSIP/315451

Schneider B, Zilli F, Facelli F, Campana M (2020) Factors driving seed Bank diversity in wetlands of a large river floodplain. Wetlands. https://doi.org/10.1007/s13157-020-01355-9

Silva FHB (2011) Efeito da expansão de *Combretum laxum* Jacq. (Combretaceae) sobre a estrutura, composição e banco de sementes em áreas de campo nativo no Pantanal de Poconé, Brasil. Dissertation, Universidade Federal de Mato Grosso

Simpson RL, Leck MA, Parker VT (1989) Seed banks: general concepts and methodological issues. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, San Diego, pp p3–p9

Souza EB, Ferreira FA, Pott A (2016) Effects of flooding and its temporal variation on seedling recruitment from the soil seed bank of a Neotropical floodplain. Acta Bot Bras 30(4):560–568. https://doi.org/10.1590/0102-33062016abb0202

Souza EB, Damasceno-Junior GA, Pott A (2019) Soil seed bank in Pantanal riparian forest: persistence, abundance, functional diversity and composition. Oecol Austr 23(4):891–903. https://doi.org/10.4257/oeco.2019.2304.13

Thompson K (1987) Seeds and seed banks. New Phytol 106(s1):23–24

Thompson K (1992) The functional ecology of soil seed banks. In: Fenner M. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, UK pp 231–258

Thompson K, Grime JP (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J Ecol 67(3):893–921. https://doi.org/10.2307/2259220

Thompson K, Bakker J, Bakker R (1997) The soil seed bank in north west Europe: methodolgy, density and longevity. Cambridge: Cambridge University Press

Tirintan G, Catian G, Luz GP, Gonçalves VM, Scremin-Dias E (2018) Plântulas e sementes de macrófitas aquáticas de lagoas do Pantanal Sul-Mato-Grossense (seedlings and seeds of aquatic macrophytes of ponds of the Pantanal Sul-Mato-Grossense). Iheringia Sér Bot 73(2):69–87. https://doi.org/10.21826/2446-8231201873201

Chapter 16
Plant Morphoanatomical Adaptations to Environmental Conditions of the Pantanal Wetland

Edna Scremin-Dias, Jane Rodrigues da Silva, Gisele Catian, Vitoria Silva Fabiano, and Rosani do Carmo de Oliveira Arruda

16.1 Introduction

Understanding the adaptations shown by wetland plants is challenging in its own right, and, considering that the Pantanal floodplain has different landscape units influenced by the intensity and/or regularity of the inundation (Pozer and Nogueira 2004; Scremin-Dias et al. 2011), as well as a highly diverse flora, the challenge becomes all the greater. The water regime shapes the landscape diversity, and the duration and volume of flooding are major drivers of spatial and temporal distribution of plants in the Pantanal floodplain (Damasceno-Junior et al. 2005; Ferreira-Júnior et al. 2016). In flooded areas, plants with different life history strategies coexist, ranging from annual aquatic macrophytes through perennial aquatic grasses to long-lived woody species (Junk et al. 2006; Scremin-Dias 2009). These species have different morphoanatomical adaptations to deal with permanent flooding or periods of flood alternating with periods of drought (Scremin-Dias et al. 2011), as well as occasional fire events (Arruda et al. 2016).

Although the term "Pantanal" refers to "swamp," in the landscape mosaic of the Pantanal floodplain, species with diverse morphoanatomical adaptations co-occur ranging from aquatic macrophytes to woody plants with functional characteristics of semiarid environments. The diverse composition of its flora is driven by the surrounding domains, with contributions from the Amazon Basin to the north, Brazilian savanna to the east and center, Chaco to the west and south, and the Atlantic Forest to the southeast (Adámoli 1982; Pott 1994). The species distribution in the Pantanal

---

E. Scremin-Dias (✉) · J. R. da Silva · G. Catian · V. S. Fabiano ·
R. do Carmo de Oliveira Arruda
Laboratório de Anatomia Vegetal, Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biociências (INBIO), Universidade Federal de Mato Grosso do Sul,
Campo Grande, Mato Grosso do Sul, Brazil
e-mail: edna-scremin.dias@ufms.br

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_16

floodplain is also determined by the slope of the plain and the fluvial morphogenesis (Damasceno et al. 2005), since the topography is relatively flat with a slope 0.3–0.5 cm/km north-south and 0.03–0.15 cm/km east-west (DNOS 1974). This slope determines the period of flooding and, consequently, affects the zoning of aquatic macrophyte and woody species in the Pantanal floodplain.

Within the Pantanal floodplain, along with annual inundation, fire also acts as an ecological filter for plants (Arruda et al. 2016; Souza et al. 2019). The flood period and the water receding period are the periods most favorable to high biomass production, especially of macrophytes and aquatic grasses (Kufner et al. 2011; Catian 2015). Such factors, combined with high temperatures, stimulate biomass gain and population density in temporary and permanent lakes (Knipling et al. 1970). High accumulation of dead plant material at the end of the dry season favors fires, natural or anthropic (Arruda et al. 2016; Catian et al. 2018). The large amount of biomass accumulated in the community stimulates the fire to reach the edge, or even penetrate into the riparian forests adjacent to the temporarily flooded areas (see also the Chap. 18 on fire and flood).

Riparian forests along the main rivers and secondary channels are characterized by the coexistence of woody plants from different taxonomic groups adapted to annual flooding (Damasceno-Junior et al. 2005). Soil flooding on riverbanks of riparian forests reduces the availability of oxygen to the plant roots, inducing morphoanatomical and metabolic responses to anoxia (Okamoto and Joly 2000). Also, the decrease in oxygen availability can affect seed germination and the establishment and growth of seedlings of woody species. Thus, riparian forests are exposed to two types of seasonal perturbations, the anoxia of the roots and stem base caused by the inundation during the flood period, and the effects of the occasional fire that can occur in the periods of low water.

This chapter synthesizes the information on morphoanatomical features of aquatic macrophytes and woody plants in different habitats in the Pantanal floodplain. We present an overview of the morphological and anatomical diversity of vegetative organs and diaspores related to flooding, drought, and fire in Pantanal plants.

16.2 Effect of Flooding, Drought, and Fire on the Morphology of Aquatic Macrophytes

Aquatic plants or aquatic macrophytes are defined as organisms visible to the naked eye with photosynthetic parts permanently or temporarily submerged, floating, or immersed in water (Murphy et al. 2019). In the Pantanal floodplain, there are 324 species of aquatic macrophytes (Pott and Pott 2000) with different life forms: amphibious, emergent, floating (free and rooted), submerged (free and rooted), and epiphytes (Tur 1972; Irgang et al. 1984; Pedralli 2000). Throughout an annual inundation cycle, the water rising, flood, water receding, and drought periods define the species and life forms of aquatic macrophytes predominant in the community (Catian et al. 2018).

According to Hutchinson (1975), aquatic macrophytes are classified as emerging species that occur in the upper littoral zone (depth 1–1.5 m) and are characterized by roots and rhizomes adapted to anaerobic conditions and aerial flowering; floating-leaved species that occur on the water surface (depth ~0.5–3 m) and have leaves with long petioles adapted to mechanical stress and floating or aerial flowers; submersed species that occur deep in the water and present ribbonlike or dissected leaves, and aerial, floating, or (rarely) submersed flowers; and freely floating species that present aerial and/or floating leaves and flowers and absorb nutrients directly from the water. If we consider the distribution of aquatic macrophytes in a pond, submerged aquatic macrophytes inhabit deeper places, followed by rooted aquatic macrophytes with floating leaves (Pott and Pott 2000). The pond's marginal zone is occupied by aquatic macrophyte species with emergent leaves. Amphibious and palustrine species occupy the littoral zones of water bodies (Sculthorpe 1967; Pott and Pott 2003). In addition, aquatic macrophytes can occur as epiphytes on top of other aquatic plants with different life forms (Fig. 16.1). Thus, the moisture gradient acts as an ecological filter, defining the community structure and the aquatic macrophyte species distribution in temporarily or permanently flooded areas in the Pantanal (Catian et al. 2018).

The morphoanatomy of the vegetative organs of aquatic macrophytes varies according to the location of an organ in the water, or in the air, and throughout the inundation cycle (Santana et al. 2019; Scremin-Dias 2000). The shape, color, and composition of the leaf tissues also differ between individuals growing in an aquatic environment vs. terrestrial soil (e.g., Scremin-Dias et al. 1999). As the water level decreases, during water receding and dry periods, the initially floating species begin

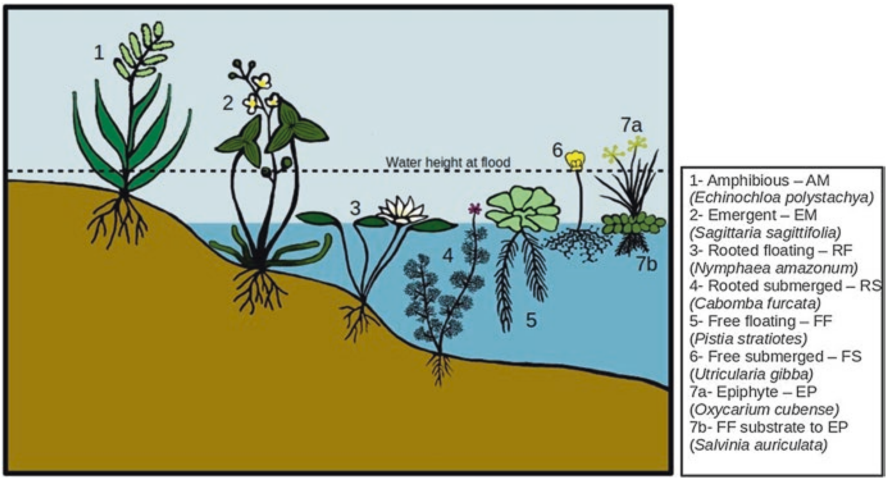


Fig. 16.1 Diagram of the distribution of life forms of aquatic macrophytes in relation to the water level. Drawn by Fabiano, VS, based on Irgang et al. (1984)

rooting into the soil. Examples are *Ludwigia helminthorriza* and *L. grandiflora*, Onagraceae (Santana et al. 2019; Silveira et al. unpublished data).

The adaptative morphoanatomical characteristics of aquatic macrophytes with different life forms are presented below, highlighting the influence of water during the ontogenesis of their vegetative organs.

16.2.1 Leaves: Structural and Adaptative Aspects

Heterophylly, i.e., the formation of emergent, submerged, and floating leaves of different shape in the same individual, is frequent in aquatic macrophytes (Sculthorpe 1967). In general, emerged and floating leaves have a consistency ranging from coriaceous, as in *Thalia geniculata*; rigid, as in *Typha domingensis* and *Victoria amazonica*; or soft, as in *Echinodorus paniculatus* and *Limnocharis flava*. In general, emergent leaves are darker in color and thicker than submerged leaves (e.g., *Eichhornia crassipes*). Floating leaves, located at the water surface (e.g., *Nymphaea gardneriana*), and the emergent leaves generally present a coriaceous texture and very variable shapes including sagittal (e.g., *Sagittaria montevidensis* and *Echinodorus grandiflorus*, Fig. 16.2a), cordiform (e.g., *Nymphaea amazonum*, Fig. 16.2b), elliptical (*Limnocharis* sp., Fig. 16.2c), and lanceolate, orbicular, to obovate (*Eichhornia azurea*, Fig. 16.2d).

Submerged leaves often have a membranous texture (e.g., *Heteranthera zosterifolia* and *Nymphaea gardneriana*), with a predominantly linear (e.g., *S. montevidensis*) or filiform shape (e.g., *Ceratophyllum demersum*, *C. submersum* var. *echinatum*). In addition to capturing light energy and absorbing carbon dioxide dissolved in water for photosynthesis, the submerged leaves can also be modified into utricles. These structures are common in Lentibulariaceae (e.g., *Utricularia* spp., Fig. 16.2h–j), and are specialized in capturing aquatic invertebrates, contributing to nutrient acquisition.

Reddish coloration is common in the floating and submerged leaves, such as in, *Echinodorus grandiflorus* (Fig. 16.2e), and *Nymphaea gardneriana* (Catian and Scremin-Dias 2015; Fig. 16.2f). This coloring results from the accumulation of anthocyanins ocurring in *Ludwigia sedioides* established on dry soil (Scremin-Dias 1992) or other pigments in the vacuole, which can provide internal tissue protection for chloroplasts and other membrane systems against photooxidation and damage caused by ultraviolet radiation (Gould et al. 1995; Chalker-Scott 1999; Evert et al. 2012). Anthocyanins, for example, absorb yellow, green, and blue radiation from the visible light spectrum, and thus provide an effective sunscreen which intercepts excess light that could be absorbed by chlorophyll, resulting in its degradation (Zhu et al. 2017). Also, these pigments may act as a defense against pathogens and herbivores (Gould et al. 1995).

Floating leaf petioles can lengthen in response to a sudden rise in water level, in a process known as depth accommodation (Ridge 1987). The lengthening of the petioles allows the leaf blade to stay at the water surface, thus avoiding the submersion of the primary photosynthetic organ of these plants (Paillisson and Marion

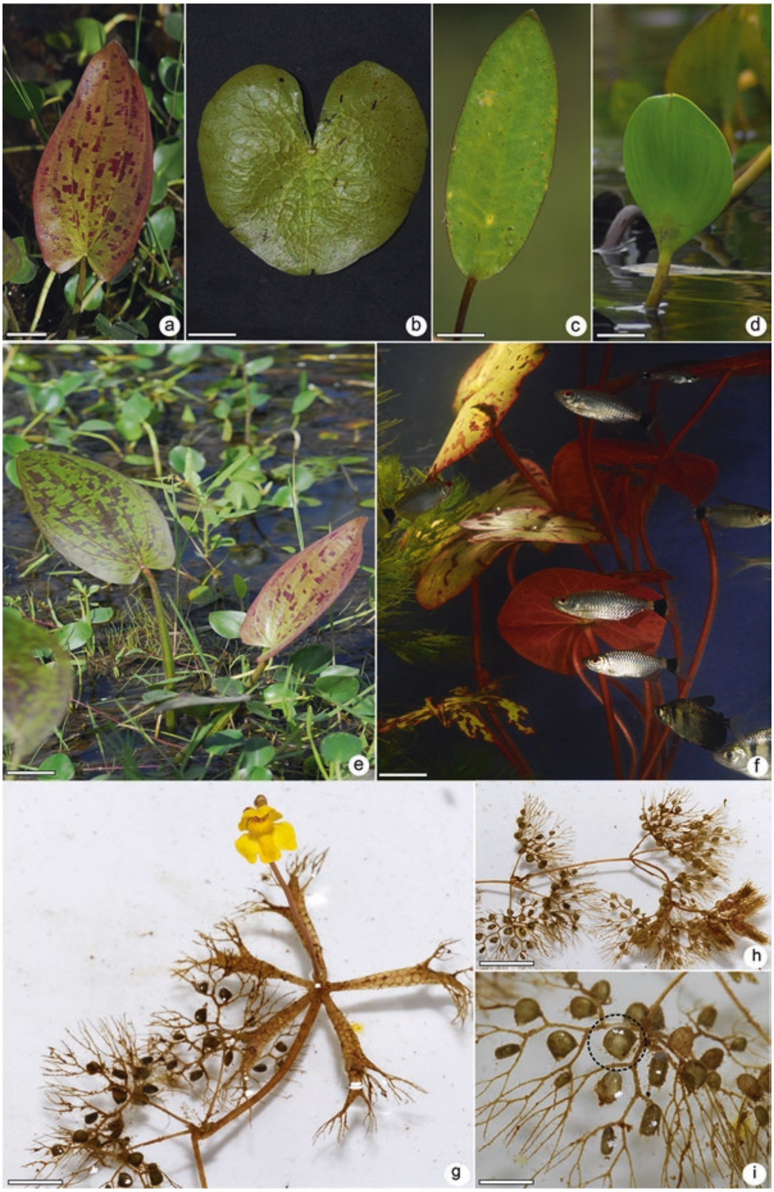


Fig. 16.2 Diverse leaf morphologies of aquatic macrophytes. Leaf with a sagittal shape in *Echinodorus grandiflorus* (**a**), cordiform in *Nymphaea* sp. (**b**), elliptical in *Limnocharis* sp. (**c**), and obovate in *Eichhornia azurea* (**d**). Leaf with a reddish color in *Echinodorus grandiflorus* (**e**) and *Nymphaea amazonum* (**f**). Modified leaves in utricles (circle) in *Utricularia breviscapa* (**g**, **i**). Utricles of *U. hydrocarpa* (**h**). Scale bars: (**a**–**d**) = 2 cm; (**d** and **e**) = 5 cm; (**g** and **h**) = 1 cm; (**i**) = 500 μm. Photos: Souza, Paulo Robson de

2006; Demetrio et al. 2014). Elongation of leaf petioles was observed in *Nymphaea amazonum*, *Victoria amazonica*, *Nymphoides grayana*, and *Sagittaria guayanensis*. In *S. guayanensis*, an increase in the diameter and biomass of petioles as well as the plant height occurs during the inundation period, resulting in plants that are more resistant to ruptures and structural damage caused by higher water flow (Demetrio et al. 2014). Petiole elongation and other stem structures are stimulated by ethylene (Wetzel 1993), and the amplitude of the elongation of a petiole is influenced by the age and/or the ontogenetic phase of an organ (Ridge 1987).

The leaf epidermis of aquatic macrophytes, as in most terrestrial plants, comprises several types of cells, such as common or ordinary epidermal cells, with little or no specialization, and specialized cells – trichomes, stomatal cells, subsidiary cells, and hydropotes. All the epidermal tissue, especially in the emerged and floating leaves, is covered by a layer of lipid compounds constituting the epicuticular wax and the cuticle that forms a protective layer impervious to water loss on the surface. Floating and emerged leaves can present a thin and shiny cuticle as an adaptive strategy for light reflection, as well as preventing water from seeping through the surface (Sculthorpe 1967). On the other hand, the cuticle is very thin in submerged leaves (Fig. 16.3).

In a frontal view of the epidermis, we observed that cell types can vary in shape, number, and morphology, according to the face of the leaf blade (upper or lower) and location of the leaf in relation to the water level. In general, common epidermal cells comprise most of the tissue and may vary in their outline (straight, sinuous) (Fig. 16.4a), the thickness of the anticline wall (thin, thick), as well as in the content, which may be transparent or contain pigments, such as anthocyanins, flavonoids, or phenolic compounds, rarely seeing chloroplasts in these cells.

One of the essential components of the leaf epidermis is the stomata, a pair of approximately reniform cells (stomatal cells or guard cells), endowed with chloroplasts that control the opening and closing of a pore, through which carbon dioxide enters, and oxygen leaves the plant. Stomata function as “gatekeepers,” and are responsible for all gaseous diffusion that is dependent on internal (physiological) and external (environmental) adjustments directing CO_2 entry and water loss by plants (Lawson and Blatt 2014). Stomata can be present on only one side or both sides of a leaf. Depending on the presence and location of the stomata, the leaves are classified as epistomatic, if the stomata are restricted to the upper side; hypostomatic (*Hydrocotyle* sp., Fig. 16.4a; *Echinodorus paniculatus*; Fig. 16.4c), when located only on the underside; and amphistomatic when present on both sides. In emergent leaves, stomata can occur on both sides of a blade (amphistomatic leaves), and they may vary in number between both surfaces, be arranged at random or in rows, distributed between the veins. The floating leaves are generally epistomatic (e.g., *Eichhornia azurea*, Fig. 16.4e), because the leaf face in contact with water is generally devoid of these structures, as carbon dioxide cannot enter via the pore opening. In submerged leaves, there are few stomata or they are even absent (e.g., *Nymphaea gardneriana* (Catian and Scremin-Dias 2015) and *Ludwigia inclinata* (Rodrigues et al. 2007), and CO_2 or $H_2CO_3^-$ absorption and release of gases occurs directly through the leaf surface.

Fig. 16.3 Leaf morphology diversity of aquatic macrophytes. Air bubbles released by submerged leaves of *Helanthium bolivianum* (**a**). Trichomes on the leaf surface of *Salvinia auriculata* (**b**) and *Pistia stratiotes* (**c**). Scale bars: (**a**) = 5 cm; (**b** and **c**) = 2 cm. Photos: Souza, Paulo Robson de

The distribution of stomata on the leaf surfaces is a characteristic that can vary. In *Ludwigia sedoides*, for example, floating leaves, with an arrangement of rosettes, are epistomatic, but on inundation-free soil, the rosette leaf pattern is lost, and stomata develop on both sides (Scremin-Dias 1992). Although Sculthorpe (1967) mentions that in submerged leaves the stomata are not functional for controlling gas exchange, functional stomata were observed in submerged seedling leaves of *Echinodorus paniculatus* (Scremin-Dias 2000). The release of oxygen as air bubbles on the entire surface of submerged leaves, e.g., in *Helanthium bolivianum*, is visible, especially in translucent water and under high sunlight (Fig. 16.3a).

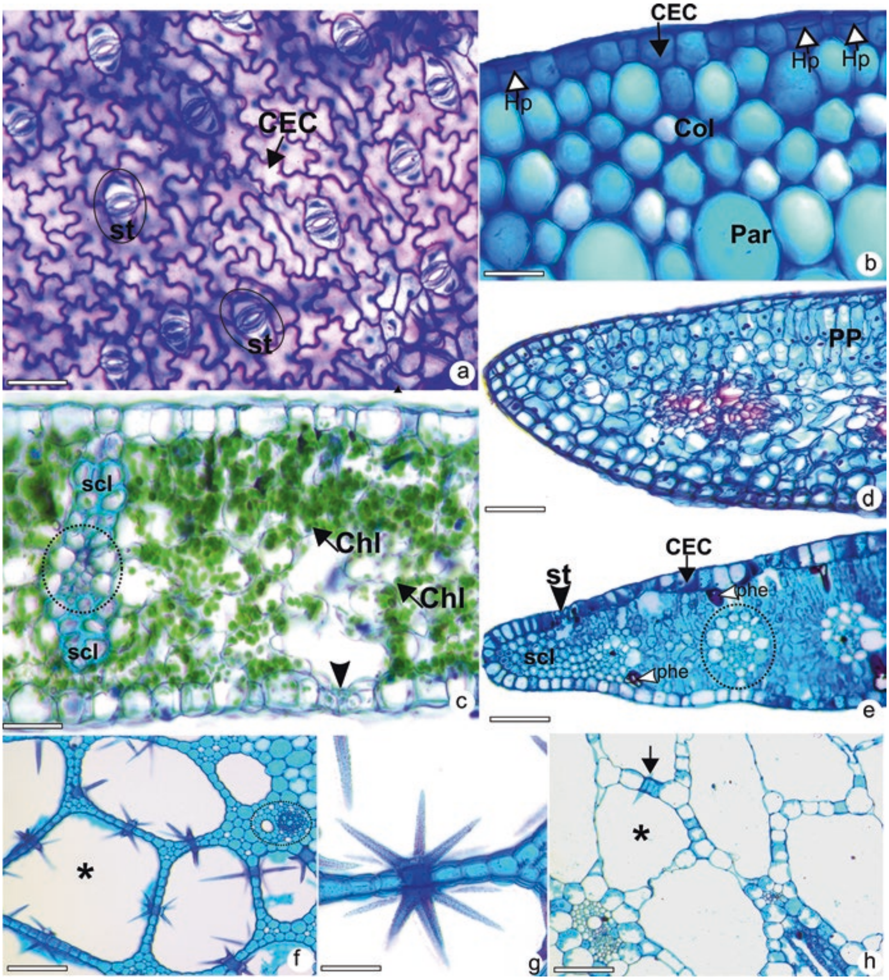


Fig. 16.4 Leaf anatomy of the species of aquatic macrophytes. (**a**) Abaxial epidermis of a floating leaf of *Hydrocotyle* sp. with stomata and common cells with sinuous walls. (**b**) Transverse section of a *Nymphaea* sp. petiole with hydropotes and common cells in the epidermis; note the subepidermal collenchyma and parenchyma in the petiole cortex. (**c**) Emerged leaf of *Echinodorus paniculatus* with isolateral mesophyll; note the vascular bundles (circle) with sclerenchyma cells extended in both sides of the leaf blade, transverse section. (**d**) Floating leaf of *Hydrocleys* sp. with dorsiventral mesophyll; note the palisade parenchyma located in the adaxial leaf surface, transverse section. (**e**) Floating leaf of *Eichhornia crassipes* with sclerenchyma cells, phenolic idioblasts, and stomata (arrowhead) in the adaxial epidermis, transverse section. (**f**–**g**) Petiole of *Nymphaea* sp. with astrosclereids in the aerenchyma (*); note the prismatic crystal on the astrosclereids surface. (**h**) Petiole of *Eichhornia crassipes* with elongated styloid crystals (arrow). *Cec* common epidermal cell, *chl* chloroplasts, *col* collenchyma, *Hp* hydropote, *par* parenchyma, *phe* phenolic idioblasts, *PP* palisade parenchyma, *scl* sclerenchyma cells, *st* stomata. Scale bars: (**a**) = 200 μm; (**b**, **c**, **d**, **e**, **f**, and **h**) = 100 μm; (**g**) = 50 μm

Trichomes can be present in aquatic plants and can be simple, nonglandular, single-celled, or glandular, as well as secretory, multicellular, and associated with the secretion of secondary metabolites, usually volatiles. Numerous trichomes give a velvety appearance and consistency to the surface of floating leaves (e.g., *Salvinia auriculata*, Fig. 16.3b, and *Pistia stratiotes*, Fig. 16.3c). In these plants, trichomes are essential for repelling water which, accumulated on the surface of the leaves, could block the stomatal pores. In some species, such as *Typha domingensis* and aquatic grasses, unicellular trichomes are distributed on the leaf margins and can be rigid due to silica impregnation on the cell wall.

The absorption of nutrients and gas exchange in submerged leaves can be accomplished through hydropotes. Hydropotes (water drinkers) are a special set of cells, present in leaves, located in the parts in contact with water, and related to the absorption of minerals (Metcalfe and Chalk 1979). In the Pantanal floodplain, this type of structure can be found in species from several families of aquatic plants: Menyanthaceae, Nymphaeaceae, Alismataceae, and Cabombaceae. It can be structured, with an organization similar to a trichome, or unstructured, comprising a set of cells distinct from other epidermal types (Metcalfe and Chalk 1979). In some Nymphaeaceae, young hydropotes form an elongated apical sharp-pointed portion, with a base composed of two or three short specialized cells. At a later developmental stage, the apical sharp-pointed portion is detached, and the mature hydropotes comprise an upper lens-shaped cell, a bowl-shaped cell, and a large foot cell (Tozin and Rodrigues 2020). Structured hydropotes are observed, for example, in floating and submerged leaves of *Nymphaea gardneriana* (Carpenter 2006; Catian and Scremin-Dias 2015; Tozin and Rodrigues 2020; e.g., *Nymphaea* sp., Fig. 16.4b), which act in direct carbon absorption of calcium carbonate from the water, used in photosynthesis (Madsen and Maberly 1991). These structures are also present in petioles or submerged organs of Cabombaceae and Nymphaeaceae (Metcalfe and Chalk 1979).

The mesophyll of the emergent leaf blade is generally thicker than the floating and submerged leaf blade. The leaf blade of aquatic macrophytes may have a dorsiventral structure, with a palisade parenchyma located only under the adaxial surface of the epidermis, as observed in species of *Nymphaea, Hydrocleys* and *Echinodorus paniculatus* (Fig. 16.4d and c). Leaves with isolateral mesophyll, with palisade parenchyma facing both sides of the blade, are common in *Eichhornia azurea* (Fig. 16.5a). Spongy parenchyma in the mesophyll can give rise to a tissue rich in wide intercellular spaces, the aerenchyma. The aerenchyma is an essential adaptation to the aquatic environment, with a function in the storage and diffusion of gases between the leaves and roots (Rich et al. 2012).

Thickness and arrangement of tissues in the leaf mesophyll vary between floating and submerged leaves within an individual. Well-developed mesophyll with enlarged air gaps in floating leaves occurs in *Eichhornia azurea* (Fig. 16.5a) and *E. crassipes*. The number of layers of palisade parenchyma and aerenchyma can be reduced in leaves in lotic environments (Sculthorpe 1967; Cutter 1987) or submerged leaves (e.g., *E. azurea*, Fig. 16.5b and c). The decrease in leaf thickness contributes to avoiding mechanical damage when the species grows in a riffle. For

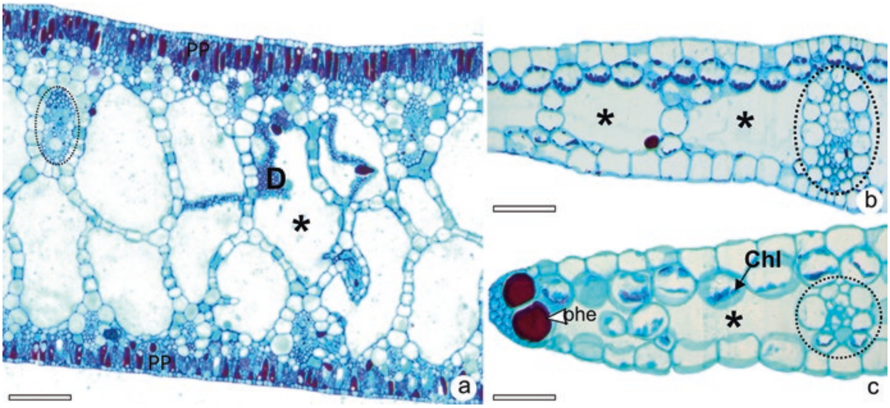


Fig. 16.5 Plasticity in leaf anatomy of *Eichhornia azurea*. (**a**) Transverse section of floating leaf with isolateral mesophyll; note the palisade parenchyma located in both leaf surfaces, and aerenchyma (*) with diaphragm, transverse section. (**b** and **c**) Transverse section of submerged leaf with mesophyll with aerenchyma (*) and reduced vascular bundles (circle); note the phenolic idioblasts in the leaf edges, without typical palisade parenchyma, transverse section. *chl* chloroplasts, *D* diaphragm, *phe* phenolic idioblasts, *PP* palisade parenchyma. Scale bars: (**a**) = 200 μm; (**b** and **c**) = 100 μm

example, submerged leaves of *Nymphaea gardneriana* (Catian and Scremin-Dias 2015), *Veronica anagallis-aquatica* (Boeger and Poulson 2003), and *Eichhornia azurea* (Fig. 16.5) have a narrower mesophyll than floating leaves.

Sclereids and idioblasts, often with phenolic and crystalline compounds, are common in floating leaves of species occurring in aquatic environments. The shape of the sclereids varies between the aquatic macrophyte species and can be elongated, tubular, columnar, or branched (astrosclereids). The mesophyll in *Nymphaea* spp. is occupied by branched sclereids, called astrosclereids that present the external surface of the cell wall with numerous prismatic crystals (Fig. 16.4f and g). The variation can be considered a relevant taxonomic attribute and can be used to identify some species of the genus (Catian and Scremin Dias 2015). In *Eichhornia crassipes* leaves, we observed elongated styloid crystals in the aerenchyma (Fig. 16.4h). In this same species, we observed numerous idioblasts with phenolic compounds among the cells of the mesophyll (Fig. 16.4e).

The median veins of the emergent leaves have the thickest and the highest number of air gaps, compared with the interveinal regions. Wide gaps are distributed in petioles that are sometimes inflated (expanded) in some species (e.g., *Nymphaea* sp., Fig. 16.4f). Plants with emerged leaves, such as *Pontederia parviflora* that occur in rivers with translucent waters, can develop fully submerged and present morphological plasticity, observed in the higher amplitude and lesser thickness of the submerged blade.

The presence of sclerenchyma and collenchyma on the edge of the leaves is common in emergent leaves of many species of aquatic macrophytes, such as *Eichhornia crassipes* (Fig. 16.4e) and *Potamogeton pectinatus* (Idestam-Almquist and Kautsky

1995). Together, collenchyma and sclerenchyma provide mechanical support, helping to maintain the leaves in the predominantly erect position (Chambers et al. 1999; Scremin-Dias 2000; Boeger and Poulson 2003).

16.2.2 Stems: Structural and Adaptative Aspects

The stems of aquatic macrophytes in the Pantanal wetlands are generally flexible. The stem epidermis is generally uniseriate and can act as a substrate for periphyton, especially in aquatic macrophytes that grow in lentic environments (*Gomphrena elegans*, Fig. 16.6a). However, the accumulation of periphyton on the stem surface decreases the diffusion of nutrients and gases.

Cortical parenchyma predominates in stems of aquatic macrophytes with wide longitudinal air gaps. Its formation can be lysigenous, schizogenous (e.g., *Gomphrena elegans*, Fig. 16.6a; *Potamogeton illinoensis*, Fig. 16.6b; and *Eichhornia crassipes*, Fig. 16.6c), or schizolysigenous (e.g., *Louisiella elephantipes*, Fig. 16.6e). In some species of aquatic macrophytes, the cells of the schizogenous aerenchyma may rupture to enlarge the air gaps (e.g., *E. crassipes*, Fig. 16.6c). These air gaps are interrupted by diaphragms in some species (e.g., *Potamogeton illinoensis*, Fig. 16.6b). The diaphragm provides support for the aerenchyma and acts as a barrier against water invasion caused by perforation or injury to the organs of aquatic macrophytes (Scremin-Dias et al. 1999). Also, the diaphragm functions as an additional area of photosynthesis as well as the passage of vascular bundles (e.g., *E. crassipes*, Fig. 16.6d). Mechanical support of the aerenchyma can also be provided through phi thickenings (e.g., *Gomphrena elegans*, Fig. 16.6a). This thickening is a lignified band formed in the anticlinal-transversal and periclinal walls of the aerenchyma cells (Bona and Morretes 2003).

In many macrophytes, e.g., *Mimosa* sp. (Fig. 16.7b) and *Neptunia prostrata* (Fig. 16.7c), subjected to flooding, the aerenchyma originates from the phellogen resulting in an aerenchymatous phellem. This tissue facilitates gas exchange between the root and the stem in plants in secondary growth that lose the cortical aerenchyma formed primarily (Stevens et al. 2002). In Onagraceae, the aerenchymatous phellem shows an expansive development pattern in most species of *Ludwigia* (Bedoya and Madriñán 2015).

The vascular system in the stem in rooted, free, and floating submerged species, in general, is surrounded by endoderm with a Casparian strip with “O”- or “U”-shaped thickenings in monocotyledons (e.g., *Potamogeton illinoensis*, Fig. 16.6f). The reduction in the primary xylem in the central cylinder occurs in many species, to the point that there is no development of conductive elements of the metaxylem, leaving only protoxylem gaps (e.g., *Victoria amazonica* and *Potamogeton illinoensis*, Fig. 16.6a). In these plants, there is a development of a large amount of primary phloem (e.g., *Potamogeton illinoensis*, Fig. 16.6a). The development of vascular cambium and secondary xylem formation occurs in the stem of some species of aquatic macrophytes (e.g., *Ludwigia sedioides*, Fig. 16.6g).

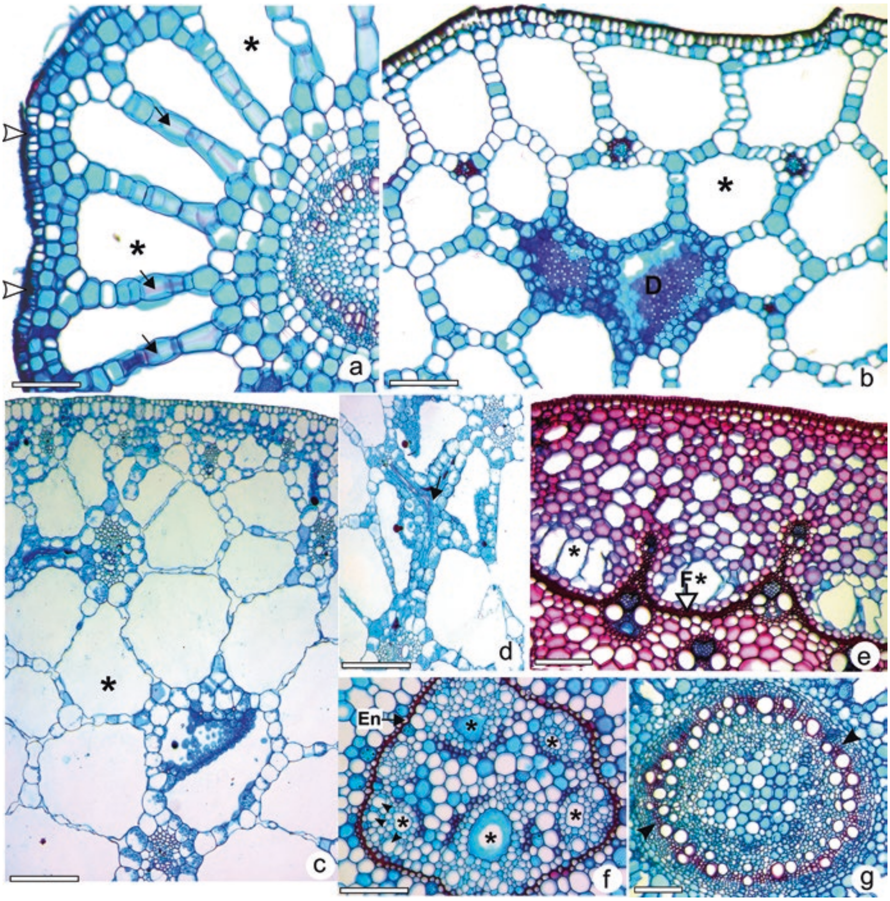


Fig. 16.6 Stem anatomy of aquatic macrophytes. (**a**) Periphyton (arrowheads) on the outer anticlinal wall of the uniseriate epidermis of the stem of *Gomphrena elegans*; note the phi thickening (arrows) in the gaps of the schizogenous aerenchyma, transverse section. (**b** and **c**) Transverse section of schizogenous aerenchyma with diaphragm on the stems of *Potamogeton illinoensis* (**b**) and *Eichhornia crassipes* (**c**); note the collapse of the aerenchyma cells (*) in *Eichhornia crassipes*. (**d**) Vascular bundles connected by the diaphragm in *Eichhornia crassipes*, transverse section. (**e**) Schizolysigenous aerenchyma (*) in *Louisiella elephantipes*, transverse section. (**f**) Vascular cylinder surrounded by the endoderm with Casparian strip with "U"-shaped thickening in *Potamogeton illinoensis*; note the presence of only conducting elements of the protoxylem (*) in the primary xylem and large sieve tube (arrowheads) in the primary phloem, transverse section. (**g**) Vascular cylinder of the stem of *Ludwigia sedioides* at the beginning of secondary growth with secondary xylem formation, transverse section. *En* endodermis, *D* diaphragm. Scale bars: (**a**, **b**, **e**, and **g**) = 200 μm; (**c** and **f**) = 100 μm; (**d**) = 50 μm

Fig. 16.7 Root and stem morphology of the aquatic macrophytes. Adventitious roots on the stem of *Sesbania virgata* (**a**), *Mimosa* sp. (**b**), and *Neptunia prostrata* (**c**); note the stem with spongy texture (aerenchymatous phellem) in *Mimosa* sp. (**b**) and *Neptunia prostrata* (**c**). Pneumatophores in *Ludwigia helminthorrhiza*, a free-floating aquatic macrophyte (**d**). Scale bars: (**a**) = 5 cm; (**b** and **c**) = 2 cm; (**d**) = 1 cm

16.2.3 Roots: Structural and Adaptative Aspects

The role of roots includes anchoring plants in the substrate, and absorbing water and minerals from the soil and water. Aquatic plants in the Pantanal floodplain form predominantly adventitious roots, regardless of the taxonomic group. For most aquatic eudicotyledons and all monocotyledons, the primary root of the embryo is ephemeral, appearing in the basal stem nodes or the cotyledonary node for monocotyledons. The roots can remain attached to the soil (rooted floating, rooted submerged, and emergent) or fixed to another substrate or on other plants, for example, epiphytes, or be free-floating.

Adventitious roots at the base or along the stem are common in aquatic macrophytes (e.g., *Sesbania virgata*, Fig. 16.7a; *Mimosa* sp., Fig. 16.7b; and *Neptunia prostrata*, Fig. 16.7c). The intense branching of the root system is also common in amphibious species that may have taproots of primary origin and, from these, extensive branching of secondary and tertiary roots. These morphological changes are adaptive characteristics of plants that grow in soil with excess water (Drew 1997; Vartaperian and Jackson 1997).

Pneumatophores are common in free-floating plants and shrink in rooted individuals (e.g., *Ludwigia helminthorrhiza*, Fig. 16.7d). Unlike the woody pneumatophores of the mangrove species (Fahn 1982), the pneumatophores of aquatic macrophytes are roots rich in aerenchyma that allows the plant to float and aerate internal tissues. The formation of pneumatophores generally occurs when the plant grows in still water, where hypoxia is more pronounced.

Aquatic plant roots generally have a large amount of aerenchyma in the cortex and, sometimes, in the vascular cylinder. Root polymorphism is common in aquatic plants, for example, in *Echinodorus paniculatus* (Scremin-Dias 2000). This monocot has thick roots anchoring plants in the soil. These roots are polyarch, with a wholly lignified vascular cylinder. The cortex may be absent in the last basal third of the root. In the rhizomes of this species and several congeners, there are smaller roots, with a vascular cylinder without lignification and up to five poles of protoxylem. These roots have numerous root hairs that play a role in absorbing nutrients and water in muddy soil. A third type of root specialized in storing starch also occurs in *E. paniculatus.* Thickened roots specialized in reserve storage are a vital attribute for survival during water receding and dry periods.

Contractile roots are also identified in aquatic macrophytes. Such roots are found in species of Alismataceae, Nymphaeaceae, and Pontederiaceae. As the water recedes, the underground organs located in the muddy soil are exposed close to the water surface. In such conditions, the parenchymatic cortex cells contract, pulling the apical meristem below the ground level, where it remains covered by the leaf sheaths throughout the dry season and is able to reestablish the aerial parts at the beginning of the subsequent flooding.

16.2.4 Adaptations of Diaspores in Aquatic Macrophytes

In habitats subject to environmental variations, the persistence of species through periods of adverse conditions is essential for their survival in the community (Pausas et al. 2018). During the dry period, aquatic grasses and macrophytes, that grew in the temporarily inundated areas, may remain dormant and/or buried in their resistant structures and diaspores (Scremin-Dias 2009; Brock 2011; Scremin-Dias et al. 2011; Catian 2015). The morphological resistant structures are represented by stolons, rhizomes, turions, and plant fragments (Sculthorpe 1967; Barrat-Segretain 1996). These morphological structures can mechanically separate from the mother plant and colonize new areas when the conditions become favorable (Barratt-Segretain et al. 1998; Kufner et al. 2011). Besides, after the flood period, diaspores of aquatic macrophytes can remain buried down to at least 5 cm in the soil (Martins and Silva 2001) and even deeper (Thompson 1992), forming a diaspore bank. Therefore, the formation of a diaspore bank in the soil and the presence of underground structures specialized in vegetative propagation are essential characteristics for in situ persistence of aquatic macrophytes and for resistance to drought and fire events.

16.2.4.1 Vegetative Propagation in Aquatic Macrophytes

Stolons, rhizomes, turions, and nonspecialized plant fragments play a major role in the vegetative propagation of aquatic macrophytes (Sculthorpe 1967; Barrat-Segretain 1996; (Fig. 16.8a–e). Turions are specialized dormant buds released by abscission or senescence of the parent plant. They occur in *Potamogeton crispus* (Sastroutomo 1981; Chambers et al. 1985), *Utricularia* spp. (Adamec 2011) and *Myriophyllum verticillatum* (Weber and Noodén 1976), *Spirodela polyrhiza*, and 15 duckweed species (Landolt and Kandeler 1987; Appenroth et al. 1989). These structures remain at the bottom of water bodies during periods unfavorable to plant growth, regrowing when the favorable conditions resume (Landolt and Kandeler

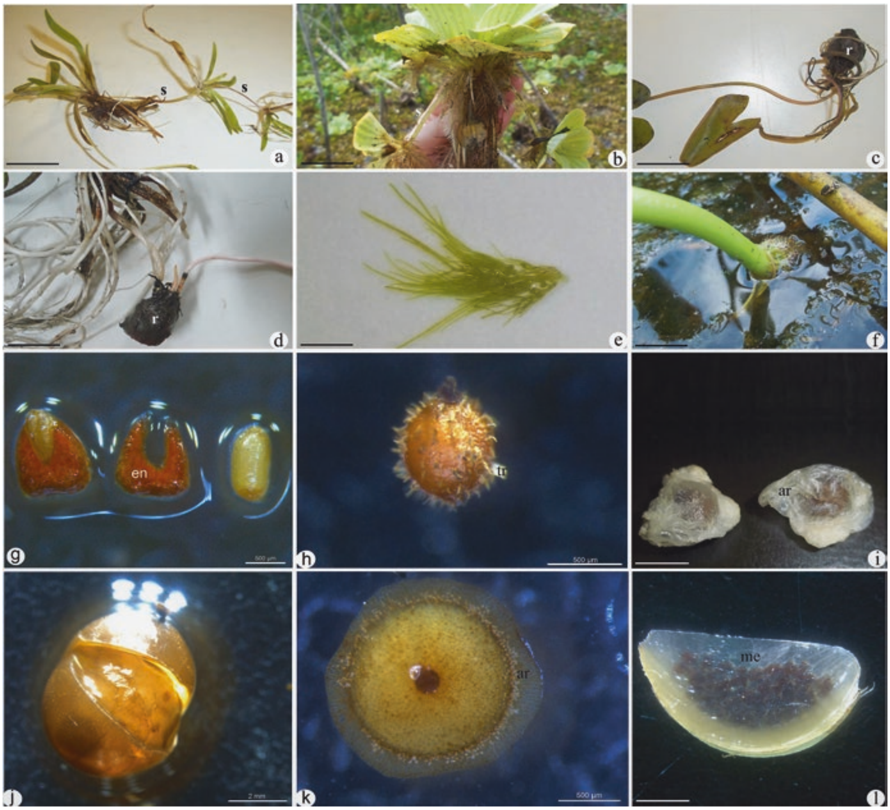


Fig. 16.8 Vegetative propagation structures and diaspores of aquatic macrophytes. (**a**) Stolons in *Helanthium tenellum* and (b) *Pistia stratiotes*. (**c** and **d**) Rhizomes in *Nymphaea amazonum*. (**e**) Plant fragments of *Utricularia gibba*. (**f**) Floral scape of *Pontederia parviflora*. (**g**) Diaspore of *Ludwigia leptocarpa* with endocarp separated from the seed. (**h**) Seed of *Nymphaea amazonum* with trichomes. (**i**) Diaspore of *Victoria amazonica* with swollen aril. (**j**) Fruit of *Utricularia foliosa* with diaspores and (**k**) diaspore of *U. gibba* with aril. (**l**) Diaspore of *Limnocharis flava* with seeds. *Ar* aril, *En* endocarp, *R* rhizome, *S* stolon, *Tr* trichome. Scale bars: (**a, b, c, d, e, f, i, l**) = 1 cm; (**j**) = 2 mm; (**g**, **h**, **k**) = 200 *µ*m. Photos: **g**, **h**, **j**, **k** = Lima, Gabriel Tirintan de

1987). In duckweeds, this structure has no roots; it has brown pigmentation spots on both sides, starch granules, reduced aerenchyma for sinking, and tannin granules for protection (Xu et al. 2018).

Rhizomes predominate in several emergent species and are able to remain dormant in the pond soil during drought. In general, rhizomes have large carbohydrate reserves which can be utilized during prolonged periods of anoxia for anaerobic respiration and which support new growth in favorable periods. In the Pantanal floodplain, rhizomes occur in rooted floating species, such as *Nymphaea amazonum* (Catian 2015; Fig. 16.8c and d), *Nymphaea* spp., and emergent species such as *Echinodorus paniculatus* and many other species of aquatic macrophytes (Pott and Pott 2000).

Stolons are present in floating species and are very important in vegetative propagation and also as a resistance structure to drought and fire. During the flood period, it is common in amphibious aquatic macrophytes to develop stolons, e.g., *Helanthium tenellum* (Fig. 16.8a); in the free-floating *Pistia stratiotes* (Fig. 16.8b), *Limnobium laevigatum*, and *Eichhornia crassipes*; and in emergent aquatic macrophytes such as *Echinodorus longiscapus* (Catian 2015).

In addition to specialized structures, stem fragments also can regrow and colonize. Stem fragments in the submerged species *Cabomba furcata*, *Utricularia gibba* (Fig. 16.8e), and *Egeria najas* are released, mainly during the water-receding season, being carried by the current (Catian 2015). In rooted plants, fragments that reach some surface or substrate may develop adventitious roots and attach themselves to the soil. In non-rooted species, such as *Utricularia* spp., an elongation of the stem fragment occurs, forming new leaves and utricles.

16.2.4.2 Dispersal of Diaspores in Aquatic Macrophytes

The product of sexual reproduction of angiosperms is seed. A seed connected to fruit or other plant tissue which assists in its dispersal is called a diaspore (Barroso et al. 1999). Diaspores can be dispersed by wind (anemochory), by animals (zoochory), by birds (ornithochory), and by fish (ichthyochory), but many plant species in wetlands tend to have an evolutionary convergence to hydrochory (Waldhoff et al. 1996).

Hydrochory is a widespread dispersal method in emergent, amphibious, epiphytic, submerged, and floating aquatic macrophytes, either with floating or sinking diaspores. Some Hydrocharitaceae and Pontederiaceae (e.g., *Pontederia parviflora*, Fig. 16.8f) bend the floral scape into the water to ripen and release the seeds (Van der Pijl 1982). Besides, the morphology of the seed coat and/or diaspore directly influences the dispersing strategy. Floating diaspores have, in general, aerenchymatous structures. We observed horseshoe-shaped structures rich in aerenchyma originating from the endocarp and comprising the seed in *Ludwigia leptocarpa* (Fig. 16.8g) and *L. lagunae* (Fabiano et al., unpublished data). Seed buoyancy can also be provided by the presence of trichomes, which increase their surface area, e.g., in *Nymphoides* sp. (Boesewinkel 1987) and *Nymphaea amazonum* (Fig. 16.8h;

Fabiano et al., unpublished data). The seed of *N. amazonum* has a globoid shape, which facilitates secondary wind dispersal (Conard 1905; Wiersema 1987). *Nymphaea* and *Victoria amazonica* seeds (Fig. 16.8i) have a whitish or translucent aril (Bonilla-Barbosa et al. 2000), with mucilage and gas bubbles, helping to float and disperse (Conard 1905). In some species, e.g., *Polygonum* spp., the seeds do not have apparent hydrochoric traits, but the persistent perianths trap air and confer buoyancy to the achenes (Staniforth and Cavers 1976).

Discoid or lenticular shapes of the diaspores also facilitate flotation. That characteristic is frequent in amphibious aquatic macrophytes, such as *Veronica* sp. and *Nymphoides* sp., and submerged species of *Utricularia* (e.g., *U. foliosa* and *U. gibba*, Fig. 16.8j and k). But some species of *Utricularia* have an anemochoric dispersal strategy (Compton 1909).

Seed size and weight are factors that influence the ability to float or sink (Marimon and Felfili 2006). *Limnocharis* (e.g., *L. flava*, Fig. 16.8l) presents floating follicle mericarps containing the seeds, which are dispersed by water, and the seeds are released by a suture and sink (Van der Pijl 1982).

Zoochoric dispersion is also typical in aquatic macrophytes. The dispersal of diaspores in *Myriophyllum* sp. occurs through transport on muddy bird feet (Fauth 1903). In such seeds, mucilage is common, which, moistened, adheres to the feet of birds or rocks (Gessner and Hammer 1962).

16.3 Adaptation to Flooding in Plants and Woody Seedlings

Flooding in the Pantanal floodplains is a key factor in the distribution of woody species throughout the riparian forest (Damasceno-Junior et al. 2005). Flooding in the riparian forests of the Paraguay River in the Pantanal floodplain can vary from 11 to 220 days per year, depending on the maximum rise attained by the river, the height of the riverbank, and the position of each tree on the levee (Damasceno-Junior et al. 2005; Fig. 16.9). Long periods of flooding make the soil anoxic, leading to a reduced

Fig. 16.9 Flooded riparian forest in the Pantanal

uptake of water and nutrients by the plant roots (Else et al. 2001; Kozlowski 2002). Under such conditions, the establishment and growth of seedlings and the survival of adult trees depend on different morphoanatomical strategies that minimize the damage caused by soil anoxia. Next, we discuss some morphoanatomical responses of seedlings to flooding and the effects of flooding on the anatomical structure of the stem bark of woody species.

16.3.1 Morphoanatomical Responses of Seedlings to Soil Flooding

The effect of flooding on stem height growth and increase in biomass of seedlings of woody species in riparian forest and wetlands in the Pantanal is variable. Under 90 days of continuous flooding of the soil, there was a decrease in height growth rate and biomass increment in *Albizia inundata*, *Banara arguta*, *Triplaris gardneriana* (Pontara et al. 2016), and *T. americana* (Pontara 2010) seedlings. The development of flooded seedlings with shorter stems and less biomass accumulation may result from a decreased carbon fixation due to stomatal closure, which hinders plant growth (Kozlowski 1997; Parad et al. 2016). Furthermore, seedlings of *A. inundata* were more prone to mortality with increased flooding time, decreasing the probability of their establishment in flooded areas. In contrast, soil flooding did not alter the height growth rate in seedlings of *Vochysia divergens* and *Tabebuia aurea* (Holsback-Menegucci 2008), and *Erythroxylum anguifugum*. Besides, *V. divergens* seedlings in experimental flooding for 120 days showed larger shoot biomass than the control (Holsback-Menegucci 2008).

The induction of hypertrophy of lenticels after soil flooding has been recorded in many woody species (Yamamoto and Kozlowski 1987a; Kolb et al. 1998; Medri et al. 1998; Parad et al. 2016). Seedlings of woody species of riparian forests of the Pantanal floodplain subjected to experimental flooding showed a high abundance of hypertrophied lenticels and adventitious roots at the stem base (e.g., *Triplaris gardneriana* (Pontara et al. 2016), *T. americana* (Pontara 2010), and *Albizia inundata*). Lenticel formation involves accelerated phellogen activity, elongation of phellem cells, dissolution of cell walls, cell hypertrophy, and cell proliferation (Angeles et al. 1986). Anatomically, in cross-sections of flooded stem seedlings of *A. inundata*, hypertrophied and radially elongated cells can be observed of the lenticel filling tissue interspersed with compact cells of the occlusion layer (Fig. 16.10). In general, the formation of lenticels and, consequently, the increase in intercellular spaces at the stem base in contact with the water surface can facilitate the diffusion of potentially toxic products, such as ethanol and acetaldehyde, from anaerobic respiration (Yamamoto and Kozlowski 1987a, b; Joly 1996).

Flooded seedlings of woody species from the riparian forest of the Pantanal floodplain present morphological and anatomical modifications in response to anoxia. Submitted to experimental flooding, they show leaf chlorosis, formation of

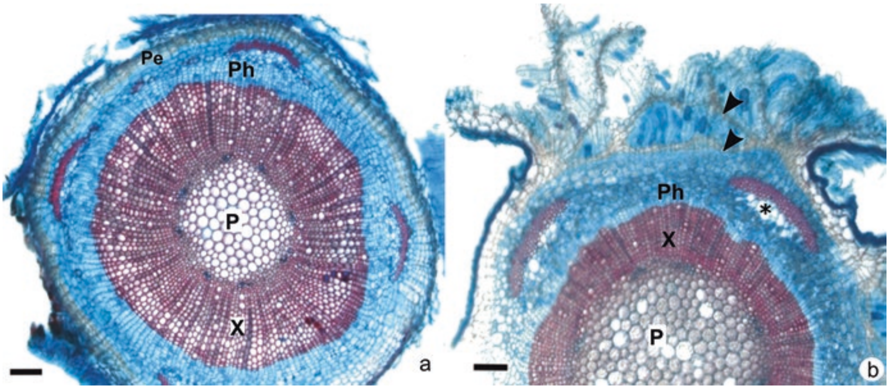


Fig. 16.10 Transverse section of the seedling stem of *Albizia inundata*. (**a**) Seedling stems grown in a drained soil, with a single periderm, pith parenchyma with few amyloplasts. (**b**) Seedling stem subjected to flooding for 90 days with hypertrophied lenticels (arrowheads), cortical parenchyma with radially elongated cells (*), amyloplasts in the radial and axial parenchyma of the secondary xylem, pith, and cortex. *P* pith, *Pe* periderm, *Ph* phloem, *X* xylem. Scale bars: (**a** and b) = 100 μm

adventitious roots, longitudinal fissures at the stem base, and increased diameters at the stem base due to lenticel hypertrophy (Holsback-Menegucci 2008; Pontara 2010; Pontara et al. 2016). Some anatomical changes are observed in the stem and root tissues, such as an increase in the volume of the cortex and pith cells (e.g., *A. inundata*, Fig. 16.10b) and a decrease in the diameter of the vessels of the secondary xylem (Pontara et al. 2016).

Furthermore, another characteristic of flood-tolerant species is the accumulation of starch in stem and root parenchyma cells (e.g., *T. gardneriana* (Pontara et al. 2016), *T. americana* (Pontara 2010), *A. inundata*, Fig. 16.10b). Large amounts of starch in flooded plant organs can be caused by the reduced transport in phloem or perhaps as a consequence of the decline in tissue metabolism under anoxic conditions (Gravatt and Kirby 1998).

16.3.2 Bark of Woody Riparian Forest Species

The stem bark plays a vital role in the survival of mature trees in riparian forests subject to periodic flooding (Angeles et al. 1986; Angeles 1992; Yáñez-Espinosa et al. 2008). Bark represents all tissues external to the vascular cambium (Esau 1965; Angyalossy et al. 2016) and includes tissues with distinct meristematic origins in well-established secondary growth stems (Roth 1981). The inner bark consists of secondary phloem and primary tissues, if any (Roth 1981; Angyalossy et al. 2016). Secondary phloem is derived from vascular cambium and plays a key role in the transport of photo-assimilates, storage of water and organic compounds, mechanical stem support, recovery from damage by biotic and abiotic agents, and protection against pathogens and herbivores (Roth 1981; Franceschi et al. 2005; Romero et al. 2009; Paine et al. 2010; Vergílio et al. 2017). Bark primary tissues, such as the cortex, are derived from primary growth and can play a role in the storage of substances (Evert 2006). On the other hand, the outer bark is a secondary protective tissue, derived from phellogen, and can be formed by a single periderm or successive periderms, called rhytidome (Evert 2006; Angyalossy et al. 2016).

Long periods of flooding make woody plants more prone to herbivory and fungal and bacterial infection (Li et al. 2005). Widely distributed tree species in riparian forests of the Pantanal floodplain show anatomical and chemical characteristics in the bark, which can act as constitutive defenses (Paine et al. 2010; Poorter et al. 2014). Phellem with numerous layers of cells impregnated with lignin (e.g., *Handroanthus heptaphyllus*, Fig. 16.11b), large sclereids with calcium oxalate crystals on the periphery of the collapsed secondary phloem (e.g., *Cassia grandis*, Fig. 16.11a and c), and calcium oxalate crystals in the parenchyma cells (e.g., druses in *Vochysia divergens*, Fig. 16.11d) are characteristics that can increase the mechanical resistance to penetration, and ingestion/mastication by small herbivorous insects (Franceschi et al. 2005). In addition, cells with phenolic compounds are common in parenchyma cells in the inner bark of some tree species of the Pantanal floodplain (e.g., *C. grandis*, Fig. 16.11a, and *Inga vera*, Fig. 16.11e). Phenolic compounds have fungicidal properties, which associated with sclereids and cells with crystals, provide an efficient chemical and mechanical protection system against the action of herbivores and a defense against pathogen infections (Roth 1981; Franceschi et al. 2005).

Adaptation of the bark in flooded environments involves the formation of intercellular spaces, allowing the flow of gases between emergent parts of the stem and the submerged parts of the stem and the root system (Yáñez-Espinosa and Terrazas 2001). Hypertrophied lenticels are also prevalent in emergent stems in riparian tree species and occur in different patterns. Hypertrophied lenticels have a longitudinal arrangement in *Albizia inundata* (Fig. 16.12a) and *Inga vera* (Fig. 16.12b) and a circular arrangement in *Triplaris gardneriana* (Fig. 16.12c) and *Genipa americana* (Fig. 16.12d). We also observed wide intercellular spaces in the periderm of *Vochysia divergens*; its cross-section shows radially elongated phellem cells, looking like a loose bark (Fig. 16.11f). According to Kawase and Whitmoyer (1980), the accumulation of ethylene in flooded plants could increase the cellulase activity, causing the formation of aerenchymatous phellem and hypertrophied lenticels.

Final Considerations and Perspectives

In this chapter, we described the morphological and anatomical diversity of aquatic macrophytes and other wetland plants in areas experiencing seasonal periods of flooding and drought, including occasional fire events in the Pantanal floodplain. The following stand out among the predominant morphoanatomical characteristics in organs of aquatic macrophytes: cuticles with variable thickness, variations in position, quantity and functionality of stomata, presence of hydropotes, anthocyanin accumulation in submerged and floating organs, position and thickness of chlorenchyma, aerenchyma with or without diaphragm, reduction or even absence

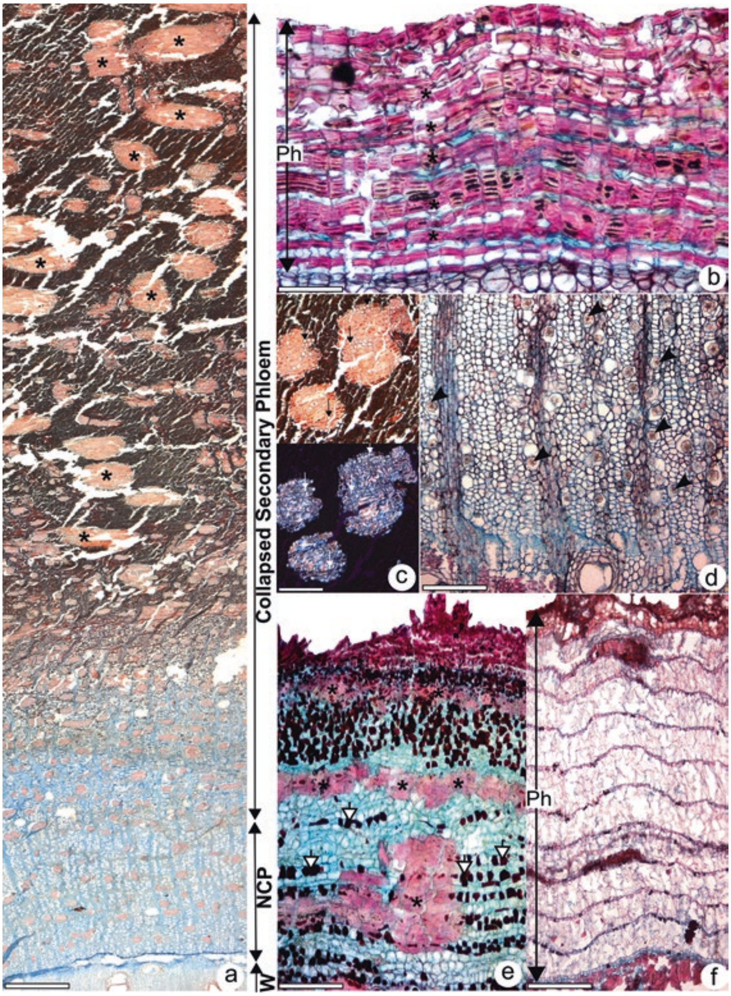


Fig. 16.11 Bark anatomy of riparian species from the Pantanal. (**a**) Transverse section of *Cassia grandis* with collapsed secondary phloem with large sclereids (stone cells; *) and parenchyma cells with phenolic content (blackish stained area). (**b**) Phellem with numerous layers of cells impregnated with lignin in *Handroanthus heptaphyllus*, transverse section. (**c**) Prismatic crystals (arrows) in parenchyma cells associated to sclerenchyma in *Cassia grandis* in stained transverse sections (above) and under polarized light (below). (**d**) Secondary phloem of *Vochysia divergens* with druses (arrowheads) in the parenchyma cells, transverse section. (**e**) Transverse sections of cortex and periderm of *Inga vera* with sclereids and parenchyma cells with phenolic content (arrows), transverse section. (**f**) Periderm of *Vochysia divergens* showing the loose aspect of aerenchymatous phellem, transverse section. *NCP* non-collapsed phloem, *Ph* phellem, *W* wood. Scale bars: (**a**) = 500 μm; (**e** and **f**) = 100 μm (**b**) = 200 μm; (**c**) = 50 μm

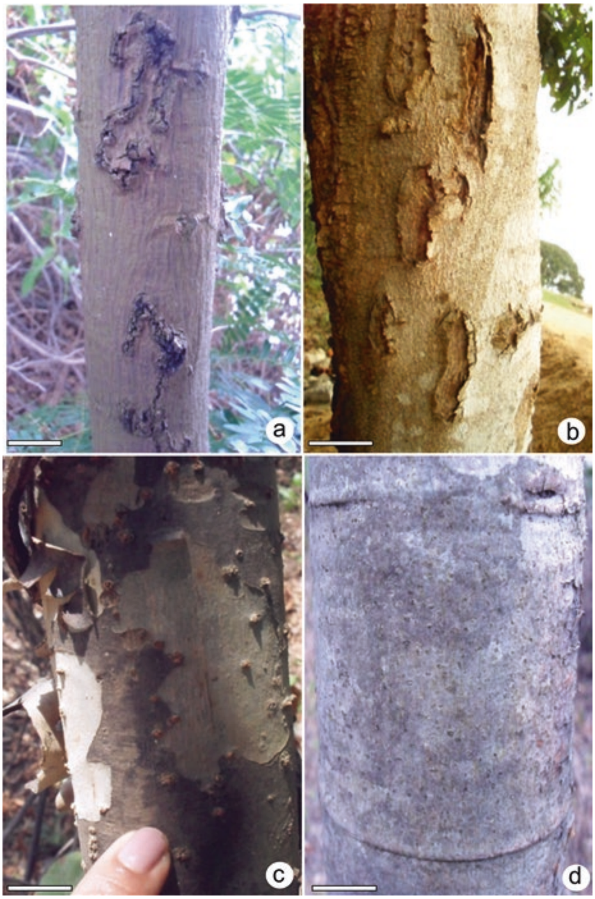


Fig. 16.12 General view of bark traits of woody trees from riparian forest of the Paraguay River Basin. (**a**) *Albizia inundata* and (**b**) *Inga vera* with smooth bark surface with longitudinal lenticels. (**c**) *Triplaris gardneriana* and (**d**) *Genipa americana* with smooth bark surface with circular lenticels. Scale bars: (**a**–**d**) = 5 cm

of metaxylem vessels in the vascular cylinder, presence of collenchyma, and formation of adventitious roots. These can occur in organs that are flooded or above the water and in response to the moisture gradient.

Flooding in several areas of the Pantanal floodplain also contributes to the dispersal of diaspores and vegetative structures. In general, aquatic macrophytes have numerous adaptations on the surface of their diaspores for hydrochoric dispersal. Also, structures with a potential for vegetative propagation, such as rhizomes, stolons, turions, and plant fragments, are common in numerous aquatic macrophytes that grow in the extensive wetlands in the Pantanal floodplain. These structures allow in situ persistence and rapid spatial recolonization during the flooding period.

Woody plants submitted to annual flooding of the riparian forests remain for short or long periods with their roots and basal stem parts in an anoxic environment. Decreased oxygen availability induces the formation of hypertrophied lenticels at the stem base, the formation of intercellular spaces in root and stem tissues, and the development of adventitious roots. Fire events can occur in riparian forests after the water-receding and subsequent dry period. Unfortunately, knowledge about the anatomical bark structure of woody species in the riparian forest in the Pantanal floodplain, as well as the synergistic effects of flooding, drought, and fire on their anatomy, is scarce. Given the predictions of the intensification of droughts and an increase in fire events in the riparian forests and other areas of the Pantanal floodplain, knowledge of the essential adaptations for the survival of woody plants and aquatic macrophytes in the wetlands is essential to understanding the effects of ongoing climate change on the plant distribution as well as for the development and application of management and conservation strategies in these areas.

Acknowledgments We are grateful to Rede de Sementes do Pantanal for support during the fieldwork that made this research project possible; to the Instituto Nacional de Áreas Úmidas (INAU) and Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul - FUNDECT (Edital PAPOS) for financial support, and to Dr. Arnildo Pott and Dra. Vali Joana Pott for English language review and plant identification.

References

Adamec L (2011) Dark respiration and photosynthesis of dormant and sprouting turions of aquatic plants. Fundam Appl Limnol/Archiv für Hydrobiol 179(2):151–158

Adámoli J (1982) O Pantanal e suas relações fitogeográficas com os Cerrados. Anais do Congresso Nacional de Botânica 32:109–119

Angeles G (1992) The periderm of flooded and non-flooded *Ludwigia octovalvis* (Onagraceae). IAWA Bull 13(2):195–200

Angeles G, Evert RF, Kozlowski TT (1986) Development of lenticels and adventitious roots in flooded *Ulmus americana* seedlings. Can J For Res 16:585–590

Angyalossy V, Pace M, Evert RF, Marcati CR, Oskolski AA, Terrazas T, Kotina E, Lens F, Mazzoni-Viveiros SC, Angeles G, Machado SR, Crivellaro A, Rao KS, Junikka L, Nicolaeva N, Baas P (2016) IAWA list of microscopic bark features. IAWA J 37:517–615. https://doi.org/10.1163/22941932-20160151

Appenroth K, Hertel W, Jungnickel F, Augstenn H (1989) Influence of nutrient deficiency and light on turion formation in Spirodela polyrhiza (L.) Schleiden. Biochem Physiol Pflanzen 184(5-6):395–403

Arruda WS, Oldeland J, Paranhos Filho AC, Pott A, Cunha NL, Ishii IH, Damasceno-Junior GA (2016) Inundation and fire shape the structure of riparian forests in the Pantanal, Brazil. PLoS One 11(6):e0156825. https://doi.org/10.1371/journal.pone.0156825

Barrat-Segretain MH (1996) Strategies of reproduction, dispersion, and competition in river plants: a review. Vegetation 123(1):13–37

Barrat-Segretain MH, Bornette G, Hering-Vilas-Boas A (1998) Comparative abilities of vegetative regeneration among aquatic plants growing in disturbed habitats. Aquat Bot 60(3):201–211

Barroso GM, Morim MP, Peixoto AL, Ichaso CLF (1999) Frutos e sementes: morfologia aplicada à sistemática de dicotiledôneas. UFV, Viçosa, 443 pp

Bedoya AM, Madriñán S (2015) Evolution of the aquatic habit in *Ludwigia* (Onagraceae): Morpho-anatomical adaptive strategies in the Neotropics. Aquat Bot 120:352–362. https://doi.org/10.1016/j.aquabot.2014.10.005

Boeger MRT, Poulson ME (2003) Morphological adaptations and photosynthetic rates of amphibious *Veronica anagallis-aquatica* L. (*Scrophulariaceae*) under different flow regimes. Aquat Bot 72:123–135

Boesewinkel FD (1987) Ovules and seeds of Trigoniaceae. Acta Bot Neerl 36(1):81–91

Bona C, Morretes BL (2003) Anatomia das raízes de *Bacopa salzmannii* (Benth.) Wettst. ex Edwall e *Bacopa monnierioides* (Cham.) Robinson (Scrophulariaceae) em ambientes aquático e terrestre. Acta Bot Bras 17(1):155–170

Bonilla-Barbosa J, Novelo A, Hornelas Orozco Y, Márquez-Guzmán J (2000) Comparative seed morphology of Mexican *Nymphaea* species. Aquat Bot 68(3):189–204

Brock MA (2011) Persistence of seed banks in Australian temporary wetlands. Freshw Biol 56:1312–1327

Carpenter KJ (2006) Specialized structures in the leaf epidermis of basal angiosperms: morphology, distribution, and homology. Am J Bot 93(5):665–681. https://doi.org/10.3732/ajb.93.5.665

Catian G (2015) Efeitos da dinâmica de inundação nas estratégias reprodutivas, na estrutura do banco de sementes e na diversidade funcional de comunidades de macrófitas aquáticas em lagoas do Pantanal. Tese de doutorado pelo programa de Pós-graduação Ecologia e Conservação, Universidade Federal de Mato Grosso do Sul, 115p

Catian G, Scremin-Dias E (2015) Phenotypic variations in leaf anatomy of *Nymphaea gardneriana* (Nymphaeaceae) demonstrate its adaptive plasticity. J Torrey Bot Soc 142(1):18–26. https://doi.org/10.3159/TORREY-D-14-00038.1

Catian G, Silva DM, Súarez YR, Scremin-Dias E (2018) Effects of flood pulse dynamics on functional diversity of macrophyte communities in the Pantanal wetland. Wetlands 38(5):975–991. https://doi.org/10.1007/s13157-018-1050-5

Chalker-Scott L (1999) Environmental significance of anthocyanins in plant stress responses. Photochem Photobiol 70(1):1–9

Chambers PA, Spence DHN, Weeks DC (1985) Photocontrol of turion formation by *Potamogeton crispus* L. in the laboratory and natural water. New Phytol 99(2):183–194

Chambers RM, Meyerson LA, Saltonstall K (1999) Expansion of Phragmites australis into tidal wetlands of North America. Aquat Bot 64(3–4):261–273

Compton RH (1909) The morphology and anatomy of *Utricularia brachiata*, Oliver. New Phytol 8(4):117–130

Conard HS (1905) The waterlilies: a monograph of the genus *Nymphaea* (No. 4). Published by the Carnegie Institution of Washington.

Cutter EG (1987) Anatomia vegetal, vol 1. Roca, São Paulo

Damasceno-Junior GA, Semir J, Santos MFA, Leitão-Filho HF (2005) Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200(2):119–135. https://doi.org/10.1016/j.flora.2004.09.002

Demetrio GR, Barbosa MEA, Coelho FF (2014) Water level-dependent morphological plasticity in *Sagittaria montevidensis* Cham. and Schl. (Alismataceae). Braz J Biol 74(3):S199–S206

DNOS (1974) Estudos Hidrológicos da Bacia do Alto Paraguai. Programa das Nações Unidas para o Desenvolvimento (Relatório Técnico), Rio de Janeiro

Drew MC (1997) Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Biol 48(1):223–250

Else MA, Coupland D, Dutton L, Jackson MB (2001) Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure and slows leaf expansion in flooded plants of castor oil (*Ricinus communis*) despite diminished delivery of ABA from the roots to shoots in xylem sap. Physiol Plantarum 111(1): 46-54. doi:https://doi.org/10.1034/j.1399-3054.2001.1110107.x.

Esau K (1965) Plant anatomy, 2nd edn. Wiley, Hoboken

Evert R (2006) Esau's plant anatomy: meristems, cells, and tissues of the plant body: their structure, function, and development. Wiley, Hoboken

Evert RF, Eichhorn SE, Raven PH (2012) Biology of plants. W. H. Freeman, New York

Fahn A (1982) Plant anatomy, 3rd edn. Pergamon Press, Oxford

Fauth A (1903) Beiträge zur Anatomie und Biologie der Früchte und Samen einiger einheimischer Wasser-und Sumpfpflanzen. Jena, G. Fischer

Ferreira-Júnior WG, Schaefer CEGR, Cunha CN, Duarte TG, Chieregatto LC, Carmo FMS (2016) Flood regime and water table determines tree distribution in a forest-savanna gradient in the Brazilian Pantanal. Anais da Academia Brasileira de Ciências 88:719–731. https://doi.org/10.1590/0001-3765201620150341

Franceschi VR, Krokene P, Christiansen E, Krekling T (2005) Anatomical and chemical defenses of confer bark against bark beetles and other pests. New Phytol 167(2):353–375. https://doi.org/10.1111/j.1469-8137.2005.01436.x

Gessner F, Hammer L (1962) Ökologisch-physiologische Untersuchungen an den Podostemonaceen des Caroni. Int Revue ges Hydrobiol Hydrogr 47(4):497–514

Gould KS, Kuhn DN, Lee DW, Oberbauer SF (1995) Why leaves are sometimes red. Nature 378:241–242. https://doi.org/10.1038/378241b0

Gravatt DA, Kirby CJ (1998) Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. Tree Physiol 18:411–417. https://doi.org/10.1093/treephys/18.6.411

Holsback-Menegucci ZR (2008) Estudo comparativo de respostas ao alagamento em plantas jovens de espécies arbóreas provenientes do Pantanal, Mato Grosso do Sul, Brasil. Dissertação de Mestrado, Programa de Pós-Graduação em Biologia Vegetal. Universidade Federal de Mato Grosso do Sul

Hutchinson GE (1975) A treatise on limnology, v. 3. Limnological botany. John Wiley & Sons, New York, London, Sydney, and Toronto, xii + 660 p

Idestam-Almquist J, Kautsky L (1995) Plastic responses in morphology of *Potamogeton pectinatus* L. to sediment and above-sediment conditions at two sites in the northern Baltic proper. Aquat Bot 52(3):205–216

Irgang BE, Pedralli G, Waechter JL (1984) Macrófitos aquáticos da Estação Ecológica do Taim, Rio Grande do Sul, Brasil. Roessléria 6(1):395–404

Joly CA (1996) The role of oxygen diffusion to the root system on the flooding tolerance of tropical trees. Rev Brasil Biol 56(2):375–382

Junk WJ, Nunes C, Wantzen KM, Petermann P, Strüssmann C, Marques MI, Adis J (2006) Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquat Sci 68:278–309. https://doi.org/10.1007/s00027-006-0851-4

Kawase MI, Whitmoyer RE (1980) Aerenchyma development in waterlogged plants. Am J Bot 67(1):18–22

Knipling ED, West SH, Haller WT (1970) Growth characteristics, yield potential, and nutritive content of water hyacinth. Proc Soil Crop Sci Soc Fl 30:51–63

Kolb RM, Medri ME, Bianchini E, Pimenta JA, Giloni PC, Correa GT (1998) Anatomia ecológica de *Sebastiania commersoniana* (Baillon) Smith & Downs (Euphorbiaceae) submetida ao alagamento. Rev Brasil Bot 21(3). https://doi.org/10.1590/S0100-84041998000300010

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiol 1(1):1–29. https://doi.org/10.1080/07352680091139196

Kozlowski TT (2002) Physiological-ecological impacts of flooding on riparian ecosystems. Wetlands 22(3):12

Kufner DCL, Scremin-Dias E, Guglieri-Caporal A (2011) Composição florística e variação sazonal da biomassa de macrófitas aquáticas em lagoa de meandro do Pantanal. Rodriguésia 62(4):803–812

Landolt E, Kandeler R (1987) The family of *Lemnaceae* – a monographic study, vol. 2. Veroff. Geobot. ETH, Stiftung Rübel, Zürich, 95 Heft

Lawson T, Blatt MR (2014) Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. Plant Physiol 164(4):1556–1570

Li S, Martin LT, Pezeshki SR, Shields FD (2005) Responses of black willow (*Salix nigra*) cuttings to simulated herbivory and flooding. Acta Oecol 28:173–180. https://doi.org/10.1016/j.actao.2005.03.009

Madsen TV, Maberly SC (1991) Diurnal variation in light and carbon limitation of photosynthesis by two species of submerged freshwater macrophyte with a differential ability to use bicarbonate. Freshw Biol 26:175–187

Marimon BS, Felfili JM (2006) Chuva de sementes em uma floresta monodominante de *Brosimum rubescens* Taub. e em uma floresta mista adjacente no Vale do Araguaia, MT, Brasil. Acta Bot Brasil 20(2):423–432

Martins L, Silva WRD (2001) Dormancy performance of *Brachiaria brizantha* seeds submitted to thermal and chemical treatments. Pesqui Agropecu Bras 36(7):997–1003

Medri ME, Bianchini E, Pimenta JA, Delgado MF, Correa GT (1998) Aspectos morfo-anatômicos e fisiológicos de *Peltophorum dubium* (Spr.) Taub. submetida ao alagamento e à aplicação de etrel. Rev Brasil Bot 21(3):261–267. https://doi.org/10.1590/S0100-84041998000300004

Metcalfe CR, Chalk L (1979) Anatomy of the dicotyledons. Vol I. Systematic anatomy of leaf and stem, with a brief history of the subject, 2nd edn. Anatomy of the dicotyledons

Murphy K, Efremov A, Davidson TA, Molina-Navarro E, Fidanza K, Betiol TCC, Chambers P, Grimaldo JT, Martins SV, Springuel I, Kennedy M, Mormul RP, Dibble E, Hofstra D, Lukács BA, Gebler D, Baastrup-Spohr L, Estrada-Urrutia J (2019) World distribution, diversity and endemism of aquatic macrophytes. Aquat Bot 158:103127

Okamoto JM, Joly CA (2000) Ecophysiology and respiratory metabolism during the germination of *Inga sessilis* (Vell.) Mart. (Mimosaceae) seeds subjected to hypoxia and anoxia. Braz J Bot 23(1):51–57. https://doi.org/10.1590/S0100-84042000000100006

Paillisson JM, Marion L (2006) Can small water level fluctuations affect the biomass of *Nymphaea alba* in large lakes? Aquat Bot 84(3):259–266

Paine CET, Stahl C, Courtois EA, Patiño S, Sarmiento C, Baraloto C (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. Funct Ecol 24(6):1202–1210. https://doi.org/10.1111/j.1365-2435.2010.01736.x

Parad GA, Kouchaksaraei MT, Striker GG (2016) Growth, morphology and gas exchange responses of two-year-old *Quercus castaneifolia* seedlings to flooding stress. Scand J For Res 31(5):458–466. https://doi.org/10.1080/02827581.2015.1072240

Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A (2018) Unearthing belowground bud banks in fire-prone ecosystems. New Phytol 217:1435–1448

Pedralli G (2000) Padrões florísticos como subsídios à conservação da biodiversidade de macrófitas aquáticas. Tópicos Atuais em Botânica, Palestras convidadas do 51 Congresso Nacional de Botânica, Brasília-DF. Brasília, EMBRAPA

Pontara V (2010) Efeitos do alagamento em plântulas de *Triplaris americana* L. e *Triplaris gardneriana* Wedd. (Polygonaceae). Dissertação de Mestrado. Programa de Pós graduação em Biologia vegetal, Universidade Federal de Mato Grosso do Sul

Pontara V, Bueno ML, Scremin-Dias E (2016) Flooding avoidance *Triplaris gardneriana* Wedd. (Polygonaceae): growth and morpho-anatomical aspects. Acta Sci Biol Sci 38(3):341–346. https://doi.org/10.4025/actascibiolsci.v38i3.31267

Poorter L, Mcneil A, Hurtado VH, Prins HHT, Putz FE (2014) Bark traits and life-history strategies of tropical dry and moist forest trees. Funct Ecol 28(1):232–242. https://doi.org/10.1111/1365-2435.12158

Pott A (1994) Ecosistema Pantanal. In: Puignau JP (ed) Utilizacion y Manejo de Pastizales. IICA-PROCISUR, Montevideo, pp 31–44

Pott VJ, Pott A (2000) Plantas aquáticas do Pantanal. EMBRAPA Comunicação para transferência de Tecnologia, Brasília

Pott VJ, Pott A (2003) Dinâmica da vegetação aquática do Pantanal. In: Thomaz SM, Bini LM (eds) Ecologia e manejo de macrófitas aquáticas. Editora da Universidade Estadual de Maringá, Maringá, pp 145–162

Pozer CG, Nogueira F (2004) Flooded native pastures of the northern region of the Pantanal of Mato Grosso: biomass and primary productivity variations. Braz J Biol 64(4):859–866

Rich SM, Ludwig M, Colmer TD (2012) Aquatic adventitious root development in partially and completely submerged wetland plants *Cotula coronopifolia* and *Meionectes brownii*. Ann Bot 110(2):405–414. https://doi.org/10.1093/aob/mcs051

Ridge I (1987) Ethylene and growth control in amphibious plants. In: Crawford RMM (ed) Plant life in aquatic and amphibious habitats. Blackwell Science Publishing, Oxford, pp 53–76

Rodrigues S, Scremin-Dias S, Medeiros SCH, Souza MC (2007) Alterações estruturais do caule e da folha de *Ludwigia inclinata* (L. f.) M. Gómez, desenvolvidos emersos e submersos no Pantanal Sul-Mato-Grossense. Revista Brasileira de Biociências 5(S1):174–176

Romero C, Bolker BM, Edwards CE (2009) Stem responses to damage: the evolutionary ecology of *Quercus* species in contrasting fire regimes. New Phytol 182(1):261–271. https://doi.org/10.1111/j.1469-8137.2008.02733.x

Roth I (1981) Structural patterns of tropical barks. Gebrüder Borntraeger, Berlin

Santana MAC, Catian G, Scremin-Dias E (2019) Respostas morfológicas de *Ludwigia helminthorrhiza* (Mart.) H. Hara (Onagraceae) à sazonalidade do Pantanal. Oecol Aust 23(4):874–890

Sastroutomo SS (1981) Turion formation, dormancy and germination of curly pondweed, *Potamogeton crispus* L. Aquat Bot 10:161–173

Scremin-Dias E (1992) Morfoanatomia dos órgãos vegetativos de *Ludwigia sedoides* (Humb. & Bonpl.) Hara (Onagraceae) ocorrente no Pantanal Sul-Mato-Grossense. Dissertação de mestrado. Universidade Federal do Paraná, Curitiba

Scremin-Dias E (2000) A plasticidade fenotípica das macrófitas aquáticas em resposta à dinâmica ambiental. In: Tópicos Atuais em Botânica: Palestras convidadas do 51 Congresso Nacional de Botânica, Brasília-DF, BR, pp 189–193

Scremin-Dias E (2009) Tropical aquatic plants: morphoanatomical adaptations. In: Del-Claro K, Rico-Gray (eds) Encyclopedia of tropical biology and conservation management. UNESCO/EOLSS, Paris, pp 84–132

Scremin-dias E, Pott VJ, Hora RC, Souza PR (1999) Nos jardins submersos da Bodoquena: guia para identificação de plantas aquáticas de Bonito e região. ECOA-Ecologia e Ação. Editora UFMS, Campo Grande

Scremin-Dias E, Lorenz-Lemke AP, Oliveira AKM (2011) The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress. Braz J Biol 71:275–282. https://doi.org/10.1590/S1519-69842011000200006

Sculthorpe CD (1967) The biology of aquatic vascular plants. Edward Arnold, London, 620p

Souza AHA, Rivaben RC, Batalha AM, Casagrande C, Assunção VA, Pott A, Damasceno-Junior GA (2019) Fire can weaken or trigger functional responses of trees to flooding in wetland forest patches. J Veg Sci 30:521–532. https://doi.org/10.1111/jvs.12719

Staniforth RJ, Cavers PB (1976) An experimental study of water dispersal in *Polygonum* spp. Can J Bot 54(22):2587–2596. https://doi.org/10.1139/b76-278

Stevens KJ, Peterson RL, Reader RJ (2002) The aerenchymatous phellem of *Lythrum salicaria* (L.): a pathway for gas transport and its role in flood tolerance. Ann Bot 89:621–625

Thompson K (1992) The functional ecology of seed banks. In: Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, pp 231–258

Tozin LRS, Rodrigues TM (2020) Revisiting hydropotes of Nymphaeaceae: ultrastructural features associated with glandular functions. Acta Bot Brasil 34(1):31–39. https://doi.org/10.1590/0102-33062019abb0120

Tur NM (1972) Un caso de epifitismo acuático. Boletin de la Sociedad Argentina de Botánica 10(4):323–327

Van der Pijl L (1982) Ecological dispersal classes, established on the basis of the dispersing agents. In: Principles of dispersal in higher plants. Springer, Berlin/Heidelberg, pp 22–90

Vartaperian BB, Jackson MB (1997) Plant adaptations to anaerobic stress. Ann Bot 79(1):3–20

Vergílio PCB, Silva JR, Blagitz M, Longo LR, Marcati CR (2017) Structural differences in the secondary phloem suggest higher support and storage potential in stems than roots of *Citharexylum myrianthum* Cham. (Verbenaceae). Botany 8(July):1–8

Waldhoff D, Saint-Paul U, Furch B (1996) Value of fruits and seeds from the floodplain forests of Central Amazonia as food resource for fish. Ecotropica 2(2):143–156

Weber JA, Noodén LD (1976) Environmental and hormonal control of turion formation in *Myriophyllum verticillatum*. Plant Cell Physiol 17(4):721–731

Wetzel RG (1993) Microcommunities and microgradients: linking nutrient regeneration, microbial mutualism, and high sustained aquatic primary production. Neth J Aquat Ecol 27(1):3–9

Wiersema JH (1987) A monograph of *Nymphaea* subgenus *Hydrocallis* (Nymphaeaceae). Syst Bot Monogr:1–112

Xu YL, Fangac Y, Li Q, Yang GL, Guo L, Che GK, Tan L, He KZ, Jin YL, Zhao H (2018) Turion, an innovative duckweed-based starch production system for economical biofuel manufacture. Ind Crops Prod 124:108–114

Yamamoto F, Kozlowski TT (1987a) Effect of flooding of soil on growth, stem anatomy, and ethylene production of *Cryptomeria japonica* seedlings. Scand J For Res 2(1–4):45–58. https://doi.org/10.1080/02827588709382445

Yamamoto F, Kozlowski TT (1987b) Effect of flooding on growth, stem anatomy, and ethylene production of *Pinus halepensis* seedlings. Can J For Res 17(1):69–79

Yáñez-Espinosa L, Terrazas T (2001) Wood and bark anatomy variation of *Annona glabra* L. under flooding. Agrociencia 35(1):51–63

Yáñez-Espinosa L, Terrazas T, Angeles G (2008) The effect of prolonged flooding on the bark of mangrove trees. Trees 22(1):77–86. https://doi.org/10.1007/s00468-007-0171-x

Zhu X, Chen J, Qiu K, Kuai B (2017) Phytohormone and light regulation of chlorophyll degradation. Front Plant Sci 8:1911

Chapter 17
Metabolomics Applied to Understand and Determine Ecological and Evolutionary Relationships, and Medicinal Potential of Plants from Pantanal

Vanessa Samúdio Santos-Zanuncio, Diomar Verçosa, Darlene Gris, Denise Brentan Silva, and Carlos Alexandre Carollo

17.1 Primary Metabolism and Secondary Plant Metabolism

Secondary metabolites, also known as natural products, are substances with biosynthesis that derives from products of primary metabolism, which are produced, accumulated, and transformed by plant enzymes, coenzymes, or organelles (Fig. 17.1) (Dewick 2002; Taiz and Zeiger 2004). Secondary metabolites originate from glucose metabolism, with two central intermediates, shikimic acid and acetate (Santos 2007; Taiz et al. 2017). Aromatic amino acids, such as tryptophan, phenylalanine/tyrosine, as well as cinnamic acid, are produced from the shikimic acid pathway, which are precursors for most of the secondary aromatic metabolites, such as coumarins and a large part of the alkaloids and tannins. However, among acetate derivatives (acetyl-CoA as a precursor), terpenoids, steroids, iridoids, and some alkaloids are yielded. Additionally, anthraquinones, flavonoids, and condensed tannins are derived from shikimate and acetate pathways (Fig. 17.1) (Santos 2007).

Differing from primary metabolites with basic and essential functions to preserve and conserve plant life, secondary metabolites can be restricted as elements of

---

V. S. Santos-Zanuncio · D. Verçosa · D. B. Silva · C. A. Carollo (✉)
Laboratório de Produtos Naturais e Espectrometria de Massas (LaPNEM), Faculdade de Ciências Farmacêuticas, Alimentos e Nutrição (FACFAN), Universidade Federal de Mato Grosso do Sul (UFMS), Campo Grande, MS, Brazil
e-mail: carlos.carollo@ufms.br

D. Gris
Laboratório de Produtos Naturais e Espectrometria de Massas (LaPNEM), Faculdade de Ciências Farmacêuticas, Alimentos e Nutrição (FACFAN), Universidade Federal de Mato Grosso do Sul (UFMS), Campo Grande, MS, Brazil

Grupo de Pesquisa em Ecologia Florestal – Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, AM, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_17

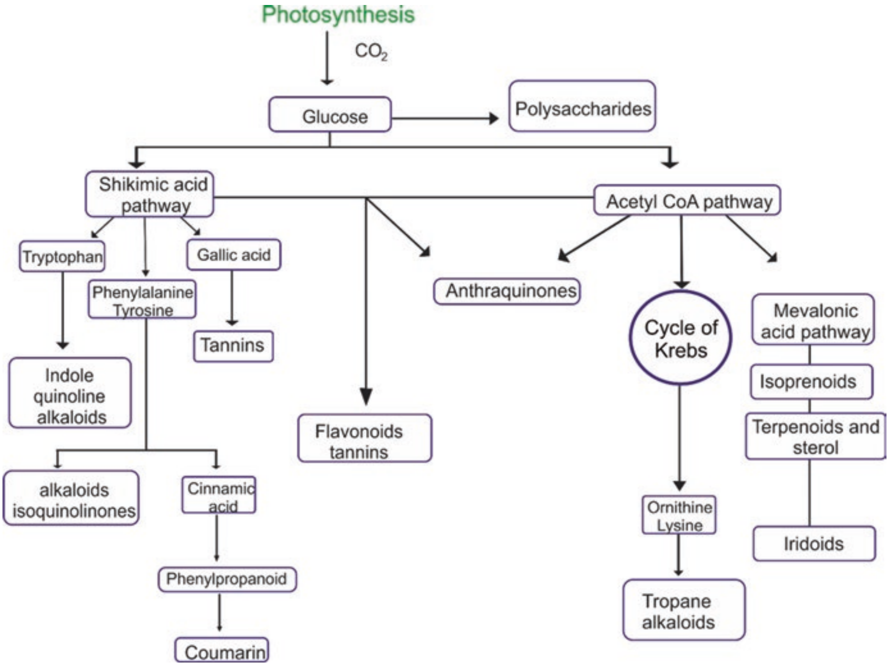


Fig. 17.1 Biosynthetic relationships between primary metabolism and some secondary metabolites. Adapted from Santos 2007

specialization in particular species or groups (Dewick 2002; Santos 2007; Taiz and Zeiger 2004; Raven et al. 2014). Sometimes, metabolic pathways of secondary metabolism appear to be activated only during certain phases of development or in response to stress, such as defense against herbivores (Mann 1987; Santos 2007).

Initially, the adaptive importance of secondary metabolites was unknown, as they were considered waste products of primary metabolism. Nowadays, secondary metabolites are known to participate in the growth and development of plants (Harborne 1996; Raven et al. 2014). These compounds play an important role in plant survival, propagation, protection against solar radiation, interaction with pollinators, pollen and seed dispersal, and especially in defense against pathogens and herbivores (Harborne 1996; Stevenson et al. 2017).

In addition, metabolites play an important role of chemical signaling in the communication between plants and the environment (Hebets and Papaj 2005; Brunetti et al. 2018). It is one of the most widespread and oldest modes of interaction between species or within the same species, representing the communication between the emitter (emission of one or more molecules) and the receiver (detects these molecules from chemical receptors), showing a complex network of connectivity in the biological organization (Dicke and Takken 2006; Meinwald and Eisner 2008; Dicke and Baldwin 2010; Wyatt 2014; Brunetti et al. 2018). Brunetti et al. (2018) present an intense review on the new tools and advances in studies of communication and chemical signals.

Consequently, variations in the composition and concentration of these compounds occur according to the plant species, stage of development, different defense needs, and environmental factors that plant populations are conditioned to (Raven et al. 2014).

The concentration and composition of secondary metabolites change between specimens since their biosynthesis is affected by the conditions of their surrounding environment (Kutchan 2001) and secondary metabolites appear to be involved in the communication and establishment of plants in the environment (Chacón et al. 2013). Considering that these metabolites represent the chemical response and communication between plants and their surrounding environment, biosynthesis is affected by environmental changes which induce plant adaptations. Thus, several factors, either separately or in combination, may qualitatively and quantitatively affect secondary metabolites (Bennett and Wallsgrove 1994; Gobbo-Neto and Lopes 2007; Behr et al. 2017; Ramakrishna and Ravishankar 2011). Some factors that influence the composition of secondary metabolites are seasonality and circadian rhythms, environmental temperature, floods, water and soil nutrient availability, UV radiation incidence, altitude and levels of air pollution, salinity, and oxygen availability (Bennett and Wallsgrove 1994; Gobbo-Neto and Lopes 2007; Behr et al. 2017; Ramakrishna and Ravishankar 2011).

Seasonality is one of the most influential factors for metabolites, since composition varies between seasons, throughout the year, and depending on the period of the day. Also, plants are usually adapted to specific ranges of temperature, altitude, and ultraviolet radiation. Thus, variations in these factors exert a strong influence on the development of these plants and secondary metabolites. Furthermore, plants have specific needs regarding water and nutrients, and changes in the availability of such factors, as well as the radiation incidence, promote changes in metabolic composition as a plant responds to biotic and abiotic stress (Gobbo-Neto and Lopes 2007) (Fig. 17.2).

The content of secondary metabolites may also vary depending on the developmental stage of a plant, with variations in the composition and concentration of metabolites between different tissues and stages (Suzuki et al. 2008). For example, in the initial phases of growth, a new plant is more vulnerable to attack by pathogens, such as insects and fungi, as well as water stress and other environmental factors. Thereby, the plant needs compounds to assist in the defense and maintenance of tissues in these early stages, while in the following stages, plants not only need to defend themselves but have to attract pollinators and disperse seeds and pollen, among other activities (Chacón et al. 2013; Raven et al. 2014).

Regarding variations between species, secondary metabolites may be specific and limited to only one species, genus, or family, and are frequently specialization subsidies for some groups (Dewick 2002; Santos 2007). This area of study, called chemotaxonomy or chemosystematics, may be another tool for plant systematics, which suggests that the content of secondary metabolites can be used to evaluate phylogenetic similarity and can clarify controversies and elucidate variations in secondary metabolism during evolution, complementing the use of reproductive

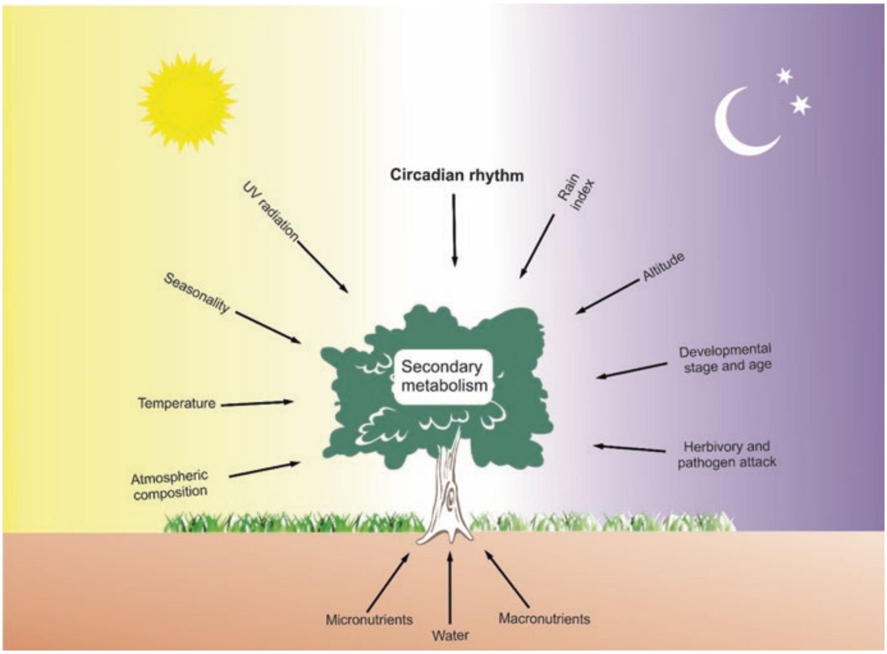


Fig. 17.2 Summary of factors that affect the composition of secondary metabolites in plants

and vegetative morphological characters when grouping plants (Pirani 2005; Liu et al. 2017).

The three main classes of secondary metabolites in plants are nitrogen compounds (alkaloids), terpenoids, and phenolic compounds (Taiz and Zeiger 2004; Raven et al. 2014). Alkaloids play a definite role in defense against biotic and abiotic stressors, mainly as repellents against herbivores and pathogens as fungi (Mithöfer et al. 2009; War et al. 2012; Matsuura and Fett-Neto 2015). For example, caffeine exhibits toxicity to both insects and fungi, and has inhibitory potential for the growth of competing plants, while nicotine, mainly synthesized in response to herbivore injury, repels mammal and insect attack (Raven et al. 2014). Terpenoids contribute to different actions in plants, i.e., carotenoids participate in pigmentation, abscisic acid and gibberellin are hormones, while saponins participate in defense against microorganisms, parasites, insects, and vertebrates (Osbourn 1996; Taiz and Zeiger 2004; Moses et al. 2014; Raven et al. 2014). Phenolic compounds include flavonoids, tannins, lignins, and salicylic acid, and are substances that accumulate in all plant parts, including roots, stems, flowers, leaves, and fruits, attracting pollinators and defending against pathogens and herbivores (Raven et al. 2014). For example, tannins present great potential as insect and vertebrate repellents (Taiz and Zeiger 2004), while flavonoids provide not only protection against herbivores, fungi, and drought but also influence the attraction of nitrogen-fixing bacteria (Grayer and Harborne 1994; Hungria and Stacey 1997; Tattini et al. 2004; War et al. 2012).

Many compounds produced by plants to maintain growth and development are used as natural products by humans. The pharmacological and medicinal use of natural products has been investigated since ancient Greece when the product of the in plants were already considered a promising source of bioactive compounds for humanity (Santos 2007; Pavarini et al. 2012). Currently, there is an increasing need for studies to elucidate and demonstrate the functions and biological and pharmacological effects of these natural products, as well as search for new compounds (Oksman-Caldenty and Inzé 2004; Santos 2007; Pavarini et al. 2012).

The pharmacological potential of several secondary metabolite classes, such as alkaloids, has been shown to benefits human health in various studies and has pharmacological and medicinal interest, mainly for physiological and psychological benefits. Alkaloids include compounds such as morphine, cocaine, caffeine, nicotine, and atropine, which present properties ranging from anesthetic to stimulant (Taiz and Zeiger 2004; Raven et al. 2014). Terpenoids, or terpenes, are the most abundant class of secondary metabolites. Monoterpenes and sesquiterpenes are common constituents in essential oils, which confer fragrance in plants and include menthol and menthone or taxol, which has anticancer properties (Raven et al. 2014). Moreover, phenolic compounds, such as salicylic acid, present broad pharmacological interest including antioxidant or analgesic properties (Raven et al. 2014).

Therefore, studies focused on the composition and variation of secondary metabolism in plants can help to clarify and establish the role of these substances in ecological (plant-plant and plant-environment) adaptive processes and evolutionary relationships, as well as in the search for new compounds and bioactive sources of pharmacological interest. Moreover, the Pantanal is a fascinating location for studying these relationships and interactions, since it is a diverse floodplain that presents exciting contrasts between environmental factors and vegetation, along with distinct phytophysiognomies with high species diversity (Damasceno-Junior and Pott 2011). Species structure, composition, and distribution of the vegetation of the Pantanal are strongly influenced by variations in the relief, topography, soil, and other factors that affect the periodical flooding and generate changes in the secondary metabolites of the plants (Campbell et al. 1992; Oliveira-Filho et al. 1994; Damasceno-Junior et al. 2005; Harborne 1996; Raven et al. 2014).

17.2 Metabolomics

In natural ecosystems, plants are exposed to biotic and abiotic factors that exert selective pressure and create new biosynthetic pathways throughout the process of plant evolution, which leads to the production of substances with an essential role in ecological interactions, designated as secondary metabolites (Cipollini et al. 2012). Metabolomics is an essential tool for monitoring these secondary metabolites; it is used to investigate variations in the chemical profile of species in response to several environmental factors and has gained popularity for qualitative and quantitative analysis of plant metabolomes (Fiehn 2002; Rodziewicz et al. 2014).

Several concepts of metabolomics have been cited in the literature, including the concept by Oliver et al. (1998), who emphasized the need to connect metabolomics and genomics to observe if the variation in metabolite concentration is related to the deletion or expression of a gene. According to Fiehn and collaborators (2000), metabolomics offers unique results that help clarify biological information, and, due to the importance of these studies for the plant, animal, or biological fluid samples, metabolomics studies have been intensifying (Wolfender et al. 2009; Jiang et al. 2010).

Metabolomics is part of the "omics" sciences: genomics (DNAs), transcriptomics (mRNAs), proteomics (proteins), and metabolomics (metabolites) (Agin et al. 2016), and is still considered a new field, emerging with great opportunities due to characterization capacity, genotype and phenotype differentiation based on metabolites, and monitoring of profile variation of these compounds (Verpoorte et al. 1999). Such determination of metabolites in a given system can be obtained through modern metabolomics tools, which are usually applied chromatographic techniques along with mass spectrometry to obtain data that is subsequently submitted to appropriate statistical analysis tools, including multivariate, and more recently the new challenger is to combine several omics strategies in a metadata profile (Aksenov et al. 2017).

Plant metabolomics help researchers understand several ecological interactions, including the interaction of plants with the environment, herbivores, and pathogens, as well as production and accumulation of specific metabolites in response to chemical, physical, and genotypic factors (Hall 2006; Wolfender et al. 2013). With the potential for worldwide expansion, metabolomics provides applicability and answers in experiments that incorporate several areas of research. Furthermore, metabolomics along with the other "omics" techniques can be used to form molecular networks which help to understand several complex biochemical processes (Lei et al. 2011; Yin and Xu 2014).

Metabolites are selected (targeted) by optimized extraction or specific separation and detection, and analysis only focuses on these substances. The selection of metabolites can be based on previous knowledge or can follow broad-scale metabolomics analyses. Different strategies are used in metabolomics analysis and can be divided into two categories known as targeted (directed) (Dudley et al. 2010) and untargeted analysis (not directed) (De Vos et al. 2007), with both categories presenting advantages and disadvantages. Targeted metabolomics consists focused analysis known of metabolites, where an analytical method is developed previously and optimize for them, including the sample preparation, and the method development. Therefore, prior knowledge of the chemical structure of the target metabolite is required for both analyses. Targeted analysis can be considered a quantitative approach, with main limitations being the need for prior knowledge about monitored compounds and a standard to compare and confirm compound identification or quantification. Such factor is limiting since some compounds have no standards in the purified form, and, consequently, a large number of compounds are unidentified in the analyzed samples (Shulaev 2006; Dudley et al. 2010).

The untargeted metabolomic approach can be fingerprinting or profiling, which consists of an analysis covering all the compounds found in a sample, including chemical compounds that do not necessarily need purified standards. Usually, the information obtained by the untargeted approach is treated using multivariate chemometric methods to reduce the extensive datasets generated from forming smaller datasets that facilitate interpretation. The significant challenge of this approach is the development of protocols, the time required for data acquisition and processing, and, consequently, more time spent on identification and characterization of compounds. However, untargeted metabolomics offers an additional advantage, the possibility of finding essential biomarkers for diagnostics and treatments, resulting in a more holistic approach (De Vos et al. 2007; Roberts et al. 2012). Due to the high chemical variety of the metabolome compounds, one single technique is insufficient and requires the combination of various techniques, even though these approaches are still not widely explored.

In recent years, using hyphenated techniques, such as liquid chromatography (LC) and gas chromatography (GC) coupled with mass spectrometry (MS), has led to better results. Other techniques, such as NMR and MS, are used in the nonselective analytical approach (Kuehnbaum and Britz-Mckibbin 2013). In Table 17.1, we show the essential characteristics of the most known and used techniques and their applications in metabolomics.

Among these techniques, LC-MS comes closest to the objectives of metabolomics, that is, it has a superior scope in detecting metabolites because it allows for the separation of compounds with a polarity range through isocratic elution (composition of the mobile phase does not vary during the chromatographic analysis) or gradient elution (composition of the mobile phase varies during the analysis) (Wolfender et al. 2013; Kuehnbaum and Britz-Mckibbin 2013).

For metabolomics analyses, sample preparation is a crucial step and requires prior investigation to verify that the steps taken will achieve the expected goal. The

Table 17.1 Principal analytical techniques applied in metabolomics studies

Analytical techniques	Characteristics	Metabolomic applications
No-hyphenated techniques		
NMR	Low sensitivity, high cost, usually coupled with a separation technique	Target(s) metabolite(s), metabolite profile (fingerprint), metabolomics and metabolite flow
MS	High sensitivity, high cost	Target(s) metabolite(s), metabolite profile, metabolic pattern (fingerprint), metabolomics and metabolite flow
Hyphenated techniques		
GC-MS	High sensitivity, volatile analytes, low cost	Target(s) metabolite(s) and metabolomics
LC-MS	High sensitivity, nonvolatile analytes, thermal unstable, high cost	Target(s) metabolite(s), metabolite profile (fingerprint)

sample preparation can be divided into four steps: harvesting, processing of the material (drying, spraying), extraction of the compounds of interest, and analytical preparation of the samples (Fig. 17.3) (Ernst et al. 2014). The need to carry out these four steps depends on the purpose of the study, the analytical method chosen, or the physical-chemical properties of the analytes monitored in the study.

After data acquisition, preprocessing is necessary to normalize and reduce the data before identification of compounds and statistical analysis. This preprocessing may be performed in the XCMS online (https://xcmsonline.scripps.edu/), which performs nonlinear alignment of time, automatic integration, extraction of peak intensities, and other relevant preprocessing so data can be used. Other software is

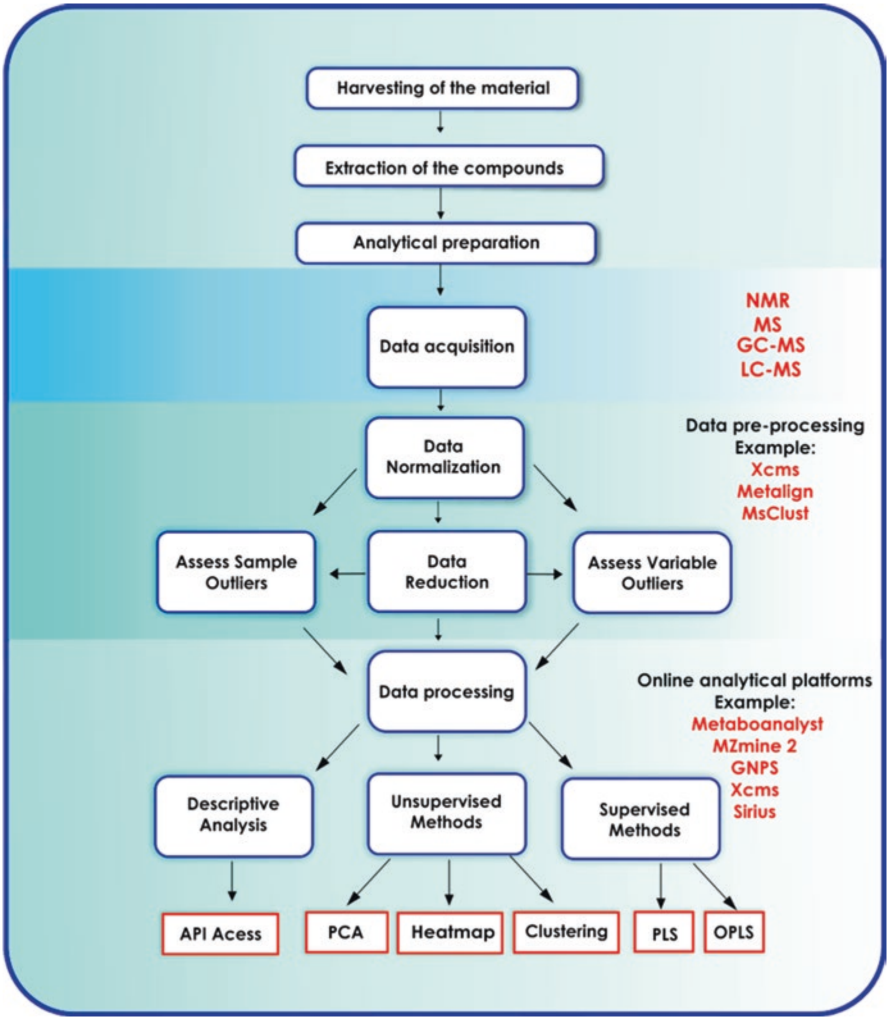


Fig. 17.3 Processing steps in metabolomics

used for preprocessing, as MZmine and MetAlign, and later the MSClust software can be used to reduce the data (Tikunov et al. 2012). The software MSClust has algorithms that can reduce the number of signals generated by the mass spectrometer, generated from molecular fragments, adducts, and isotopes, and this software can group the signals into presumably intact metabolites for subsequent identification of these compounds.

The increase in metabolomics research number with natural origin products has led to the inevitable adjustment of advanced techniques for the analysis of chemical profile of plants, microorganisms, and animals, as well as the creation of databases for the storage of information about the compounds. Currently, important bases are found on open access platforms (Table 17.2), and these databases have virtual screening of natural compounds and can aid in their use (Clark et al. 2010).

The GNPS (Global Natural Products Social Molecular Networking) is a free database, nowadays considered as a natural products global network; it is responsible

Table 17.2 Natural plant product databases, number of entries, references, and links for access

Database	Information	References
NPCARE	Compounds and fractions of extracts	Choi et al. (2017)
Super Natural II	Structures 2D	Banerjee et al. (2014)
NuBBE	Compounds of Brazilian sources	Valli et al. (2013)
TCM	Structures 3D	Xie et al. (2015)
NANPDB (Northern African Natural Products Database)	–	Ntie-Kang et al. (2017)
SuperToxic	Demonstrates the risk of use of compounds	Xie et al. (2015)
3DMET	Structures 3D	Xie et al. (2015)
ConMedNP	Structures 3D	Ntie-Kang et al. (2014)
AfroDb	Structures 3D	Ntie-Kang et al. (2013)
SANCDB	–	Hatherley et al. (2015)
DDP (Drug Discovery Portal)	Structures 2D and 3D	Clark et al. (2010)
GNPS (Global Natural Products Social Molecular Networking)		Wang et al. (2016)
NPACT		Mangal et al. (2012)
Universal Natural Product Database	Structures 3D	Gu et al. (2013)
Drug Discovery Portal	Natural products and synthesized	Clark et al. (2010)
TCMID	Traditional Chinese medicine	Xue et al. (2012)
CVDHD (cardiovascular disease herbal database)	Structures 3D	Gu et al. (2013)

for analyzing, navigating, and combining large datasets, performing the comparison with your spectral database (Watrous et al. 2012).

The results available are given in order to present a molecular network and emerged as a tool to integrate similar elements of proteomic data (Watrous et al. 2012). In addition, the molecular network has been applied in metabolomics studies, using MS/MS fragmentation data and gathering classes of metabolites with similar spectral profile (Watrous et al. 2012; Yang et al. 2013).

After preprocessing the data, different mathematical and statistical methods can be applied to the chemical data, including principal component analysis (PCA) and hierarchical grouping analysis (HCA), which are unsupervised multivariate analyses to recognize patterns and trends generated by chemical data and non-direct groupings of the sample set used, while partial least squares (PLS) and its orthogonal variant known as OPLS are supervised multivariate analyses because the data generated by the cluster follows a previously reported trend (a targeting) for the analysis. Therefore, according to Rencher (2002), both PCA and PLS are techniques used for dimensionality reduction.

Metabolomics studies generate a massive amount of data to be treated with several statistical analyses, such as multivariate analyses to facilitate the interpretation of these large datasets. The identification of compounds takes a long time, and depending on the study, is required. Compound identification can be performed using online data banks (for electrospray ionization (ESI)-MS) and libraries (electron ionization (EI)-MS) when available or manually by comparing UV signals or mass spectra with library reference for electrospray ionization mass spectrometry (ESI-MS), which takes much longer.

Plant metabolomics has been widely utilized in chemosystematics, which emerged in the 1970s to help taxonomic classification (Wink et al. 2010). This survey of the chemical profile of plants offers much information to phytochemists, pharmacists, botanists, and taxonomists since chemosystematics is used to uncover biosynthetic pathways of isolated natural products, which may be useful in explaining uncertain taxa positions and phylogenetic trends (Sampaio-Santos et al. 1995). Moreover, metabolomics can be applied to chemical profiling for several plant groups and can establish and help determine new bioactive compounds.

17.3 Application of Metabolomics in the Pantanal

The presence of monodominant patches is a peculiarity in the Pantanal and generates exceptional interest among researchers to understand the possible causes of such a phenomenon. Therefore, several studies were developed to address aspects of composition and floristic structure of these monodominant formations (Arieira and Nunes Da Cunha 2006; Amador et al. 2012; Bueno et al. 2014). Only in the past few years have studies investigated the composition and variation of secondary metabolites of Pantanal species using metabolomics techniques. Studying these aspects can help understand and establish the ecological role of these substances and set the precedent of searching for bioactive compounds. The variation in composition and concentration of secondary metabolites may be related to plant defense against herbivorous and pathogen attack or may even occur as a form of adaptation to the different environmental factors that different plant populations experience. Herein, we discuss recent studies that apply metabolomics techniques.

The first monodominant formation (Chap. 8) in the Pantanal to be studied was the "paratudal," which consists of the predominant species *Tabebuia aurea* (Bignoniaceae) (Fig. 17.4) and is one of the most extensive formations in the Pantanal (Soares and Oliveira 2009; Bueno et al. 2014). *Tabebuia aurea* has wide geographic distribution in the tropical and subtropical regions of the American continent (Pott and Pott 1994; Lorenzi and Matos 2008). This tree species is widely used for ornamental purposes due to the exuberant beauty of its yellow flowers, along with its medicinal potential to treat various diseases (Lorenzi and Matos 2008). For a long time, *T. aurea* was used by Brazilian Indians, and currently, human residents of the Pantanal chew its bark in the field to aid stomach and liver diseases, anemia, worms, and diabetes (Pott and Pott 1994).

When it comes to chemicals in the iridoid class, *Tabebuia* is the most abundant representative of this compost class within Bignoniaceae (Von Poser et al. 2000). These compounds are essential mediators for interactions between plants and herbivores, acting as toxins and deterrents of several generalist herbivores. However, specialist herbivores use these compounds as clues for food and oviposition (Kelly and Bowers 2016). Iridoid compounds can be sequestered by specialist herbivores who use them for their defense (Jamieson and Bowers 2010). Furthermore, these compounds present several biological activities (Villasenor 2007; Viljoen et al. 2012). The barks of some *Tabebuia* species present large amounts of lapachol, a

Fig. 17.4 Monodominant formation of *Tabebuia aurea* "paratudal"

naphthoquinone recognized for its various biological activities, such as antineoplastic, anti-inflammatory, trypanocidal, leishmanicidal, antimicrobial, antifungal, analgesic, antimalarial, and insecticide effects (De Moura et al. 2001; Barbosa-Filho et al. 2004; Hussain et al. 2007).

Verçosa et al. (2020) studied the variation of *T. aurea* secondary metabolites among individuals located at the edge and center of a formation during dry and flood periods in the Pantanal. In this study, metabolomics target analysis was performed using liquid chromatography techniques. The chromatographic profile of the stem bark presented a main compound, which was used to quantify and monitor the variation. When comparing the NMR and MS data with the literature, Verçosa determined the compound was specioside, a glycoside iridoid that was isolated for the first time from leaves of *Catalpa speciosa* Warder (Bignoniaceae) by El-Naggar and Doskotch (1980).

This study demonstrated that flooding affected the concentration of metabolites in the monodominant formation, with individuals located at the edge presenting a lower concentration of specioside during the flood period. Therefore, plants at higher sites had higher concentrations of metabolites during the flood period due to lower stress caused by flooding. Also, they observed higher concentrations of specioside in the stem bark compared to leaves, which explains why residents in the Pantanal use stem bark for various diseases. This study indicates that plants located in higher regions favor higher concentrations of metabolites.

Although the literature reports the presence of lapachol in *T. aurea* (Barbosa-Filho et al. 2004), Verçosa did not find it in extracts of the stem bark and leaves sampled. To eliminate the possibility of an inadequate method for detecting this substance, injections of authentic lapachol pattern and extracts of *T. impetiginosa*, which produces lapachol in great quantity, were used. Therefore, we verified that the method of extraction and analysis in HPLC-DAD is sensitive for this compound, which was verified in phytochemical studies carried out by Guerbas Neto (2003).

17.4 The Role of Metabolomics in Chemosystematics of Pantanal Species

Due to high complexity, species classification is an arduous task for systematists. Even though there have been significant advances in separation techniques in recent years, there is still a high demand for the development and application of new techniques. Recently, there has been a reorganization of some species between the genera *Tabebuia* and *Handroanthus,* a genus that presents some controversial classification. In this sense, Santos et al. (2017) tested the efficiency of metabolomics techniques as a tool for identifying genera and species by comparing the chemical profile of species with taxonomic classification and molecular phylogeny. The objective of this study was to use metabolomics to solve controversies of taxonomic classification between the genera *Tabebuia* and *Handroanthus*. For this, Santos et al. analyzed stem bark from seven species of *Tabebuia* s.l., four *Handroanthus* and three *Tabebuia s. str.* species (Grose and Olmstead 2007; Gentry 1992). Analyses were carried out in HPLC-DAD-MS/MS, and data was processed, aligned, and statistically evaluated using multivariate statistical analysis.

Santos et al. characterized 23 compounds of high relevance distributed in four classes of metabolites: iridoids, phenylpropanoids, benzoic acid derivatives, and lignans for the taxonomic separation of the genera. They found unique compounds for each genus and some compounds in both genera: seven exclusive compounds for *Handroanthus*, six compounds for *Tabebuia*, and ten compounds in both genera. These findings indicate that the chemical composition is relevant for classification of species among genera since species showed a different set of compounds that can be applied for chemosystematics.

Some compounds occur in both genera, although their storage capacity was different (Fig. 17.5). Higher amounts of compounds as quinic acid (1), verbascoside (4), 10-*O*-benzoyl-scandoside (5), and 6-*O*-(4-hydroxybenzoyl) ajugol (3) were found in species of *Handroanthus*, while higher amounts of the compounds specioside (6), verminoside (2), and minecoside (7) occur in species of *Tabebuia*. These results agree with the study by Verçosa et al. (2020), who found a high concentration of specioside in stem bark of *T. aurea*. High storage of iridoids has significant implications for plant performance since these compounds are effective defenders of plants against herbivores and pathogens. Furthermore, these results reveal the potential of Pantanal species for the discovery of new bioactive compounds, and those species seem a promising source for bioactive compounds in high concentrations.

Besides *Tabebuia* and *Handroanthus*, metabolomics was applied to clarify species classification in the genus *Byrsonima* (Malpighiaceae). Species of this genus occur in monodominant formations and cover extensive areas of the Pantanal, i.e.,

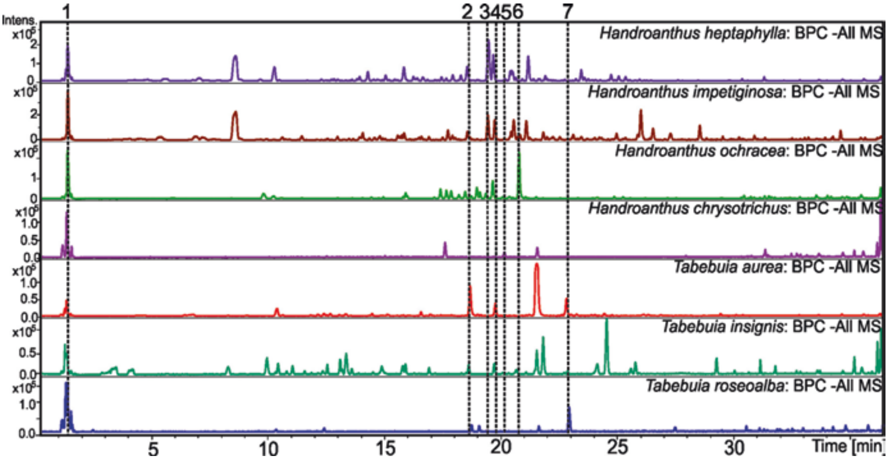


Fig. 17.5 Chromatogram of four *Handroanthus* and three *Tabebuia* species studied

Byrsonima cydoniifolia also known as "canjiqueirais" (Fig. 17.6) (Pott and Pott 1994). Santos Zanuncio. (2020) evaluated the metabolite profiles of *Byrsonima* species from the subgenus *Byrsonima* and *Macrozeugma* Nied., a group of plants considered natural, by applying metabolomics in the systematics of the group and relating chemosystematics with phylogenetic classification and morphological characters. In this study, stem bark fragments of 42 specimens of 15 *Byrsonima* species were analyzed in HPLC-DAD-MS/MS, and the data was processed, aligned, and statistically evaluated using multivariate analysis.

The application of several metabolomics techniques led to the characterization of 37 compounds, with mostly flavonoids. Both the genus *Byrsonima* and the subgenera

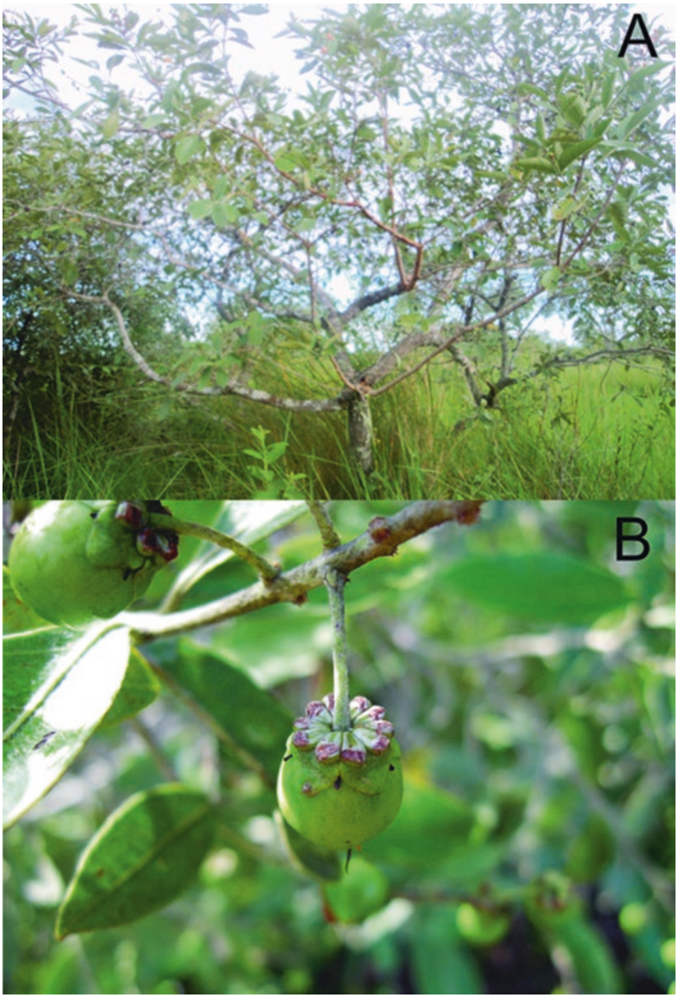


Fig. 17.6 (**a**) Monodominant formation of *Byrsonima cydoniifolia* – canjiqueirais. (**b**) Fruit of *Byrsonima cydoniifolia*

Byrsonima and *Macrozeugma* presented high similarity of the chemical profile, showing very conserved metabolites for these subgenera and no different compounds among the species' metabolic profiles, which included flavan-3-ol and proanthocyanidins. The chemical homogeneity from branches of *Byrsonima* observed in Santos et al. (2017) indicates that the primary clades of this genus have diversified in a short time. Consequently, these species have diversified in the Cerrado and have not chemically diversified yet (Fig. 17.7). These studies performed with *Tabebuia* and *Byrsonima* demonstrate that metabolomics techniques are useful tools for solving issues in chemotaxonomic studies (Santos et al. 2017, Santos-Zanuncio et al. 2020).

17.4.1 Effects of Environmental Factors on the Concentration of Secondary Metabolites in Early Development Stages

In the Pantanal, plants are subject to flooding and sporadic fire events, which can be determinant factors for the establishment of new plants, particularly in their initial and most vulnerable phases of development (Chacón et al. 2013). As a biological response, the composition of secondary metabolites may vary depending on the plant's needs in different developmental phases or in different tissues (Suzuki et al. 2008). For example, in a recent study, Gris (2017) applied metabolomics techniques to understand how plants respond to stress caused by fire and flooding in the early stages of development and how the secondary metabolite composition varies in these stages of *Erythrina fusca* (Fig. 17.8). *E. fusca* naturally occurs in riparian forests (Russo and Baguinon 1997) and also forms monodominant formations in parts of the Pantanal, representing approximately 77% of all the arboreal individuals (Gris 2017).

Gris (2017) analyzed extracts from seeds and seedlings submitted to simulated flooding and fire conditions using an HPLC-DAD-MS/MS, and the data was processed, aligned, and statistically evaluated using multivariate analysis. Gris (2017) characterized 55 metabolites, belonging to four classes of compounds: erythrinian alkaloids, triterpene saponins, flavonoids (flavone, isoflavone, flavonol, and pterocarpan), and amino acid derivatives. There was a clear separation between the metabolic profile of seeds and seedlings of *E. fusca* (Fig. 17.9), where the first axis (PC 1) explained 85.1% of the variation. The translocation of some compounds from seeds to seedlings was also detected, while some compounds were found exclusively in seedlings. When seeds and seedlings were exposed to flood and fire stress factors, isoflavones and alkaloids, defense-related compounds, increased. The study by Gris (2017) suggests that plants invest in the production and accumulation of defense metabolites, such as alkaloids, in the early stages of development, mainly when subjected to stress factors.

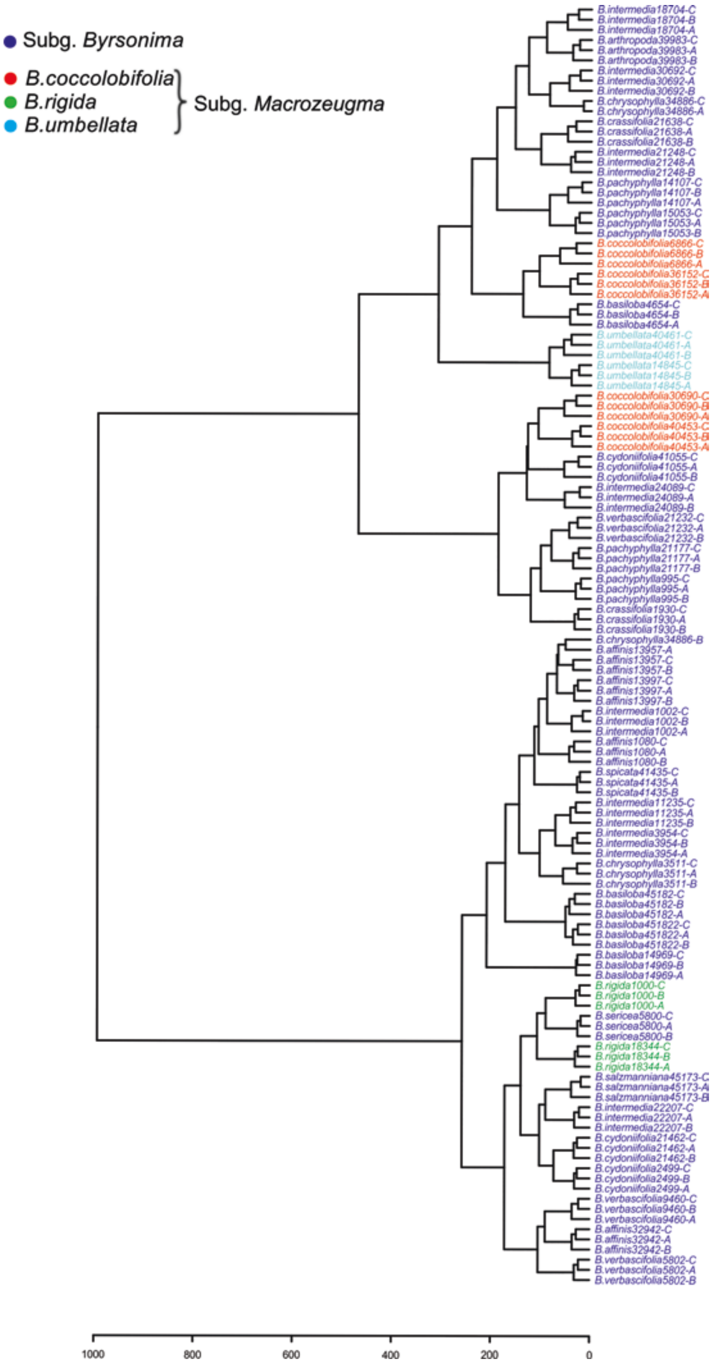


Fig. 17.7 Dendrogram of *Byrsonima* species subgenus *Byrsonima* and subgenus *Macrozeugma*

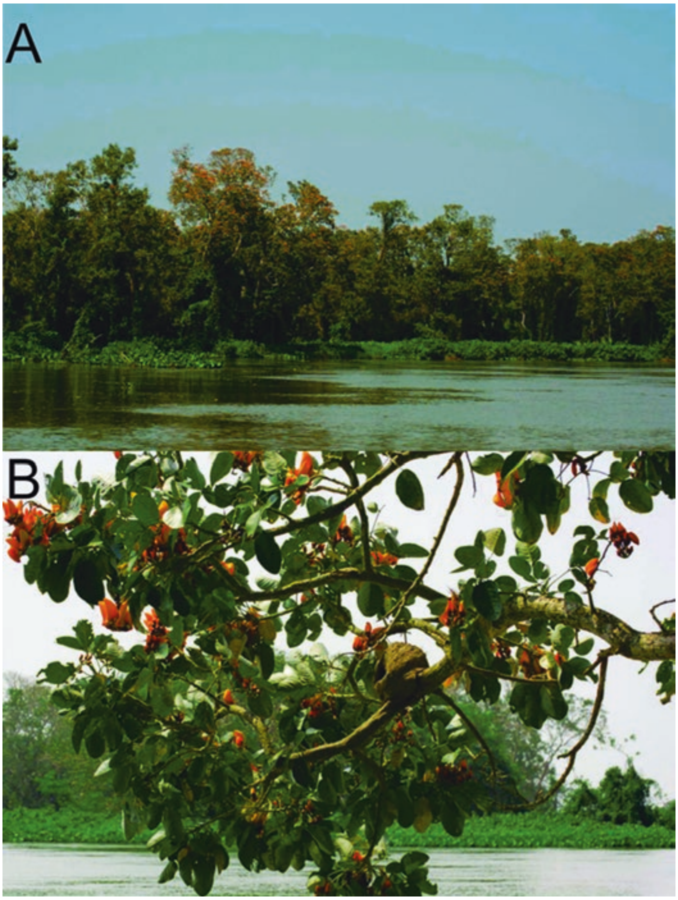


Fig. 17.8 (**a**) Monodominant stand of *Erythrina fusca* (tree in the photo). (**b**) Flowering *E. fusca* on Taimã Ecological Station, Cáceres, Mato Grosso, Brazil

17.4.2 Biological Activities and Nutraceutical Potential of Fruits

The Pantanal harbors plant families that are used by humans as food and medicine. Previous studies have investigated the bioactivities of plant extracts from the Pantanal, including extracts from *Tabebuia aurea* (a species responsible for the "paratudal" monodominant formation) stem bark. Based on reports of the widespread use of *T. aurea* to treat the effects of snakebites, Reis et al. (2014) evaluated the effects of hydroethanolic extracts of *T. aurea* stem bark on mice injected with *Bothrops neuwiedi* snake venom. They observed that the hydroethanolic extract inhibited edema in mice, indicating anti-inflammatory, antihemorrhagic, and antimyotoxic activities. Evidence of this magnitude not only supports the use of

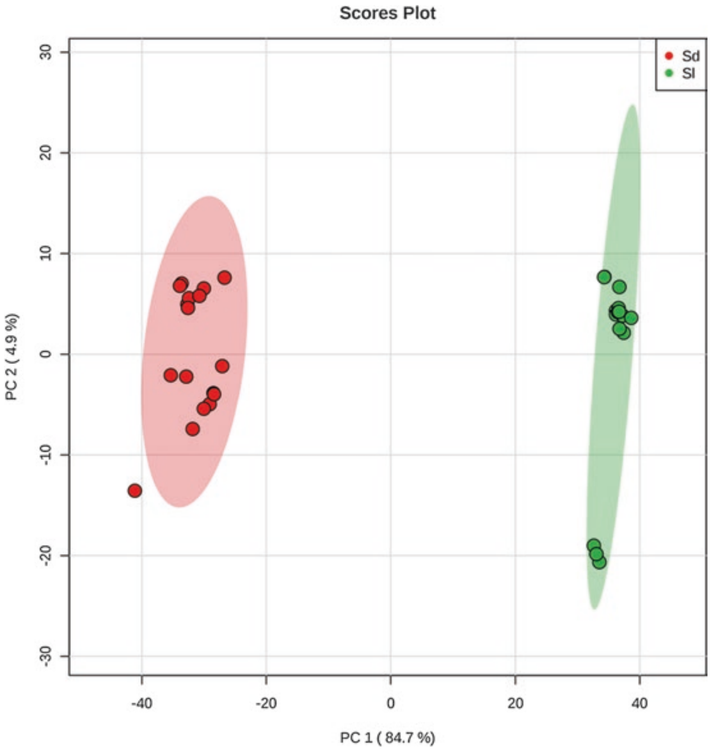


Fig. 17.9 The principal component analysis (PCA) of metabolites from seedlings (Sl=green) and seeds (Sd=red) of *Erythrina fusca* subjected to flooding and fire stress factors

T. aurea extract in popular medicine against snakebite but also opens a range of future research in the Pantanal.

Besides Bignoniaceae, the family Malpighiaceae presents several genera with nutraceutical fruits, such as *Byrsonima* sp., whose fruits are known as "murici" with potential commercialization throughout Brazil (Guilhon-Simplicio and Pereira 2011). The term nutraceutical comes from the junction of nutritional and pharmaceutical, in other words, fruits that have nutritional properties and chemical compounds that generate health benefits, i.e., antioxidant and anti-inflammatory (Espín et al. 2007). There are few studies related to the fruit of *Byrsonima* species, even though they have several commercial and medicinal uses. In general, most studies focus on the leaves of plants from this genus, with anti-inflammatory activities reported in several studies of *B. intermedia* and *B. verbascifolia* (Moreira et al. 2011; Saldanha et al. 2016), antimicrobial activities for *B. fagifolia, B. basiloba* and *B. intermedia,* (Michelin et al. 2008), and antiulcerogenic activities for *B. crassa* (Sannomiya et al. 2005).

Byrsonima cydoniifolia constitutes another monodominant formation in the Pantanal, and Santos et al. (2017) revealed that the hydroethanolic extract of *B. cydoniifolia* fruits shows anti-inflammatory and antihyperalgesic activity. The chemical profile of *B. cydoniifolia* fruits analyzed by HPLC-DAD-MS/MS indicates flavonoids and stilbene derivatives, such as trans-piceatannol and resveratrol, as the main secondary metabolites. In the study about the anti-inflammatory and antihyperalgesic properties of the fruit of *B. cydoniifolia*, carried out on mice, the hydroethanolic extract of the fruit reduced edema and migration of polymorphonuclear cells into the peritoneal cavity and decreased abdominal torsions. For the first time, the presence of stilbenoids was reported for the genus *Byrsonima* and demonstrated the anti-inflammatory and antihyperalgesic effect of *B. cydoniifolia* fruits, supporting its use as a nutraceutical food (Santos et al. 2017).

Studies of this magnitude highlight the importance of studying the variation of secondary metabolites in Pantanal species.

17.4.3 Future Perspectives

The recent studies mentioned in this chapter show significant advances in research related to the metabolomic profiles of Pantanal species. In this context, future research can investigate the composition and concentration of secondary metabolites from other important medicinal species in high and low regions that are subject to different flooding regimes to demonstrate how these factors may or may not change the chemical characteristics of these species. Furthermore, few studies have correlated herbivory rates with variations in secondary metabolites of wetland plants or how herbivores respond to periods of drought and flood. Therefore, studies focused on the composition and concentration of secondary metabolites of Pantanal plants and comparisons to studies carried out with these species in other biomes are needed to verify if the environmental peculiarities of the Pantanal influence the secondary metabolite composition of such species.

References

Agin A, Heintz D, Ruhland E, Chao de la Barca JM, Zumsteg J, Moal V, Gauchez AS, Namer IJ (2016) Metabolomics – an overview. From basic principles to potential biomarkers (part 1). Méd Nucl 40:4–10

Aksenov AA, da Silva R, Knight R, Lopes NP, Dorrestein PC (2017) Global chemical analysis of biology by mass spectrometry. Nat Rev Chem 1:0054

Amador GA, Damasceno-Júnior GA, Casagrande JC, Sartori ALB (2012) Structure of two communities dominated by *Copernicia Alba* and associations with soil and inundation in Pantanal Wetland, Brazil. Oecol Aust 16:846–858

Arieira J, Nunes da Cunha C (2006) Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae), no Pantanal Norte, MT, Brasil. Acta Bot Bras 20:569–580

Banerjee P, Erehman J, Gohlke BO, Wilhelm T, Preissner R, Dunkel M (2014) Super Natural II – a database of natural products. Nucleic Acids Res 43:D935–D939

Barbosa-Filho JM, Lima CSA, Amorim ELC, Sena KXFR, Almeida JRGS, Da Cunha EVL, Silva MS, De Fatima M, Braz-Filho R (2004) Botanical study, phytochemistry and antimicrobial activity of *Tabebuia aurea*. Phyton 53:221–228

Behr JH, Bouchereau A, Berardocco S, Seal CE, Flowers TJ, Zörb C (2017) Metabolic and physiological adjustment of *Suaeda maritima* to combined salinity and hypoxia. An Bot 119:965–976

Bennett RN, Wallsgrove RM (1994) Secondary metabolites in plant defence mechanisms. New Phytol 127:617–633

Brunetti AE, Carnevale Neto F, Vera MC, Taboada C, Pavarini DP, Bauermeister A, Lopes NP (2018) An integrative omics perspective for the analysis of chemical signals in ecological interactions. Chem Soc Rev 47:1574–1591

Bueno ML, Damasceno-Junior GA, Pott A, Pontara V, Seleme EP, Fava WS, Salomão AKD, Ratter JA (2014) Structure of arboreal and herbaceous strata in a neotropical seasonally flooded monodominant savanna of *Tabebuia aurea*. Braz J Biol 74:325–337

Campbell DG, Stone JL, Rosas A Jr (1992) A comparison of the phytosociology and dynamics of three floodplain (Várzea) forests of known ages, rio Juruá, western Brazilian Amazon. Bot J Linn Soc 108:213–237

Chacón IDLC, Riley-Saldaña CA, González-Esquinca AR (2013) Secondary metabolites during early development in plants. Phytochem Rev 12:47–64

Choi H, Cho SY, Pak HJ, Kim Y, Choi JY, Lee YJ et al (2017) NPCARE: database of natural products and fractional extracts for cancer regulation. J Cheminform 9:2

Cipollini D, Rigsby CM, Barto EK (2012) Microbes as targets and mediators of allelopathy in plants. J Chem Ecol 38:714–727

Clark RL, Johnston BF, Mackay SP, Breslin CJ, Robertson MN, Harvey AL (2010) The Drug Discovery Portal: a resource to enhance drug discovery from academia. Drug Discov Today 15:679–683

Damasceno-Junior GA, Pott A (2011) Métodos de amostragem em estudos fitossociológicos sugeridos para o Pantanal. In: Felfili JM, Eisenlohr PV, Melo MMRF, Andrade LA, Meira Neto JAA (eds) Fitossociologia no Brasil-Métodos e estudos de casos, vol 1. Editora UFV, Viçosa, pp 213–230

Damasceno-Junior GA, Semir J, Santos FAM, Leitão-Filho HF (2005) Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200:119–135

De Moura KCG, Emery FS, Neves-Pinto C, Pinto MDFR, Dantas AP, Salomao K, De Castro SL, Pinto AV (2001) Trypanocidal activity of isolated naphthoquinones from *Tabebuia* and some heterocyclic derivatives: A review from an interdisciplinary study. J Braz Chem Soc 12:325–338

De Vos RCH, Moco S, Lommen A, Keurentjes JJB, Bino RJ, Hall RD (2007) Untargeted large-scale plant metabolomics using liquid chromatography coupled to mass spectrometry. Nat Protoc 2:778–791

Dewick PM (2002) Medicinal natural products: a biosynthetic approach, 2nd edn. Wiley, Nottingham

Dicke M, Baldwin IT (2010) The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help'. Trends Plant Sci 15:167–175

Dicke M, Takken W (2006) Chemical ecology: from gene to ecosystem. Springer, Berlin

Dudley E, Yousef M, Wang Y, Griffiths WJ (2010) Targeted metabolomics and mass spectrometry. Adv Protein Chem Struct Biol 80:45–83

El-Naggar SF, Doskotch RW (1980) Specioside – a new iridoid glycoside from *Catalpa-speciosa*. J Nat Prod 43:524–526

Ernst M, Silva DB, Silva RR, Vêncio RZ, Lopes NP (2014) Mass spectrometry in plant metabolomics strategies: from analytical platforms to data acquisition and processing. Nat Prod Rep 31:784–806

Espín JC, García-Conesa MT, Tomás-Barberán FA (2007) Nutraceuticals: facts and fiction. Phytochem 68:2986–3008

Fiehn O (2002) Metabolomics – the link between genotypes and phenotypes. Plant Mol Biol 48:155–171

Fiehn O, Kopka J, Dörmann P, Altmann T, Trethewey RN, Willmitzer L (2000) Metabolite profiling for plant functional genomics. Nat Biotechnol 18:1157–1161

Gentry AH (1992) Bignoniaceae: Part II (Tribe Tecomeae). Flora Neotrop 25:1–370

Gobbo-Neto L, Lopes NP (2007) Plantas medicinais: fatores de influência no conteúdo de metabólitos secundários. Quim Nova 30:374–381

Grayer RJ, Harborne JB (1994) A survey of antifungal compounds from higher plants, 1982-1993. Phytochem 37:19–42

Grose SO, Olmstead RG (2007) Evolution of a charismatic neotropical clade: Molecular phylogeny of *Tabebuia* s.l., *Crescentieae*, and allied genera (Bignoniaceae). Syst Bot 32:650–659

Gu J, Gui Y, Chen L, Yuan G, Lu HZ, Xu X (2013) Use of natural products as chemical library for drug discovery and network pharmacology. PloS One 8:e62839

Guerbas Neto P (2003) Estudo químico da casca, folhas e cerne de um espécime de *Tabebuia aurea* (Bignoniaceae) coletado no Pantanal. Dissertação de Mestrado, Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul

Guilhon-Simplicio F, Pereira MM (2011) Aspectos químicos e farmacológicos de *Byrsonima* (Malpighiaceae). Quim Nova 34:1032–1041

Gris D (2017) Monodominance of Erythrina fusca Lour.: influence of environmental factors, chemical ecology and dendroecology. Tese de doutorado. Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul

Hall RD (2006) Plant metabolomics: from holistic hope, to hype, to hot topic. New Phytol 169:453–468

Harborne JB (1996) Plant secondary metabolism. In: Crawley MJ (ed) Plant ecology, 2nd edn. Blackwell Publishing, Oxford, pp 132–155

Hatherley R, Brown DK, Musyoka TM, Penkler DL, Faya N, Lobb KA, Bishop ÖT (2015) SANCDB: a South African natural compound database. J Cheminform 7:29

Hebets EA, Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol 57:197–214

Hungria M, Stacey G (1997) Molecular signals exchanged between host plants and rhizobia: Basic aspects and potential application in agriculture. Soil Biol Biochem 29:819–830

Hussain H, Krohn K, Ahmad VU, Miana GA, Green IR (2007) Lapachol: an overview. Arkivoc 2:145–171

Jamieson MA, Bowers MD (2010) Iridoid Glycoside Variation in the Invasive Plant Dalmatian Toadflax, *Linaria dalmatica* (Plantaginaceae), and Sequestration by the Biological Control Agent, *Calophasia lunula*. J Chem Ecol 36:70–79

Jiang Y, David B, Tu P, Barbin Y (2010) Recent analytical approaches in quality control of traditional Chinese medicines – a review. Anal Chim Acta 657:9–18

Kelly CA, Bowers MD (2016) Preference and performance of generalist and specialist herbivores on chemically defended host plants. Ecol Entomol 4:308–316

Kuehnbaum NL, Britz-Mckibbin P (2013) New advances in separation science for metabolomics: resolving chemical diversity in a post-genomic era. Chem Rev 113:2437–2468

Kutchan TM (2001) Ecological Arsenal and developmental dispatcher. The paradigm of secondary metabolism. Plant Physiol 125:58–60

Lei ZH, David V, Sumner LW (2011) Mass spectrometry strategies in metabolomics. J Biol Chem 286:25435–25442

Liu K, Abdullah AA, Huang M, Nishioka T, Altaf-Ul-Amin M, Kanaya S (2017) Novel approach to classify plants based on metabolite-content similarity. BioMed Res Int

Lorenzi H, Matos FJDA (2008) Plantas medicinais no Brasil: nativas e exóticas, 2nd edn. Inst Plantarum, Nova Odessa, SP

Mangal M, Sagar P, Singh H, Raghava GP, Agarwal SM (2012) NPACT: naturally occurring plant-based anti-cancer compound-activity-target database. Nucleic Acids Res 41:D1124–D1129

Mann J (1987) Secondary metabolism, 2nd edn. Oxford University Press, Oxford

Matsuura HN, Fett-Neto AG (2015) Plant alkaloids: main features, toxicity and mechanisms of action. In: Gopalakrishnakone P, Carlini CR, Ligabue-Braun R (eds) Plant toxins. Springer, Dordrecht, pp 1–15

Meinwald J, Eisner T (2008) Chemical ecology in retrospect and prospect. Proc Natl Acad Sci 105:4539–4540

Michelin DC, Sannomiya M, Figueiredo ME, Rinaldo D, dos Santos LC, Souza-Brito ARM, Vilegas W, Salgado HRN (2008) Antimicrobial activity of *Byrsonima* species (Malpighiaceae). Rev Bras Farm 18:690–695

Mithöfer A, Boland W, Maffei ME (2009) Chemical ecology of plant-insect interactions. In: Parker J (ed) Annual plant reviews: molecular aspects of plant disease resistance. Wiley-Blackwell, Chichester, pp 261–291

Moreira LQ, Vilela FC, Orlandi L, Dias DF, Santos AL, Da Silva MA, Paiva R, Alves-da-Silva G, Giusti-Paiva A (2011) Anti-inflammatory effect of extract and fractions from the leaves of *Byrsonima intermedia* A. Juss. in rats. J Ethnopharmacol 138:610–615

Moses T, Papadopoulou KK, Osbourn A (2014) Metabolic and functional diversity of saponins, biosynthetic intermediates and semi-synthetic derivatives. Crit Rev Biochem Mol Biol 49:439–462

Ntie-Kang F, Telukunta KK, Döring K, Simoben CV, Moumbock AF, Malange YI et al (2017) NANPDB: a resource for natural products from Northern African sources. J Nat Prod 80:2067–2076

Ntie-Kang F., Zofou D, Babiaka SB, Meudom R, Scharfe M, Lifongo LL, ... Efange SM (2013) AfroDb: a select highly potent and diverse natural product library from African medicinal plants. PloS one, 8(10), e78085

Ntie-Kang F, Onguéné PA, Scharfe M, Owono LCO, Megnassan E, Mbaze LMA, ... Efange S M (2014) ConMedNP: a natural product library from Central African medicinal plants for drug discovery. Rsc Advances, 4(1), 409–419

Oksman-Caldentey KM, Inzé D (2004) Plant cell factories in the post-genomic era: new ways to produce designer secondary metabolites. Trends Plant Sci 9:433–440

Oliveira-Filho AT, Vilela EA, Gavilanes ML, Carvalho DA (1994) Effect of flooding regime and understorey bamboos on the physiognomy and tree species composition of a tropical semideciduous forest in southeastern Brazil. Vegetatio 113:99–124

Oliver SG, Wilson MK, Kell DB, Baganz F (1998) Systematic functional analysis of the yeast genome. Focus 16:373–378

Osbourn A (1996) Saponins and plant defence – a soap story. Trends Plant Sci 1:4–9

Pavarini DP, Silva DB, Carollo CA, Portella AP, Latansio-Aidar SR, Cavalin PO, Oliveira VC, Rosado BHP, Aidar MPM, Bolzani VS, Lopes NP, Joly CA (2012) Application of MALDI-MS analysis of Rainforest chemodiversity: a keystone for biodiversity conservation and sustainable use. J Mass Spectrom 47:1482–1485

Pirani JR (2005) Sistemática: tendências e desenvolvimento, incluindo impedimentos para o avanço do conhecimento na área. www.cgee.org.br/atividades/redirect/1678. Accessed 2018 July

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa – Centro de Pesquisa Agropecuária, Corumbá-MS

Ramakrishna A, Ravishankar GA (2011) Influence of abiotic stress signals on secondary metabolites in plants. Plant Signal Behav 6:1720–1731

Raven PH, Evert RF, Eichhorn SE (2014) Biologia vegetal. Guanabara Koogan S.A., Rio de Janeiro

Reis FP, Bonfa IMS, Cavalcante RB, Okoba D, de Souza Vasconcelos SB, Candeloro L, de Oliveira Filiu WF, Monreal ACD, da Silva VJ, Santa Rita PH, Carollo CA, Toffoli-Kadri MC (2014) *Tabebuia aurea* decreases inflammatory, myotoxic and hemorrhagic activities induced by the venom of *Bothrops neuwiedi*. J Ethnopharmacol 158:352–357

Rencher AC (2002) Methods of multivariate analysis, 2nd edn. Bringhan Young University, Provo

Roberts LD, Souza AL, Gerszten RE, Clish CB (2012) UNIT 30.2 Targeted metabolomics. Curr Protoc Mol Biol 30:30.2.1–30.224

Rodziewicz P, Swarcewicz B, Chmielewska K, Wojakowska A, Stobiecki M (2014) Influence of abiotic stresses on plant proteome and metabolome changes. Acta Physiol Plant 36:1–19

Russo RO, Baguinon NT (1997) *Erythrina fusca* Loureiro. In: Faridah Hanum I, van der LJG M (eds) Plant resources of South-East Asia No. 11: auxiliary plants. Backhuys Publisher, Leiden, pp 121–123

Saldanha AA, Do Carmo LF, Do Nascimento SB, De Matos NA, De Carvalho VC, Castro AHF, De Vos RC, Klein A, De Siqueira JM, Carollo CA, do Nascimento TV, Toffoli-Kadri MC, Soares AC (2016) Chemical composition and anti-inflammatory activity of the leaves of *Byrsonima verbascifolia*. J Nat Med 70:760–768

Sampaio-Santos MI, Kaplan MAC, Gottlieb OR (1995) Iridoid polarizations in Angiospermae. Acad Bras Cienc 67:413–424

Sannomiya M, Fonseca VB, Da Silva MA, Rocha LRM, dos Santos LD, Hiruma-Lima CA, Souza Brito ARM, Vilegas W (2005) Flavonoids and antiulcerogenic activity from *Byrsonima crassa* leaves extracts. J Ethnopharmacol 97:1–6

Santos RI (2007) Metabolismo básico e origem dos metabólitos secundários. In: Simões CMO, Schenkel EP, Gosmann G, Mello JCP, Mentz LA, Petrovick PR (eds) Farmacognosia: da planta ao medicamento, 6th edn. UFSC, Porto Alegre, pp 403–434

Santos-Zanuncio VS, Alves FM, Silva DB, Carollo CA (2020) Chemosystematic implications based on metabolic profiling of the genus *Byrsonima* (Malpighiaceae). Folia Geobotanica, 55(4), 289–300

Santos VS, Macedo FA, Vale JS, Silva DB, Carollo CA (2017) Metabolomics as a tool for understanding the evolution of *Tabebuia* sensu lato. Metabolomics 13:72

Shulaev V (2006) Metabolomics technology and bioinformatics. Brief Bioinform 7:128–139

Soares JJ, De Oliveira AKM (2009) O Paratudal do Pantanal de Miranda, Corumbá-MS, Brasil. Rev Arvore 33:339–347

Stevenson PC, Nicolson SW, Wright GA (2017) Plant secondary metabolites in nectar: impacts on pollinators and ecological functions. Funct Ecol 31:65–75

Suzuki H, Sasaki R, Ogata Y, Nakamura Y, Sakurai N, Kitajima M, Takayama H, Kanaya S, Aoki K, Shibata D, Saito K (2008) Metabolic profiling of flavonoids in *Lotus japonicus* using liquid chromatography Fourier transform ion cyclotron resonance mass spectrometry. Phytochem 69:99–111

Taiz L, Zeiger E (2004) Fisiologia vegetal, 3rd edn. Artmed, Porto Alegre

Taiz L, Zeiger E, Møller IM, Murphy A (2017) Fisiologia e desenvolvimento vegetal, 3rd edn. Artmed, Porto Alegre

Tattini M, Galardi C, Pinelli P, Massai R, Remorini D, Agati G (2004) Differential accumulation of flavonoids and hydroxycinnamates in leaves of *Ligustrum vulgare* under excess light and drought stress. New Phytol 163:547–561

Tikunov Y, Laptenok S, Hall R, Bovy A, De Vos R (2012) MSClust: A tool for unsupervised mass spectra extraction of chromatography-mass spectrometry ion-wise aligned data. Metabolomics 8:714–718

Valli M, Dos Santos RN, Figueira LD, Nakajima CH, Castro-Gamboa I, Andricopulo AD, Bolzani VS (2013) Development of a natural products database from the biodiversity of Brazil. J Nat Prod 76:439–444

Verçosa D, Santos-Zanuncio VS, do Amaral Albrez E, de Lima DP, Paranhos Filho AC, Marques, M R, Carollo CA (2020) Seasonal and spatial variation of the iridoid specioside in monodominant formation of *Tabebuia aurea* in the Brazilian Pantanal wetland. Brazilian Journal of Development, 6(9), 68771–68786

Verpoorte R, Van Der Heijden R, Ten Hoopen HJG, Memelink J (1999) Metabolic engineering of plant secondary metabolite pathways for the production of fine chemicals. Biotechnol Lett 21:467–479

Viljoen A, Mncwangi N, Vermaak I (2012) Anti-inflammatory iridoids of botanical origin. Curr Med Chem 19:2104–2127

Villasenor IM (2007) Bioactivities of Iridoids. Anti-Inflamm Anti-Allergy Agents Med Chem 6:307–314

Von Poser GL, Schripsema J, Henriques AT, Jensen SR (2000) The distribution of iridoids in Bignoniaceae. Biochem Syst Ecol 28:351–366

Wang M, Carver JJ, Phelan VV, Sanchez LM, Garg N, Peng Y et al (2016) Sharing and community curation of mass spectrometry data with Global Natural Products Social Molecular Networking. Nat Biotechnol 34(8):828–837

War AR, Paulraj MG, Ahmad T, Buhroo AA, Hussain B, Ignacimuthu S, Sharma HC (2012) Mechanisms of plant defense against insect herbivores. Plant Signal Behav 7:1306–1320

Watrous J, Roach P, Alexandrov T, Heath BS, Yang JY, Kersten RD et al (2012) Mass spectral molecular networking of living microbial colonies. Proc Natl Acad Sci 109:E1743–E1752

Wink M, Botschen F, Gosmann C, Schäfer H, Waterman PG (2010) Chemotaxonomy seen from a phylogenetic perspective and evolution of secondary metabolism. Plant Rev 40:364–433

Wolfender JL, Glauser G, Boccard J, Rudaz S (2009) MS-based plant metabolomic approaches for biomarker discovery. Nat Prod Commun 4:1417–1430

Wolfender JL, Rudaz S, Hae Choi Y, Kyong Kim H (2013) Plant metabolomics: from holistic data to relevant biomarkers. Curr Med Chem 20:1056–1090

Wyatt TD (2014) Pheromones and animal behavior: chemical signals and signatures. Cambridge University Press, Cambridge

Xie T, Song S, Li S, Ouyang L, Xia L, Huang J (2015) Review of natural product databases. Cell Prolif 48:398–404

Xue R, Fang Z, Zhang M, Yi Z, Wen C, Shi T (2012) TCMID: traditional Chinese medicine integrative database for herb molecular mechanism analysis. Nucleic Acids Res 41:D1089–D1095

Yang JY, Sanchez LM, Rath CM, Liu X, Boudreau PD, Bruns N et al (2013) Molecular networking as a dereplication strategy. J Nat Prod 76:1686–1699

Yin P, Xu G (2014) Current state-of-the-art of nontargeted metabolomics based on liquid chromatography-mass spectrometry with special emphasis in clinical applications. J Chromatogr A 1374:1–13

Chapter 18
Fire, Flood and Pantanal Vegetation

Geraldo Alves Damasceno-Junior, Alexandre de Matos Martins Pereira, Jens Oldeland, Pia Parolin, and Arnildo Pott

18.1 Introduction

Fire in periodically flooded floodplains sounds like a contradictory issue: fire and flood are opposite phenomena, and, in many cases, it is not so common to imagine how they can interact together influencing the structure of biological communities. However, many tropical wetlands in the world are subject to the strong influence of periodical floods and fires which act on their plant communities. That is the case, among others, in the Okavango Delta in Botswana; the Kafue floodplains in Zambia (Ellenbroek 1987), Kakadu region in Northern Australia (Parolin and Wittmann 2010; Tsheboeng and Murray-Hudson 2013); Cameia region in Angola (Zigelski et al. 2018); Everglades in Florida, USA (Newman et al. 1998; Ruiz et al. 2013); the Llanos in the Orinoco river basin in Colombia and Venezuela

---

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/978-3-030-83375-6_18.

G. A. Damasceno-Junior (✉) · A. Pott
Laboratório de Ecologia Vegetal, Instituto de Biociências, Federal University
of Mato Grosso do Sul, Campo Grande, MS, Brazil

A. d. M. M. Pereira
Centro Nacional de Prevenção e Combate aos Incêndios Florestais (Prevfogo)/Instituto
Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA),
Campo Grande, MS, Brazil

J. Oldeland
Biodiversity, Evolution, and Ecology of Plants, Institute of Plant Sciences and Microbiology,
University of Hamburg, Hamburg, Germany

P. Parolin
Université Côte d'Azur, INRAE, CNRS, ISA, Sophia Antipolis, France

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_18

(Armenteras et al. 2015); some floodable grasslands in the northern extreme of the Amazon such as Roraima (Ab'Sáber 1998); and the Pantanal (Oliveira et al. 2014; Arruda et al. 2016).

18.1.1 Flooding

Flooding has strong impacts on the vegetation, but if it is periodically recurring, the plants can adapt and develop strategies to cope with the impact of a priori lethal phenomenon for terrestrial organisms. The inundation has many effects on vegetation. At the individual level, inundation can induce oxygen deprivation in roots and change plant metabolism (Armstrong and Hull 1994). It can interfere with seed germination. Some species cannot germinate under flooding conditions (Parolin et al. 2002). Others, even being adapted to seasonally flooded environments, need drained soils to germinate, and after that, the sapling can be recruited under flooded conditions (Marques and Joly 2000). Some seedlings of trees can survive in darkness and underwater without oxygen during floods (Parolin 2009). Many species change their metabolism during floods using alternative metabolic pathways without oxygen such as malate, ethanol, alanine, or lactate for ATP production (Armstrong and Hull 1994). Some species have aerenchyma in the roots as an oxygen transport mechanism to the lower parts of the plant to overcome anaerobic conditions and turn the species more competitive in flooded environments (De Simone et al. 2002; Sairam et al. 2008). Moreover, there are some adaptations such as growth variations which lead to the presence of annual rings in the wood, hypertrophied lenticels, adventitious roots and new leaves produced above the water surface during floods, resprouting after inundation and reduction of growth, and states of dormancy, among others (Parolin et al. 2004) (see the Chap. 16 on Plant Morphoanatomical Adaptations).

On the landscape level, species are distributed along the flooding gradient, reflecting their ability to use these adaptations to cope with different levels, frequencies, and duration of inundation. That is true for forested environments, savannas, and grasslands (Fortney et al. 2004; Damasceno-Junior et al. 2005; Ferreira-Júnior et al. 2016). Diaspores in most species are released directly into the water in the high-water period, contributing to define the distribution of species (Kubitzki and Ziburski 1994; Ferreira and Stohlgren 1999; Damasceno-Junior et al. 2005; Casco et al. 2010; Parolin et al. 2013). Inundation can diminish the number of tree individuals and species in the low-lying parts of the gradient which are flooded for more extended periods (Ferreira 2000; Wittmann et al. 2008; Rodríguez-González et al. 2010; Oliveira et al. 2014; Arruda et al. 2016). Tree species have lower basal areas and consequently less biomass in places where the time of inundation is longer (Rodríguez-González et al. 2010; Arruda et al. 2016). The position of species along the flooding gradient can vary according to fluctuations in the interannual cycles of inundation. Despite an overall high flood tolerance, exceptional periods of flooding much longer than usual can kill trees (Damasceno-Junior et al. 2004), and, on the other hand, some woody species can spread in lower parts of the gradient in subsequent series of dry years (Pott and Pott 1994).

18.1.2 Fire

The occurrence of fire in floodplains is related to the seasonality under distinct rainy and dry seasons. During the rainy season, there is inundation and high production of biomass that can burn in the dry season as a consequence of anthropogenic management (Gould et al. 2002) or natural phenomena such as lightning (Ramos-Neto and Pivello 2000; Rorig and Ferguson 2002; Pettit and Naiman 2007a). The effects of fire on ecosystems are related to frequency, intensity, and time of occurrence. It is also affected by the climatic conditions, type of vegetation, amount of fuel, and vegetation physiognomy (Pettit and Naiman 2007b). Fire or the smoke effect (Zirondi et al. 2019) stimulates germination of some species, e.g., by reducing seed testa hardness, as found in Fabaceae. It can also synchronize flowering of some species, such as *Stirlingia latifolia* R. Br. in the woodlands of Australia (Bowen and Pate 2004) or wet prairie grasses in Florida (Main and Barry 2002). In contrast, it can prevent the flowering of grasses, such as in the case of a Cerrado area where, after burning, all grasses stayed 1 year without flowering (Neves and Damasceno-Junior 2011). Fire can also diminish the number of tillers in grasses (Silva and Klink 2001). Fire can consume a large amount of biomass, kill individuals, or stimulate resprouting of some species (Cirne and Scarano 2001; Lukac et al. 2011). The ability to remain for many years resprouting in a given environment submitted to strong filters such as fire has been called the persistence niche (Bond and Midgley 2001). Some traits contribute to protecting trees from being killed during fire events, such as bark thickness, a larger trunk diameter, flammability of tissues (mainly leaves), the presence of starch or other reserves in roots and underground systems to support resprout after fire, as well as the ability of dispersal after fire and the persistence of propagules (Oliveira Filho and Ratter 2002; Otterstrom and Schwartz 2006; Lukac et al. 2011). Fire can also reduce plant height because of the top kill of trees (Bond and Keeley 2005). In the Cerrado, some seeds can be fire resistant (Fichino et al. 2016). Some signs left by fire can be observed years later, such as fire scars on the trunk basis, frequently forming a hole where the bark died and did not regenerate, and broom-like sprouting on the upper side of branches not licked by flames where the buds survived.

In fire-prone ecosystems such as savannas, the spatial coexistence of grasses and trees is mediated by fire, and by the ability of trees to resprout and their variability in recruitment rates (Higgins et al. 2000). Grasses benefit from the fire because of their underground systems, such as rhizomes or buds very close to the soil surface. On the other hand, some grasses, e.g., *Aristida* spp., have hygroscopic awns that help diaspores being buried to a depth that permits the seed to escape the fire heat on the soil surface (Garnier and Dajoz 2001). By producing high amounts of biomass during the rainy season that can increase fire risk and intensity during the dry season, grasses can eliminate trees in severe fire events. Most tree seedlings or young trees die during the burning process, thus diminishing the out-shading of the grasses by trees (Higgins et al. 2000). By consuming biomass, fire opens space to more individuals and consequently, more species may establish (Otterstrom and Schwartz 2006).

18.1.3 Effects of Flooding and Fire

The mixed effects of flooding and fire in wetlands have been mainly studied for single wildfires in temperate headwater systems (Bixby et al. 2015). At the soil level, fire can mobilize nutrients, increasing runoff with consequences in potential erosion. Fire can affect the variation of temperature and relative humidity over the transition between wetlands and riparian zones. Fire can also decrease the concentration of O_2 available in the water because of the decomposition of debris (Bixby et al. 2015).

In several ecosystems, like in the Mediterranean climate, burning can influence the runoff and flood magnitude because of water repellency in the soil after a fire (Soto and Díaz-Fierros 1998; Candela et al. 2005). This phenomenon is poorly understood for tropical systems. On the other hand, in the tropical Okavango Delta, fire frequency is higher in more floodable areas because of the high production of grass biomass during flooding time that can turn into fuel (Heinl et al. 2007), likewise in the Pantanal.

The effects of fire on the vegetation of riparian environments and wetlands are still poorly understood. In the Everglades, Florida, the succession of vegetation depends on the levels of inundation and the number of fire events. The occurrence of frequent or severe fires at a given level of inundation can lead to a *Cladium mariscus* marsh (sawgrass marsh), one of the most resistant types of vegetation in the region (Richardson 2010). *Cladium mariscus* marshes also occur on the Miranda River upper basin. One effect of this interaction is the formation of woody debris. Woody debris is formed in forests along rivers by fire and by normal and extreme flooding events. Fire can also produce much woody debris that can interfere in water runoff; inundation can kill trees, make leaves and branches drop, and as a consequence increase fire intensity in riparian areas and cause tree death. That is described for highlands in tropical and temperate environments (Pettit and Naiman 2007b; Bendix and Cowell 2010). The recovery of vegetation after a fire event can vary according to the slope of the terrain, differences between riparian and adjacent vegetation, and the amount of rainfall in a given region (Pettit and Naiman 2007a).

The Pantanal is one of the largest tropical floodplains of the world, with a total of circa 160,000 km^2 (nearly 140,000 km^2 in Brazil), under a seasonal climate (Junk and Nunes da Cunha 2012). The inundation in the Pantanal is mainly caused by its rivers' overflow, and the vegetation can be flooded from nearly 20 or 30 to more than 270 days a year (Damasceno-Junior et al. 2005). Because of the marked seasonal climate with a decreasing mean level of rainfall from east to west (1300–1000 mm/year), fire events are recurrent in the region (Schroeder et al. 2005). The effects of fire on the vegetation are still poorly understood in the Pantanal. Many publications about fire in the Pantanal only say that fire is a problem or cite fire as a frequent issue in this system (Prance and Schaller 1982; Junk and Nunes da Cunha 2012; Tomas et al. 2019).

This chapter aims to describe the fire regime in the floodplain of the Pantanal and to review the available literature on what is known about the effects of fire and the combination with flooding on its vegetation.

18.2 Methods

We searched in the Web of Science and SciELO using the keywords *Pantanal* and *fire* in English and Portuguese to have a comprehensive view of what has been published about fire in the Pantanal. We selected only publications related to vegetation and we also included information from books.

To analyze the fire regime, we verified the spatial distribution of wildfires inside the Pantanal using kernel density of heat spots maps between 1999 and 2020. Data was gathered from the Brazilian National Institute for Spatial Research site (INPE/Brasil 2017). The available data of fire comes from reference satellite images previously processed. From January 1, 1999, to July 3, 2002, we used the NOAA-12 (AVHRR sensor, obtaining the images taken at the end of the afternoon); after that, we used the AQUA_M-T images (MODIS sensor, getting images taken in the early afternoon). We downloaded data about fire occurrences in point shapefile format and processed them using the free software QGIS, version 3.10.12 (QGIS 2017) with the system of coordinates defined in SIRGAS 2000 (Sánchez et al. 2013). We generated fire maps using a kernel density estimator from a cloud of point locations of fire events inside the Pantanal. We grouped the data in circles of 10 km diameter using the formula:

$$f(x) = \frac{1}{nh}\sum_{i=1}^{n} K\left(\frac{x - Xi}{h}\right)$$

with K = kernel function, h = radius of searching, x = center position of each raster, X_i position of the Ith point that comes from the centroid of each polygon, and n = total number of pixels.

The kernel estimator creates a neighborhood circle around each sampled point were 1 corresponds to the center of the circle and 0 to the outer limit. The value of the circle is the sum of all overlapping circles with information of fire divided by each radius (Silverman 1986). For this study, the radius $h = 10$ km.

After the generation of maps, we reclassified the raster generated data based on the image rendering. We applied false color according to the concentration of fire pixels: white (without fire), blue (very low – $0 < x \leq 20$ fire events in a circle of 10 km of radius), green (low $20 < x \leq 40$ fire events), yellow (medium $40 < x \leq 60$), orange (high $60 < x \leq 80$), and red (very high $x > 80$). The categories were set up based on the year 2020, which had the highest number of fire pixels. We also set up a map with all analyzed years and used the following definitions for the false colors: $0 < x \leq 90$ fire events in a circle of 10 km of radius, blue; $90 < x \leq 179$, green; $179 < x \leq 268$, yellow; $268 < x \leq 358$, orange; and $x > 358$, red.

18.3 Results and Discussion

18.3.1 Fire Regime

The origin of fires in the Pantanal is unknown from scientific data; however, from observation, we can say that most fires either originate from lightning or are anthropogenic fires. Cattle ranchers can set fire to renew pastures. The human riverine population can set fire to clean around their houses. Inadvertently anthropogenic fires can also occur on roadsides. Over the period observed by us in the satellite images (1999–2020), we can say that there was no area, considering our scale of work, without a fire event inside the floodplain. In this period, the Pantanal burned almost completely (Figs. 18.1 and 18.2), of course at different times of the year and with different intensities. The incidence of fire varies in the number of foci over the years. In most areas, a high fire incidence in a given year is followed by a low fire incidence in the following year. The years 2002, 2005, and 2020 had a very high number of events, with more than 12,000 recorded fire spots in 2002 and 22,116 in 2020. The years with the lowest number of fire events were 2000, 2014, and 2018, with 2000 or fewer fire events per year (Fig. 18.3). Considering the size of the circles, approximately less than 15–30% of the Pantanal remain without fire events in a radius of 10 km per year (Figs. 18.1 and 18.2). The frequency of fire (from medium to very high) is nearly every second year in the used sampling unit (Figs. 18.1 and 18.2). Regarding its relationship with floods, fire incidence tends to be higher in years when the extent and time of inundation in the Paraguay River are low. In other words, fires spread more when, during the dry season, the Paraguay River level is very low, and subsequent rains are not enough to make the river overflow. The fire then usually comes from the hills and burns the floodplains, which in normal years would not burn because they still would have water during the dry season. This phenomenon occurred in 2020 on the Serra do Amolar and other hills along the Paraguay River. That is similar to the reported fire synchrony on riparian and adjacent upland forests in eastern Oregon, USA (Harley et al. 2020). When the opposite occurs, the incidence of fire is lower (Fig. 18.4). As the Paraguay River is the main river of the Pantanal and accumulates waters that overflow, this relationship is expected because it reflects the inundation levels in the whole Pantanal and the availability of fire-prone dry areas. Other climatic features affect fire frequency in the Pantanal, such as accumulated sun radiation load, relative humidity, and temperature (Viganó et al. 2018). In the dry season, the air humidity tends to be very low; it can be as low as 20% and often goes together with strong winds, which increases the fire risk (Viganó et al. 2018). Extreme droughts such as occurred in

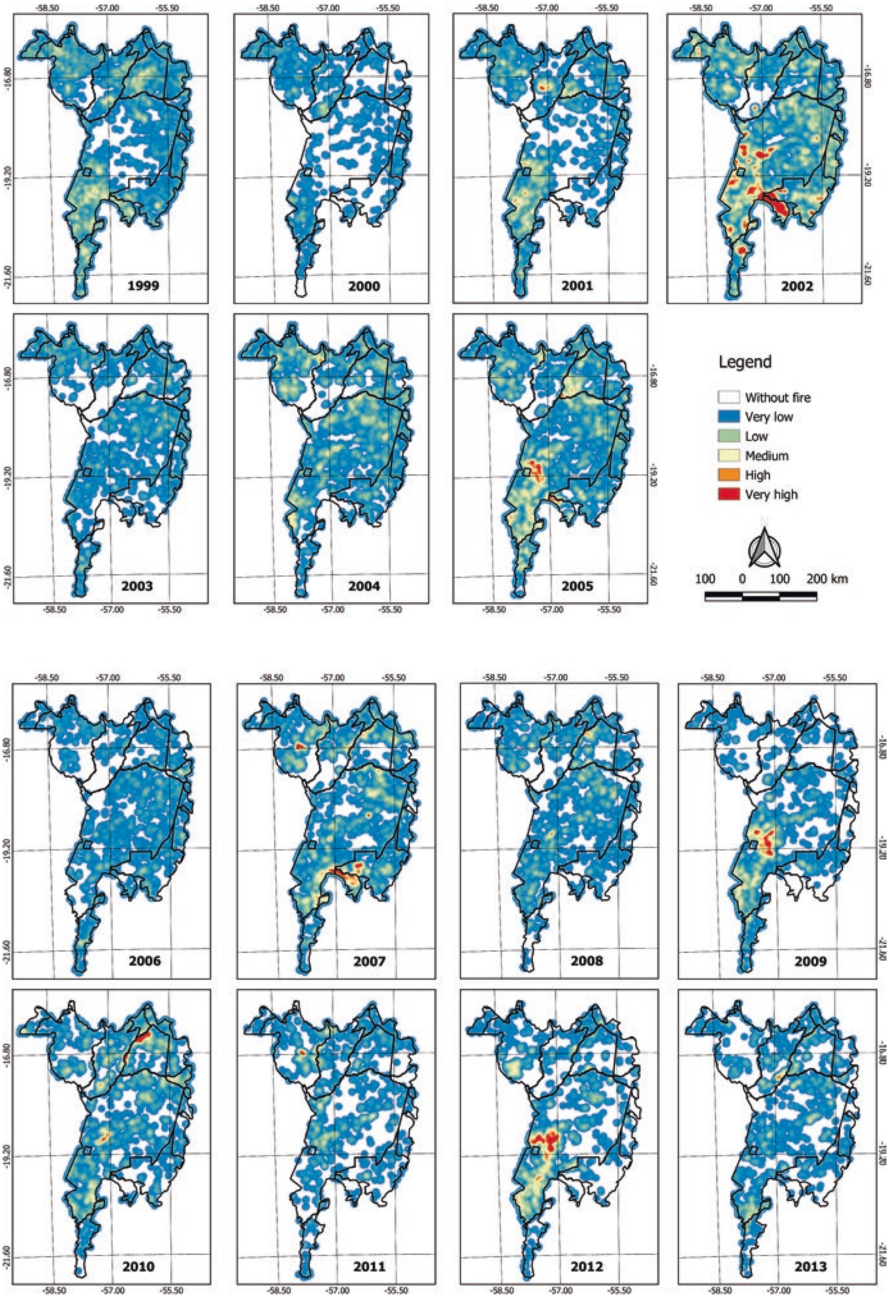


Fig. 18.1 Distribution of fire from 1999 to 2013 in the Pantanal, accessed by heat spots using a circle of 10 km radius as sampling unit. White (without fire), blue (very low – $0 < x \leq 20$ fire events within a circle of 10 km radius), green (low $20 < x \leq 40$ fire events), yellow (medium $40 < x \leq 60$), orange (high – $60 < x \leq 80$), and red (very high $x > 80$)

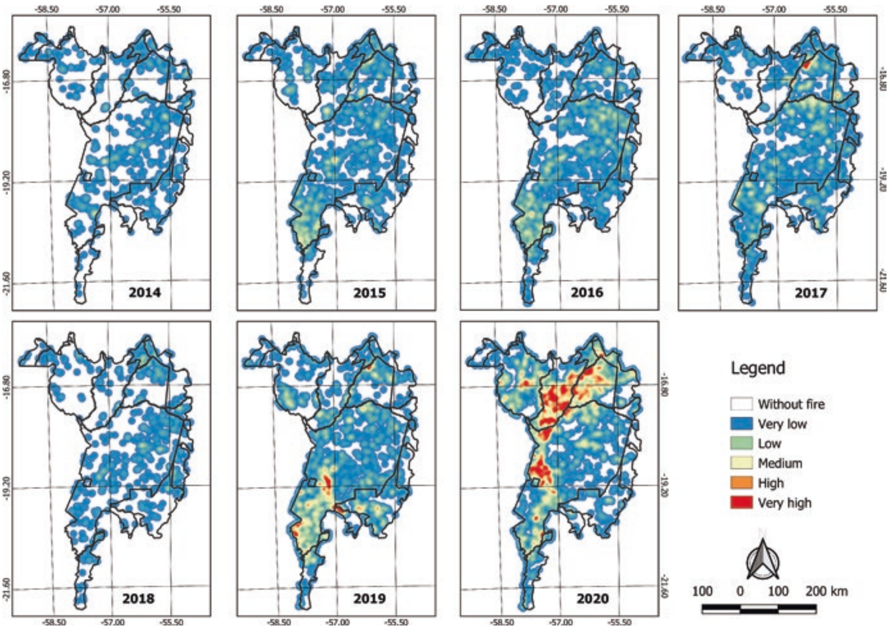


Fig. 18.2 Distribution of fire from 2014 to 2020 in the Pantanal, accessed by heat spots using a circle of 10 km radius as sampling unit. White (without fire), blue (very low – $0 < x \leq 20$ fire events within a circle of 10 km radius), green (low $20 < x \leq 40$ fire events), yellow (medium $40 < x \leq 60$), orange (high – $60 < x \leq 80$), and red (very high $x > 80$)

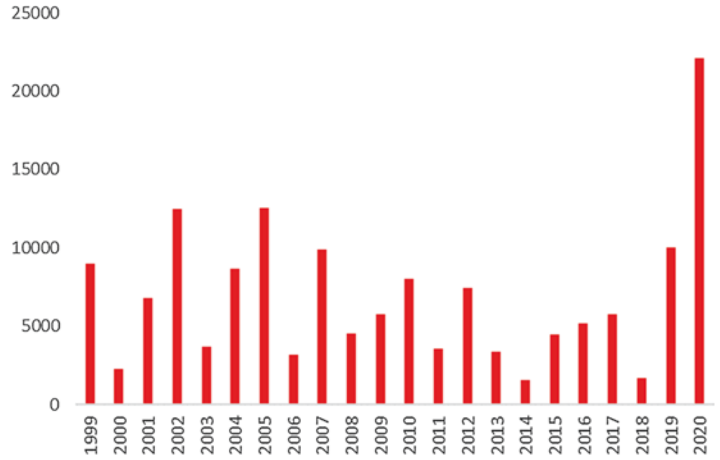


Fig. 18.3 Number of heat foci in the Pantanal from 1999 to 2020. Data obtained from NOAA-12 and AQUA_M-T satellites. (INPE/Brazil)

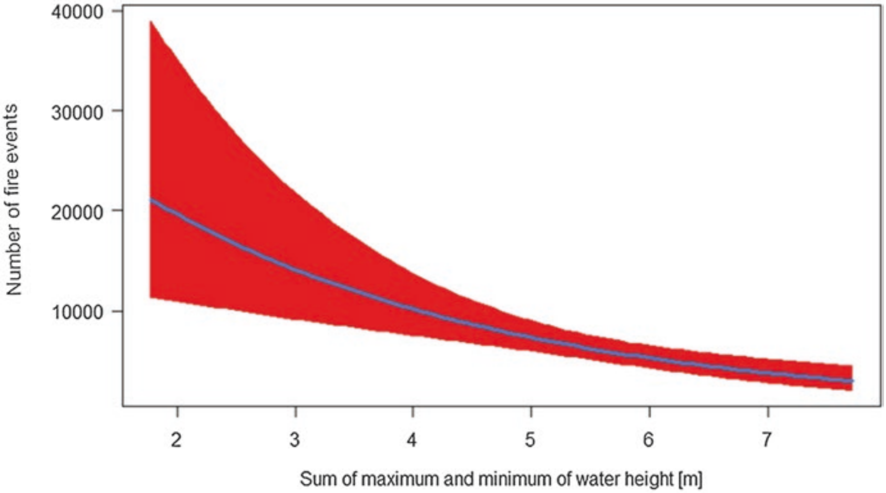


Fig. 18.4 Generalized linear model showing the relationship between the sum of annual maximum and the minimum level of inundation of the Paraguay River and annual fire frequency in the whole Pantanal from 1999 to 2020 (pseudo $R^2 = 0.44$). The sum of maximum and minimum reflects the inundation time on adjacent grasslands. When the sum is low, the inundation-free period in (part of) the floodplain is more extended, and when the sum is high, the duration of inundation is long

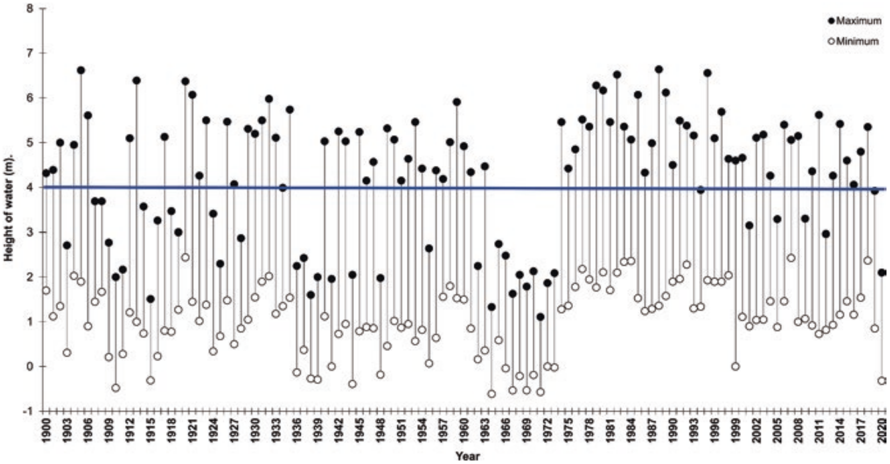


Fig. 18.5 Annual maximum and minimum of the Paraguay River height in the Ladário hydrometric gauge from 1900 until 2020. The blue line represents the level when the Paraguay River overflows. (Data from Brazilian Navy)

2020 can lead to catastrophic fires. The year 2020 was the seventh driest in 120 years of records taken in the Ladário hydrometric gauge (Fig. 18.5). Under such a combination of conditions, the flammability threshold was one of the highest since 1980 (Libonati et al. 2020). As a consequence, more than 30% of the Pantanal area burned (LASA 2020). Rainfall in the upper Paraguay basin is highly related to the sea surface temperatures, mainly the central South Atlantic system, which explain circa 80% of the rain in the region (Thielen et al. 2020). As aforementioned, lightning can ignite a fire, mostly when dry thunderstorms occur, at the change of seasons (Ramos-Neto and Pivello 2000). Occasional frosts cause massive leaf death and consequently contribute to bushfires.

Fires were less frequent in areas around the National Park of Pantanal, near the big lakes such as Gaíva and Uberaba in the north, and also in the Taquari alluvial fan in lower areas of Nhecolândia and Paiaguás (Figs. 18.2 and 18.3). The highest fire incidence was around the city of Corumbá along the Paraguay River, the Taquari fan delta, the Miranda River until its mouth at the Paraguay River, and the Nabileque subregion. These areas are among the most inundated in the Pantanal (Fig. 18.6). With some exceptions, we can say the most fire-prone areas in the Pantanal are those more subjected to prolonged and high inundation levels. Based on the map of

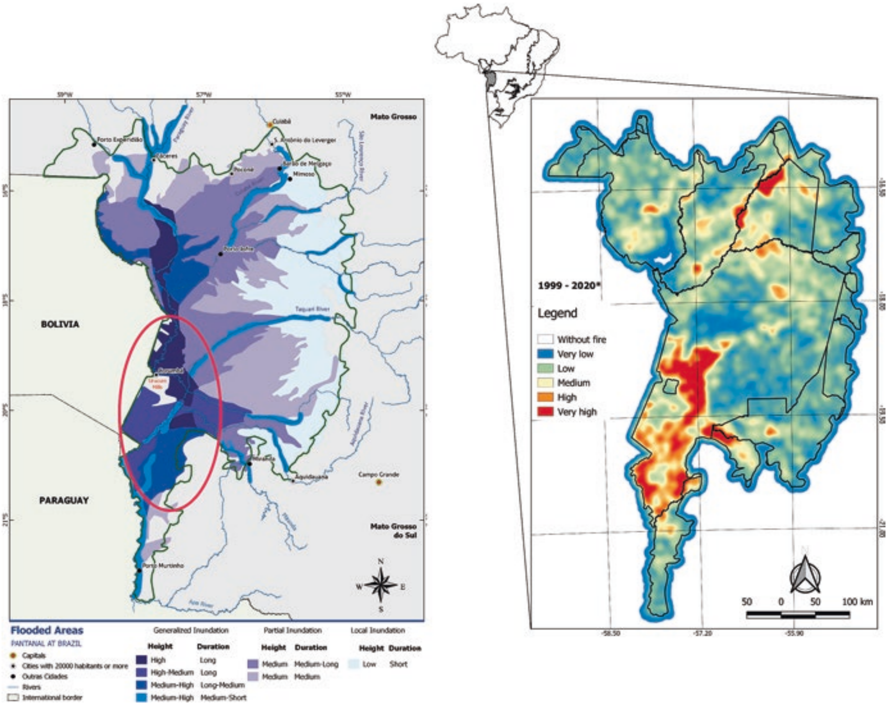


Fig. 18.6 Inundation levels in the Pantanal, on the left, and number of fire events in the Pantanal from 1999 to 2020, on the right. (Source of inundation map (GEF et al. 2004)). The area within the red ellipse (left) corresponds to the *corridor of fire and flood* (area with the highest levels of inundation and fire)

fire and flood, we can call this region *the corridor of fire and flood of the Pantanal* (Fig. 18.6).

This big area where wildfires occur more intensely (corridor of fire and flood) produces massive biomass because of the higher flooding levels. These areas frequently have monodominant stands and extensive grasslands, in many cases dominated by *Oryza* spp., *Paspalum fasciculatum*, *P. wrightii*, *Hymenachne amplexicaulis*, and *H. pernambucense*. Most of these grasses can grow amazingly fast and stay, by continuous growth, at least 1 m above the water level during the flooding process (Bertazzoni and Damasceno-Junior 2011). Therefore, the production of biomass during flooding is very high and fast. Some of the main grasses in this area, during flooding, can reach a length of 5 or 6 m. When the waters recede, there is a considerable amount of drying biomass available for the frequent, widespread fires (Fig. 18.7). The accumulated biomass in these areas remain available as fuel because the grasslands cannot be grazed or remain undergrazed because of cattle ranching restrictions imposed by deep flooding. Still, the fire and flood corridor includes large urban centers as Corumbá and Ladário, with a higher risk of anthropogenic fires.

Fires around the Paraguay River only occur in two situations: (1) when the flood level does not reach 4 m in the Ladário gauge and (2) when there are at least 1 or 2 weeks without rain in January and the Paraguay River is at its lowest level (Oliveira

Fig. 18.7 Grasslands burning in the *corridor of fire and flood* of the Pantanal in the Paraguay subregion (Picture by Angelo Rabelo)

et al. 2014; Arruda et al. 2016). In 2020, both phenomena occurred because of the extreme drought of meteorological and hydrometric conditions. The phenomenon of a high fire incidence in the more inundated areas was also observed in the Okavango Delta (Heinl et al. 2008).

18.3.2 Fire and Pantanal Vegetation

Fire in the Pantanal can be considered an ecological filter. We presume that fire has been occurring in the Pantanal since it was established as a floodplain within a seasonal climate zone. The most comprehensive historical data on fire in the Pantanal were obtained from analyses of charcoal, pollen, and diatomaceous Gaíva Lake sediments (Power et al. 2016). In that study, fire signs were recorded over the entire period of 12,000 years (Fig. 18.8). To whom believes that fire is just an anthropogenic issue in the Pantanal, it is worth mentioning that the most ancient archaeological site in the Pantanal is dated 8000 years, found along the Paraguay River (Peixoto and Arruda 2015). The highest fire frequency detected in Gaíva Lake was from 12,000 to 10,000 ybp, i.e., at least 2000 years before the first record of human presence in the region (Fig. 18.8). Nonetheless, fire magnitude increased when humans settled in this region (Fig. 18.8) (see the Chap.2 on Paleopalynology).

The Pantanal has a low number of endemic species (see the Chap. 3 on Flora) because of its recent origin (Pott et al. 2011). Nevertheless, it is noteworthy that one of the endemic species of the Pantanal, *Zephyranthes pantanalensis* (Pott and Pott 1994), can flower 2 days after a fire event, showing an obvious fire adaptation (Fig. 18.9). Fire has been used in the Pantanal as a management tool to promote regrowth of native pastures, mainly on the most dystrophic soils with scleromorphic grasses such as *Andropogon* spp., *Paspalum carinatum*, and *P. lineare* (Pott 1994). Monodominant stands of *Elionurus muticus* ("caronais") are frequently burned.

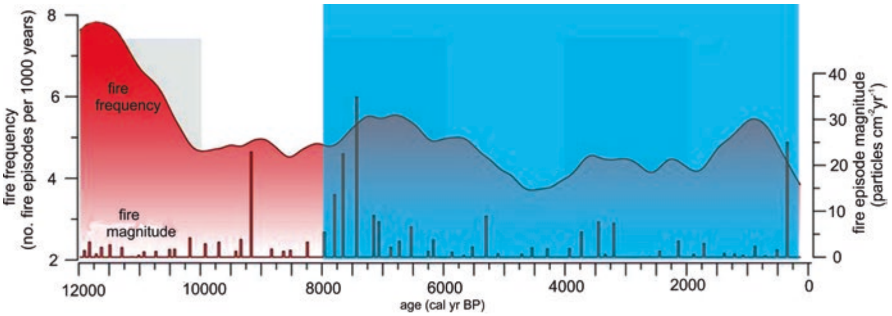


Fig. 18.8 Diagram showing the fire frequency for the last 12,000 years. In red: the number of fire episodes per 1000 years, and the magnitude of the fires (in the red histogram) representing the charcoal amount in Gaíva Lake, Pantanal (modified from Power et al. 2016). The blue part of the diagram represents the human presence in the region of the presently most ancient archaeological site recorded for the Pantanal. (Peixoto and Arruda 2015) (see Chap. 12 on Paleopalynology)

Fig. 18.9 *Zephyranthes pantanalensis*, an endemic species of the Pantanal, flowering 2 days after a fire event in 2019

Fig. 18.10 Prescribed fire experiment in an ungrazed floodable grassland of *Andropogon hypogynus* and an adjacent area of *Elionurus muticus* in the Nhecolândia subregion of the Pantanal

This species contains essential oils that increase flammability. The species grows between the floodable and the flood-free zones and is the only monodominant species in the Pantanal whose monodominance is not related to inundation, despite the water table nearly reaching the soil surface at high floods. We believe that its high flames help to largely eliminate shrubs and trees that occasionally are recruited in these grasslands. Only a few woody species survive the fires, e.g., the short Cerrado tree *Mouriri elliptica*, with a corky bark and coriaceous leaves. As far as the monodominant grassland stands of *Elionurus muticus* are concerned, not only fire but probably also local edaphic conditions, such as leached sandy soils, seem to favor its monodominance (Fig. 18.10). That should be investigated in future studies. Even though the species is associated with fire, a fire can lead to a reduced biomass of these grasslands by 36 %, and if burned in two consecutive years, by 50% (Cardoso et al. 2000). This species is grazed by cattle soon after a fire (Pott 1994) (see the Chap. 10 on Grasslands). Other monodominant stands, such as *Tabebuia aurea* (*paratudais*) and *Copernicia alba* (*carandazais*), are frequently burned (Pott 1994) (see the Chap.8 on Monodominants). Wildfires in *C. alba* are practically uncontrollable and can jump over rivers and roads. Even when the burning is prescribed, it may easily escape and go on for days. In contrast, the Nhecolândia subregion has natural barriers of ponds and nearly evergreen short grasslands (e.g., *Axonopus purpusii* and *Reimarochloa* spp.).

Fire is an essential issue for nearly all vegetation types of the Pantanal. We built a list of 805 species of different growth habits from the Pantanal (from a total of 2568; see Chap. 3 on Checklist) containing 232 species from Pott and Pott (1994) and the others from field observations; 159 species are fire-tolerant and survive fires (Fig. 18.11 see also supplementary 1). Some of these species are from the Cerrado areas inside the Pantanal and have corky barks, e.g., *Himatanthus obovatus*, *Handroanthus ochraceus*, *Pseudobombax longiflorum*, *Connarus suberosus*, *Curatella americana*, *Vatairea macrocarpa*, and *Erythroxylum suberosum*. In *Curatella americana*, the bark is composed of several suberous layers working as insolation, with dormant axillary buds underneath for eventual sprouting. As observed in the Paiaguás subregion, *C. americana* grows as a dwarfed multi-stemmed treelet under recurrent fires and floods and is very persistent (Pott and Pott 1994). There are also species with a thick bark from semideciduous and deciduous forests, such as *Cedrela fissilis*, *Rhamnidium elaeocarpum*, *Sideroxylon obtusifolium*, and *Zanthoxylum caribaeum*, as well as others without much suber, such as

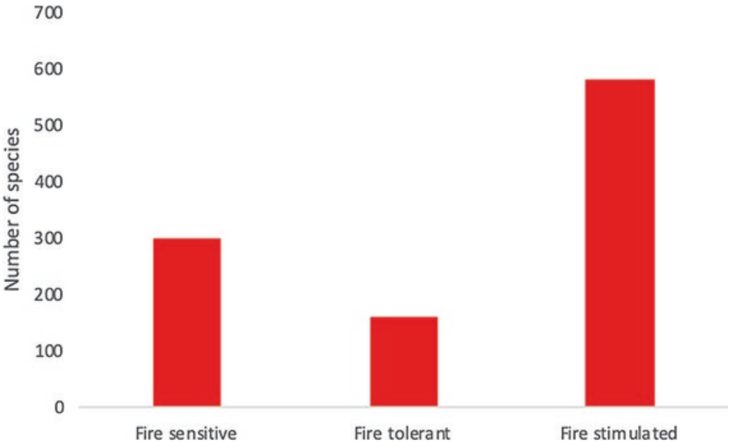


Fig. 18.11 Behavior of 806 plant species of the Pantanal after fire according to Pott and Pott (1994) and our field observations. There is some overlap of species because some species can be sensitive to fire and die, but their seeds are promoted by fire and thus are also included in the fire stimulated category. Some species are fire-tolerant but flower after fire and are also in the fire stimulated category

Jacaranda cuspidifolia, *Combretum leprosum*, and *Dilodendron bipinnatum*. Moreover, some riparian species have corky barks, such as *Handroanthus heptaphyllus*, and other trees of flooded habitats, such as *Tabebuia aurea*. In floodable grasslands, we believe that *Couepia uiti* has both a fire-avoidance strategy: it positions its canopy close to the ground, thus shading out most grass; as a result, fires do not easily reach the stems, and a fire-tolerance strategy as it resprouts from the crown.

Straight short-branched trees such as *Casearia gossypiosperma* can regrow from axillary buds. When, in this species, the bark is consumed by fire, the exposed xylem is vulnerable to burn in subsequent fire events and wood-decay agents, such as insects and fungi, leading to a progressive stem hollowing and consequent decrepitude or treefall. Nevertheless, some species have outstanding resilience and may survive with just a small undamaged part of the bark, or even resprout shoots after collapsing, e.g., *Handroanthus ochraceus* (from gemmiferous roots) and *Maclura tinctoria* (Fig. 18.12). Likewise, some riparian trees felled by the floods can resist dying, e.g., *Andira inermis*, *Inga vera*, *Symmeria paniculata* (plus basal shoots), and *Vitex cymosa* (Fig. 18.12).

Non-arboreal plants may have other adaptations. Bromeliaceae such as *Dyckia leptostachya* have crasseous leaves that get scorched only at the apex, so the basis and the apical bud remain preserved inside the rosette, and *Bromelia balansae* recovers from rhizomes even after a complete top kill. Herbs, shrubs, or vines can resprout from the basis or have underground systems as a fire-escape strategy, including *Andira humilis*, *Annona cornifolia*, *A. dioica*, *Heteropterys tomentosa*, *Staelia thymoides*, *Waltheria albicans*, *Piriqueta corumbensis*, *Cissus erosa*, *Pfaffia glomerata*, and *Anacardium humile*. Some plants with bulbs survive well and flower

Fig. 18.12 *Vitex cymosa* in a semideciduous and riparian forest resprouting after a severe fire event at Caiman ranch. The branch apexes were burned, and the plant is resprouting mainly from thicker parts of the branches

after a fire, e.g., *Cipura paludosa*, *Zephyranthes pantanalensis* (Fig. 18.9), and *Hippeastrum puniceum*. Some species can increase their cover after a fire by resprouting from many points in the underground system, e.g., *Heteropterys tomentosa*, or by germination of seeds, such as *Microstachys hispida*. The fruticose *M. hispida* is a good indicator of burned grassland (Pott and Pott 1994). Trees, such as *Trema micrantha* and *Cecropia pachystachya*, also germinate better after a fire because of canopy openness, as their seeds are positive photoblastic (Válio and Scarpa 2001).

Most Pantanal palms are quite fire-tolerant. They protect their first bud by burying the hypocotyl during the germination (even if the seed is aboveground). These strategies make them safe from fire and herbivory. In the acaulescent palm *Allagoptera leucocalyx*, the growing point remains underground during the entire life span. The palm *Attalea phalerata* increases its relative abundance after severe fires in forested islets (locally called *capões*) surrounded by grasslands. It can survive the fire mainly because of its sheaths that remain surrounding the stem after leaf fall. However, it can die from fire after the protective old sheaths are lost (Rivaben et al. 2021). The palm *Bactris glaucescens* has thin stems that are often top-killed by fire, but, being sympodial, it regrows from rhizomes. Fire increases the abundance of *Copernicia alba* (Pott and Pott 1994) in the so-called pyrophytic savanna. When its stem is smooth, it indicates that old sheaths are lost to fire. Curiously, the orchid *Catasetum fimbriatum* finds a habitat on this palm: it grows on the stems of *C. alba*. Its thick pseudobulbs buffer some of the heat during a fire; it drops its leaves and only dies when the flames are intense above 2–3 m.

Grasses benefit from the fire in savanna vegetation or grasslands, except most of the aquatic species. From a list of 157 species of Poaceae, 115 can resprout after a fire, e.g., *Andropogon bicornis* and *A. hypogynus.* These two species cover extensive areas in the Pantanal, are very fibrous, and little grazed. After a fire, they resprout with new soft leaves and are palatable until becoming tough again. Despite being consumed by cattle, they increase in density (Allem and Valls 1987) until becoming tough again (except under heavy grazing). Twenty-eight species of grasses increase under fire, 52 are sensitive, 56 have an underground system, and 43 decrease. As grasslands cover most of the Pantanal, these species play a primary role in the fires because they are the principal flammable biomass providers.

Many aquatic species can survive fire mainly because of underground systems, e.g., *Cyperus giganteus* (Rocha et al. 2015). Aquatic species such as *Cyperus blepharoleptos* can produce flammable biomass because it can grow over other aquatic species and over itself (Fig. 18.13; also see Chap. 4 on Aquatic Plants). These characteristics create a thick histosol in more flooded areas of the Pantanal. Some areas remained completely covered by these histosols for over 20 years until 2020 when the extreme drought occurred. This species, among others, produces many areas with histosols in the Pantanal. That created an exceedingly difficult type of fire to fight against, an underground fire. The biomass of these aquatic plants caught fire during the 2020 fire events. Many reports showed underground fires that were one of the biggest challenges for the firemen during those catastrophic events (Fig. 18.14)

Fig. 18.13 Aquatic environment in the Pantanal showing *Cyperus blepharoleptos* growing up over other aquatic plants. (Picture by Geraldo A. Damasceno-Junior)

Fig. 18.14 Piece of histosol burning on a glove of a firefighter. This is the main cause of underground fires in the Pantanal. (Picture by Saul Schramm)

(for the adaptation of Pantanal plants to flooding, see the Chap. 4 on Aquatics and the Chap. 16 on Adaptations).

The ability of Pantanal vegetation to become green again after a fire is due to many adaptations described above and also because of the reaction of the seed bank. Many herbaceous species, aquatic and terrestrial, whose seeds are stored in the seed bank, can germinate just after fire events (Souza et al. 2019b; Kohagura et al. 2020) (see the Chap.15 on Seed Bank). Some seeds are protected from fire inside the fruits such as *Sesbania virgata* (Soares et al. 2021) that is spreading after 2020 fire events.

18.3.3 Fire, Inundation, and Their Combined Effects on Vegetation

The combined effects of fire and flooding on shaping plant communities in the Pantanal are beginning to be understood. In terms of species richness, inundation can decrease the number of species because relatively few are adapted to oxygen deprivation in the roots. That applies especially to trees (Damasceno-Junior et al. 2005). On the other hand, fire can open gaps in the vegetation and increase post-fire colonization by more species (Oliveira et al. 2014). Studies conducted in Paraguay River riparian forests show that the occurrence of fire can affect plant richness in the regeneration along the flooding gradient. In areas of riparian forest that remained unburned for 10 years, the total number of species in the regenerating group of plants tended to decrease with increasing flooding levels; however, the difference in the species number in the two extremes of the gradient was small. A similar tendency was observed in areas that experienced three fire episodes during the same period (Oliveira et al. 2014). There were more species in the less inundated part of the gradient due to fire gaps; however, in the lower part of the gradient, the combination of fire and deeper flooding more strongly reduced species richness. That is because the fire may kill many individuals, and after the fire, inundation prevents the recruitment of species non-tolerant to flooding (Oliveira et al. 2014). Thus, on higher spots, which are relatively briefly inundated, fire creates open spaces on which lianas, trees, and shrubs may settle. For adult trees in the same area and conditions, the effect of fire on species richness along the flooding gradient was even more noteworthy. Without fire for 10 years, species richness proved higher in lower and more inundated areas and diminishes toward the higher ground. With three fire events during a 10-year period, the tendency of the richness among adult trees along the flooding gradient inversed. As a result, the tendency in the richness of adult trees along the flooding gradient after fire becomes similar to the regeneration described above (Fig. 18.15) (Arruda et al. 2016).

Regarding the abundance of individuals, the variation along the flooding gradient is the same for regenerating and adult trees and shrubs. The number of individuals is not altered along the flooding gradient in these riparian forests without fire occurrence. Recurrent fires change this tendency. In recurrently burned areas, the number of individuals becomes higher in less flooded parts of the gradient and lower in low-lying parts. That is for the same reasons that cause the variation in richness after a fire (Oliveira et al. 2014; Arruda et al. 2016). In this situation, fire can open gaps for recruiting new individuals on the higher parts of the gradient, and these individuals can succeed. However, fire also opens spaces in the lower zones by killing some trees and shrubs, but the prolonged flooding prevents colonizing by new individuals.

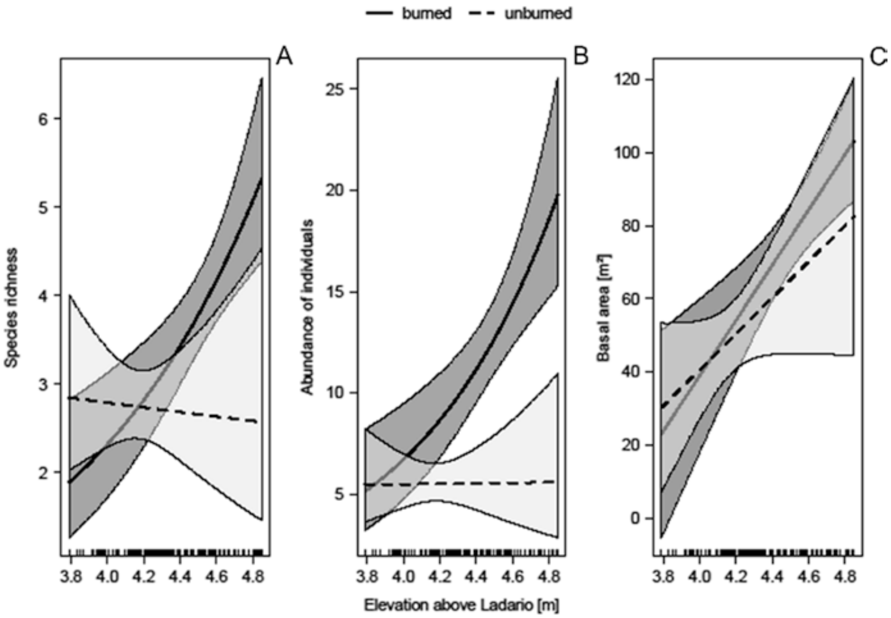


Fig. 18.15 Variation in species richness, abundance of individuals, and basal area of trees and shrubs with and without fire along the ground topographic variation measured in relation to the Paraguay River hydrometric gauge at Ladário. (Arruda et al. 2016)

As a result of this combined effect, fire reduces the number of individuals and species in the lower areas, turning these environments more open. These lower areas of the gradient are surrounded by grasslands that provide most fuel for such fire events; thus, we may expect a higher fire intensity there than under closed woods. Nevertheless, the 2020 wildfire scorched dense forests.

The basal area of adult trees and shrubs tends to decrease in areas with a long flooding duration. The occurrence of fires does not alter this tendency (Arruda et al. 2016). Fire can kill many big trees, but the regeneration of many small individuals may compensate for the basal area lost during fires in all parts of the flooding gradient (Fig. 18.15).

Fire can also change the tendency of some plant traits along the flooding gradient. A study comparing traits of forest patches burned 17 years ago with recently burned ones (Souza et al. 2019a) showed remarkable trends. For example, LDMC (leaf dry matter content), which is a proxy of leaf flammability, increases along the flooding gradient without fire, but after being burned, the fire risk decreases. Therefore, the deepest flooded environments become less fire-prone after a fire event. The allocation of resources represented by SLA (specific leaf area) and LT (leaf thickness) decreases toward the low-lying areas over the flooding gradient. Nevertheless, in recently burned areas, this tendency is smoothed, indicating that differences in leaf traits over the flooding gradient tend to reduce post-fire. It was also found that fire triggers the response of relative bark thickness (RBT) along the flooding gradient. Without fire, there is no relation between RBT and inundation; however, in recently burned areas, RBT increases with increased flooding, contributing to oxygen exchange across the bark during floods and bark protection against fire (Souza et al. 2019a).

With regard to soil nutrients, there is little information on fire effects for the Pantanal in the literature. One example is that in the Abobral subregion, where 7 years after fire, the amount of N in the soil was not different from unburned areas (Souza et al. 2019a). Similarly, the total N lost from the burned vegetation in a Cerrado area was compensated by atmospheric N input within 3 years (Pivello and Coutinho 1992).

In floodable savannas, the responses are not well established; however, there are indications that fire helps in maintaining the savanna physiognomy as the occupation of trees in grasslands is influenced by flood and fire. Grasslands in the Pantanal can be taken over by trees and shrubs such as *Tabebuia aurea*, *Byrsonima cydoniifolia*, and *Vochysia divergens.* Some species, such as *V. divergens*, tend to occupy grasslands in pluriannual cycles of high inundation levels, increasing the cover of woody elements and decreasing the volume of grasses available to cattle and native ungulate fauna of the Pantanal (see the encroachment Chap. 11). On the other hand, fire reduces the number of *V. divergens* individuals, and in this way, keeps more open physiognomies (Cunha and Junk 2004). Besides, the growth of *V. divergens* is reduced in years with low rainfall related to ENSO (El Niño-Southern Oscillation) (Fortes et al. 2018). This tree is, therefore, a typical colonizer of wet years and controlled by fire. On the other hand, the Pantanal has an unpredictable cycle of multiannual dry and wet years. In dry years, there is a tendency of some species typical of higher areas to migrate into the grasslands, such as *Erythroxylum anguifugum*, *Hymenaea stigonocarpa*, and even *Cereus bicolor*, being set back again in wetter years. In the long floodless period of 1960–1974, trees grew inside dry ponds and old river beds (Pott et al. 2014). The combination of fire and inundation can also clean such areas (Pott et al. 2014).

The corridor of fire and flood in the Pantanal (Fig. 18.6) is rich in monodominant stands. They form vast grasslands and savannas such as extensive areas of *Copernicia alba* in the Nabileque subregion and also areas of *Tabebuia aurea* and *Byrsonima cydoniifolia* (see the Chap. 2 on Vegetation Mapping and Chap. 8 on Monodominant Stands). It seems that these species can benefit from the condition of higher floods and fires (Fig. 18.16). For *Tabebuia aurea*, the combination of fire and flood also contributes to its monodominance (Manrique-Pineda et al. 2021). There are herbaceous monodominants, such as *Oryza* spp. The flooded grasslands with *Oryza latifolia*, *O. rufipogon*, *Hymenachne amplexicaulis*, and *Leersia hexandra* are the largest continuous areas of treeless grasslands in the Pantanal (Fig. 18.17), and we believe the interaction of fire and flood is shaping this physiognomy.

Sharp transitions between grassland and forest have been attributed mainly to flood gradients caused by topographic levels (Adámoli and Pott 1996). That is more the case of woody vegetation on *cordilheiras* (ridges or ancient levees) and forest islets. Nevertheless, in a vegetation study conducted along the Paraguay River, Arruda et al. (2016) found that the response of trees per species along the flooding

Fig. 18.16 Monodominant stands of *Tabebuia aurea* in the corridor of fire and flood in the Pantanal during a year-cycle of flooding (first photograph), dry phase (second), and fire (last)

gradient can change if the area is subjected to fire. After burning, many tree species can reduce the range of occurrence in the flooding gradient, making the transition from forest to grassland more abrupt. Thereby, sharp grassland-forest contrasts are primarily defined by fire/flood interaction. The fire alone can also be responsible for sharp grassland-forest transitions in non-flooded tropical savannas (Werger 1983). We believe that there such sharp grassland-forest transitions occur by additive effects since flooding favors grasses and grasses promote fire occurrence, and the opposite happens regarding fire-tolerant trees. Similar mosaic landscapes occur in

Fig. 18.17 Open grassland area dominated by *Oryza* spp. in the Pantanal of the Paraguay subregion (In the back: Serra do Amolar, western border of the Pantanal)

other tropical wetlands, such as Llanos (Armenteras et al. 2015), Everglades (Newman et al. 1998), and other such tropical or subtropical systems.

18.3.4 Fire, Flood, and the Management of Pantanal

It is almost a consensus about the Pantanal that if we exclude cattle and/or anthropogenic fire from grasslands, the biomass accumulation can promote catastrophic wildfires, even burning the tree crowns (Pott et al. 2014) with the risk of losses in flora and fauna. The exclusion of fire and grazing can lead to strong dominance of some grasses such as *Andropogon* spp., which accumulate a large amount of dry biomass, very flammable, as we witnessed in an experimental burning after 4 years, in the Nhecolândia subregion (Fig. 18.10). In many subregions, we have observed the buildup of fuel and practically inevitable wildfire. The Nhumirim preserve of 600 ha, a small area in the Pantanal, in a research farm of Embrapa, surrounded by a 10 m wide firebreak, caught fire in the fourth year of cattle exclosure. Likewise, besides an extraordinary fire control structure, the largest private reserve (SESC RPPN) of the Pantanal burned several times, though partially because of an intense fire watch. Different from African savannas, the Pantanal lacks large herds of native grazing animals, and this is why the ecosystem did not degenerate after cattle introduction, as these animals beneficially reduce the surplus of grass that otherwise would become fuel. There is a discussion on the role of cattle as firefighters in the Pantanal. Indeed, for the reasons explained above, cattle are particularly relevant. Besides, cattle ranching is the main economic activity in the Pantanal. Nevertheless, this role needs to be studied in experiments in various vegetation types to evaluate the benefits of cattle grazing as biomass consumers preventing fuel accumulation, thereby helping to control fires.

Floating meadows and long-flooded areas accumulate organic soil, mainly histosol, which burns in periodic very dry years, together with its seed bank. Such deeply burned areas are colonized by incoming seeds via water, wind, or animals. One of such pioneer species is *Cecropia pachystachya* that indicates burned areas (Arruda et al. 2016) and can grow on the floating meadows. (For the effects of fire and flood on the soil seed bank, see the Chap.15 on Seed Bank.)

The use of prescribed fire is still being evaluated for the Pantanal. There are some actions supported by Universidade Federal de Mato Grosso do Sul and IBAMA/PREVFOGO, where the main question is to find the best time of the year to set fire. Strategic, controlled burning can be applied to reduce damaging wildfires. We believe that it will be possible to create regulations for prescribed fire in the Pantanal within 4 or 5 years. Nowadays, the use of fire has many restrictions by the Brazilian Federal and the State legislations of Mato Grosso and Mato Grosso do Sul. The fire can be used as a management tool under controlled conditions and in certain months of the year, depending on the state.

In conclusion, we may say that fire is part of the Pantanal landscape and plays an essential role in determining its open and savanna-like physiognomy, mainly when combined with flooding. Fire has been occurring in the Pantanal on a long-timescale and may be considered an evolutive filter on selecting species and traits at the community level. Proper management of the Pantanal must include reliable information on fire and flood interactions and their consequences for the biota. At a global scale, climate changes can, in many cases, change the frequency and intensity of fires (Vanniére et al. 2011; Bixby et al. 2015). As a fire-prone environment, the Pantanal cannot stay without fire and is sensitive to climatic changes. Nevertheless, unplanned and catastrophic fires can negatively impact atmospheric conditions for aircraft, increase respiratory diseases, and destroy houses, bridges, and other infrastructures for local human populations. However, the strategic use of fire can help to control damaging wildfires. The administration of Everglades National Park in the USA burns each year many areas next to Miami, Florida, to prevent the impacts of smoke and uncontrolled fire (Everglades National Park et al. 2015). One essential tool is satellite monitoring that can track flood and fire and, allied to the knowledge on vegetation and its response to these phenomena, can help to set up a system to prescribe fire for this floodable savanna.

References

Ab'Sáber AN (1998) Roraima: os paradoxos de um grande incêndio ao fim do milênio. Estudos Avançados 12:227–231

Adámoli J, Pott A (1996) Estudo fitossociológico e ecológico do Pantanal dos Paiaguás. In: II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal, pp 215–225

Allem AC, Valls JFM (1987) Recursos Forrageiros Nativos do Pantanal Mato-Grossense. EMBRAPA, Brasilia

Armenteras D, Romero M, Galdino G (2015) Vegetation fire in the savannas of the Llanos Orientales of Colombia. Geophysical Res Abstracts 7:00463

Armstrong W, Hull H (1994) Mechanisms of flood tolerance plants. Acta Bot Neerl 43:307–358

Arruda WDS, Oldeland J, Paranhos Filho AC, Pott A, Cunha NL, Ishii IH, Damasceno-Junior GA (2016) Inundation and fire shape the structure of riparian forests in the Pantanal, Brazil. PLoS One 11:e0156825. https://doi.org/10.1371/journal.pone.0156825

Bendix J, Cowell CM (2010) Impacts of wildfire on the composition and structure of Riparian Forests in Southern California. Ecosystems 13:99–107

Bertazzoni EC, Damasceno-Júnior GA (2011) Aspectos da biologia e fenologia de *Oryza latifolia* Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Bot Brasilica 25:476–786

Bixby RJ, Cooper SD, Gresswell RE, Brown LE, Dahm CN, Dwire KA (2015) Fire effects on aquatic ecosystems: an assessment of the current state of the science. Freshw Sci 34:1340–1350

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol Evol 20:387–394

Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51

Bowen BJ, Pate JS (2004) Effect of season of burn on shoot recovery and post-fire flowering performance in the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). Austral Ecol 29:145–155

Candela A, Aronica G, Santoro M (2005) Effects of forest fires on flood frequency curves in a Mediterranean catchment. Hydrol Sci J 50:193–206

Cardoso EL, Crispim SMA, Rodrigues CAG, Barioni Júnior W (2000) Biomassa aérea e produção primária do estrato herbáceo em campo de *Elyonurus muticus* submetido à queima anual, no Pantanal. Pesqui Agropec Bras 35:1501–1507

Casco SL, Neiff JJ, de Neiff AP (2010) Ecological responses of two pioneer species to a hydrological connectivity gradient in riparian forests of the lower Paraná River. Plant Ecol 209:167–177

Cirne P, Scarano FR (2001) Resprouting and growth dynamics after fire of the clonal shrub *Andira legalis* (Leguminosae) in a sandy coastal plain in south-eastern Brazil. J Ecol 89:351–357

Cunha CND, Junk WJ (2004) Year-to-year changes in water level drive the invasion of *Vochysia divergens* in Pantanal grasslands. Appl Veg Sci 7:103–110

Damasceno-Junior GA, Semir J, dos Santos FAM, Leitão-Filho HF (2004) Tree mortality in a riparian forest at Rio Paraguai, Pantanal, Brazil, after an extreme flooding. Acta Bot Bras 18:839–846

Damasceno-Junior GA, Semir J, dos Santos FAM, Leitão-Filho HF (2005) Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200:119–135

De Simone O, Müller E, Junk WJ, Schmidt W (2002) Adaptations of Central Amazon tree species to prolonged flooding: root morphology and leaf longevity. Plant Biol 4:515–522

Ellenbroek GA (1987) Ecology and productivity of an African wetland system, Geobotany 9. Dr. W. Junk Publishers, The Hague, 267pp

Everglades National Park, Homestead F, National Park Service, US Department of the Interior (2015) Everglades National Park 2015 fire management plan. Washington, DC

Ferreira LV (2000) Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. Biodivers Conserv 9:1–14

Ferreira LV, Stohlgren TJ (1999) Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120:582–587

Ferreira-Júnior WG, Schaefer CEGR, Cunha CN, Duarte TG, Chieregatto LC, Carmo FMS (2016) Flood regime and water table determines tree distribution in a forest-savanna gradient in the Brazilian pantanal. An Acad Bras Cienc 88

Fichino BS, Dombroski JRG, Pivello VR, Fidelis A (2016) Does fire trigger seed germination in the neotropical Savannas? Experimental tests with six cerrado species. Biotropica 48:181–187

Fortes CF, Nunes-da-Cunha C, Rosa SA, Paixão E, Junk WJ, Schöngart J, Paixão E, Junk WJ (2018) Dendrochronological records of a pioneer tree species containing ENSO signal in the Pantanal, Brazil. Braz J Bot 41:167–174

Fortney RH, Benedict M, Gottgens JF, Walters TL, Leady BS, Rentch J (2004) Aquatic plant community composition and distribution along an inundation gradient at two ecologically-distinct sites in the Pantanal region of Brazil. Wetl Ecol Manag 12:575–585

Garnier LKM, Dajoz I (2001) Evolutionary significance of awn length variation in a clonal grass of fire-prone. Source Ecol 82:1720–1733

GEF, ANA, PNUMA, OEA (2004) Programa de Ações Estratégicas para o Gerenciamento Integrado do Pantanal e da Bacia do Alto Paraguai. Brasilia

Gould KA, Fredericksen TS, Morales F, Kennard D, Putz FE, Mostacedo B, Toledo M (2002) Post-fire tree regeneration in lowland Bolivia: implications for fire management. For Ecol Manage 165:225–234

Harley GL, Heyerdahl EK, Johnston JD, Olson DL (2020) Riparian and adjacent upland forests burned synchronously during dry years in eastern Oregon (1650–1900 CE), USA. Int J Wildl Fire. https://doi.org/10.1071/WF19101

Heinl M, Frost P, Vanderpost C, Sliva J (2007) Fire activity on drylands and floodplains in the southern Okavango Delta, Botswana. J Arid Environ 68:77–87

Heinl M, Sliva J, Tacheba B, Murray-Hudson M (2008) The relevance of fire frequency for the floodplain vegetation of the Okavango Delta, Botswana. Afr J Ecol 46:350–358

Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. J Ecol 88:213–229

INPE/Brasil (2017) Banco de Dados de Queimadas. Inst Pesqui Espac. http://www.inpe.br/queimadas/bdqueimadas/. Last accessed 20 Aug 2019

Junk W, Nunes da Cunha C (2012) Pasture clearing from invasive woody plants in the Pantanal: a tool for sustainable management or environmental destruction? Wetl Ecol Manag 20:111–122

Kohagura C, De Souza EB, Bao F, Ferreira FA, Pott A (2020) Flood and fire affect the soil seed bank of riparian forest in the Pantanal wetland. Rodriguésia 71:e00052018

Kubitzki K, Ziburski A (1994) Seed dispersal in flood plain forests of Amazonia. Biotropica 26:30

LASA (2020) Área queimada Pantanal 2020. Rio de Janeiro. https://lasa.ufrj.br/noticias/area-queimada-pantanal-2020/. Last accessed 10 Mar 2021

Libonati R, DaCamara CC, Peres LF, Sander de Carvalho LA, Garcia LC (2020) Rescue Brazil's burning Pantanal wetlands. Nature 588:217–219. https://doi.org/10.1038/d41586-020-03464-1

Lukac M, Pensa M, Shiller G (2011) Tree species' tolerance to water stress, salinity and fire. In: Forest management and the water cycle: an ecosystem-based, vol 212, pp 453–469

Main MB, Barry MJ (2002) Influence of season of fire on flowering of wet prairie grasses in South Florida, USA. Wetlands 22:430–434

Manrique-Pineda DA, de Souza EB, Paranhos Filho AC, Encina CCC, Damasceno-Junior GA (2021) Fire, flood and monodominance of Tabebuia aurea in Pantanal. For Ecol Manage 479:118599. https://doi.org/10.1016/j.foreco.2020.118599

Marques MCM, Joly CA (2000) Germinação e crescimento de *Calophyllum brasiliense* (Clusiaceae), uma espécie típica de florestas inundadas. Acta Bot Bras 14:113–120

Neves D, Damasceno-Junior G (2011) Post-fire phenology in a campo sujo vegetation in the Urucum plateau, Mato Grosso do Sul, Brazil. Braz J Biol 71:881–888

Newman S, Schuette J, Grace JB, Rutchey K, Fontaine T, Reddy KR, Pietrucha M (1998) Factors influencing cattail abundance in the northern Everglades. Aquat Bot 60:265–280

Oliveira Filho AT, Ratter JA (2002) Vegetation physiognomies and woody flora of the cerrado biome. cerrados Brazil Ecol an Nat Hist a Neotrop savanna (Oliveira PS, Marquis RJ (eds)). Columbia University Press, New York, pp 91–120

Oliveira MT d, Damasceno-Junior GA, Pott A, Paranhos Filho AC, Suarez YR, Parolin P (2014) Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence. For Ecol Manage 331:256–263

Otterstrom SM, Schwartz MW (2006) Responses to fire in selected tropical dry forest trees 1. Biotropica 38:592–598

Parolin P (2009) Submerged in darkness: adaptations to prolonged submergence by woody species of the Amazonian floodplains. Ann Bot 103:359–376

Parolin P, Wittmann F (2010) Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems. AoB Plants 2010:plq003

Parolin P, Oliveira AC, Piedade MTF, Wittmann F, Junk WJ (2002) Pioneer trees in Amazonian floodplains: three key species form monospecific stands in different habitats. Folia Geobot 37:225–238

Parolin P, De Simone O, Haase K, Waldhoff D, Rottenberger S, Kuhn U, Kesselmeier J, Kleiss B, Schmidt W, Piedade MTF, Junk WJ (2004) Central Amazonian Floodplain Forests: tree adaptations in a pulsing system. Bot Rev 70:357–380

Parolin P, Wittmann F, Ferreira LV (2013) Fruit and seed dispersal in Amazonian floodplain trees–a review. Ecotropica 19:19–36

Peixoto JL, Arruda AA de (2015) Interação regional dos grupos indígenas pré-coloniais que ocuparam a região das Grandes Lagoas do Pantanal e da Chiquitania. In: Alconini S, Betancourt CJ (eds) En el corazón de América del Sur 3 (Arqueología de las tierras bajas de Bolivia y zonas limítrofes). Imprenta 2E, Santa Cruz de la Sierra, pp 41–66

Pettit NE, Naiman RJ (2007a) Fire in the Riparian zone: characteristics and ecological consequences. Ecosystems 10:673–687

Pettit NE, Naiman RJ (2007b) Postfire response of flood-regenerating Riparian vegetation in a semi-arid landscape. Ecology 88:2094–2104

Pivello VR, Coutinho LM (1992) Transfer of macro-nutrients to the atmosphere during experimental burnings in an open cerrado (Brazilian savanna). J Trop Ecol 8:487–497

Pott A (1994) Ecossistema Pantanal. In: Puignau JP (ed) Utilizacion y manejo de pastizales. Montevideo, IICA-PROCISUR, pp 31–44

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa, Corumbá

Pott A, Oliveira A, Damasceno-Junior G, Silva J (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71:265–273

Pott A, Damasceno-junior GA, Pereira M (2014) Características da Bacia Hidrográfica do Rio Miranda. Rev GeoPantanal 16:125–140

Power MJ, Whitney BS, Mayle FE, Neves DM, de Boer EJ, Maclean KS (2016) Fire, climate and vegetation linkages in the Bolivian Chiquitano seasonally dry tropical forest. Philos Trans R Soc B Biol Sci 371:20150165

Prance G, Schaller GB (1982) Preliminary study of some vegetation types of the Pantanal, Mato Grosso. Brazil Brittonia 4

QGIS (2017) Guia do Usuário QGIS. https://docs.qgis.org/2.18/pt_BR/docs/user_manual/index.html. Last accessed 20 Aug 2019

Ramos-Neto MB, Pivello VR (2000) Lightning fires in a Brazilian Savanna National Park: rethinking management strategies. Environ Manage 26:675–684

Richardson CJ (2010) The Everglades: North America's subtropical wetland. Wetl Ecol Manag 18:517–542

Rivaben RC, Pott A, Bueno ML, Parolin P, Cordova MO, Oldeland J, da Silva RH, Damasceno-Junior GA, (2021) Do fire and flood interact to determine forest islet structure and diversity in a Neotropical wetland?. Flora 281:151874

Rocha M, Santos Júnior C, Damasceno-Júnior G, Pott V, Pott A, Rocha M, Santos Júnior C, Damasceno-Júnior G, Pott V, Pott A (2015) Effect of fire on a monodominant floating mat of *Cyperus giganteus* Vahl in a neotropical wetland. Braz J Biol 75:114–124

Rodríguez-González PM, Stella JC, Campelo F, Ferreira MT, Albuquerque A (2010) Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe. For Ecol Manage 259:2015–2025

Rorig ML, Ferguson SA (2002) The 2000 fire season: lightning-caused fires. J Appl Meteorol 41:786–791

Ruiz PL, Sah JP, Ross MS, Spitzig AA (2013) Tree Island response to fire and flooding in the short-hydroperiod marl prairie grasslands of the Florida everglades, USA. Fire Ecol 9:38–54

Sairam RK, Kumutha D, Ezhilmathi K, Deshmukh PS, Srivastava GC (2008) Physiology and biochemistry of waterlogging tolerance in plants. Biol Plant 52:401–412

Sánchez L, Seemüller W, Drewes H, Mateo L, González G, Silva A, Pampillón J, Martínez W, Cioce V, Cisneros D, Cimbaro S (2013) Long-Term Stability of the SIRGAS Reference Frame and Episodic Station Movements Caused by the Seismic Activity in the SIRGAS Region. In: Altamimi Z, Collilieux X (Eds.) Reference Frames for Applications in Geosciences, IAG Symposia 138:153–161. https://doi.org/10.1007/978-3-642-32998-2_24. Springer Berlin Heidelberg.

Schroeder W, Morisette JT, Csiszar I, Giglio L, Morton D, Justice CO, Schroeder W, Morisette JT, Csiszar I, Giglio L, Morton D, Justice CO (2005) Characterizing vegetation fire dynamics in Brazil through multisatellite data: common trends and practical issues. Earth Interact 9:1–26

Silva D, Klink CA (2001) Dinâmica de foliação e perfilhamento de duas gramíneas C4 e uma C3 nativas do Cerrado. Rev Bras Bot 24:441–446

Silverman BW (1986) Density estimation for statistics and data analysis. Chapman and Hall, New York

Soares VC, Scremin-Dias E, Daibes LF, Damasceno-Junior GA, Pott A, de Lima LB (2021) Fire has little to no effect on the enhancement of germination, but buried seeds may survive in a Neotropical wetland. Flora 151801. https://doi.org/10.1016/j.flora.2021.151801

Soto B, Díaz-Fierros F (1998) Runoff and soil erosion from areas of burnt scrub: comparison of experimental results with those predicted by the WEPP model. Catena 31:257–270

Souza AHA, Batalha MA, Casagrande JC, Rivaben R, Assunção VA, Pott A, Damasceno-Junior GA (2019a) Fire can weaken or trigger functional responses of trees to flooding in wetland forest patches. J Veg Sci 30:521–532

Souza EB, Damasceno-Junior GA, Pott A (2019b) Soil seed bank in Pantanal riparian forest: persistence, abundance, functional diversity and composition. Oecologia Aust 23:891–903

Thielen D, Schuchmann KL, Ramoni-Perazzi P, Marquez M, Rojas W, Quintero JI, Marques MI (2020) Quo vadis Pantanal? Expected precipitation extremes and drought dynamics from changing sea surface temperature. PLoS One 15:1–25. https://doi.org/10.1371/journal.pone.0227437

Tomas WM, de Oliveira RF, Morato RG, Medici PE, Chiaravalloti RM, Tortato FR, Penha JMF, Izzo TJ, Garcia LC, Lourival RFF, Girard P, Albuquerque NR, Almeida-Gomes M, Andrade MHS, Araujo FAS, Araujo AC, Arruda EC, Assunção VA, Battirola LD, Benites M, Bolzan FP, Boock JC, Bortolotto IM, Brasil MSS, Camilo AR, Campos Z, Carniello MA, Catella AC, Cheida CC, Crawshaw PG, Crispim SMA, Junior GAD, Desbiez ALJ, Dias FA, Eaton DP, Faggioni GP, Farinaccio MA, Fernandes JFA, Ferreira VL, Fischer EA, Fragoso CE, Freitas GO, Galvani F, Garcia AS, Garcia CM, Graciolli G, Guariento RD, Guedes NMR, Guerra A, Herrera HM, Hoogesteijn R, Ikeda SC, Juliano RS, Kantek DLZK, Keuroghlian A, Lacerda ACR, Lacerda ALR, Landeiro VL, Laps RR, Layme V, Leimgruber P, Rocha FL, Mamede S, Marques DKS, Marques MI, Mateus LAF, Moraes RN, Moreira TA, Mourão GM, Nicola RD, Nogueira DG, Nunes AP, Nunes da Cunha C, Oliveira MD, Oliveira MR, Paggi GM, Pellegrin AO, Pereira GMF, Peres IAHFS, Pinho JB, Pinto JOP, Pott A, Provete DB, dos Reis VDA, dos Reis LK, Renaud PC, Ribeiro DB, Rossetto OC, Sabino J, Rumiz D, Salis SM, Santana DJ, Santos SA, Sartori ÂL, Sato M, Schuchmann KL, Scremin-Dias E, Seixas GHF et al (2019) Sustainability agenda for the Pantanal wetland: perspectives on a collaborative interface for science, policy, and decision-making. Trop Conserv Sci 12

Tsheboeng G, Murray-Hudson M (2013) Spatial variation of population size structure of selected riparian tree species in the Okavango Delta, Botswana. Biodivers Ecol 5:341–350

Válio IFM, Scarpa FM (2001) Germination of seeds of tropical pioneer species under controlled and natural conditions. Rev Bras Bot 24:79–84

Vanniére B, Power MJ, Roberts N, Tinner W, Carrión J, Magny M, Bartlein P, Colombaroli D, Daniau AL, Finsinger W, Gil-Romera G, Kaltenrieder P, Pini R, Sadori L, Turner R, Valsecchi V, Vescovi E (2011) Circum-mediterranean fire activity and climate changes during the mid-holocene environmental transition (8500–2500 cal. BP). Holocene 21:53–73

Viganó HHG, de Souza CC, Reis Neto JF, Cristaldo MF, de Jesus L (2018) Previsão e Modelagem das Ocorrências de Incêndios no Pantanal. Rev Bras Meteorol 33:306–316

Werger MJA (1983) Tropical grasslands, savannas, woodlands: natural and manmade. In: Holzner W, Werger MJA, Ikusima I (eds) Man's impact on vegetation. Dr. W. Junk Publishers, The Hague/Boston/London, pp 107–137

Wittmann F, Zorzi BT, Tizianel FAT, Urquiza MVS, Faria RR, Sousa NM, Módena ÉS, Gamarra RM, Rosa ALM (2008) Tree species composition, structure, and aboveground wood biomass of a Riparian forest of the Lower Miranda River, Southern Pantanal, Brazil. Folia Geobot 43:397–411

Zigelski P, Lages F, Finckh M (2018) Seasonal changes of biodiversity patterns and habitat conditions in a flooded savanna – The Cameia National Park Biodiversity Observatory in the Upper Zambezi catchment, Angola. In: Revermann R, Krewenka KM, Schmiedel U, Olwoch JM, Helmschrot J, Jürgens N (eds) Climate change and adaptive land management in southern Africa: assessments, changes, challenges, and solutions. University of Hamburg, Hamburg, pp 438–449

Zirondi HL, Silveira FAO, Fidelis A (2019) Fire effects on seed germination: Heat shock and smoke on permeable vs impermeable seed coats. Flora Morphol Distrib Funct Ecol Plants 253

Chapter 19
Wild Food Plants of the Pantanal: Past, Present, and Future

Ieda Maria Bortolotto, Paulo Robson de Souza, Arnildo Pott, and Geraldo Alves Damasceno-Junior

19.1 Introduction

The food plants traditionally utilized by local people have been the target of several ethnobotanical studies aiming to identify species that were important for human populations in the past and persist nowadays or those that were abandoned (Arenas and Scarpa 2007; Turner and Turner 2008; Turner and Von Aderkas 2012; Cámara-Leret et al. 2014). Besides identifying temporal changes in the use of wild plants, the studies aim to identify the reasons for such changes (Turner and Von Aderkas 2012; Kalle and Sõukand 2016).

Considering that many species associated with several human cultures have been abandoned by the communities (Keller et al. 2005), and became scarce by deforestation, with the decline in the availability of plants (Hanazaki et al. 2013), there occurs, for example, a progressive loss of the biocultural heritage. The combined loss of species and associated know-how leads to a collapse of knowledge nets and undermines the resilience of the communities that depend on that biocultural connection (Cámara-Leret et al. 2019). Regarding the abandonment of the traditional use of plants in indigenous communities, for example, Arenas and Scarpa (2007) discuss that their traditional preparation methods are maintained when traditional foods are eaten.

Several projects have been developed in South America that aim to rescue and conserve the biocultural diversity and assure the food and nutritional security and sovereignty (Alcorn et al. 2010; Depenthal and Yoder 2017), also in Brazil (May

---

I. M. Bortolotto (✉) · A. Pott · G. A. Damasceno-Junior
Laboratório de Botânica, Instituto de Biociências, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil

P. R. de Souza
Laboratório de Prática de Ensino, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_19

and Vinha 2013; MMA 2016; Bortolotto et al. 2017), and to the benefit of the communities. The Program Plants for the Future, developed by the Brazilian government, organized a series of publications by regions of Brazil highlighting regionally important species that also have the potential of economic utilization for the future (MMA 2016). The Central-West region of Brazil, where the Pantanal is located, harbors a high number of traditionally used species that have a relevant potential for the future, though are as yet neglected. The Pantanal is particularly rich in plant species (see the Chap. 3 on Flora), and many of them have a high food potential (Pott and Pott 1994; Pott and Pott 2000; Bortolotto et al. 2018; Bortolotto et al. 2021). The conservation of these species implies their sustainable use and gains critical importance for close relatives of cultivated species, such as wild rice (Bertazzoni and Damasceno-Junior 2011), as they offer potential germplasm for genetic improvement (Karasawa et al. 2007).

Besides strengthening the communities with the valorization of the traditional foods that are part of their diet, the conservation of these species, tested and confirmed by traditional use, offers a range of opportunities to strengthen and propose new food products and services, including neglected or abandoned species. Moreover, to associate culture with the recognition of flood plants for present and future use is of great importance, particularly in countries with a high biological and cultural diversity, as is the case of Brazil.

In this chapter, we aimed to gather information on the native food species that were most important in the past and that were maintained or neglected (or abandoned) in urban and rural communities located along the Paraguay River, on the western edge of the Brazilian Pantanal, and that have a potential for alimentary use in the future. We also compiled information on the main peoples that traditionally inhabited the Pantanal and who were sources of knowledge on food plants.

19.2 Biocultural Diversity in the Pantanal

Brazil encompasses most of the Pantanal area of 138,183 km^2 (Silva and Abdon 1998) (78%), one of the largest continuous wetlands in the world, which also stretches into the territory of Bolivia (18%) and Paraguay (4%) (Adámoli 1982). The Brazilian Pantanal is located in the states of Mato Grosso (35.36%) and Mato Grosso do Sul (64.64%). The Pantanal plain is divided into 11 subregions (Silva and Abdon 1998). According to that subdivision, the floodplain of the Paraguay River, which runs north-south through the Pantanal, is called Pantanal of the Paraguay River, corresponding to 5.9% of the Pantanal plain. The western edge of the Pantanal comprises a floodplain on the border of Brazil with Bolivia and Paraguay; it also includes the residual uplands Urucum-Amolar (Brasil 1982), adjacent to the Paraguay River (Fig. 19.1).

The vegetation is a mosaic of floras from the Cerrado, Amazonia, the Chaco, and the Atlantic Forest (Adámoli 1982). In the various vegetation physiognomies that occur on floodplains and highlands (Prance and Schaller 1982), up to 1065 m

Fig. 19.1 Amolar hill adjacent to the Paraguay River in Corumbá, Mato Grosso do Sul, Brazil. Picture by Geraldo Alves Damasceno Junior

altitude (Brasil 1982), the Pantanal shelters over 2500 species of angiosperms (see the Chap. 3 on Flora). Besides that species richness, there is also a diverse cultural heritage formed by indigenous populations with different matrices (Bespalez 2015) and by non-indigenous populations that live in urban and rural areas, in traditional and nontraditional communities (Neuburger and Silva 2011), including small riverside communities and large cattle ranches (Silva and Silva 1995), or even small populations dispersed over some small areas along the Paraguay River, but within the Pantanal (Silva 2020). The composition of these peoples resulted from the migration of farmer peoples enforced by the Inca conquests in the Andean and tropical zones (Métraux 1946; Oliveira and Viana 2000), including indigenous people of the Chaco (Súsnik and Chase-Sardi 1995). The various ethnicities were composed of hunters, collectors, fishers, or farmers that occupied both uplands (hilly countries) and lowlands (floodable areas) (Oliveira 2002).

The Guató, canoeing and collector Indians, occupied large areas extending along the Paraguay River (Oliveira 2002). The Bororo occupied areas in the northern stretch of the upper Paraguay basin, including the São Lourenço River until its junction with the Cuiabá (Frič and Radin 1906). The Mbayá (belonging to the Guaicuru linguistic family, ancestors of the Kadiwéu that nowadays occupy a reserve in an area south of the Pantanal), lived along the Paraguay River in the Chaco. The same happened with the Layana, Terena, and Kinikinao (Métraux

Table 19.1 Indigenous People in the Pantanal (Mato Grosso do Sul – MS or Mato Grosso – MT, Brazil) mentioned in this Chapter; native language, past and current location, and source (reference)

Indigenous communities	Native language	Past location	Current location	Source
Payaguá (+)	*Payaguá (extinct and little-known language)	**Along the Paraguay River	No current record	*Barros (2013); **Oliveira (2002)
Mbayá: ancestors of the Kadiwéu (+)	Guaikuru linguistic family	Along the Paraguay River	No current record	Métraux (1946)
Kadiwéu (!)	Guaikuru linguistic family, Kaiwéu language	Chaco	Kadiwéu indigenous reserve (MS)	ISA (2020)
Guató (†, !)	*Macro-Jê linguistic trunk; Guató linguistic family, Guató language	** On the shores of Lakes Guaíba and Uberaba and the connected rivers such as the Paraguay River	***Ilha Ínsua (MS); Baia Guató and Barão de Melgaço municipality (MT)	*ISA (2020); **Métraux (1942); ***Oliveira (1996)
Chamacoco (!)	*Zamuco linguistic family, Chamacoco language	**Baía Negra (municipality of Porto Murtinho), south of Forte Coimbra (municipality of Corumbá) and surroundings	**Kadiwéu Indigenous Reserve (MS)	*Martins and Chamorro (2015); **Fabre (2007)
Terena (!)	*Aruak linguistic family, Terena language	**Along the Paraguay River	**Spread over seven municipalities (MS)	*Castro (2015); **ISA (2020)
Kinikinau (†, !)	*Aruak linguistic family, Kinikinau language	*Along the Paraguay River	**Kadiwéu Indigenous Reserve (MS)	*Castro (2015) **ISA (2020)
Layana (†, !)	*Aruak linguistic family	Along the Paraguay River	Scattered Indians (remnants), some live among the Terena and Kinikinau (MS)	*Castro (2015)
Umutina (!)	*Macro-Jê linguistic trunk; Bororo linguistic family, Umutina	**Along the Paraguay River	**Paraguay River (upper basin) and Barra dos Bugres (MT)	*ISA (2020); **Neuburger and Silva (2011)

(continued)

Table 19.1 (continued)

Indigenous communities	Native language	Past location	Current location	Source
Bororo (!)	*Macro-Jê linguistic trunk; Bororo linguistic family, Bororo language	**Northern stretch of the upper Paraguay basin including the São Lourenço River until its junction with the Cuiabá River	***Village of Teresa Cristina and village of Pirigara, upper basin (MT); ****on the banks of the São Lourenço River (MT)	*ISA (2020); **Frič and Radin (1906); ***Neuburger and Silva (2011); **** Silva (2020)

Symbols of the legend: + (considered extinct); † (considered extinct in the past); ! (remaining peoples) and * to **** (in the column source gives the source that cited the information presented in the other columns)

1946). Before they migrated to the Pantanal, Brazil, they lived in the Spanish colony that became Paraguay in 1811 (Table 19.1).

Among the remaining peoples, some with small populational groups still live in the Pantanal. They are peoples with distinct languages and cultures (Table 19.1) that still keep their ways of life and utilize resources as part of their diet (Oliveira 1996; Bittencourt and Ladeira 2000; Ribas et al. 2001; Bortolotto et al. 2015). Several indigenous peoples were considered extinct in the Pantanal or in the process of extinction, such as the Payaguá, known as “lords of the river” (Oliveira 2002) and the Mbayá (Métraux 1946). In the years 1940 and 1941, Schmidt (1949) met a Payaguá Indian woman in Assunción (Paraguay) who was a representant, at that time one of the few remaining members of that ethnic group that was so populous in the past. The author commented that there might be others “on the other bank of the Paraguay River,” but it would be difficult to identify them. According to Barros (2013), the last Payaguá speaker died in 1940, and both the Mbayá language and Payaguá are extinct (Table 19.1). Indeed, there is no record of this ethnicity in the Pantanal today. However, as other peoples seen as extinct in the past are emerging and are in the process of recognition, like Guató, Kinikinau, and Layana (Table 19.1), it is possible to think that these ethnic groups, or at least the biological descendants, are only hidden and not extinct. Many of these indigenous communities face the rapid decline of their ancestral languages. The Guató, Kinikinau and Chiquitano languages (Table 19.1) are classified as critically endangered, and Umutina language is considered extinct (Moseley 2010).

Nowadays, besides the Guató, considered extinct in the past, but living on the edge of the Uberaba Lake (Fig. 19.2), which is linked to the Paraguay River (Table 19.1), there are also isolated Indians and descendants living in small traditional communities, among big cattle ranches and the towns of Corumbá, Ladário, and Porto Murtinho, the latter in the Chaco area. Others migrated to the uplands, like the Bororo, or elsewhere in the Pantanal, away from the Paraguay River, e.g., the Terena, Kinikinau, and Kadiwéu (Table 19.1).

Fig. 19.2 View of the Guató village, on the edge of the Uberaba Lake, Corumbá, Mato Grosso do Sul, Brazil. (Picture by Ieda Maria Bortolotto)

Many Indians continued to stay in villages and small traditional communities located along the Paraguay River (Fig. 19.3), on the western edge of the Pantanal, next to descendants of European and African origin (Bortolotto and Amorozo 2012). The Albuquerque community is one of the oldest along the Paraguay River, founded at the end of the eighteenth century, in an area that was occupied by indigenous dwellers of various ethnicities (Bortolotto and Guarim-Neto 2004). Nowadays, the traditional communities and the Guató live from hunting, fishing, growing small subsistence crops, keeping some animal husbandry, craftsmanship, and, increasingly, tourism (Bortolotto and Amorozo 2012). Recent studies have discussed aspects related to sustainability in the rural area and demand public policies that respect essential social aspects of human life, intrinsically related to nature (Bortolotto et al. 2017; Chiaravalloti et al. 2017; Chiaravalloti 2019; Tomas et al. 2019).

19.3 Material and Methods

19.3.1 Historical Background

The data presented in this work were compiled from ethnobotanical and ethnographic studies or reports of chroniclers with information on the uses of food plants that occur in the Pantanal, especially for the Pantanal of the Paraguay River,

Fig. 19.3 Amolar community, Paraguay River, and hills in the background. (Picture by Ieda Maria Bortolotto)

Nhecolândia, Miranda, and Aquidauana (Silva and Abdon 1998), on the western edge of the Pantanal. We used primary and secondary sources (from the literature), mainly since the nineteenth century, but also used data on plants used by human populations since the European arrival in the sixteenth century. The species indicated as food by the indigenous peoples of the Chaco that moved to the borders of Paraguay, Bolivia, Argentina, and Brazil (Métraux 1942, 1946; Oberg 1949) were included when it concerned plant species that occur in the Pantanal vegetation (in Brazil) or were used by groups that migrated to Brazil.

As regards presently used food plants, we included species recently cited in ethnobotanical studies carried out along the Paraguay River (Bortolotto et al. 2015), (Bortolotto et al. 2019) or species used in cooking workshops carried out in communities in the Pantanal (Damasceno-Junior et al. 2010; Bortolotto et al. 2017). Edible species mentioned by some authors (Pott and Pott 1994; Pott and Pott 2000; Bortolotto et al. 2018) have been included to indicate the potential use of plants native to the Pantanal. Vernacular names (in Portuguese and the indigenous language) were included, as shown in the consulted literature. We also included species that occur on the hills of residual relief that remained in the floodplain.

For homonymous ethnospecies, such as *bocaiuva*, *ata*, *canjiqueira*, *jatobá*, wild rice, and *algarobo* belonging to genera such as *Acrocomia*, *Annona*, *Byrsonima*, *Hymenaea*, *Oryza*, and *Prosopis*, respectively, we added known food species that occur in the Pantanal nowadays and that are mentioned in other reports (Pott and Pott 1994; Pott and Pott 2000; Bortolotto et al. 2018; Sartori et al. 2018). We also included the recently described species of *bocaiuva* (*Acrocomia corumbaensis* S.A.Vianna) (Vianna 2017). Cavalcanti and Albuquerque (2013) defined as "hidden diversity" a set of different homonymous ethnospecies "hidden" under the same common name among the medicinal plants of the Northeast of Brazil. We will follow that line regarding food plants, thus widening the information on species richness with food uses occurring in the Pantanal.

19.3.2 Sources of Data on Plants

In the Pantanal, as well as in other Brazilian regions and other South American countries, the first reports on plants utilized by indigenous peoples were made by European colonizers; they used indigenous vernacular names or their own names (in the conqueror's language), often associating with similar food plants in their countries of origin, but these generally were not documented with botanical collections. A recent study that analyzed documents of the Portuguese crown that colonized the Brazilian coast after 1500 (Tomchinsky and Ming 2019) identified 183 native and exotic edible plant species used in the sixteenth to eighteenth centuries in Brazil. That study used letters and original documents, as well as textual descriptions and images available in old works, with information on the origin, distribution area, and the common names, to identify the mentioned species.

Unlike what occurred on the coast, the western Brazilian area now known as Pantanal started to be appropriated by the Spanish crown by provisions in the "Tratado de Tordesilhas" after the beginning of the sixteenth century (Cintra 2012). Thus, the letters and reports of travelers and chroniclers who participated in the Spanish crown expeditions are sources of historical and ethnographic data for the sixteenth to eighteenth centuries (Schuch 1995) and also represent the first historical sources on the indigenous food plants of the Pantanal. Of course, the indigenous ethnicities that lived in that region shared a territory without the borders presently established with the neighboring countries (Paraguay and Bolivia).

The Spanish conqueror Alvar Nuñez Cabeza de Vaca who entered the Pantanal in 1543 (Cabeza de Vaca 1555, Costa 1999), and Ulrico Schmidl (Schmidl 1903), a German soldier, who participated in Iberian expeditions in the period of 1536–1548 (Kloster and Sommer 1942), made the firsts reports on the plants used by the indigenous people. Georg Heinrich von Langsdorff, who led a scientific expedition between the years 1826 and 1828 (Silva et al. 1997), and Hercules Florence, one of the two illustrators in the team (Florence 2007), narrated several facts pertinent to the results of that expedition. They crossed the Pantanal and collected hundreds of specimens of the local fauna and flora, and they recorded usages and objects in drawings (Silva et al. 1997). Alfredo d'Escragnolle Taunay (Taunay 1868; Taunay 1931) was a military who was in the Aquidauana and Miranda Pantanal during the Paraguayan War at the end of the nineteenth century; he recorded mainly on the Chané and Guaná, but he also mentioned the Terena, Kinikinau, Laiana, Guaikurús, and other indigenous groups.

Max Schmidt, an ethnologist (Schmidt 1942), and Alberto Vojtěch Frič, an ethnographer and botanist (Frič and Radin 1906), studied the Guató and Bororo, respectively, both at the beginning of the twentieth century. Alfred Métraux was an anthropologist who assembled many data written about the Indian cultures of the Chaco from the sixteenth to the mid-twentieth centuries (Métraux 1946). Among the indigenous groups studied by them are those who lived in the north of the Chaco and the south and west of the state of "Matto Grosso" (Métraux 1942), presently being the State of Mato Grosso do Sul, created after the division of the former State of Mato Grosso in 1977. Kalervo Oberg was an anthropologist who studied the Terena and the Caduveo in the Pantanal (Oberg 1949).

Tekla Hartmann (Hartmann 1967) was, probably, the first researcher to use the term ethnobotany in a scientific report on the Pantanal and the first research woman in this region. She studied the nomenclature of plants used by the Bororo Indians in the second half of the twentieth century. In the same period, Jorge Eremites Oliveira carried out a study on the ethnohistory among the Guató, providing several names of food plants with their respective names in the Guató language (Oliveira 1996). Other historians collected primary data about the Pantanal indigenous human culture, including information on food plants used by them (Schuch 1995; Herberts 1998).

Many botanists (Conceição and Paula 1984; Berg 1986; Conceição and Paula 1990; Pott and Pott 1994; Guarim Neto et al. 2000; Pott and Pott 2000) gathered information about useful plants collected in the Pantanal. They made observations at the collection sites and linked that to literature sources and plant specimens deposited in herbaria. Several ethnobotanical studies carried out in communities along the Paraguay River have focused specifically on indigenous and traditional communities in Mato Grosso do Sul (Bortolotto and Damasceno-Junior 1998; Bortolotto 1999; Bortolotto et al. 2015; Bortolotto et al. 2019; Bortolotto 2006; Seleme et al. 2020), while other studies focusing on populations in Mato Grosso (Carniello 2007; Santos et al. 2016; de Morais and da Silva 2010) provided information on food plants used by them.

19.4 Results

19.4.1 Historical Background

The history of utilization of native food plants of the Pantanal is associated with the indigenous peoples that inhabited the region before European arrival in the sixteenth century. Archeological studies in the Pantanal suggest that the first human populations arrived circa 8000 years ago (Bespalez 2015); they explored animal and plant food resources all over the surroundings, i.e., in the floodplain, already

Fig. 19.4 Rock inscriptions at Caracará Hill, Poconé, Mato Grosso, Brazil. (Picture by Geraldo Alves Damasceno Junior)

using canoes, as well as on the slopes of the uplands of Urucum-Amolar. The farmer groups Guarani and Guaná that founded more stable settlements in the hills probably arrived after the first millennium of our era (Schmitz 2015). Besides the traces of those peoples at archeological sites, there are rupestrian inscriptions (sites of rupestrian art) at several points (Fig. 19.4) along the Paraguay River or lakes (Aguiar 2015).

When the first Iberic explorers reached the Pantanal, the indigenous populations of the Pantanal already cultivated food plants domesticated in the Americas (Costa 1999). In 1542, Domingos Martínez de Irala and Alvar Nuñez Cabeza de Vaca found the “Xaray”[1] on the Upper Paraguay River, which were good agriculturists, as were other indigenous tribes in the Upper Paraguay (Métraux 1942). Ulrich Schmidl mentioned “mannduis, turkish wheat, and the ‘mandeochade’” (Schmidl 1903), names that refer, respectively, to *Arachis hypogea* L., *Zea mays* L., and *Manihot esculenta* Crantz. Ulrich Schmidl mentioned two varieties of cassava consumed after being cooked.

In chronicler reports of the sixteenth century, there is little information on native food plants. Generally, the chroniclers referred to “fruits,” “heart of palms,” “roots,” or “seeds” consumed by the Indians. One of these, mentioned by Ulrich Schmidl in the contact period, would be the *mbocaja* palm fruits (*Acrocomia* sp.) (Schmidl 1903; Métraux 1942). Native and cultivated plants were also mentioned by Hercule Florence (Florence 2007) and by Georg Heinrich von Langsdorff (Silva

---

[1] Xaray were no longer known in the eighteenth century; “*In documents produced by Spanish conquerors of the 16th century, the Xaray are written as Xarayes or Jarayes, probably a Guarani nickname: savages of the river” (chara = unkempt, rude, “whooly” and y = water, river)*” (Oliveira and Viana 2000).

et al. 1997), between 1826 and 1828, during a scientific expedition lead by Langsdorff. Besides them, several ethnologists, ethnographers, and more recently ethnobotanists also recorded cultivated and wild plants used by indigenous peoples, especially for the Terena, Chamacoco, Kadiwéu, Guató, and Bororo (Taunay 1868; Frič and Radin 1906; Métraux 1942; Schmidt 1942; Hartmann 1967).

19.4.2 Wild Food Plants Used in the Past

We identified 67 ethnospecies of native plants cited in the literature as food in the past (between the sixteenth and mid-twentieth centuries) (Table 19.2). Those mentioned at the genus level, whose species are included in those listed in Table 19.2, are not considered here. Some ethnospecies were mentioned only by their genus or common name, such as rice, *bocaiuva* (*mbocaja* palm), acuri or uakuri, *algarobo*, and *guavira* (respectively *Oryza*, *Acrocomia*, *Attalea*, *Prosopis*, and *Campomanesia*) (Taunay 1868; Frič and Radin 1906; Métraux 1942; Schmidt 1942; Oberg 1949; Hartmann 1967; Silva et al. 1997; Florence 2007).

Some species were cited with synonyms or were certainly wrong. "Auassú," for example, was mentioned as *Attalea spectabilis* Mart., but that species does not occur in the Pantanal (see the Chap. 3 on Flora). The popular name auassú (babaçú) is traditionally associated with *Attalea speciosa* (Table 19.2). On the other hand, in Hartmann's work (1967), there is also possibly an identification error for "acuri or uakuri" (Table 19.2). Frič and Radin (1906) cited only the popular name "uakuri," and Hartmann (1967) mentioned *Attalea speciosa* Mart. ex Spreng. for the acuri palm. However, in the Pantanal, acuri is a popular name for *Attalea phalerata* and babaçu for *Attalea speciosa*, as mentioned above. Because of this, we are considering that both referred to *Attalea phalerata* when they mentioned the acuri or uakuri for the Bororo indigenous people. Also, other species were possibly mistaken in their identification. *Copernicia prunifera* (Mill.) H. E. Moore (mentioned by the synonym *Copernicia cerifera* (Arruda) Mart.), cited by Métraux (1946) for an indigenous group of the Chaco, probably is *Copernicia alba* (carandá); it is used as a food source by various indigenous people of the South American Chaco (Arenas and Scarpa 2007; Scarpa 2009). Other comments like this will be presented in the text below.

Even though some plants have been mentioned at the species level in other reports, it is likely that the indigenous peoples used all closely related, similar species and not only the one specifically mentioned by the researchers. Métraux (1946), for example, cited *Oryza perennis* Moench (synonym of *Oryza rufipogon* Griff.) for the Payaguá and Gauchi (extinct peoples) and the Mbayá, as will be discussed below. *Oryza rufipogon* is one of the three species of *Oryza* occurring in the Pantanal (Flora do Brasil 2020). To the list of plants with the same common names (ethnospecies) cited in the past (Table 19.2), we added 12 species as possible correspondent to those mentioned in the historical studies: bocaiuva (addition of 1 species), ata (2), guavira (5), arroz (2), and algaroba (2). But several species

Table 19.2 Wild food plants used in the past (from the fifteenth to the mid-twentieth century) mentioned in literature sources

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Alismataceae	*Echinodorus grandiflorus* (Cham. & Schltr.) Micheli	Chapéu-de-couro	Tuber	+	–	22
Alismataceae	*Limnocharis flava* (L.) Buchenau	Camalote	Leaf, stem, inflorescence	–	–	22
Alismataceae	*Sagittaria guayanensis* Kunth	Lagartixa, largatissa	Rhizome	–	–	22
Amaranthaceae	*Amaranthus viridis* L.	Caruru	Leaf	–	–	21
Anacardiaceae	*Anacardium humile* A. St.-Hil.	Cajuzinho-do-mato, cajuí, cajuzinho-do-cerrado, cajuzinho-do-campo	Seed (nut), succulent pedicel	–	+	1, 21
Anacardiaceae	*Spondias mombin* L.	Cajá, acaiá, caiá	Fruit	–	+	1, 2, 21
Annonaceae	*Annona aurantiaca* Barb. Rodrig.	Ata	Fruit	‡	–	5
Annonaceae	*Annona cacans* Warm.	Ariticum-cagão	Fruit	–	–	23
Annonaceae	*Annona coriacea* Mart.	Araticum, marolo, pinha-do-cerrado	Fruit	–	+	1
Annonaceae	*Annona cornifolia* A. St.-Hil.	Ata-do-campo	Fruit	+	+	2, 17, 21
Annonaceae	*Annona crassiflora* Mart.	Ata	Fruit	–	+	3
Annonaceae	*Annona dioica* A.St.-Hil.	Arixicum, ariticum	Fruit	–	–	21
Annonaceae	*Annona emarginata* (Schltdl.) H.Rainer	Arixicum-do-mato	Fruit	–	–	21
Annonaceae	*Annona montana* Macfad.	Ata	Fruit	–	–	23
Annonaceae	*Annona nutans* (R.E.Fr.) R.E.Fr.	Ata-brava	Fruit	–	+	2, 3
Annonaceae	*Annona sylvatica* A. St.-Hil.	Ata	Fruit	‡	–	5
Annonaceae	*Annona* sp.	Ata-do-campo	Fruit	–	+	2
Annonaceae	*Duguetia furfuracea* (A.St.-Hil.) Saff.	Ariticunzinho	Fruit	–	–	21
Annonaceae	*Xylopia aromatica* (Lam.) Mart.	Pimenta-de-macaco, pindaíva, pindaíba	Seed	–	+	1, 21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Apocynaceae	*Hancornia speciosa* Gomez	Mangaba, mangabeira, *báto í (Bo, 13)	Fruit	+	+	1, 2, 13, 21
Araceae	*Pistia stratiotes* L.	Alface-d'água	Cooked leaf	–	–	22
Araceae	*Urospatha sagittifolia* (Rudge) Schott	–	Rhizome	+	–	22
Araceae	*Xanthosoma striatipes* (Kunth & Bouché) Madison	Almeirão-do-brejo, banana-do-brejo	Spadix, tuber	+	–	22
Arecaceae	*Acrocomia aculeata* (Jacq.) Lodd. ex Mart. (mentioned by the synonym *Acrocomia glaucophylla* Drude (13)	Bocaiuva, macaúba, *áku (Bo, 13), *maguedji (Gt, 16), namogologi (Mb, 17)	Fruit pith, palm heart, seed, sap	+	+	1, 2, 3, 4, 13, 16, 17, 21
Arecaceae	*Acrocomia corumbaensis* S.A.Vianna	Bocaiuva, macaúba	Fruit, pith, palm heart, seed, sap	‡	+	5
Arecaceae	*Acrocomia* spp. (mentioned only by popular name (bocaiuva = similar to macaúba – *Acrocomia* sp.)	Bocaiuva, macauba, mbocaiá, *ecaié (Te, 18), *áku (Bo, 13), amukaya (Ki, 19)	Fruit, pith, palm heart, seed, sap, stipe	+	+	3 15, 18, 19, 20
Arecaceae	*Acrocomia totai* Mart.	Bocaiuva, macauba, mbocaiá, *namogologi (M-G, 11)	Fruit, pith, palm heart, seed, sap, long fibers in the lower part of the trunk (stipe)	+	+	11, 17
Arecaceae	*Allagoptera leucocalyx* Drude	Buri	Fruit, seed	–	+	2, 21
Arecaceae	*Attalea phalerata* Mart. ex Spreng. (mentioned by the synonym *Scheelea phalerata* (Mart. ex Spreng.) Burret (17); *Attalea speciosa* Mart. ex Spreng. (13) and with acepted name)	Acuri, *aucury (6), *mudjí (Gt, 16), *ápe or apído (Bo, 13), *exate (Ki, 19), *etchate (Kw, 17)	Fruit, leaf	+	+	1, 2, 3, 4, 6, 7, 9, 10, 13, 16, 17, 19, 21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Arecaceae	*Attalea speciosa* Mart. ex Spreng. (mentioned with the popular name "auassú" and as *Attalea spectabilis* Mart.)	Babaçu, auassú or Chatellôd (Gk, 6)	Fruit, seeds	+	–	6, 21
Arecaceae	*Bactris glaucescens* Drude	Tucum-azedo, tucum-preto, tucum-roxo, tucum-verde, tucum, *magueto (Gt, 16)	Fruit	+	+	1, 2, 3, 4, 16, 21
Arecaceae	*Bactris major* Mart.	Tucum-branco	Fruit	–	+	2
Arecaceae	*Bactris riparia* Barb. Rodr.	Tucum-vermelho	Fruit	–	+	2
Arecaceae	*Bactris* spp. (mentioned by the popular name tucum)	Tucum	Fruit	+	–	10
Arecaceae	*Butia leptospatha* (Burret) Noblick	–	Seed	–	–	23
Arecaceae	*Butia paraguayensis* Barb. Rodr. (mentioned by the synonym *Cocos paraguayensis* Barb. Rodr.)	Butiá, cabeçudo, *yatái-guazú (Mb, 11)	Palm heart, fruit, pith	+	+	1, 11
Arecaceae	*Copernicia alba* Morong ex Morong & Britton (mentioned by the synonym *Copernicia australis* Becc.)	Carandá, *mufá (Gt, 16); *hérena (Gu or Ch, 6); *tugúri (Bo)	Fruit, kernels, pith, palm heart, long fibers in the lower part of the trunk (stipe)	+	+	2, 3, 6, 11, 13, 16, 21
Arecaceae	*Desmoncus orthacanthos* Mart.	Urubamba, tucum-preto	Fruit	–	+	1, 2
Arecaceae	*Mauritia flexuosa* L. f. (mentioned by the synonym *Mauritia vinifera* Mart. and accepted name)	Buriti, *bority or *mority (Tp, 6), *bority maiana heréna (Gu or Ch, 6)	Fruit, stipe	+	–	1, 6, 21
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman	Jerivá, coquinho	Fruit, seed	–	+	1

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Arecaceae	*Syagrus flexuosa* (Mart.) Becc.	Acumã, acuman	Fruit, seed	–	–	21
Arecaceae	*Trithrinax schizophylla* Drude (mentioned by popular name carandaipé)	Carandaipé (11), carandilla, Carandaí		+	–	11, 23
Asteraceae	*Bidens pilosa* L.	Picão	Flower	–	–	21
Asteraceae	*Pacourina edulis* Aubl.	Pacurina	Floral receptacle	–	–	22
Asteraceae	*Stevia rebaudiana* (Bertoni) Bertoni	Caá-êhê (Gr, 23)	Plant	–	–	23
Balanophoraceae	*Langsdorffia hypogaea* Mart.	Paratudo	Inflorescence	–	–	21
Bignoniaceae	*Handroanthus heptaphyllus* (Vell.) Mattos	Piúva, piúva-do'pantanal, piúva-do-campo, piúva-roxa, peúva	Flower (petals)	–	–	21
Bignoniaceae	*Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore	Paratudo	Flower (petals)	–	–	21
Bixaceae	*Bixa orellana* L.	Urucu	Root	+	–	17
Bromeliaceae	*Ananas ananassoides* Baker	Abacaxizinho	Fruit	+	+	1, 2, 17, 21
Bromeliaceae	*Bromelia balansae* Mez.	Sussa, caraguatá (Bo, 21), gravatá, gravateiro	Fruit, young leaf	–	+	3, 21
Bromeliaceae	*Bromelia interior* L.B.Sm.	–	Fruit	–	–	23
Bromeliaceae	*Pseudananas sagenarius* (Arruda) Camargo	Abacaxi-do-mato	Fruit	–	–	23
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand	Almecega, almésca, armésca, amécicla	Seed (aryl)	–	–	21
Cactaceae	*Brasiliopuntia brasiliensis* (Willd.) A. Berger	–	Fruit	–	–	23
Cactaceae	*Cereus bicolor* Rizzini & Mattos	Urumbeva	Fruit	–	+	2
Cactaceae	*Opuntia* sp. (mentioned as *Opuntia* sp.)	Tuna (Barbary figs)	Fruit	+	–	11, 15

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Cactaceae	*Pereskia sacharosa* Griseb.	Amapola	Fruit	–	–	21
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg. (mentioned by the synonym *Celtis pubescens* Spreng.)	Taleira	Fruit	–	+	3, 21
Cannaceae	*Canna glauca L.*	Cana-do-brejo cana, bananinha-do-brejo, cana-do-brejo	Rhizome	–	–	21
Capparaceae	*Anisocapparis speciosa* (Griseb.) Cornejo & Iltis (mentioned by the synonym *Capparis speciosa* Griseb.)	Mangaba-brava, naranja del monte (spanish name)	Fruit, seed	+	+	1, 11
Capparaceae	*Capparicordis tweediana* (Eichler) Iltis & Cornejo	–	Fruit	–	–	23
Capparaceae	*Crateva tapia* L.	*Pajaguanaranka (Gr, 3), cabaceira, cabaceira-do-pantanal,cabeceira	Fruit	–	+	1, 21
Capparaceae	*Cynophalla retusa* (Griseb.) Cornejo & Iltis (mentioned by the synonym *Capparis retusa* Griseb.)	Poroto del monte (spanish name)	Pods	+	–	11, 21
Caricaceae	*Jacaratia corumbensis* Kuntze (mentioned by the synonym *Jacaratia hassleriana* Chodat)	Jaracatiá, cipoy (Chaco Indians)	Tuber, fruit	+	+	1, 11, 21
Caryocaraceae	*Caryocar brasiliense* Cambess.	Pequi, piqui, pequi-do-campo, pequizeiro, *éko í (Bo, 13)	Fruit	+	+	1, 2, 3,4, 6, 13, 21
Celastraceae	*Salacia elliptica* (Mart. ex Schult.) G. Don	Siputá, sitoba, mats´í (Gt, 16)	Fruit	+	+	1, 2, 9, 10, 17
Celastraceae	*Peritassa campestris* (Cambess.) A.C. Sm.	Bacupari	Fruit	–	–	23

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Celastraceae	*Tontelea micrantha* (Mart. ex Schult.) A.C. Sm.	Bacupari-do-cerrado, siputá-do-cerrado	Fruit	–	–	23
Chrysobalanaceae	*Couepia grandiflora* (Mart. & Zucc.) Benth.	Genciana, suquiana	Fruit	–	–	21
Chrysobalanaceae	*Couepia uiti* (Mart. & Zucc.) Benth. ex Hook.f.	Pateiro, fruta-de-pato, bola-de-bugio	fruit	–	+	1, 2, 3, 4, 21
Clusiaceae	*Garcinia gardneriana* (Planch. & Triana) Zappi	Acupari, cupari, bacupari	Fruit	–	+	1, 2, 21
Combretaceae	*Terminalia argentea* Mart. et Zucc.	Capitão	Trunk bark (tea)	–	–	21
Combretaceae	*Terminalia corrugata* (Ducke) Gere & Boatwr. (mentioned by the synonym *Buchenavia tomentosa* Eichler)	Tarumarana	Fruit	–	+	1, 2, 21
Convolvulaceae	*Ipomoea alba L.*	Viuviu, abre-noite-fecha-dia	Flower (chalice), seed	–	–	21
Costaceae	*Costus arabicus* L.	Caninha-do-brejo, cana- brava	Rhizome	–	–	21
Dilleniaceae	*Curatella americana* L.	Lixeira	Seed (aryl)	–	–	21
Dilleniaceae	*Doliocarpus dentatus* (Aubl.) Standl.	Cipó-de-fogo	Sap	–	–	21
Dioscoreaceae	*Dioscorea hassleriana* Chodat	–	Tuber	–	–	23
Dioscoreaceae	*Dioscorea trifida* L.	Japecanga	Tuber	–	–	21
Ebenaceae	*Diospyros lasiocalyx* (Mart.) B.Walln. (mentioned by the synonym *Diospyros hispida* A.DC.)	Fruta-de-boi, olho-de-boi	Fruit	–	+	2, 21
Ebenaceae	*Diospyros dalyom* B.Walln. (mentioned as *Diospyros obovata* Jacq.)	Olho-de-boi	Fruit	–	+	2, 21
Fabaceae	*Canavalia mattogrossensis* (Barb. Rodr.) Malme	Feijão-bravo, fijão-do-mato, faveirinho	Seed	–	–	21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Fabaceae	*Cassia grandis* L. (mentioned by the popular name)	Canafístula	Fruit	+	+	2, 12
Fabaceae	*Copaifera coriacea* Mart.	Guaranazinho	Seed (aryl)	–	–	21
Fabaceae	*Dipteryx alata* Vogel	Cumbaru, baru	Seed	–	+	1, 21
Fabaceae	*Discolobium pulchellum* Benth	Cortiça	Flower	–	–	22
Fabaceae	*Geoffroea spinosa* Jacq. (mentioned by the synonym *Geoffroea striata* (Willd.) Morong)	Amendoim-do-mato	Fruit, seed	–	+	3
Fabaceae	*Hymenaea courbaril* L.	Jatobá-mirim, jatobá-preto, jatobá	Seed (sarcotesta)	–	+	1, 2, 4, 21
Fabaceae	*Hymenaea martiana* Hayne	Jatobá	Fruit	–	+	23
Fabaceae	*Hymenaea* sp.	Jatobá, *muku (Gt, 9, 16), jatobá-da-floresta (13), *bokwadí (Bo 13)	Seed (sarcotesta)	+	–	6, 9, 13, 16
Fabaceae	*Hymenaea stigonocarpa* Mart. ex Hayne	Jatobá-cascudo, jatobá, jatobá-do-cerrado (13), rumága í (Bo, 13)	Seeds (sarcotesta)	+	+	1, 2, 4, 13, 21
Fabaceae	*Inga laurina* (Sw.) Willd.	Ingá	Fruit	–	+	3
Fabaceae	*Inga vera* Willd.	Ingá	Fruit	–	+	1, 2, 3
Fabaceae	*Phaseolus lunatus* L.	Feijãozinho, fejão-fava	Seed	–	–	23
Fabaceae	*Prosopis alba* Griseb.	Algaroba, algarobo	Fruit	+	–	11
Fabaceae	*Prosopis nigra* Hieron.	Algaroba, algarobo	Fruit	+	–	11
Fabaceae	*Prosopis rubriflora* Hassl.	Algarobo-preto	Fruit	‡	+	3
Fabaceae	*Prosopis ruscifolia* Griseb.	Algarobo	Fruit	‡	+	3, 21
Fabaceae	*Prosopis* spp. (mentioned only as popular name)	Algarobo, *havahú (Pa, 12)	Fruit	+	–	11, 12, 17

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Fabaceae	*Samanea tubulosa* (Benth.) Barneby & J.W. Grimes	Farinha-seca	Fruit	–	–	21
Fabaceae	*Senna occidentalis* (L.) Link	Fedegoso	Seed	–	+	1, 2, 3, 21
Fabaceae	*Vachellia farnesiana* (L.) Wight & Arn.	Aromita	Fruit	–	+	3
Icacinaceae	*Emmotum nitens* (Benth.) Miers	Sobre	Fruit	–	–	23
Lamiaceae	*Vitex cymosa* Bertero ex Spreng.	Tarumã, taruma (7), *madô (Gt, 16)	Fruit, flower	+	+	1, 2, 3, 7, 9, 10, 16, 21
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke(mentioned as the synonym *Vitex montevidensis* Cham.)	Tarumá	Fruit, flower	+	–	6, 11
Lecythidaceae	*Eschweilera nana* (O. Berg) Miers	Ovo-frito	Seed	–	–	23
Malpighiaceae	*Byrsonima arthropoda* A.Juss.	Uvinha	Fruit	–	+	1, 4, 21
Malpighiaceae	*Byrsonima chrysophylla* Kunth	Mureci-penina	Fruit	+	–	6
Malpighiaceae	*Byrsonima coccolobifolia* Kunth	Canjiqueira	Fruit	–	–	21
Malpighiaceae	*Byrsonima crassifolia* (L.) Kunth	Canjicão	Fruit	–	–	21
Malpighiaceae	*Byrsonima cydoniifolia* A.Juss. (mentioned as *B. orbignyana* A. Juss.)	Canjiqueira, canjiquinha, canjica, murici	Fruit	–	+	1, 2
Malpighiaceae	*Byrsonima intermedia* A. Juss.	Murici-do-campo	Fruit	–	–	23
Malpighiaceae	*Byrsonima verbascifolia* (L.) DC.	Mureci-do-pantanal	Fruit	+	–	6, 21
Malvaceae	*Guazuma ulmifolia* Lam.	Chico-magro, mutambo	Fruit	–	+	1, 2, 21
Malvaceae	*Sterculia apetala* (Jacq.) H. Karst	Mandovi, manduvi, manduvizeiro, amendoim-de-bugre	Seed	–	+	1, 21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Malvaceae	*Sterculia striata* A.St.-Hil. & Naudin (mentioned with the popular name mandubiru)	Manduvi, amendoim-de-arara, xixá, mandubirú (12)	Seed	+	+	1, 2, 12
Marantaceae	*Thalia geniculata L.*	Caeté, acité, banana-d'água	Rhizome	–	–	21
Melastomataceae	*Clidemia biserrata* DC.	Cambucá-do-campo, cambucá-do-firme	Fruit	–	+	1, 4
Melastomataceae	*Mouriri elliptica* Mart.	Coroa-de-frade, coroa	Fruit	–	+	1, 21
Melastomataceae	*Mouriri guianensis* Aubl.	Roncador, *môguâadô (Gt, 16)	Fruit	+	+	2, 16, 21
Menispermaceae	*Abuta grandifolia* (Mart.) Sandw.	Grão-de-galo	Fruit	–	+	1, 2. 4
Menispermaceae	*Disciphania ernstii* Eichler	Uva-do-mato	Fruit	–	+	1
Moraceae	*Sorocea saxicola* Hassl. (mentioned as *Sorocea sprucei* (Baill.) J.F. Macbr.)	Figueirinha, figueirinha-do-pantanal, leiteiro	Fruit	–	+	21
Moraceae	*Brosimum gaudichaudii* Trec.	Mama-cadela, algodãozinho, chiclete-do-cerrado	Fruit	–	+	1, 21
Moraceae	*Ficus pertusa* L.f.	Figueirinha* ou figueira-de-folha miúda	Fruit	–	–	23
Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	Amora-brava, taiuva	Fruit	–	+	1, 2, 21
Myrtaceae	*Campomanesia adamantium* (Cambess.) O. Berg	Guavira, gabiroba, guabiroba,	Fruit	‡	+	1, 3, 4
Myrtaceae	*Campomanesia eugenioides* (Cambess.) D. Legrand ex Landrum	Guavira, gabiroba, guabiroba,	Fruit	‡	–	21
Myrtaceae	*Campomanesia lineatifolia* Ruiz & Pav.	Guavira, gabiroba, guabiroba,	Fruit	‡	–	5

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Myrtaceae	*Campomanesia pubescens* (Mart. ex DC.) O. Berg	*Jokukuietái (Bo, 13)	Fruit	+	+	1, 4, 13
Myrtaceae	*Campomanesia sessiliflora* (O.Berg) Mattos	Guavira, gabiroba, guabiroba,	Fruit	‡	+	1, 21
Myrtaceae	*Campomanesia* sp. (mentioned as *Eugenia* spp.)	Guavira, guabiroba, araçá-do-campo	Fruit	+	–	6
Myrtaceae	*Campomanesia xanthocarpa* (Mart.) O.Berg	Guavira, gabiroba	Fruit	‡	–	5
Myrtaceae	*Eugenia aurata* O. Berg	–	Fruit	–	–	21
Myrtaceae	*Eugenia dysenterica* (Mart.) DC.	Cagaita, cagaiteira	Fruit	+	+	1, 6
Myrtaceae	*Eugenia egensis* DC.	–	Fruit	–	–	21
Myrtaceae	*Eugenia florida* DC.	–	Fruit	–	–	21
Myrtaceae	*Eugenia inundata* DC.	–	Fruit	–	–	21
Myrtaceae	*Eugenia involucrata* DC.	Cereja-do-cerrado	Fruit	–	+	1
Myrtaceae	*Eugenia matogrossensis* Sobral	Guariroba	Fruit	–	–	1
Myrtaceae	*Eugenia pitanga* (O. Berg) Kiaersk.	Pitanga	Fruit	–	+	1
Myrtaceae	*Eugenia punicifolia* (Kunth.) DC.	–	Fruit	–	–	23
Myrtaceae	*Eugenia pyriformis* Cambess.	Eucaliptinho	Fruit	–	–	21
Myrtaceae	*Eugenia stictopetala* Mart. ex DC. (mentioned by the synonym *Eugenia tapacumensis* O. Berg)	Cambucá, língua-de-cachorro	Fruit	–	–	21
Myrtaceae	*Eugenia repanda* O. Berg	–	Fruit	–	–	23
Myrtaceae	*Eugenia subterminalis* DC.	–	Fruit	–	–	23
Myrtaceae	*Eugenia uniflora* L.	Pitanga	Fruit	–	+	2, 3

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Myrtaceae	*Myrcia palustris* DC. (mentioned by the synonym *Gomidesia palustris* (DC.) Kaussel)	Balsemim, jacarezinho	Fruit	–	–	21
Myrtaceae	*Myrcia splendens* (Sw.) DC. (mentioned by the synonym *Myrcia fallax* (Rich.) DC.)	Miguá (Gt, 16)	Fruit	+	–	16, 21
Myrtaceae	*Plinia cauliflora* (DC.) Kausel	Jabuticaba, jabuticaba-nativa	Fruit	+	+	1, 3, 10
Myrtaceae	*Psidium acutangulum DC.*	Araçá	Fruit	–	+	1
Myrtaceae	*Psidium guineense* Sw.	Araçá	Fruit	–	–	21
Myrtaceae	*Psidium* sp.	Goiabinha, goiabinha-do-mato	Fruit	–	+	2
Myrtaceae	*Psidium* sp. (mentioned with the popular name)	Araçá-de-corôa	Fruit	+	–	6
Myrtaceae	*Psidium striatulum* Mart. ex DC. (mentioned by the synonym *Psidium persicifolium* O. Berg)	Goiabinha	Fruit	–	–	21
Myrtaceae	*Psidium sartorianum* (O. Berg) Nied.	Araçá	Fruit	–	–	23
Nymphaeaceae	*Nymphaea amazonum* Mart. & Zucc.	Lagartixa	Rhizome	+	–	22
Nymphaeaceae	*Victoria amazonica* (Poepp.) J.C. Sowerby* (mentioned with the popular name (9, 11) forno d-água and with the accepted name)	Forno d'água, vitória-régia, muguãtã (Gt, 16)	Seed, rhizome, petiole	+	+	1, 2, 9, 11, 16, 22
Olacaceae	*Ximenia americana* L.	Limão-bravo, limãozinho	Fruit	–	–	21
Opiliaceae	*Agonandra brasiliensis* Miers ex Benth & Hook.f.	Pau-marfim, tinge-cuia	Fruit	–	+	1, 21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Orchidaceae	*Vanilla palmarum* (Salzm. ex Lindl.) Lindl.	Baunilha-de-acuri	Fruit	–	+	1, 21
Passifloraceae	*Passiflora amethystina* J. C. Mikan	Maracujá	Fruit	–	–	23
Passifloraceae	*Passiflora cincinnata* Mast.	Maracujá-do-mato	Fruit	–	+	2
Passifloraceae	*Passiflora edulis* Sims	Maracujá	Fruit	–	+	23
Passifloraceae	*Passiflora foetida* L.	Maracujá-do-mato	Fruit	–	–	23
Passifloraceae	*Passiflora gibertii* N. E. Br.	Maracujazinho, maracujá-bravo, maracujá-do-mato	Fruit	–	+	1
Passifloraceae	*Passiflora misera* Kunth	Maracujá-do-mato, maracujá-nativo	Fruit	–	+	2
Passifloraceae	*Passiflora* sp. (mentioned by popular name maracujá)	Maracujá	Fruit	+	–	10
Piperaceae	*Piper aduncum* L.	Pimenta-do-mato	Fruit	–	+	21
Piperaceae	*Piper arboreum* L.	Pimenta-do-mato, pimenta-de-macaco, dedo- de-urubu	Fruit	–	–	21
Poaceae	*Leersia hexandra* Sw.	Felpudinho, grameiro, arrozinho, grama-do-brejo, capim-navalha	Seed	–	–	22
Poaceae	*Oryza grandiglumis* (Döll) Prod.	Arroz-do-campo	Seed	‡	–	5
Poaceae	*Oryza latifolia* Desv.* (sometimes mentioned as the synonym *Oryza alta* Swallen)	Arroz-do-campo, arroz-bravo, arroz-do-brejo, matchamo (Gt, 16)	Seed	+	+	1, 2, 4, 5, 16, 22, 23
Poaceae	*Oryza rufipogon* Griff. (Sometimes mentioned as the synonym *O. glumaepatula* Steud.)	Arroz-do-campo, *matchamo (Gt, 16)	Seed	+	–	1, 2, 4, 5, 11, 22, 23

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Poaceae	*Oryza* spp. (mentioned only as popular name or as *Oryza sativa* L.)	Wild rice, rice, nacacú (Gu or Ch 6)	Seed	+	–	6, 7, 8, 9, 10, 12, 14, 15
Polygonaceae	*Coccoloba ochreolata* Wedd.	Porô	Fruit	–	+	3
Polygonaceae	*Coccoloba parimensis* Benth.	Canjiquinha, rosarinho, uvinha	Fruit	–	+	2, 21
Polygonaceae	*Coccoloba rigida* Willd. ex Meisn.	Poró	Fruit, seed, pith, leaf	–	+	3
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	Camalote	leaf, flower	–	+	3, 22
Pontederiaceae	*Pontederia cordata* L.	Guapé, aguapé	Seed	–	–	22
Portulacaceae	*Portulaca grandiflora* Hook. (mentioned by the synonym *Portulaca fluvialis* D. Legrand)	Nove-horas, nove-hora, onze-horas	Leaf	–	–	21
Rhamnaceae	*Rhamnidium elaeocarpum* Reissek	Cabriteira	Fruit	–	+	2, 3, 21
Rhamnaceae	*Sarcomphalus mistol* (Griseb) Hauenschild.	Mistol	Fruit	+	+	3, 11
Rhamnaceae	*Ziziphus oblongifolius* Moore	Fruto-de-cabra, veludinho, olho-de-boi, *macariguá (Gt, 16)	Fruit	+	+	2, 16, 21
Rubiaceae	*Alibertia edulis* (Rich.) A. Rich. ex DC. (mentioned as "marmelada, from the Rubiaceae family")	Marmelo, marmelada, marmelada-olho-de-boi, marmelada-de-bola	Fruit	+	+	1, 2, 4, 6, 21
Rubiaceae	*Cordiera sessilis* (Vell.) Kuntze	Marmelada, marmelada- preta, marmelada-de-cachorro	Fruit	+	–	6, 21
Rubiaceae	*Genipa americana* L.	Jenipapo, jenipapeiro, *mató (Gt, 16); *bíe í (Bo, 13), *notiquigó (M-G)	Fruit	+	+	1, 2, 3, 13, 16, 21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Rubiaceae	*Randia heteromera* Judkevich & R.M. Salas (mentioned as *Randia armata* (Sw.) DC.)	Veludo-de-espinho, espinheiro, unha-de-gato	Fruit	–	–	21
Rubiaceae	*Rudgea viburnoides* (Cham.) Benth.	Veludo	Fruit	–	–	23
Rutaceae	*Esenbeckia almawillia* Kaastra	Côca (tea)	Leaf	–	+	2
Salicaceae	*Casearia sylvestris* Sw.	Chá-de-frade	Fruit	–	–	21
Sapindaceae	*Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	Cuncun	Fruit	–	–	23
Sapindaceae	*Allophylus pauciflorus* Radlk.	Cuncun	Fruit	–	–	23
Sapindaceae	*Cardiospermum halicacabum* L.	Poca	Seed, leaf	–	–	21
Sapindaceae	*Dilodendron bipinnatum* Radlk.	Mulher-pobre, maria- pobre, mãe-pobre	Seed	–	–	21
Sapindaceae	*Melicoccus lepidopetalus* Radlk.	Água-pomba, *mapó' (Gt, 16)	Fruit, seed	+	+	1, 2, 6, 16, 21
Sapindaceae	*Paullinia elegans* Cambess.	–	Seed (aryl)	–	–	21
Sapindaceae	*Paullinia pinnata* L.	Cipó-cinco-folha, fruta-de- pomba (1)	Seed (aryl)	–	–	21
Sapindaceae	*Talisia esculenta* (A. St.-Hil.) Radlk.	Pitomba	Fruit	–	+	1, 2
Sapotaceae	*Chrysophyllum marginatum* (Hook. & Arn.) Radlk	Leiteirinho, uvinha, pimenteira-de-aranquã	Fruit	–	–	21
Sapotaceae	*Pouteria gardneri* (Mart. & Miq.) Baehni	Frutinha-de-veado	Fruit	–	–	23
Sapotaceae	*Pouteria glomerata* (Miq.) Radlk.	Laranjinha-de-pacu, laranjinha, moranguinha, parada, *macondjê (Gt, 16)	Fruit	–	+	1, 2, 4, 21

(continued)

Table 19.2 (continued)

Family	Species and original source	Popular name; *indigenous name (ethnic group, source)	Edible plant parts	Pa	Pr	Pu (sources)
Sapotaceae	*Pouteria ramiflora* (Mart.) Radlk.	Fruta-de-veado, fruteira	Fruit	–	–	21
Sapotaceae	*Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn.	Guajuviraí, laranjinha-preta	Fruit	–	–	21
Solanaceae	*Capsicum baccatum* L.	Pimenta	Fruit	–	–	23
Solanaceae	*Physalis peruviana L.*	–	Fruit	–	–	21
Solanaceae	*Solanum paniculatum* L.	Jurubeba	Fruit	–	+	1, 3
Talinaceae	*Talinum fruticosum* (L.) Juss. (mentioned as the synonym *Talinum triangulare* (Jacq.) Willd.)	Caruru, alfavaca	Leaf, bud	–	–	21
Typhaceae	*Typha domingensis* Pers. (mentioned with the popular name totora)	Totora, taboa	Rhizome, seed, bud, pollen, young plant	+	–	17, 22
Urticaceae	*Cecropia pachystachya* Trec.	Embaúba, embauva	Fruit	–	+	2, 4, 21
Urticaceae	*Urera aurantiaca* Wedd.	Urtiga-de-pacu, urtiga, casanção	Fruit	–	–	21
Verbenaceae	*Lantana trifolia* L.	Cidreira (falsa), uvinha- do-campo	Fruit	–	–	21
Verbenaceae	*Lippia alba* (Mill.) N.E. Br. ex Britton & P. Wilson	Cidreira-do-campo, chá-de-zezinho	Leaf (tea)	–	–	23
Vitaceae	*Cissus campestris* (Baker) Planch.	Cipó-de-arraia	Fruit	–	–	21

Common Portuguese name and indigenous name, family and plant species (scientific name in original source), vegetation type, edible plant parts, and literature

popular name; *indigenous name (indigenous ethnicity): Bo (Bororo), Gu or Ch (Guaná or Chané), Gr (Guarani), Gk (Guaikuru), Gt (Guató), M-G (Mbayá-Guaikuru), Mb (Mbayá), Pa (Payaguá), Te (Terena). Pa (past), Pr (present), Pu (potential use). Confirmed use (+), no information (–), use in the past suggested in this work (‡). **Sources: 1** = Damasceno-Junior et al. (2010)**, 2** = Bortolotto et al. (2015)**, 3** = Bortolotto et al. (2019)**, 4** = Bortolotto et al. (2017)**, 5 = this work , 6** = Taunay (1868)**, 7** = Frič and Radin (1906)**, 8** = Silva et al. (1997)**, 9** = Schmidt (1942)**, 10** = Métraux (1942)**, 11**= Métraux (1946)**, 12** = Schmidt (1949)**, 13** = Hartmann (1967)**, 14** = Florence (2007)**, 15** = Oberg (1949)**, 16** = Oliveira (1996)**, 17** = Herberts (1998)**, 18** = Bittencourt and Ladeira (2000)**, 19** = Souza (2008)**, 20** = Schmídel (1903)**, 21** = Pott and Pott (1994)**, 22** = Pott and Pott (2000)**, 23** = Bortolotto et al. (2018)

identified so far only with their local name and mentioned by Hartmann (1967) for the Bororo still need proper botanical identification. That is the case for wild varieties such as “kanho,” “mxi,” or “óko,” which were not included here.

19.4.3 Wild Food Plants Used in the Present and with Potential Use

Besides the species used in the past, we included 96 known to be eaten nowadays in the Pantanal and 87 edible species occurring in the Pantanal with potential use. This totals to 211 species belonging to 134 genera and 61 botanical families (Table 19.2). All of these species have food potential for the future. Among the 67 species cited between the sixteenth and mid-twentieth centuries, 33 were not mentioned in the recent ethnobotanical studies (Bortolotto et al. 2015; Bortolotto et al. 2019). Some of these are well-known as food plants, e.g., *Prosopis alba* Griseb., *P. nigra* Hieron., *Attalea speciosa* Mart. *ex* Spreng., *Mauritia flexuosa* L.f., *Mouriri elliptica* Mart., *Byrsonima verbascifolia* (L.) DC., *Cynophalla retusa* (Griseb.) Cornejo & Iltis and *Typha domingensis* Pers. That omission may be partly due to the scarcity of recent studies on ethnobotany in the Pantanal (Ritter et al. 2015) that document the knowledge of local people based on botanical collection and identification. Further studies in other regions of the Pantanal would certainly result in a higher number of species.

However, it is possible that many of the edible species mentioned in Table 19.2 and which have not yet been recorded in ethnobotanical studies are not used or not known as food plants by current populations. Indeed, some traditionally used species have been totally abandoned and others only some uses have been maintained. However, as we will discuss below, these plants are relevant food resources for raw consumption; for the production of flours, oils, and drinks; and to supplement the diet; or they can be commercialized and linked to the traditional culture of local populations, and there are also species with a potential utilization as a medicine, or as building materials, or habitat for animals (Bortolotto and Amorozo 2012).

The species with the highest number of citations in the literature as a traditional diet of indigenous groups in the past are *Acrocomia* spp. (8), *Attalea phalerata* (8), *Oryza* spp. (8), *Copernicia alba* Morong *ex* Morong & Britton (4), *Prosopis* spp. (4), *Hymenaea* spp. (4), *Vitex* sp. (4), and *Victoria amazonica* (Poepp.) J.C. Sowerby (3). The most cited species in the literature sources consulted are presented in greater detail below.

19.4.4 Acrocomia spp.

Two species of *Acrocomia* are specifically cited for the Pantanal in the Lista de Espécies do Brasil (Table 19.2): *Acrocomia corumbaensis* S.A.Vianna and *Acrocomia totai* (Vianna 2017). *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. also occurs in Mato Grosso do Sul (Vianna and Campos-Rocha 2020) and is cited as a traditional food currently used (Bortolotto et al. 2015; Bortolotto et al. 2019), and for the Bororo also in the past, where it was cited under the synonym *Acrocomia glaucophylla* Drude. The mentioning of the palm tree as part of the diet as early as the sixteenth century possibly covered all these species, given the considerable dynamics of indigenous ethnicities at the time, and considering the diversity of indigenous names for *Acrocomia* spp. They are called bocaiuva and macauba in Portuguese, and in many indigenous languages their name is mbocaiá, namogologi (Mbayá-Guaicuru), ecaié (Terena), mudjí (Guató), áku (Bororo), and amukaya (Kinikinau).

There are few studies on the botanical classification by the indigenous peoples of the Pantanal, but the studies by Hartmann (1967) showed that the Bororo indigenous people distinguished more than one species of *Acrocomia*. According to this study, akó is the indigenous name for coconut of macaíba (*A. aculeata*) and akoréu í – akó the indigenous name for a variety of macaíba (*Acrocomia* sp.) – (réu = similar and í = tree), meaning: "tree with fruits similar to macaíba coconuts" or "bacaiúva."

A. aculeata has been used in South America since 11,200 B.P., and its probable spread from South America to Central South America would have been eased by the characteristics of the fresh fruits, representing an excellent food option to migrating people (Morcote-Ríos and Bernal 2001). These authors discuss that the fruits of *Acrocomia* spp. (Fig. 19.5a) have a fleshy and abundantly oily mesocarp, protected by an exocarp that is easily removable (Fig. 19.5b) during the trip. The seed can be discarded intact when the endocarp does not break readily.

Besides the fleshy mesocarp, the three local species of *Acrocomia* produce edible nuts and heart of palm. Metraux (1946) mentioned that the "mbocayá" fruits (*A. totai*) were eaten raw or boiled to make a thick mush; the kernels were eaten raw or were first roasted in the ashes to extract the seeds. According to the author, the Mbayá extracted the long fibers embedded in the starch from the lower part of the trunk and also drank the slightly fermented sap of the mbocaya palm (*Acrocomia* sp.,); sometimes they allowed the mush made of the fruits of this palm to ferment, but this beverage was hardly alcoholic and larvae which grew in the decayed stipe were much relished as food. Processed products, such as oils and flours from nut and pulp, are currently cited as part of the diet in communities along the Paraguay River in the Pantanal, but the oil was reported to be used only in the past (Bortolotto et al. 2015). On the Ínsua island, indigenous people drink a juice know as a nonalcoholic "chicha" prepared from the pulp of *Acrocomia* sp. (Bortolotto and Damasceno-Junior 1998).

Fig. 19.5 Palm (**a**) and fruits (**b**) of *Acrocomia* sp. (Pictures by Paulo Robson de Souza. Source of the picture b: Damasceno-Junior et al. (2010))

Nowadays, the species occur in various natural landscapes of the Pantanal, in seasonal forests, and in Cerrado, Chaco, and anthropic areas, such as home yards, old cropland, pastures, and roadsides, and build monodominant formations (Table 19.2). The oldest citation of a native species is of *bocaiuva* (*mbocaya*), already utilized (and possibly managed) by indigenous peoples in the past; it remains a most important species in the Pantanal (Bortolotto et al. 2015), demonstrating strong resilience. Cooking workshops to produce cake, juice, cookies, and loaves of bocaiuva flour have been developed to promote the eating and valorization of this species in the Pantanal (Bortolotto et al. 2017).

19.4.5 Attalea phalerata Mart. ex Spreng

Locally known as *acuri* (Table 19.2), *Attalea phalerata* (Fig. 19.6) occurs in monodominant formations (*acurizal*) in the Pantanal (Pott and Pott 1994) and had uses closely associated with the diet and culture of the Guató in the past (Schmidt 1942). That author discussed that the Indians practiced a type of agriculture, moving earth from the floodplain to build small mounds to cultivate. The seeds, pulp (Fig. 19.6), and palm heart of *A. phalerata* were used in the diet of the Guató (Schmidt 1942), the nuts being broken in small cavities in rocks (Métraux 1942). According to Schmidt (1942), each family had its areas of *A. phalerata* (*acurizal*) for *chicha* production, a slightly fermented alcoholic drink that the Indians much appreciated. Even though removing the leaves from the palm top to obtain the sap and prepare *chicha* caused the palm's death, there existed such extensive areas with *A. phalerata* that its sustainability and culture was maintained over time.

Frič and Radin (1906) observed and described the process of producing *chicha* from *A. phalerata*, as well as its consumption in 1905 while visiting the Bororo who lived on the banks of the São Lourenço River, an affluent of the Paraguay River, in quite the same way as described for the Guató. Those authors recorded that the sap was obtained from a hollow dug into the stem top of the "uakuri" (*A. phalerata*). The fermented juice was sucked up through a bamboo straw and then spit into a bowl (made of dry fruit).

That report demonstrated the concern about the influence of civilization on the Bororo and its impact on their traditional lifestyle (Frič and Radin 1906). *A. phalerata* is still known as a food plant (Bortolotto et al. 2015) (Bortolotto et al. 2019), but the consumption of *chicha* obtained from the fermented sap was not mentioned in those studies, nor in Hartmann (1967). *A. phalerata* was considered a pasture weed (Nunes 2001).

Fig. 19.6 Ripe fruits (**a**) and dehydrated pulp (**b**) of *Attalea phalerata.* (Pictures by Ieda Maria Bortolotto (**a**) and Paulo Robson de Souza (**b**). Source of the picture **a**: Bortolotto et al. (2017). Source of the picture **b**: Damasceno-Junior et al. (2010))

19.4.6 Oryza spp.

Several authors in different epochs mentioned the natural *arrozais* or stands of wild rice (*Oryza* spp.) and its consumption (Table 19.2) for various indigenous ethnicities, such as the Guató (Métraux 1946; Oliveira 1996; Silva et al. 1997; Florence 2007), the extinct Payaguá (Schmidt 1949), and the Terena and Kadiwéu (Métraux 1946; Oberg 1949). Possibly, the *arrozais* have drawn attention because they form more conspicuous, monodominant formations (see the Chap. 8 on Monodominants) that occupy extensive areas in the Paraguay River floodplain (Bertazzoni and Damasceno-Junior 2011). These are species similar to the cultivated rice (*O. sativa* L.). Langsdorff reported in his diary that he had observed the *arrozais* in December and January. That means that he did not see it in fructification since that occurs only in the flood period (May and June) (Bertazzoni and Damasceno-Junior 2011). Even so, he wrote that the grain had a black shell and that for 40 years it occupied those areas without management. That evidently is information that he heard from the riverside people or from somebody who knew. About management practices, Hercule Florence, illustrator of the Langsdorff Expedition, mentioned that for "lack of cultivation, the grain has quality inferior to ours," indicating the Eurocentric vision of that time.

At present, three species of *Oryza* are recorded for the Pantanal (Tables 19.1 and 19.2) (see the Lista de Espécies da Flora do Brasil) (Filgueiras et al. 2015). However, in several sources, wild rice is generally mentioned only by its common name. About the rice that he saw the Guató harvesting near the Lake Gaíba, Schmidt (1951) thought it was *O. sativa* (and not the American wild rice) left by the Spanish on their first voyages to the region. Nevertheless, he comments that the plant would not have any cultivation practice once the rice "sown by the Spanish" kept growing as a wild plant without the influence of the Guató on its propagation (the same observation was made by Langsdorff, cited above). The occurrence of three species of *Oryza* in the Pantanal indicates that Schmidt would be mistaken about the origin of the species. Métraux (1946), in turn, referred to *O. perennis* Moench, a synonym of *O. rufipogon* Griff., as one of the species identified for the Pantanal.

Wild rice was widely consumed by the Indians of the Paraguay River. At flood time, the Guató and Payaguá harvested the rice shaking the grains into their canoes and store that (Métraux 1942; Schmidt 1942; Florence 2007). A similar process is described for the harvest of the wild rice *Zizania* spp. in North America (Métraux 1946). Pott and Pott (1994) mentioned the use of wild rice (*Oryza* spp.) in the Pantanal by people of the Paraguay River at the end of the twentieth century. However, at the beginning of the twenty-first century, such use was no longer observed (Bortolotto et al. 2015). In contrast, in North America, until today, *Zizania aquatica* is harvested still using the traditional process (Turner and Von Aderkas 2012). A strategy that contributed favorably to the incorporation of the indigenous species to the diet was the name "wild rice," adopted for *Zizania*, thus giving it a meaning to people familiar with eating cultivated rice (*O. sativa*) (Turner and Von Aderkas 2012). The vernacular name "rice" was also adopted in the Pantanal, but different from what happened with *Zizania* spp., the native species were kept restricted to the local people, not being incorporated into the diet countrywide.

That has changed somewhat in the later years: the Guató indigenous people and other riverside communities of the Paraguay River became involved in projects aiming to recover this cultural practice (Bortolotto et al. 2017). These projects developed the utilization of the rice with harvest practices similar to those described above. The postharvest process includes stamping the grains and separation of the shell using a sieve. Métraux (1946) commented, based on José Sánches Labrador (Sánches Labrador 1910), that the Indians ate the rice without removing the shell. In the mentioned workshops, however, the process of removing the shell was adopted, since an elderly Guató woman (still speaking the Guató language) told us that when she was a child, that practice was used, and she learned it from her mother.

Most rice species, such as *O. latifolia* and *O. rufipogon*, have an awn that can be removed by stamping and sieving. *O. rufipogon*, for example, has awns (Fig. 19.7 a) of 6 to 16 cm in length (Rosa et al. 2006). The awn was mentioned as one of the inconveniences at harvest time, as it was necessary to protect one's eyes, mouth, nose nostrils, and ears to prevent irritation. These species are also strategic for in situ conservation of germplasm, as they are close relatives of the cultivated species. *O. rufipogon* has an AA genome, the same type as *O. sativa*, and has potential for genetic improvement of cultivated rice (Karasawa et al. 2007).

19.4.7 Copernicia alba Morong ex Morong & Britton

Copernicia alba is a palm (Fig. 19.8) typical of the Chaco, and it occurs in monodominant formations in the Pantanal called *carandazal*, frequently around alkaline ponds locally named *salinas* (Pott and Pott 1994). The fruit, nut, and palm heart were mentioned as part of the culture of the Guató, Terena, Bororo, and Kadiwéu (Métraux 1946; Oberg 1949; Hartmann 1967). Taunay (1868) commented that oil was extracted from the fruits and that it was edible. Especially, the Chaco Indians consumed the palm heart fresh, cooked in water or baked in ashes; the flour obtained from the grilled and ground heart of palm was used for cakes and porridge; the nut was consumed fresh or roasted (Métraux 1946).

The fruits (Fig. 19.8) and the palm heart are still used as food items in Porto Murtinho, where this species is one of the most valuable for use, also considering the importance of the stipe and leaves for construction and handicrafts (Silva 2018; Bortolotto et al. 2019; Seleme et al. 2020). A recent doctoral thesis discussed strategies for the sustainable use of *C. alba*, especially for the use of fruit pulp, which has nutritional value and is an excellent food potential (Silva 2018). In neighboring countries, such as Argentina, Paraguay, and Bolivia, this species has been reported as part of the Gran Chaco indigenous people diet (Schmeda-Hirschmann 1994; Arenas and Scarpa 2007; Scarpa 2009).

Fig. 19.7 Rice (*Oryza spp.*) (**a**) with awn (*Oryza rufipogon*) and peeled grain (*Oryza latifolia)* (**b**). (Pictures by Paulo Robson de Souza (**a**) e Ieda Maria Bortolotto (**b**))

19.4.8 *Prosopis* spp.

Algarobo is a popular name for species of *Prosopis* in the Gran Chaco. The algaroba pods are known to be part of the diet of the Chaco indigenous peoples for production of flour, the preparation of bread and cakes, and brewing an alcoholic drink (beer) (Table 19.2). *Prosopis alba* Griseb. and *P. ruscifolia* Griseb. were cited as being used in the past, and currently *P. ruscifolia* and *P. rubriflora* Hassl. were recorded for Porto Murtinho (Souza-Lima et al. 2017; Sartori et al. 2018). Algaroba pods were among the main plant foods of the Chamacoco, Mbayá, and other Chaco Indians (Métraux 1946). Many forms of consumption and preparation of the pods were mentioned. Algaroba pods (Fig. 19.9) were crushed in a mortar and eaten as mush, and the algaroba flour could be stored and used to make cakes. During the algaroba season (November to February), large quantities of beer were brewed every day (Métraux 1946).

Fig. 19.8 *Copernicia alba* palm with fruits. (Picture by Paulo Robson de Souza)

Fig. 19.9 Algaroba (*Prosopis* sp.) fruits. (Picture by Paulo Robson de Souza)

The utilization of fruits of *P. ruscifolia* and *P. rubriflora* was mentioned for the production of flour in Porto Murtinho, Brazil, as well as a *chicha* (beer) (Bortolotto et al. 2019), but with an inferior use value. An algaroba beer prepared with *P. alba* fruits is also consumed in Argentina and Bolivia (Cano et al. 2020). Algaroba beer and the flour produced from *Prosopis* pods are also used in several countries in South America (Lévi-Strauss 1952). Despite its potential use, even with the possibility of being stored, its present use in the Pantanal is minimal. Moreover, it is the same in other countries of the Gran Chaco (Bolivia and Argentina), where alternative projects in poor communities promote the commercialization of algarobo flour (*Prosopis alba*, “native carob”) (Alcorn et al. 2010).

19.4.9 *Hymenaea* spp.

Jatobá is the popular name for three *Hymenaea* species in the Pantanal, *H. courbaril* L., *H. martiana* Hayne, and *Hymenaea stigonocarpa* Mart. ex Hayne (see the Chap. 3 on Flora). These tree species also occur in the Cerrado (*H. stigonocarpa*) and in the seasonal forests and riparian forests (Table 19.2) with fruits that are traditionally (Fig. 19.10) used in the diet because of the farinaceous pulp (sarcotesta). In addition to the name *jatobá*, residents currently distinguish these species with several other names (Table 19.2). In Bororo language, bokwadí means “jatobá-da-floresta” (*Hymenaea* sp.) and rumága í means “jatobá-do-cerrado” (*H. stigonocarpa*) (Hartmann 1967), again showing the potential of indigenous peoples in species differentiation, even though they are morphologically very similar.

The farinaceous pulp has a strong aroma, has a high caloric value, and is rich in magnesium and copper (Damasceno-Junior and Souza 2010). People who are not familiar with the strong aroma may reject the raw flour, but it becomes mild in derived dishes. However, in many indigenous and traditional communities in Brazil, the *Hymenaea* species are strongly associated with local culture and are

Fig. 19.10 *Hymenaea* sp. (jatobá) fruits, with farinaceous pulp. (Picture by Paulo Robson de Souza. Source: Bortolotto et al. 2017)

traditionally used in the diet (Lévi-Strauss 2004). It can be consumed unprocessed or used in cakes, bread, juices, porridge, and other dishes (Damasceno-Junior and Souza 2010). The nuts were also reported to have food value for the South American Indians (Lévi-Strauss 1952). The *Hymenaea* species are used for very different purposes, including medicinal, fuel, and wood source uses (Lévi-Strauss 1952; Bortolotto et al. 2015; Miguéis et al. 2019). Although it is an important food resource, with a rich nutritional value, with abundant fruit, and indeed was much used in the past, these species presently are neglected in the Pantanal. Nevertheless, they have been the target of extension actions for their valorization as food plants.

19.4.10 *Vitex cymosa* Bertero ex Spreng.

Tarumã (*Vitex* spp.) are arboreal species from riparian forests of the Pantanal, with fleshy drupes, whose color varies from purple to black when ripe (Fig. 19.11). Besides *V. cymosa*, which is very common, Taunay (1931) mentioned *Vitex megapotamica* (Spreng.) Moldenke (Table 19.2), whose characteristics are similar. According to him, in December 1866, it was the main food of the Kinikinao people of the hills. Fruits of both species can be consumed naturally or as sweets and are a traditional food in South America (Lévi-Strauss 1952; Guevara et al. 2020). Raw fruits have a strong odor considered unpleasant by those not used to consume them (the taste is a bit bitter), softened at processing. Fruits are abundant and an excellent resource to add to a diet. As a result, its use has been encouraged in recent years (Bortolotto et al. 2017). Cooking workshops have been developed in the communities where the production of preserved sweets of *Vitex* has been the main

Fig. 19.11 *Vitex cymosa* (*tarumã*) ripening fruits. (Picture by Paulo Robson de Souza)

item. When added to a traditional coconut sweet (produced with *Cocos nucifera* L.), it produces different flavors with contrasting colors.

19.4.11 Victoria amazonica Planch. ex Casp.

Victoria amazonica or vitória-régia, the Victoria lily, a rooted floating plant known as forno-d'água (probably because the leaf shape resembles a baking sheet) in the Pantanal subregion of the Paraguay River, "with floury grains similar to corn," is also mentioned as edible for the Guató (Métraux 1942, 1946; Schmidt 1942; Oliveira 1996). This species was one of the three aquatic food species mentioned as presently used by riverside communities of the Paraguay River (Bortolotto et al. 2015). In that report, the residents cited its use for starch made from the seeds after being peeled and crushed with a pestle (Fig. 19.12). Considering that the seeds are essential to regenerate the small population in the Pantanal, it was suggested to use them with restriction (Damasceno-Junior and Souza 2010). While hydrophytes grow abundantly in the Pantanal and 21 species of hydrophytes with food potential were listed, they still constitute a little-utilized potential in the area (Pott and Pott 2000; Bortolotto et al. 2018).

19.4.12 Other Native Food Species of the Pantanal

In addition to these species, which are among the most cited in historical sources and that are still used in some way or have their use stimulated at present, there are several native food plants that occur in the Chaco areas in the south of the Pantanal. Some of those species are abundant but not mentioned in recent ethnobotanical studies in the Pantanal. We highlight *Typha domingensis* Pers., the cattail, a hydrophyte with a wide geographical distribution. It is best known for using some of its plant parts for the confection of handmade mats and pillows. However, the pollen provides excellent food to indigenous groups of the Chaco in Argentina and Paraguay, both because of its nutritional value and availability in periods of scarcity of fruits and vegetables (Arenas and Scarpa 2003). Their rhizomes contain starch, and their "palm hearts" (Fig. 19.13) are edible. The species is frequent in the Pantanal and has a good potential for utilization as a food source or as fibers for handicrafts, with little danger of hampering its regeneration because it readily regrows and, in fact, often behaves like a weed (Silveira et al. 2012).

Other neglected food species that were eaten in the past in the Pantanal are *Anisocapparis speciosa* (Fig. 19.14), called *mangaba-brava* (Portuguese) or *naranja del monte* (Spanish), and *Cynophalla retusa*, both species belonging to the Capparaceae (Table 19.2). Their fleshy fruits must be cooked several times in fresh water to remove the bitter taste; afterward, they used to be stamped and sun-dried (Lévi-Strauss 1952). The people of the Chaco (biome) consumed fruits *in natura*

Fig. 19.12 Fruits (**a**) and seeds (**b**) of *Victoria amazonica*. (Pictures by Paulo Robson de Souza. Source of the picture **a**: Damasceno-Junior et al. 2010)

(raw), cooked or baked, and processed their pulp and nuts to produce oils, flours, and drinks; their "palm hearts" were eaten raw, cooked or baked, and their roots were cooked or baked (Métraux 1946). Food processing, such as *algarobo* flour, baked "palm heart," nuts that could be stored for several months, was an essential procedure for shortage periods. Lévi-Strauss also mentioned food storage in the Chaco "...as soon as the rains stop, in April, the surplus of wild fruits are put to dry in the sun, for provisions for the winter and the plantation plots are prepared" (Lévi-Strauss 2004). These species cited for the Chaco were also mentioned in several studies in the nearby countries (Argentina, Paraguay, and Bolivia) (Schmeda-Hirschmann 1994; Arenas and Scarpa 2007; Scarpa 2009).

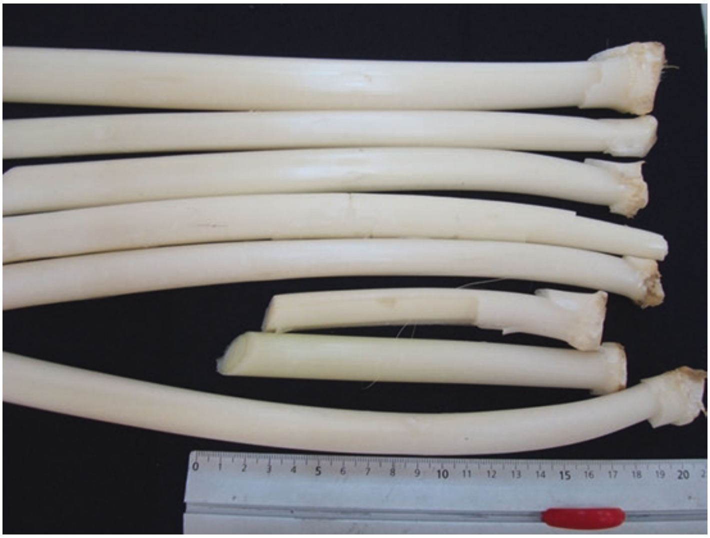


Fig. 19.13 "Palm heart" of *Typha domingensis*. (Picture by Iria Hiromi Ishii)

Fig. 19.14 *Anisocapparis speciosa* fruits and seeds. (Pictures by Paulo Robson de Souza)

A report on the Terena and Kadiwéu (Miranda, MS) mentioned, besides *algarobo* (*Prosopis* sp.) and wild rice (*Oryza* spp.), a great variety of palms (Table 19.1) and the Barbary fig (*Opuntia* sp.) (Métraux 1946). The species of *Opuntia* were not mentioned in recent ethnobotanical studies in the Brazilian Chaco (Bortolotto et al. 2019), despite their occurrence in native landscapes (Sartori et al. 2018): they occur with nine species in ethnobotanical studies on ten ethnicities of the Grand Chaco (Scarpa 2009).

There are few data on the plants that were part of the food habits of the Payaguá, who became already extinct in the seventeenth century. Apart from the rice already mentioned, that people consumed *algaroba*, *canafístula*, and *mandubiru* (Schmidt 1949). That author mentioned only the common names, but his description suggested that these were *Prosopis* spp., *Cassia grandis* L.f., and *Sterculia striata*

A.St.-Hil. & Naudin, respectively. About *algaroba* (*algarobo*), he mentioned that they had fruits very similar to those used for *chicha* by neighboring tribes of the Chaco. The *cana fístula* (*canafístula*) was described as a big, large-canopied tree, which fruits of a hand palm and a half long, that could be consumed after dilution in water. About *mandubiru*, he mentioned that these were medium-sized trees, with fruits containing seeds like peanuts (referring to *Arachis* seeds; the Portuguese name *amendoim* derives from the Tupy term *mandu'wi* = *mandubi*). The raw seeds are bitter, but the Indians consumed them after boiling them several times in fresh water. The uses for *mandubiruu* and *cana fístula* were based on information of José Sanches Labrador (Sánches Labrador 1910).

The fruits (pulp and nuts) are the main part utilized of most species (Table 19.2), but the leaves (including palm heart), stem (xylopodium), and flowers were also mentioned. For the palm species, both palm heart, stipe, and the fruits (pulp and nuts) were mentioned (Table 19.2). The most common species, often abundant and forming part of monodominant formations, have products that could be stored, such as oil, flour, or dehydrated pulp. This certainly made these species of strategic importance for feeding these peoples, in addition to the cultivated plants already mentioned. The uses of starchy fibers present in palm trees such as *Acrocomia* spp., *Copernicia alba*, and *Mauritia flexuosa* have not been mentioned recently; thus, they may no longer be part of people's diet as in the past. They seem to have become a neglected resource.

Nowadays, in the Pantanal, while *chicha* (juice), made from fruits of the *Acrocomia* spp., is consumed in the Guató community, another *chicha* (a fermented drink made from fruits of the *Prosopis* spp.) is only known in Porto Murtinho, but it is not manufactured. The fermented *chicha* beverage obtained after excavating the apex of the palm tree (*Attalea phalerata*) also is in disuse. Thus, in the Pantanal, the name *chicha* was used for both fermented and non-fermented drinks from different species, produced in the present and past times. The origin of the word "chicha" is not fully understood, but the Spaniards used to describe both alcoholic and nonalcoholic beverages produced since pre-Hispanic times in American countries (Pardo 2004; Goldstein et al. 2009). The consumption of corn *chicha* was widespread in America, but it was also prepared from roots and tubers, with the mead of the agaves and the sap of the palms and with many fruits from different species (Pardo 2004).

Despite the abandonment of some species or common uses in the past, the recent ethnobotanical studies have pointed to the species richness that still is part of the culture of indigenous and traditional communities in the western edge of the Pantanal. For example, the Guató, who now live on the Ínsua island in the Pantanal, are among those who, compared to other communities along the Paraguay River, best know the native food plants (Bortolotto et al. 2015). Wild food plants are still part of the diet of the Terena, such as *bocaiuva* (*Acrocomia aculeata*), *araticum* (*Annona dioica*), *jatobá* (*Hymenaea stigonocarpa*), *jenipapo* (*Genipa americana*), *coroa-de-frade* (*Mouriri elliptica*), *buriti* (*Mauritia flexuosa*), *pequi* (*Caryocar brasiliense*), *jurubeba* (*Solanum paniculatum*), *ingá* (*Inga vera*), *guariroba*

(*Syagrus oleracea*), *araçá* (*Psidium guineense*), *urucum* (*Bixa orellana*), and *caraguatá* (*Bromelia balansae*) (Ribas et al. 2001).

The fact that species were abandoned and the consumption of resources that were important in the past diminished significantly in the present (Bortolotto et al. 2015), associated with the increased demand for human food resources in the Pantanal, has stimulated the development of projects aiming at the rescue of information and the reestablishment of old knowledge for the benefit of the present human populations, improving either their diet or their income based on biodiversity (Bortolotto et al. 2017). However, even while the harvest of species such as rice and the preparation of fruits, flours, and oils have been abandoned or neglected, the results obtained in recent projects (Bortolotto et al. 2017) point to a new scenario involving the cooperation of local communities and production chains.

19.4.13 Future: Challenges for Conservation

Over the past two decades, projects focused on the sustainable use of biodiversity with the utilization of native fruits and economic and social benefits to the Pantanal communities, have aimed to stimulate the use of native food species in the diets and their economic utilization (Bortolotto 2017; Bortolotto et al. 2017). In workshops about food plants, several dishes were developed with *acuri* (*A. phalerata*), such as coconut sweet (Fig. 19.15) and regional donut ("bolinho de chuva") (Fig. 19.15), as well as the production of pulp flour that started to be commercialized with a label mentioning the nutritional value (Damasceno-Junior and Souza 2010).

Much progress was made, not only in the Pantanal but also in rural communities outside the Pantanal that search for income alternatives based on the utilization of native food plants. In the Pantanal, the traditional and indigenous communities have adhered to the strategies of use known food plants in their diet, participating in projects aiming at conservation of the species and improving their source of income. About six communities in the Pantanal started to harvest fruits and produce jams and realized an increment in the production of oil and flour obtained from the pulp of *bocaiuva* (Fig. 19.16) *Acrocomia* spp. (Bortolotto et al. 2017).

Thus, we observed a recent change in the relationship of the people with the plants in small rural communities, aiming to rescue their values and culture. In this process, the plants that had priority value for subsistence (food security) and culture acquired economic value and associated with it created new demands and challenges for the conservation of natural resources. Several studies have reported the utilization of fruits from the Pantanal as jam, flour, and others (Hiane et al. 2006; Prates et al. 2015; da Silva et al. 2017). These activities have stimulated the communities and helped to develop their activities.

There is an ongoing debate on whether or not the lands for nature and production should be segregated (land sparing) or integrated into the same geographical space (land sharing, wildlife-friendly farming) (Tscharntke et al. 2012). To assure

Fig. 19.15 "Acuri coco sweet" (**a**) and "acuri donut" (**b**) made of seeds and pulp of *Attalea phalerata* fruits, respectively. (Pictures by Paulo Robson de Souza. Source of the picture **b**: Damasceno-Junior et al. 2010)

Fig. 19.16 *Bocaiuva* flour (*Acrocomia* spp.). (Pictures by Ieda Maria Bortolotto)

the production of sufficient food, it is necessary to establish a dialogue with the people who live or have properties in the rural area (*besides* the indigenous and traditional communities) on conserving strategic species to assure food purposes. Much of these resources are in rural properties (large cattle ranches). Nowadays, 95% of the Pantanal is occupied by private ranches (Santos et al. 2011). The National Park of the Pantanal and the private Conservation Units (RPPNs) are of great importance for conservation of biodiversity, though, ungrazed, needing a robust integrated management program to keep them free from periodic wildfires. Nevertheless, there still is a demand for public policies focused on sustainable use involving the human populations and their culture.

19.5 Final Considerations

While domesticated plant species, widely cultivated globally, have been much researched, the wild food or semi-domesticated species still require many more studies to show their potential utilization; reveal their morphology, distribution, and ecology; and demonstrate their nutritional value and postharvest treatment.

Extension actions also need to be intensified in the rural area, considering the abandonment of ancient food plants. Such species represent a potential resource for food and nutritional security of the local human populations, and projects in this line aiming to incite their cultural rescue are essential.

There is a certain gap regarding ethnobotanical studies in present indigenous communities (Bortolotto and Damasceno-Junior 2021): we need more projects that take into consideration the local culture, forms of uses and management, as well as projects that reveal the knowledge of species used in the past, as available in primary historical documents not analyzed here. Knowledge on the species used in the past, maintained or abandoned, is essential for developing strategies for their conservation in situ and food security.

The study on historical ethnobotany based on primary sources of the Portuguese crown (Tomchinsky and Ming 2019) and covering the eastern part of Brazil, which has flora and indigenous cultures distinct from the Pantanal, discusses species utilized as food plants that are different from those utilized for food in the Pantanal. None of the species here mentioned (*Oryza* spp., *Prosopis* spp., *Copernicia alba*, or *Attalea phalerata*) are reported in that study. That is characteristic of a country with a very diverse biological and cultural heritage, where many studies are still needed to understand the past and the present and plan for the future.

Acknowledgments To the Universidade Federal de Mato Grosso do Sul for infrastructure and support. We thank the National Council for Scientific and Technological Development (CNPq) for the researcher grants to G. A. D.J., process number 307429/2019-9, and A. Pott, process number 303191/2017-1.

References

Adámoli J (1982) O Pantanal e suas relações fitogeográficas com os cerrados: discussão sobre o conceito de complexo do Pantanal. In: Anais do 32° Congresso nacional da Sociedade Botânica do Brasil. Universidade Federal do Piauí, Teresina, pp 109–119

Aguiar LS d (2015) A Arte rupestre em Mato Grosso do Sul Rodrigo. In: Chamorro G, Combés I (eds) Povos indígenas em Mato Grosso do Sul: História, cultura e transformações sociais. UFGD, Dourados, p 51

Alcorn JB, Zarzycki A, de la Cruz LM (2010) Poverty, governance and conservation in the Gran Chaco of South America. Biodiversity 11:39–44. https://doi.org/10.1080/14888386.2010.9712645

Arenas P, Scarpa GF (2003) The consumption of Typha domingensis pers. (Typhaceae) pollen among the ethnic groups of the Gran Chaco, South America. Econ Bot 57:181–188. https://doi.org/10.1663/0013-0001(2003)057[0181:TCOTDP]2.0.CO;2

Arenas P, Scarpa GF (2007) Edible wild plants of the Chorote Indians, Gran Chaco, Argentina. Bot J Linn Soc 153:73–85. https://doi.org/10.1111/j.1095-8339.2007.00576.x

Barros JPV (2013) La hipótesis de parentesco Guaicurú-Mataguayo: estado actual de la cuestión. Rev Bras Linguística Antropológica 5:293–333. https://doi.org/10.26512/rbla.v5i2.16269

Berg MEVD (1986) Formas atuais e potenciais de aproveitamento das espécies nativas e exóticas do Pantanal Mato-grossense. In: EMBRAPA (ed) Simpósio sobre recursos naturais e sócio-econômicos do Pantanal. Brasília, pp 131–136

Bertazzoni EC, Damasceno-Junior GA (2011) Aspectos da biologia e fenologia de Oryza latifolia Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Bot Bras 25:476–486. https://doi.org/10.1590/S0102-33062011000200023

Bespalez E (2015) Arqueologia e história indígena no Pantanal. Estud Avancados 29:45–86. https://doi.org/10.1590/S0103-40142015000100005

Bittencourt CM, Ladeira ME (2000) A História do Povo Terena. MEC, Brasília

Bortolotto IM (1999) Educação e uso de recursos naturais: um estudo na comunidade de Albuquerque, Corumbá – Mato Grosso do Sul. Universidade Federal de Mato Grosso, Pantanal

Bortolotto IM (2006) Etnobotânica nas comunidades do Castelo e Amolar, Borda Oeste do Pantanal brasileiro. Universidade Estadual Paulista “Júlio de Mesquita Filho”

Bortolotto IM (org.) (2017) Conservação da biodiversidade, alimentos e cultura em Mato Grosso do Sul. Campo Grande: Editora UFMS. 68 p. (Coleção Saberes do Cerrado e do Pantanal, v. 2)

Bortolotto IM, Amorozo MC de M (2012) Aspectos históricos e estratégias de subsistência nas comunidades localizadas ao longo do rio Paraguai em Corumbá-MS. In: Moretti EC, Banducci Junior Á (eds) Pantanal: territorialidades, culturas e diversidade. UFMS, Campo Grande, pp 57–88

Bortolotto IM, Damasceno-Junior GA (1998) O uso de plantas e animais pelos índios Guató, Ilha Ínsua, Pantanal Sul-Mato-Grossense. Corumbá (Relatório).

Bortolotto IM, Guarim-Neto G (2004) Albuquerque: aspectos históricos, socioambientais e educacionais do Distrito de Albuquerque, Corumbá, no Pantanal Sul-Mato-Grossense. Rev Geogr. Campo Grande ANO X:42–52

Bortolotto IM, de Mello Amorozo MC, Neto GG, Oldeland J, Damasceno-Junior GA (2015) Knowledge and use of wild edible plants in rural communities along Paraguay River, Pantanal, Brazil. J Ethnobiol Ethnomed 11. https://doi.org/10.1186/s13002-015-0026-2

Bortolotto IM, Hiane PA, Ishii IH, de Souza PR, Campos RP, Juraci Bastos Gomes R, Farias CS, Leme FM, de Oliveira Arruda R d C, de Lima Corrêa da Costa LB, Damasceno-Junior GA (2017) A knowledge network to promote the use and valorization of wild food plants in the Pantanal and Cerrado, Brazil. Reg Environ Chang 17:1329–1341. https://doi.org/10.1007/s10113-016-1088-y

Bortolotto IM, Damasceno-Junior GA, Pott A (2018) Preliminary list of native food plants of Mato Grosso do Sul, Brazil. Iheringia - Ser Bot 73:101–116. https://doi.org/10.21826/24468231201873s101

Bortolotto IM, Seleme EP, de Araújo IPP, Moura S d S, Sartori ÂLB (2019) Conhecimento local sobre plantas alimentícias nativas no Chaco brasileiro. Oecol Aust 23:764–775

Bortolotto IM; Damasceno-Junior, G A (2021) Plantas alimentícias do Chaco brasileiro: uma contribuição da etnobotânica às estratégias de conservação. In: Sartori ALB, Souza PR, Arruda, RCO (Ed). Chaco: caracterização, riqueza, diversidade, recursos e interações. Editora UFMS, Campo grande, p. 284-304

Bortolotto IM, Guimarães R de CA, Campos RP, Lopes MR da S, Silva LPR da, Silva RH, Damasceno-Junior GA, Pott A, Hiane PA (2021) Food Composition Data: Edible Plants in Pantanal. In: Jacob MCM, Albuquerque UP (ed). Local Food Plants of Brazil. Ethnobiology. Springer, Cham

Brasil (1982) Projeto RADAMBRASIL. Folha SE. 21 Corumbá e parte da folha SE 20. Levantamento de Recursos Naturais. Rio de Janeiro

Cabeza de Vaca AN (1555) La relación y comentarios del gouvernador Alvar Nuñez Cabeza de Vaca, de lo acaescido en las dos jornadas que hizo a las Indias. Valladolid

Cámara-Leret R, Paniagua-Zambrana N, Balslev H, Macía MJ (2014) Ethnobotanical knowledge is vastly under-documented in northwestern South America. PLoS One 9. https://doi.org/10.1371/journal.pone.0085794

Cámara-Leret R, Fortuna MA, Bascompte J (2019) Indigenous knowledge networks in the face of global change. Proc Natl Acad Sci U S A 116:9913–9918. https://doi.org/10.1073/pnas.1821843116

Cano ANH, Cano ANH, Suárez ME, Suárez ME (2020) Ethnobiology of algarroba beer, the ancestral fermented beverage of the Wichí people of the Gran Chaco I: a detailed recipe and a thorough analysis of the process. J Ethn Foods 7:1–12. https://doi.org/10.1186/s42779-019-0028-0

Carniello MA (2007) Estudo etnobotânico nas comunidades de Porto Limão, Porto Alambrado e Campo Alegre, na fronteira Brasil-Bolívia, Mato Grosso Brasil. Universidade Estadual Paulista “Julio de Mesquita Filho”

Castro IQ (2015) Os Kinikinau: persistência e percepções. In: Chamorro G, Combés I (eds) Povos indígenas em Mato Grosso do Sul: História, cultura e transformações sociais. UFGD, Dourados, p 268

Cavalcanti DR, Albuquerque UP (2013) The “hidden diversity” of medicinal plants in northeastern Brazil: diagnosis and prospects for conservation and biological prospecting. Evidence-based Complement Altern Med 2013:5–7. https://doi.org/10.1155/2013/102714

Chiaravalloti RM (2019) The displacement of insufficiently ‘traditional’ communities: local fisheries in the Pantanal. Conserv Soc 15:173–183. https://doi.org/10.4103/cs.cs

Chiaravalloti RM, Homewood K, Erikson K (2017) Sustainability and Land tenure: who owns the floodplain in the Pantanal, Brazil? Land Use Policy 64:511–524. https://doi.org/10.1016/j.landusepol.2017.03.005

Cintra JP (2012) O mapa das cortes e as fronteiras do Brasil. Bol Ciencias Geod 18:421–445. https://doi.org/10.1590/s1982-21702012000300005

Conceição CA, Paula JE de (1984) Contribuição para o conhecimento da flora do Pantanal mato-grossense e sua relação com a fauna e o homem. In: Anais do I Simpósio Sobre Recursos Naturais e Sócio-Econômicos do Pantanal, 1984. Empresa Brasileira de Pesquisa Agropecuária, pp 107–136

Conceição CA, Paula JE d (1990) Contribuição para o conhecimento da flora do Pantanal mato-grossense. Rev Científica e Cult 5:13–22

Costa M d F (1999) História de um país inexistente: o Pantanal entre os séculos XVI e XVIII. Estação Liberdade, São Paulo

Damasceno-Junior GA, Souza PR (2010) Sabores do Cerrado e Pantanal: Receitas e boas práticas de aproveitamento. Editora UFMS, Campo Grande

Damasceno-Junior GA, Souza PR, Bortolotto IM, Ramos MIL, Hiane PA, Braga Neto JA, Ishii IH, Costa DC, Ramos-Filho MM, Gomes RJB, Barbosa MM, Rodrigues RB (2010) Sabores do Cerrado & Pantanal: Receitas e boas práticas de aproveitamento. In: Damasceno-Junior GA, Souza PR (eds). Editora UFMS, Campo Grande, p 141

Depenthal J, Yoder LSM (2017) Community use and knowledge of Algarrobo (Prosopis pallida) and implications for Peruvian dry forest conservation. Rev Ciencias Ambient 52:49. https://doi.org/10.15359/rca.52-1.3

Fabre A (2007) Los pueblos del Gran Chaco y sus lenguas, cuarta parte: Los zamuco. Supl Antropológico 42:271–323

Filgueiras TS, Valls JFM, Oliveira RP (2015) Oryza. In: List. Espécies da Flora do Bras. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB24298

Florence H (2007) Viagem fluvial do Tietê ao Amazonas de 1825 a 1829, Volume 93. Edições do Senado Federal, Brasília

Frič V, Radin P (1906) Contributions to the Study of the Bororo Indians. J Anthropol Inst Gt Britain Irel 36:382–406

Goldstein DJ, Goldstein RCC, Williams PR (2009) You are what you drink: a sociocultural reconstruction of pre-hispanic fermented beverage use at Cerro Baúl, Moquegua, Peru. In: Drink, power, and society in the Andes, pp 133–166

Guarim Neto G, Santana SR, da Silva JVB (2000) Notas etnobotânicas de espécies de Sapindaceae Jussieu. Acta Bot Bras 14:327–334. https://doi.org/10.1590/S0102-33062000000300009

Guevara M, Valdés-Silverio LA, Granda-Albuja MG, Iturralde G, Jaramillo-Vivanco T, Giampieri F, Santos-Buelga C, González-Paramás AM, Battino M, Álvarez-Suarez JM (2020) Pechiche (Vitex cymosa Berteo ex Speng), a nontraditional fruit from Ecuador, is a dietary source of phenolic acids and nutrient minerals, in addition to efficiently counteracting the oxidative-Induced damage in human dermal fibroblasts. Antioxidants 9. https://doi.org/10.3390/antiox9020109

Hanazaki N, Herbst DF, Marques MS, Vandebroek I (2013) Evidence of the shifting baseline syndrome in ethnobotanical research. J Ethnobiol Ethnomed 9:1–12. https://doi.org/10.1186/1746-4269-9-75

Hartmann T (1967) Nomenclatura Botânica dos Borôro (Materiais para um ensaio etno-botânico). Instituto de Estudo Brasileiros – Universidade de São Paulo, São Paulo

Herberts AL (1998) OS Mbayá-Guaikurú: área, assentamento, subsistência e cultura material. Universidade Vale do rio dos Sinos

Hiane PA, Baldasso PA, Marangoni S, Macedo MLR (2006) Chemical and nutritional evaluation of kernels of bocaiuva. Ciência e Tecnol Aliment Campinas 26:683–689. https://doi.org/10.1590/S0101-20612006000300031

ISA – Instituto Socioambiental (2020) Povos Indígenas no Brasil. https://pib.socioambiental.org/pt/Página_principal. Accessed 24 July 2020

Kalle R, Sõukand R (2016) Current and remembered past uses of wild food plants in Saaremaa, Estonia: changes in the context of unlearning debt. Econ Bot 70:235–253. https://doi.org/10.1007/s12231-016-9355-x

Karasawa MMG, Vencovsky R, Silva CM, Zucchi MI, Oliveira GCX, Veasey EA (2007) Genetic structure of Brazilian wild rice (Oryza glumaepatula Steud., Poaceae) populations analyzed using microsatellite markers. Genet Mol Biol 30:400–410. https://doi.org/10.1590/S1415-47572007000300017

Keller GB, Mndiga H, Maass BL (2005) Diversity and genetic erosion of traditional vegetables in Tanzania from the farmer's point of view. Plant Genet Resour 3:400–413. https://doi.org/10.1079/pgr200594

Kloster W, Sommer F (1942) Ulrico Schmidl no Brasil Quinhentista. Tipografia Gutemberg, São Paulo

Lévi-Strauss C (1952) The use of wild plants in tropical South America. Econ Bot 6:252–270. https://doi.org/10.1007/BF02985068

Lévi-Strauss C (2004) Do mel às cinzas. In: Mitológicas 2. Cosacnaify, São Paulo, p 500

Martins AMS, Graciela Chamorro (2015) Diversidade linguística em Mato Grosso do Sul. In: Chamorro G, Combés I (eds) Povos indígenas em Mato Grosso do Sul: História, cultura e transformações sociais. UFGD, Dourados, p 732

May P, Vinha VdV (2013) Investing in sustainable use of biodiversity for social benefit in Brazil. In: Muradian R, Rival L (eds) Governing the provision of ecossystem services. Springer, pp 21–47

Métraux A (1942) The native tribes of Eastern Bolivia and Western Matto Grosso. Smithsonian Institution, Washington, DC

Métraux A (1946) Ethnography of the Chaco. In: Steward JH (ed) Handbook of South American Indians. Smithsonian Institution, Washington, DC, p 370

Miguéis GS, Silva RH, Damasceno-Junior GA, Guarim-Neto G (2019) Plants used by the rural community of Bananal, Mato Grosso, Brazil: aspects of popular knowledge. PLoS One 14:1–20. https://doi.org/10.1371/journal.pone.0210488

MMA (2016) Espécies nativas da flora brasileira de valor econômico atual ou potencial: plantas para o futuro – região Centro-Oeste. Brasília

Morais FF d, da Silva CJ (2010) Conhecimento ecológico tradicional sobre fruteiras para pesca na comunidade de estirão comprido, Barão de Melgaço – Pantanal Matogrossense. Biota Neotrop 10:197–203

Moseley C (ed), (2010) Atlas of the World's Languages in Danger, 3rd edn. Paris, UNESCO Publishing. http://www.unesco.org/culture/en/endangeredlanguages/atlas

Morcote-Ríos G, Bernal R (2001) Remains of palms (palmae) at archaeological sites in the new world: a review. Bot Rev 67:309–350. https://doi.org/10.1007/BF02858098

Neuburger M, da Silva CJ (2011) Ribeirinhos between ecological adaptation and modernism. In: Yunk WJ, da Silva CJ, da Cunha CN, Wantzen KM (eds) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft Publishers, Sofia-Moscow, pp 673–694

Nunes SG (2001) Controle de plantas invasoras em pastagens cultivadas nos cerrados. Embrapa Gado de Corte, Campo Grande

Oberg K (1949) Terena and the Caduveo of Southern Mato Grosso, Brazil. Smithsonian Institution, Washington, DC

Oliveira JE de (1996) Guató: Argonautas do Pantanal. Edipuc, RS, Porto Alegre

Oliveira JE de (2002) Da pré-história à história indígena: (re) pensando a arqueologia e os povos canoeiros do Pantanal. Pontifícia Universidade Católica do Rio Grande do Sul

Oliveira JE de, Viana SA (2000) O Centro-Oeste Antes De Cabral. Rev USP 0:142. https://doi.org/10.11606/issn.2316-9036.v0i44p142-189

Pardo BO (2004) Las chichas en el Chile precolombino. Chloris Chil 7

Pott A, Pott VJ (1994) Plantas do Pantanal. Embrapa – SPI, Corumbá

Pott VJ, Pott A (2000) Plantas Aquáticas do Pantanal. Embrapa, Brasília

Prance GT, Schaller GB (1982) Preliminary study of some vegetation types of the pantanal, mato grosso, Brazil. Brittonia 34:228–251. https://doi.org/10.2307/2806383

Prates MFO, Campos RP, da Silva MMB, Macedo MLR, Hiane PA, Ramos Filho MM (2015) Nutritional and antioxidant potential of canjiqueira fruits affected by maturity stage and thermal processing. Ciência Rural 45:399–404. https://doi.org/10.1590/0103-8478cr20131272

Ribas DLB, Sganzerla A, Zorzatto JR, Philippi ST (2001) Nutrição e saúde infantil em uma comunidade indígena Teréna, Mato Grosso do Sul, Brasil. Cad Saude Publica 17:323–331. https://doi.org/10.1590/s0102-311x2001000200007

Ritter MR, da Silva TC, Araújo EL, Albuquerque UP (2015) Bibliometric analysis of ethnobotanical research in Brazil (1988–2013). Acta Bot Bras 29:113–119. https://doi.org/10.1590/0102-33062014abb3524

Rosa MS, dos Santos PP, Veasey EA (2006) Caracterização agromorfolólogica interpopulacional em Oryza glumaepatula. Bragantia 65:1–10. https://doi.org/10.1590/S0006-87052006000100002

Sánches Labrador J (1910) El Paraguay católico. Imprenta de Coni Hermanos, Buenos Aires

Santos SA, Desbiez ALJ, Crispin SMA, Filho JAC, de Abreu UGP, Rodela LG (2011) Natural and cultivated pastures and their use by cattle. In: Junk WJ, da Silva CJ, da Cunha CN, Wantzen KM (eds) The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensofy, Sofia-Moscow, pp 327–352

Santos TAC, Carniello MA, Barros FB (2016) Práticas agroecológicas e conhecimentos tradicionais na Chácara Santo Antônio, Cáceres-MT, Brasil. Gaia Sci 10:106–116. https://doi.org/10.21707/gs.v10.n04a08

Sartori ALB, Pott VJ, Pott A, De Carvalho FS (2018) Checklist of angiosperm from the Chaco of Mato Grosso do Sul. Iheringia – Ser Bot 73:22–33. https://doi.org/10.21826/24468231201873s22

Scarpa GF (2009) Wild food plants used by the indigenous peoples of the South American Gran Chaco: a general synopsis and intercultural comparison. J Appl Bot Food Qual 83:90–101

Schmeda-Hirschmann G (1994) Plant resources used by the Ayoreo of the Paraguayan Chaco. Econ Bot 48:252–258. https://doi.org/10.1007/BF02862325

Schmidl U (1903) Viaje ao Rio De La Plata, 1534–1554, Biblioteca. Cabaut y Cía, Buenos Aires

Schmidt M (1942) Estudos de Etnologia Brasileira. Nacional, Companhia Editorra, São Paulo

Schmidt M (1949) Los Payagua. Rev do Mus Paul 1. https://doi.org/10.1017/CBO9781107415324.004

Schmidt M (1951) Anotaciones sobre las plantas de cultivo y los metodos la agricultura de los indígenas sudamericanos. Rev do Mus Paul 5:1–476. https://doi.org/10.1017/CBO9781107415324.004

Schmitz PI (2015) Arqueologia em Mato Grosso do Su. In: Chamorro G, Cambés (eds) Povos indígenas em Mato Grosso do Sul: História, cultura e transformações sociais. Dourados, pp 27–38

Schuch MEJ (1995) Xaray e Chaué: índios frente à expansão espanhola e portuguesa no Alto-Paraguai. Universidade do Vale do Rio dos Sinos – UNISINOS

Seleme EP, Bortolotto IM, Sartori ALB (2020) Riqueza e uso de recursos vegetais por moradores do Chaco brasileiro. In: Silva CJ, Guarim Neto G (eds) Comunidades tradicionais do Pantanal. UNEMAT/Entrelinhas, Cáceres/Cuiabá, p 164

Silva RH (2018) Estabelecimento de protocolo para uso sustentável de *Copernicia alba* Morong ex Morong & Briton. Universidade Federal de Mato Grosso do Sul

Silva CJ d (2020) Povos e comunidades tradicionais do Pantanal. In: Silva CJ d, Neto GG (eds) Comunidades tradicionais do Pantanal. UNEMAT/Entrelinhas, Cáceres/Cuiabá, pp 21–38

Silva J d SV d, Abdon MM (1998) Delimitação do Pantanal Brasileiro e suas sub-regiões. Pesqui Agropecu Bras 33:1703–1711

Silva CJ, Silva JAF (1995) No ritmo das águas do Pantanal. NUPAUB/USP, São Paulo

Silva DGB da, Komissarov BN, Becher H, Levy PM, Braga MP (1997) Os diários de Langsdorff Vol. 3

Silva VMd, Campos RP, Borsato AV, Candido CJ, Donadon JR (2017) Bocaiuva jelly: preparation , physicochemical and sensory evaluation / Geleia de bocaiuva: elaboração, avaliação fisico-quimica e sensorial. Rev Bras Frutic 40. https://doi.org/10.1590/0100-29452018846

Silveira TCL, Rodrigues GG, de Souza GPC, Würdig NL (2012) Effect of *Typha domingensis* cutting: response of benthic macroinvertebrates and macrophyte regeneration. Biota Neotrop 12:124–132. https://doi.org/10.1590/s1676-06032012000300014

Souza-Lima ES d, Sinani TR, Pott A, Sartori ÂLB (2017) Mimosoideae (Leguminosae) in the Brazilian Chaco of Porto Murtinho, Mato Grosso do sul. Rodriguesia 68:263–290. https://doi.org/10.1590/2175-7860201768131

Súsnik B, Chase-Sardi M (1995) Los indios del Paraguay. Editorial Mafre, Madrid

Taunay A'E (1868) Scenas de viagem. Tipografia Americana, Rio de Janeiro

Taunay V de (1931) Entre os nossos índios: Chanés, Terenas, Kinikinaus, Guanás, Laianas, Guatós, Guaycurús, Caigangs. Comp. Melhoramentos de São Paulo, São Paulo

Tomas WM, de Oliveira RF, Morato RG, Medici PE, Chiaravalloti RM, Tortato FR, Penha JMF, Izzo TJ, Garcia LC, Lourival RFF, Girard P, Albuquerque NR, Almeida-Gomes M, Andrade

MHS, Araujo FAS, Araujo AC, Arruda EC, Assunção VA, Battirola LD, Benites M, Bolzan FP, Boock JC, Bortolotto IM, Brasil MS, Camilo AR, Campos Z, Carniello MA, Catella AC, Cheida CC, Crawshaw PG, Crispim SMA, Damasceno-Junior GA, Desbiez ALJ, Dias FA, Eaton DP, Faggioni GP, Farinaccio MA, Fernandes JFA, Ferreira VL, Fischer EA, Fragoso CE, Freitas GO, Galvani F, Garcia AS, Garcia CM, Graciolli G, Guariento RD, Guedes NMR, Guerra A, Herrera HM, Hoogesteijn R, Ikeda SC, Juliano RS, Kantek DLZK, Keuroghlian A, Lacerda ACR, Lacerda ALR, Landeiro VL, Laps RR, Layme V, Leimgruber P, Rocha FL, Mamede S, Marques DKS, Marques MI, Mateus LAF, Moraes RN, Moreira TA, Mourão GM, Nicola RD, Nogueira DG, Nunes AP, Nunes da Cunha C, Oliveira MD, Oliveira MR, Paggi GM, Pellegrin AO, Pereira GMF, Peres IAHFS, Pinho JB, Pinto JOP, Pott A, Provete DB, dos Reis VDA, dos Reis LK, Renaud PC, Ribeiro DB, Rossetto OC, Sabino J, Rumiz D, Salis SM, Santana DJ, Santos SA, Sartori ÂL, Sato M, Schuchmann KL, Scremin-Dias E, Seixas GHF, Severo-Neto F, Sigrist MR, Silva A, Silva CJ, Siqueira AL, Soriano BMA, Sousa LM, Souza FL, Strussmann C, Sugai LSM, Tocantins N, Urbanetz C, Valente-Neto F, Viana DP, Yanosky A, Junk WJ (2019) Sustainability agenda for the Pantanal wetland: perspectives on a collaborative interface for science, policy, and decision-making. Trop Conserv Sci 12. https://doi.org/10.1177/1940082919872634

Tomchinsky B, Ming LC (2019) As plantas comestíveis no Brasil dos séculos XVI e XVII segundo relatos de época. Rodriguésia 70. https://doi.org/10.1590/2175-7860201970040

Tscharntke T, Clough Y, Wanger TC, Jackson L, Motzke I, Perfecto I, Vandermeer J, Whitbread A (2012) Global food security, biodiversity conservation and the future of agricultural intensification. Biol Conserv 151:53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Turner NJ, Turner KL (2008) “Where our women used to get the food”: cumulative effects and loss of ethnobotanical knowledge and practice; case study from coastal British Columbia. Botany 86:103–115

Turner NJ, Von Aderkas P (2012) Sustained by First Nations: European newcomers’ use of Indigenous plant foods in temperate North America. Acta Soc Bot Pol 81:295–315. https://doi.org/10.5586/asbp.2012.038

Vianna SA (2017) A new species of Acrocomia (Arecaceae) from Central Brazil. Phytotaxa 314:45–54. https://doi.org/10.11646/phytotaxa.314.1.2

Vianna SA, Campos-Rocha A (2020) Acrocomia. In: Flora do Bras. 2020 em construção. Jardim Botânico do Rio de Janeiro. http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB15662

Chapter 20
Ecological Restoration of Pantanal Wetlands

Letícia Couto Garcia, Letícia Koutchin Reis, Suzana Maria Salis, Angélica Guerra, Zefa Valdevina Pereira, Marcia Raquel Avalos Bogarín, and Arnildo Pott

20.1 Introduction

Ecological restoration is the process of enhancing the recovery of a degraded, damaged, or destroyed ecosystem through actions to reestablish its structure, the ecological processes, and the conservation of its biodiversity, forming a new functional ecosystem closely similar to the original one (Bradshaw 1996; Allen et al. 2001; SER 2014). Therefore, many scientists have suggested the utilization of native species or key functional groups to compose restoration layouts (Kirmer et al. 2008; Alday et al. 2011; Garcia et al. 2015).

L. C. Garcia (✉) · L. K. Reis · M. R. A. Bogarín
Laboratório de Botânica, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

Laboratório Ecologia da Intervenção (LEI), Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

S. M. Salis
Embrapa Pantanal- Empresa Brasileira de Pesquisa Agropecuária (Embrapa), Corumbá, MS, Brazil

A. Guerra
Laboratório Ecologia da Intervenção (LEI), Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

Z. V. Pereira
Faculdade de Ciências Biológicas e Ambientais, Universidade Federal da Grande Dourados (UFGD), Dourados, MS, Brazil

A. Pott
Laboratório de Botânica, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_20

In the Pantanal, restoring the functionality of ecosystems requires an understanding of the spatiotemporal heterogeneity in wetland plant communities, which form mosaics in the landscape. Hence, identifying and explaining the role of each functional group in these ecosystems and their dynamics, as well as a means to restore these groups, is a critical aspect in the Pantanal context. The Pantanal is the Brazilian biome with the smallest quantities of published studies about restoration actions (Guerra et al. 2020a); in this chapter, we firstly review the literature to give a world context for wetland restoration focusing on progress and bottlenecks, and then, we show a synthesis of experiments that we conducted or revised.

20.2 Restoration Activities in Wetlands All Over the World

The ongoing extensive degradation in wetlands in the world reaches 64% of the original area (Ramsar 2015), showing the need for wetland restoration. Utilizing ecological restoration, we can recover a great part of the biodiversity and consequently also the lost ecosystem services (Zedler 2000; Rey-Benayas et al. 2009). However, the efficacy of wetland restoration is a challenge, since current methods need improvements to allow the recovery of the biological components, ecosystem structure, and functioning (Zedler and Kercher 2005; Moreno-Mateos et al. 2012). Recognizing and implementing disturbances (e.g., fire and flood), such as increasing plant density and diversity and improving alien species control, may help restoration (King et al. 2009). One of the factors hindering the evaluations of the positive and negative points of restoration are the different methods and patterns used to assess the results (Zedler 2000).

In a bibliometric search in the database Web of Science, utilizing the keywords "ecological restoration" and "wetlands," from 1945 until June 2018, we found 1300 publications addressing wetland restoration. The majority of studies was on passive/unassisted natural succession and/or active/assisted interference in wetland ecosystems or mentioned ecological restoration in wetlands in the USA (36%) and China (20%). Other countries, such as Holland, Canada, England, and Australia, made up between 5 and 7%. In 1970, the USA invested enormous resources in wetland restoration, implemented by the Clean Lakes Program, which joined the Commission of Restoration of Aquatic Ecosystems of 1989 for a global assessment on ecological restoration (Dong et al. 2013). After this pioneering initiative, European and Asian countries started the discussions about plans for the restoration of their aquatic ecosystems (Zhang and Wang 2001). However, in Brazil, where we find the world's largest tropical wet zones, the quantity of studies on restoration activities is only 0.81%. Among them, the studies encompass ecosystem services in wetlands (Periotto and Tundisi 2013), regeneration and recruitment in degraded mangroves (Vogt et al. 2014; Rezende et al. 2015), photosynthetic performance in restored and natural mangroves (Rovai et al. 2013), impacts of degradation in central Amazonia (Zelarayán et al. 2015), *restingas* under natural regeneration (Rodrigues et al. 2010), and active restoration in the coastal swampy forest (Zamith and Scarano 2010).

Restoration actions in the Brazilian Pantanal are recent; however, they became necessary owing to the high degradation level in the last years (Abdon et al. 2007; Paranhos Filho et al. 2014; Roque et al. 2016; Guerra et al. 2020b; 2020c).

Ecological restoration actions can increase biodiversity by 19% compared with degraded wetlands and can reach reference levels (i.e., non-degraded wetlands) (Meli et al. 2014). The diversity of restored wetlands can become similar to that of natural wetlands taken as the reference for restoration. This resemblance is observed in the diversity of plants, aquatic invertebrates, and even protists (Rey-Benayas et al. 2009). As regards organisms, restoration is capable of increasing the diversity of vertebrates by 53%, invertebrates by 15%, and regarding plant organisms, aquatic plants by 45%, and terrestrial plants by 17%, but no improvement has yet been observed in aquatic macroinvertebrates (Meli et al. 2014; Barral et al. 2015). Also significant is the diversity in non-native plants: it may be 44% lower in the restored areas since in most cases there is management for weed control (Meli et al. 2014, Barral et al. 2015).

Our bibliometric search on restoration in wetlands showed that the research reports predominantly include organisms as a way of monitoring (86%), plants being represented by 54%, followed by invertebrates (27%), vertebrates (22%), and microorganisms (5%). In most of these ecosystems, the vegetation is restored, reducing the loss of surface water, which is one of the main objectives of restoration in wetlands (Labadz et al. 2002). Studies on ecosystem functions, we found mostly on nutrients of soils and/or water (40%) and water relations (28%), are scarce, while trophic interactions are as yet overlooked (Zedler and Kercher 2005; Moreno-Mateos et al. 2012). The best-represented ecosystem type found in a meta-analysis of peer-reviewed studies on wetlands is the riparian zone (38%), followed by lacustrine (27%), estuarine (18%), and palustrine ecosystems (17%) (Meli et al. 2014). Besides, most research was based on comparisons in the field, either on active or passive restoration, and very few under controlled greenhouse conditions (Meli et al. 2014).

20.3 Abiotic and Biotic Filters and Restoration in the Pantanal

The restoration success may depend not only on the applied methods but also on the effect of ecological filters acting directly on the results. The transition of a degraded/fragmented ecosystem occurs through the interactions between abiotic and biotic filters, called “the dynamic environmental filter model” (DEFM) (Fattorini and Halle 2004). These filters, once classified, become more specific and can generate useful models to compare restoration practices for each type of ecosystem (Hobbs and Norton 2004). Restoration in the Pantanal plain, as in other wetlands, can be affected by abiotic and biotic filters as much as by anthropogenic factors.

In wet systems, abiotic filters are the most reported, mainly focusing on flood. Flood causes a series of metabolic and physiological changes in plants that may allow them to survive in wetlands (Kozlowski 1984, 2002). Such communities are highly adapted to the stresses caused by floods, but these stresses can be met up to a threshold value, and passing that it can lead to plant mortality (Crawford 1992; Cherry et al. 2015). On the other hand, a decreased flooding period in the Pantanal results in explosive recruitment from seed banks composed of annual herbs and graminoids (Souza et al. 2016). Hence, diaspore transfer can be useful for ecological restoration via a nucleation technique (see Box 20.4). A fact not always perceived are small interannual climatic fluctuations affecting the periodical water level amplitude (Cherry et al. 2015). In the Pantanal, when the flood pulse is lost, several factors become maladjusted by which many species are conditioned (Rebellato and Cunha 2005). Changes in rainfall level interfere directly in the flood pulse, affecting the food web by reducing fish, reptiles, birds, and aquatic herbivores; some of these animals only occur at sites where small flood pulses exist (Resende 2008). Therefore, owing to the Pantanal's complexity of the seasonal dynamics, with high fluctuations in flood levels, the recovery of its ecosystems may be difficult (Pott et al. 2018).

The conservation of stream headwaters in the Cerrado surrounding upland directly influences the flood regime of the Pantanal plain; however, their recovery has yet been little studied. A trial with sapling planting showed satisfactory survival (over 70%) in two degraded stream headwaters in the Cerrado (Pregelli et al. 2008), actually the tops of *veredas*. Various studies on Cerrado tree species have researched which species are tolerant of periodical flooding and what the mechanisms are that they develop to survive hypoxia/anoxia stress (Joly and Crawford 1982; Oliveira et al. 2015; Oliveira and Gualtieri 2017). In restoration by direct sowing on watercourse margins, the seasonal flood can hinder germination. For a seed to germinate, the availability of water and oxygen is essential; however, under an excess of water, the germination process can be inhibited by oxygen deficiency (Lobo and Joly 1998; Marques and Joly 2000). That leads to a selection of flood-tolerant species whose germination can occur underwater. Some species of *Inga*, for example, do not lose their germination capacity even after a considerable period of submersion and waterlogging (Okamoto 1998). Amazonian species, which also occur in Pantanal may germinate under flooded conditions, such as *Inga affinis*, *Sesbania virgata, Nectandra amazonum* (author names of plants also native to the Pantanal are given in the chapter on Flora Chap. 3) (Lobo and Joly 1998; Parolin and Junk 2002). Moreover, together with flood in Pantanal, fire can act as another biotic filter decreasing germination (Ferreira et al. 2021; Soares et al. 2021).

When transplanted saplings are under prolonged flood, they can meet aeration problems, i.e., hypoxia (low oxygen pressure) in the roots (Drew 1997; Colmer and Voesenek 2009). That can affect both growth and development as well as inhibit metabolic activity, decreasing adenosine triphosphate (ATP) until the plant dies (Crawford 1992; Drew 1997; Colmer and Voesenek 2009). If plants undergo such conditions for a long time, damages can become irreversible even after drainage (Arruda and Calbo 2004). Soil inundation generally reduces the root system, lowering its drought stress tolerance in the subsequent dry period because plants cannot adequately replenish transpiration losses (Kozlowski 1997). Hence, the periodic flooding in riparian zones produces a selective effect on the variety of species, allowing the survival of the most tolerant species dependent on the increase or decrease of the water saturation gradient (Metzger et al. 1998; Capon 2005), which in Pantanal also has concomitant influence of fire (Oliveira et al. 2014). The successful establishment of a species in flooded areas consists primarily in its capacity to survive, develop, and reproduce under such conditions (Marques and Joly 2000). Accordingly in Pantanal, the spectrum of flood-tolerant species is determined by the success of sapling establishment under waterlogging conditions and fire (Oliveira et al. 2014), and, therefore, the identification of such functional groups is necessary for restoration within the belts of the confined riverbed of the Areas of Permanent Preservation (APPs, Box 20.1).

As regards biotic filters, seed availability can depend on dispersal from surrounding remnants via seed rain or can be provided by the autochthonous seed bank (Nuttle 2007). Native fruit plant dispersers of the Pantanal are mainly large native mammals, such as tapir (*Tapirus terrestris*), peccaries (*Tayassu pecari* and *Pecari tajacu*), and frugivore birds, such as piping guans (*Aburria nattereri*) and toucans (*Ramphastos toco*) (Donatti et al. 2007). Bats, monkeys, and coatimundi are also important seed dispersers. Cattle spread *Acrocomia aculeata* (Jacq.) Lodd. and *Attalea phalerata* Mart. ex Spreng fruits, expelling them at rumination. Focusing on non-predatory plant-frugivorous interactions in the Pantanal, mammals were responsible for the dispersion of 56% of all zoochoric tree species, while birds dispersed 47%, and both together 21% (Donatti et al. 2007). The presence of vigorous populations of birds (Nunes et al. 2006) and mammals (Tomas et al. 2010) in the Pantanal is critical to facilitate the seed dispersal of zoochoric plants on the floodplain and consequently the restoration of anthropized areas. Therefore, restoration activities in the Pantanal must consider the attraction of these large frugivores for seed dispersal. Restoration actions can include zoochoric species dispersed in different periods to attract animals throughout the year (Garcia et al. 2009, 2014). In the propagation via dispersal from elsewhere, the availability of seeds from the species pool in the nearest remnant also acts as a biotic filter (Nuttle 2007), and this can be measured by the natural regeneration success. However, we found only one publication about the potential of tree species recruitment in the Pantanal (e.g., in semideciduous forests in the *Nhecolândia* subregion of the Pantanal; Cardoso et al. 2017), on a high-resilient site burned in the past to be used as agriculture, and near-natural remnants. Even in such good conditions, this site required at least three decades to reach reference levels (Box 20.2).

Herbivory is also an environmental biotic filter that influences the success of the ecological restoration of wetlands owing to its effects on plant communities. Herbivory with another continuous stress can reduce plant growth of many species (Grace and Ford 1996). For example, in coastal marshes under degradation by prolonged flood and saltwater intrusion plus soil nutrient alterations, herbivory becomes more destructive and lethal to the plants (Lori and Lee 2005). These factors involve the need for interventions, of maintenance and monitoring of the plantings for extended periods (He and Silliman 2015). The increase of nutrients intensifies plant-herbivore interactions in salty swamps, and such effects on the interactions also increase with latitude (He and Silliman 2015). Interaction of disturbances such as flood and grazing occurs in wetlands in the USA and Australia, and the prominent effect is mostly from large (bison and elk) and small herbivores (rats) (LaGrange 2010). In Brazil, in the Cerrado of the upper watershed of the Pantanal, occurs a large population of rats feeding on root systems since most saplings present xylopodia. In the Pantanal, the most damaging are invertebrates (ants) and native (tapir, deer, capybara, peccaries) and domestic mammals (cows, sheep, horses, pigs). Therefore, preventive anti-herbivory measures (Reis et al. 2019; Reis et al. 2021) should precede active restoration to overcome this strong biotic filter in the Pantanal (Box 20.3).

20.4 Low Availability of Restoration Studies in the Region: Defining Gaps and Suggesting Improvements

Since restoration methods in wetlands were first applied, we gathered experience with the reintroduction of species in highly fragmented landscapes and with the transfer of soil from donor areas to degraded areas (Pfadenhauer and Grootjans 2009). Wetland restoration has been considered a field of ecological research of utmost interest and has seen a considerable increase in theoretical and practical studies in recent years. The European Union, for example, acknowledged the importance of habitat restoration and agreed on a target to restore 15% of those environments in the Strategy for Biodiversity 2020 (Jørgensen 2015). In Brazil, the National Plan for Native Vegetation Recovery (PLANAVEG) was decreed in 2017 as a national policy to achieve a restoration goal of 12.5 million ha by 2030 (Garcia et al. 2019).

Many recent studies have tried to establish efficient techniques for the ecological restoration of Brazilian ecosystems. In Mato Grosso do Sul, although already some knowledge has been gathered, there are yet huge scientific gaps on this theme for the Pantanal region, mainly for the plain areas (Rodrigues et al. 2019). Most conspicuously in this regard are our understanding of the role of functional groups in these ecosystems, our understanding of the effects of facilitator species in the dynamics of the natural regeneration, and the evaluation of the results of various combined techniques in different ecosystems. Moreover, there is a need to stimulate the creation of seed collector networks and nurseries for the genetic conservation of local species. Besides, new techniques are necessary to conserve this genetic diversity (e.g., transplantation of seedlings of natural regeneration dominant species from remnants (Box 20.3)) and to control invasive alien species, since African grasses have been introduced for cattle ranching), which particularly hamper restoration of grasslands.

Finally, and this is important, it is worth mentioning that all reports consider forest restoration. However, there are no studies assessing the restoration of grassland vegetation (see the chapter on Native Grasslands Chap. 10 for remarks on grassland dynamics). Restoration goals in the Pantanal are as yet incidental, and the main reason is the lack of awareness, information, finance, and political support. Furthermore, most projects have financial support for only less than 3 years, which hinders successful restoration. The high costs also provide a barrier for restoration. Nevertheless, such obstacles hamper restoration projects all over the world. Therefore, the development of cheaper and more efficient techniques controlling invasive alien species, prioritising areas (Oliveira et al. 2021; Martins et al. in press), as well as mapping the resilience of degraded areas, has been an important focal point of research aimed at scaling up ecological restoration.

20.5 Environmental Efforts for Mapping the Resilience of Brazilian Biomes and the Pantanal

The concept of the term biome used here is broader than that described in ecology (Coutinho 2006); it refers to a biogeographic province, in correspondence with its definition in the Brazilian legislation. Hence, the Pantanal would not strictly be a biome (Coutinho 2006).

The Ministry of Environment, consulting external experts, organized workshops for mapping the resilience of Brazilian Biomes including the Pantanal, focusing mainly on areas with a high potential for passive restoration. This activity aims to facilitate decision-making on the legal enforcement of the principal Brazilian environmental legislation, the Native Vegetation Protection Law, commonly called the "New Forest Code" (Brasil 2012), which has recently been changed (see details in Brancalion et al. 2016). Compliance with this new law requires restoring 12.5 million ha, an area that is less than half the area envisaged in the previous law (Soares-Filho et al. 2014). The PLANAVEG (a national restoration common) aims to achieve this restoration goal by 2030 (Garcia et al. 2019) and the recovery target in the Pantanal is 50,000 ha. Natural regeneration is an alternative that helps to scale up restoration and to reduce the costs, given the size of Brazil and given the costs associated with restoration. The higher the environmental resilience, the lower the restoration costs. Furthermore, gains in biodiversity tend to be optimized when highly resilient areas are selected for passive restoration. On the other hand, active restoration is highly recommendable for increasing ecosystem services in low-resilient, degraded areas where there is no natural regeneration. To decide on active or passive restoration, not only resilience but also land-use history and the landscape context are essential when planning management strategies (Holl and Aide 2011).

To create the resilience models (Pott et al. 2018), we firstly identified in each Pantanal watershed the main vegetation type (i.e., the predominance of forests or grasslands). Next, we used several relevant layers for resilience modeling (e.g., land use, history and recent vegetation loss, slope, average distance between native vegetation fragments (forest or non forest), and pasture productivity). Cluster analysis

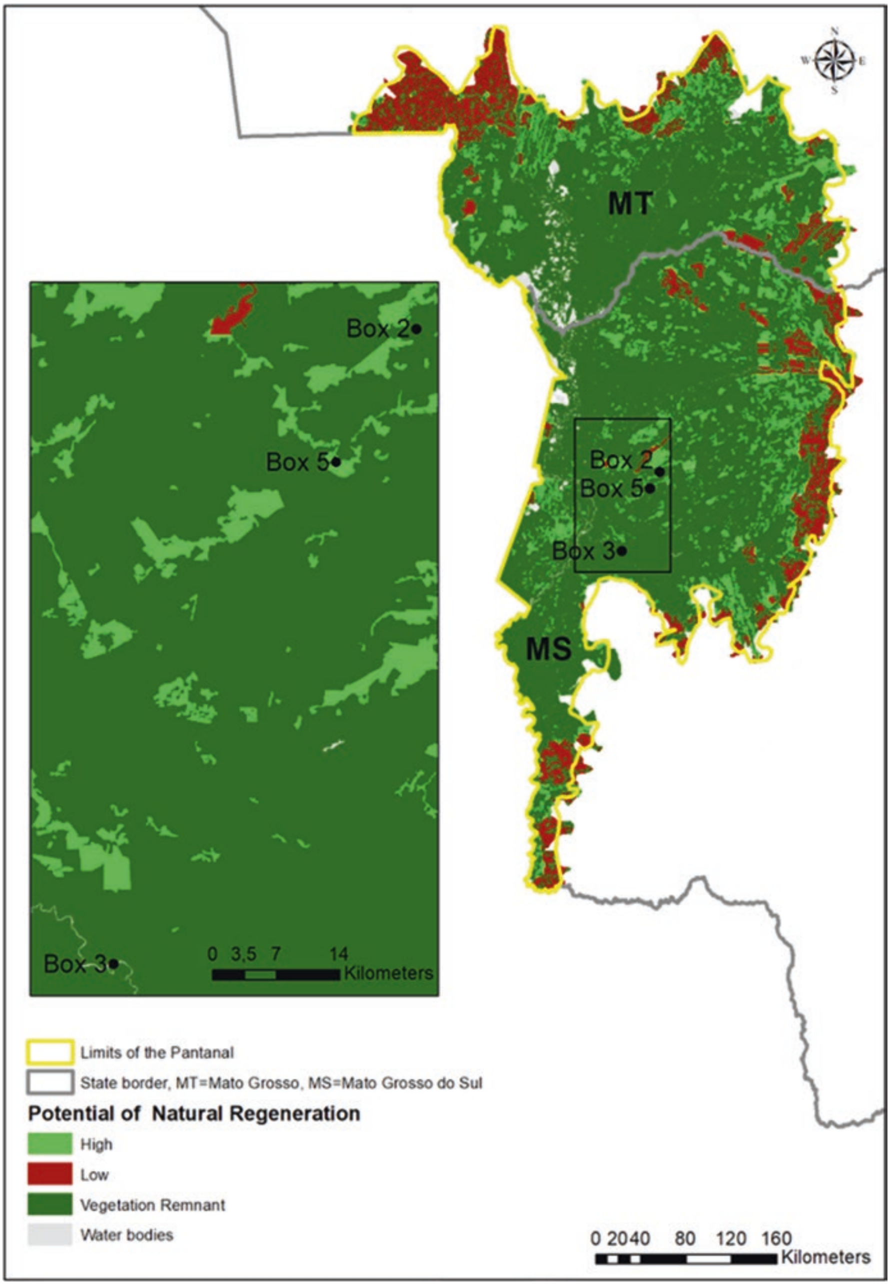


Fig. 20.1 Resilience map of the Pantanal with the study areas. (Adapted from Pott et al. 2018)

produced several groups that were evaluated and classified by experts in the categories as areas of (1) high resilience (2) and low resilience (Fig. 20.1). Although this approach may seem somewhat subjective, this classification was very much welcomed by experts who considered the results quite similar to the real situation.

Despite the assumption that the Pantanal is the Brazilian biome with least environmental liability, it is also the most difficult to restore owing to its hydrologic dynamism (Pott et al. 2018). As regards anthropogenic disturbances in the Pantanal, 54% of the sites belong in the category "low-resilient" (mainly the subregions of Paiaguás, lower Barão de Melgaço, southern Aquidauana, and southern Apa-Amonguijá-Aquidabã). Meanwhile, 46% of the sites were considered as "high-resilient," spread over several subregions. However, it is important to highlight that the wildfire event in 2020 may be triggering restoration actions particularly in low-resilient sites, but even in fire-sensitive vegetation high-resilient sites over the huge affected area (impacting almost one-third of the Pantanal and four million hectares (Libonati et al. 2020) almost half of which had not been burnt previously in the last two decades (Garcia et al. 2021)).

The map resulting from this classification (Fig. 20.1) should be used carefully for setting restoration strategies because local conditions must be considered. However, it is a good basis for large-scale planning and public policies (Martins et al. in press). So far, we lack precise information on the duration natural regeneration takes in the various subregions of the Pantanal considered as high- or low-resilient. Our given example of a natural regeneration study in the Pantanal (see Box 20.2 and Cardoso et al. 2017) refers to deforestation areas surrounded by original vegetation remnants. The Brazilian legislation framework presumes that 20 years are needed to reach restoration in Legal Reserves (LR) (Brasil 2012). Hence, if sites in near-pristine areas take 30 years for natural regeneration in the Pantanal (see Box 20.2 and Cardoso et al. 2017), some additional active restoration techniques will be needed to abbreviate that in low-resilient sites to achieve levels of restoration time as required by law (i.e., to reach restoration in Legal Reserves).

20.6 Examples of Studies Carried Out in Brazil: Active and Passive Restoration

While emphasizing that the kind of restoration to be applied should be fine-tuned to the environmental mosaic and degradation level, here we present five boxes with different examples of active (or assisted) restoration and passive (or unassisted) natural regeneration.

Box 20.1: Identifying Flood-Tolerant Species for Restoring Pantanal Wetlands

The "New Forest Code" (2012) reduced the Areas of Permanent Preservation (APP) and that negatively affects them (Garcia et al. 2013, 2016; Soares-Filho et al. 2014; Brancalion et al. 2016). The APP is now restricted to the regular watercourse bed, instead of covering the wider seasonally overflown bed, and thus reduces the legally protected riparian belt (Garcia et al. 2013, 2016; Soares-Filho et al. 2014). Hence, the restoration projects in these areas will experience a higher seasonal variation and that can hinder the running of restoration programs (Garcia et al. 2013, 2016). Owing to this specific change in the law, the species for restoration of this seasonally flooded zone should be tolerant of flood periods and proceed with their growth at the end of the flooding.

Taking into account the Cerrado influence on the vegetation of the Pantanal (Pott et al. 2011), we refer to a study (Bogarín et al. In Prep) whose objective was to identify Cerrado and Pantanal species tolerant of short inundation. Our question was: Do species found in the flood-prone edges of the regular watercourse bed in the Cerrado and the Pantanal develop special morphological structures and in greater quantity during the stress period of flooding and are they more resistant to hypoxia? This concerned 13 species: *Calophyllum brasiliense* Cambess (Clusiaceae), *Cecropia pachystachya* Trécul (Urticaceae), *Cedrela odorata* L. (Meliaceae), *Copaifera langsdorffii* Desf. (Fabaceae), *Croton urucurana* Baill. (Euphorbiaceae), *Guibourtia chodatiana* Hassl (Fabaceae), *Inga laurina* (Sw.) Willd. (Fabaceae), *I. vera* Willd. (Fabaceae), *Ormosia arborea* (Vell.) Harms (Fabaceae), *Pterogyne nitens* Tul. (Fabaceae), *Tabebuia insignis* (Miq.) Sandwith (Bignoniaceae), *Triplaris americana* L. (Polygalaceae), and *Vitex cymosa* Bertero ex Spreng (Lamiaceae). Their seedlings were acquired from local nurseries, planted in soil in plastic boxes, and kept under the same conditions of radiation and temperature (Fig. 20.2). We submerged the soil of the seedling boxes in 5 cm of circulating water. Circulating water was assumed to simulate the flow of the floodwater on the riverbanks. We assessed the responses of the following variables: the dry matter of roots, stems, and leaves, plant height, basal stem diameter, presence and number of adventitious roots and lenticels, leaf fall, and renewal. The experimental inundation period was 56 days, and after that, the plants received a further 56 days of post-inundation recovery. As regards flood tolerance and survival of the species, we found that the species that develop special morphological structures during the flooding period are not necessarily the most tolerant of hypoxia since all species survived and grew. However, a few developed some morphological structures to better adapt to the stress period, e.g., *I. vera*, *C. urucurana*, and *C. pachystachya*. Only *T. insignis* showed a reduced root mass, and *I. vera* showed a reduced height and diameter, but both survived the 2 months of flood stress. Their growth affected by flood was unexpected since the treelet *T. insignis* occurs on floating meadows and in Cerrado wetlands (*veredas*), and *I. vera* is abundant in flooded riparian forests. The four species mentioned are widespread and also native to the Pantanal. The only species non-native to the Pantanal are *C. odorata* and *O. arborea*, but they occur in the upper watershed (i.e., Cerrado surrounding areas called as *plateau*).

Fig. 20.2 Experiment of flood simulation on riparian forest saplings in plastic boxes filled with 5 cm of circulating water above soil level for 56 days in the greenhouse at Embrapa Gado de Corte, Campo Grande, Mato Grosso do Sul

Box 20.2: Method Used to Restore the Pantanal: Passive Restoration Via Natural Regeneration

Deforested study sites (0.5–2 ha), after clearing (axe-logging and burning) and cultivation (mainly cassava), were abandoned for 18, 28, and 30 years and then compared with adjacent pristine remnants (Cardoso et al. 2017). Note that fire in this case was not a wildfire (as occurred in 2020; see Libonati et al. 2020), but a fire used to clean the site for cultivation. After terminating cultivation, the bare ground left to secondary succession becomes first colonized by exotic herbs and shrubs, later by native trees. Most species participating in the natural regeneration also occur in the remnants of native vegetation (Fig. 20.3) (Cardoso et al. 2017), but their range of importance value seems to decrease over time (Fig. 20.4). Photographs were taken for a visual comparison of the studied areas (Figs. 20.5, 20.6, and 20.7). The soil fertility level in the regenerated patches was generally similar to that of the nearby native remnants, except for lower carbon stock in the 28-year site. However, considering

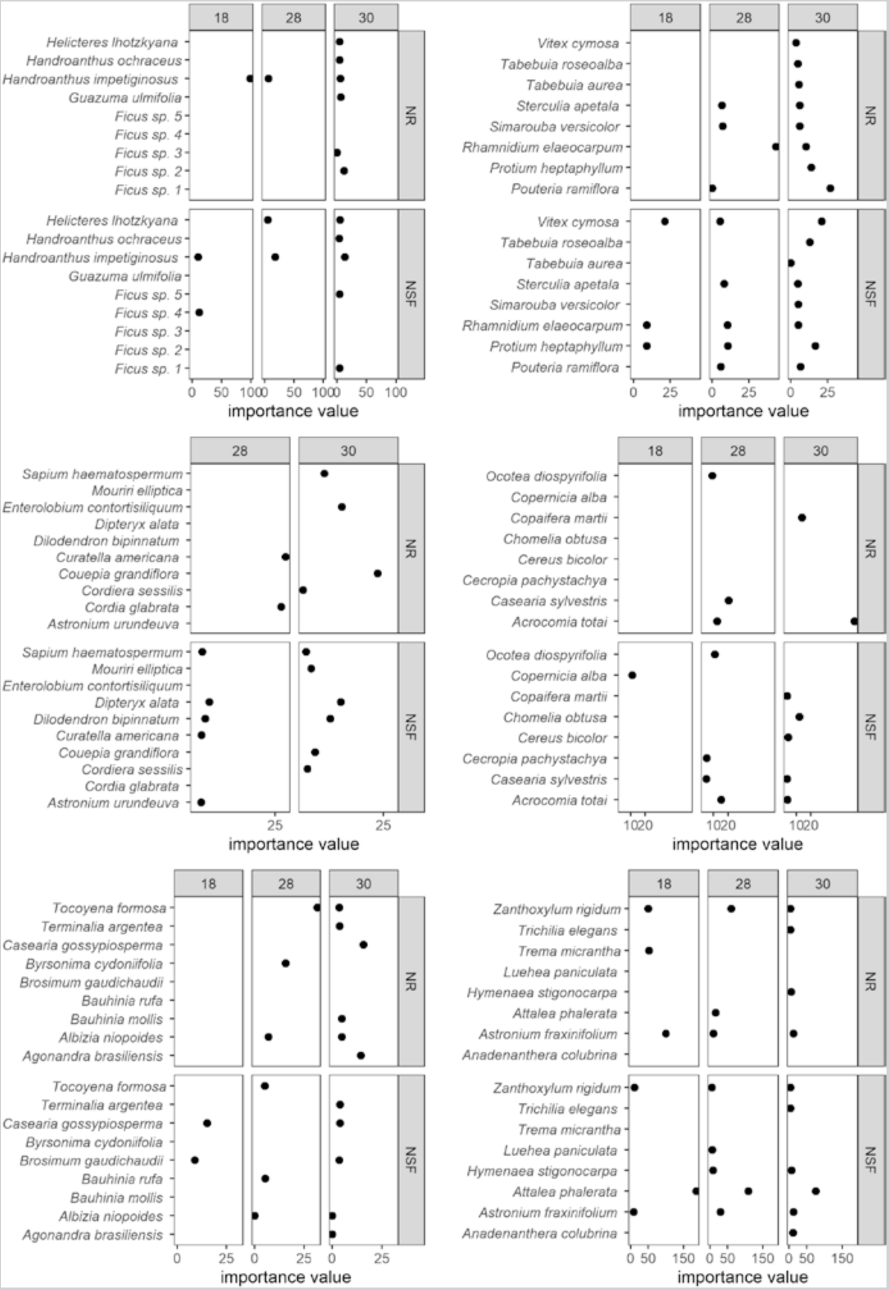


Fig. 20.3 Importance value (IV) of tree species sampled in preserved native semideciduous forest (NSF) adjacent to the and natural regeneration (NR) of deforested semideciduous forests abandoned for 18, 28, and 30 years, at Nhumirim ranch, Nhecolândia subregion of the Pantanal, Corumbá, MS, Brazil. Raw data source: Cardoso et al. (2017)

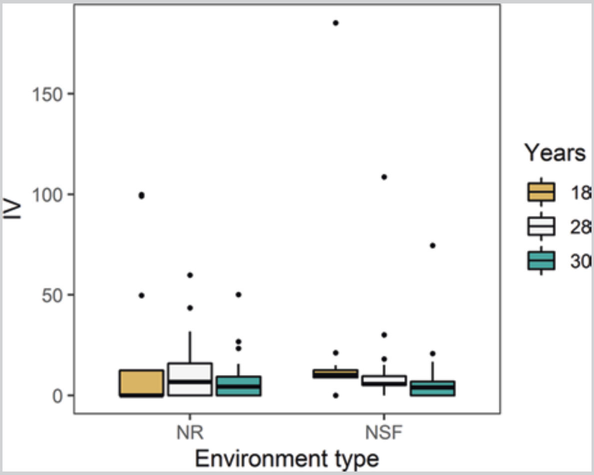


Fig. 20.4 Importance value (IV) range of tree species sampled in preserved native semideciduous forest (NSF) adjacent to the and natural regeneration (NR) of deforested semideciduous forests abandoned for 18, 28, and 30 years, at Nhumirim ranch, Nhecolândia subregion of the Pantanal, Corumbá, MS, Brazil. Raw data source: Cardoso et al. (2017)

Fig. 20.5 Original semideciduous forest area (**a**) and natural regeneration area without management for 30 years after deforestation, considered fully restored (**b**), at Nhumirim ranch, Nhecolândia subregion in the Pantanal, Corumbá, MS, Brazil. (Source: Cardoso et al. (2017). Photos: Suzana Maria Salis)

Fig. 20.6 Native semideciduous forest area (**a**) and 28-year natural regeneration of deforested area still showing some gaps with exotic grasses (**b**), at Nhumirim ranch, Nhecolândia subregion in the Pantanal, Corumbá, MS, Brazil. (Source: Cardoso et al. (2017). Photos: Suzana Maria Salis)

Fig. 20.7 Original semideciduous forest area (**a**) and 18-year natural regeneration deforested area (**b**) at Nhumirim ranch, Nhecolândia subregion in the Pantanal, Corumbá, MS, Brazil. (Source: Cardoso et al. (2017). Photos: Suzana Maria Salis)

forest structure and composition, only the 30-year site reached the levels of adjacent reference sites, where the vegetation was considered fully restored. The 30-year regenerated vegetation had a similar height and species richness (29 species) as the natural sites (31), while the 28-year stand had fewer species (15) than the natural (23). The floristic composition differed, as the regenerated forest still contained pioneer tree species such as *Albizia niopoides*, *Cecropia pachystachya*, *Cordia glabrata*, *Guazuma ulmifolia*, and *Tabebuia aurea*. The most abundant species was the palm *Attalea phalerata*. In the 18-year regeneration stand, there grew many young plants of the palm (Cardoso et al. 2017). Many of these were still stemless, with leaves sprouting from the underground part of the stem as well from the buried hypocotyl. It is one of the best species for forest restoration in the Pantanal.

Cerrado woodlands ("*Cerradão*") have been cleared mostly in the eastern and northwestern parts of the Pantanal for sowing African *Urochloa* spp. Mismanaged or abandoned pastures undergo regeneration, with secondary succession mainly from the resprouting from the persistent underground plant parts (e.g., *Annona* spp. and *Copaifera martii*). Cerrado tree and shrub species compete more successfully with exotic grasses than do forest species. In the upland, the Cerrado woodland regenerated in a 20-year cattle exclosure, the remaining trees and underground regrowth working as nuclei. Many native species of the so-called pasture weeds are excellent species for regeneration either in forest or Cerrado areas. For example, in cleared areas of Atlantic Forest in Mato Grosso do Sul, some of the principal pioneer woody plants are *Croton floribundus*, species of Lauraceae and Myrtaceae, *Peltophorum dubium*, *Senegalia* spp., *Sparattanthelium leucanthum*, *Tabernaemontana catharinensis*, and *Trema micrantha*. Some pioneer species of dry forest on calcareous soils are *Astronium urundeuva*, *Cenostigma pluviosum*, and *Vachellia farnesiana*.

There is little information on regeneration in the unique Chaco areas in the southwest of the State, there is also little information on regeneration, but after clearing a dense recovery from the seed bank occurs, mainly of legumes, e.g., *Mimosa* spp., *Muellera nudiflora*, *Parkinsonia praecox*, *Prosopis ruscifolia*, and *Vachellia* spp., as well as *Schinopsis balansae*. There are still other scattered data regarding riparian forest restoration in the Pantanal and surrounding ecosystems (plateau where the spring-fed rivers occur, part of Cerrado and Amazon). On a small scale, shifting cultivation (slash and burn) subsistence agriculture occurred along the rivers until it was forbidden in the 1980s. Subsequently, these areas became revegetated. Two other chapters of this book report on important factors of vegetation regeneration in the Pantanal. One, on fire (Chap. 18), mentions the seedling regeneration of the riparian forest of the Paraguay River, driven by flood and fire, while the second refers to seed banks (Chap. 15). Another chapter of this book addresses the dynamics of the aquatic vegetation (Chap. 4), and we highlight that restoration of aquatic vegetation of Pantanal is a knowledge gap.

Box 20.3: Method Used to Restore the Pantanal: Active Restoration by Transplanting Seedlings from Natural Regenerating Stands and Protection against Herbivory

In Brazil, the low diversity of local forest seedlings and saplings in nurseries is one of the handicaps faced by active restoration (Viani et al. 2012; Calegari et al. 2011; Pott et al. 2018). That has strongly reduced the possibilities of restoring the biological and genetic diversity of degraded areas by restoration projects. In the Pantanal region, lack of knowledge about species regeneration and recruitment restricts restoration success. Moreover, transporting seedlings or nursing them in remote places is costly. However, an on-farm nursery could be viable in tourist resorts, while presently native trees are often

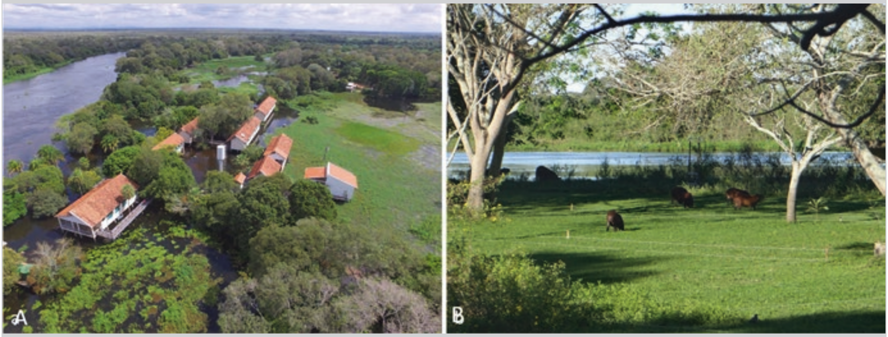


Fig. 20.8 (**a**) Base de Estudos do Pantanal (BEP), research station of the Universidade Federal de Mato Grosso do Sul, in the flood period, with the Miranda River overflowing in the rainy season. (**b**) Study site at the BEP on the deforested levee before planting the saplings for ecological restoration, showing some pegs of the experiment, a few regenerating riparian trees, and a secondary grassland kept short by mowing and grazing by capybara (*Hydrochoerus hydrochaeris*), a herbivore native to the Pantanal, with the Miranda River in the back (Reis et al. 2021)

Fig. 20.9 (**a**) Seedlings of *Ocotea diospyrifolia,* removed from naturally regenerated stands in a riparian forest for transplanting to the restoration area, showing their lignotubers; (**b**) Nursery at the *Base de Estudos do Pantanal*, screened to 70% sunlight for acclimation of the saplings in plastic bags; (**c**) Sapling of *Inga vera*, with their stem resprouting 90 days after planting; (**d**) Sapling of *I. vera*, with new leaves after flooding lasted 6 months; (**e**) Protection of wire mesh cages around saplings against mammal herbivory, and the small image on the right shows the assessment of insect damage (in red) on a leaf of *I. vera* (Reis et al. 2021)

replaced by exotic ornamentals. The high cost of various restoration techniques applied in Brazil has been limiting, and new, cheaper alternatives should be developed. Transplantation of seedlings may be a good alternative for the Pantanal to preserve the local genetic diversity (Pott et al. 2018; Reis et al. 2021). Other barriers are posed by the ecological filters that are characteristic of the Pantanal, e.g., the flood as a limiting factor in the recruitment of native species. Besides, herbivory and predation are also factors interfering with restoration success.

The technique of transplanting seedlings consists of a partial removal of the most abundant recruits from fragments with a high regeneration potential (Viani et al. 2012). In this process, seedlings of the selected species (most abundant) should be dug up with minimal harm to their root structure (Fig. 20.8a), though inevitably disrupted taproots will cause some failure. Subsequently, the seedlings should be pruned, preferably to 50% of their leaves, in order to reduce water stress after the uprooting and to enable identification (Calegari et al. 2011). Next, the seedlings have to be transported to the nursery in buckets or bags, to prevent wilting. There, the seedlings should receive further care, such as the addition of substrate to specific bags, until the root system recovers. Then the seedlings should acclimatize by gradually diminishing watering and increasing exposure to the sun. Last, the already hardened seedlings have to be transplanted in the field and surveilled.

We conducted a seedling transplant trial (Reis et al. 2021 on the *Pantanal Study Base* (19°34′37″S and 57°00′42″ W) of the Universidade Federal de Mato Grosso do Sul, at the margin of the Miranda River, Corumbá, MS. The deforested area (Fig. 20.8, Box 20.3) is an Area of Permanent Preservation (APP) since it is on the riverside, and the State environmental agency (Institute for the Environment – *Imasul*) requested its restoration. We collected naturally recruited seedlings from the adjacent seasonally flooded riparian forest. We choose four predominant pioneer species of different life forms, all zoochoric and bird-attracting: *Inga vera* (Fabaceae), *Attalea phalerata* (Arecaceae), *Ocotea diospyrifolia* (Lauraceae), and *Psychotria carthagenensis* (Rubiaceae).

In the experiment, we tested if the technique of transplanting seedlings from naturally regenerated stands in the riparian forest, with protection against herbivory (Fig 20.9c), is feasible as regards costs, growth, and survival. Variables relevant in the establishment, survival, and growth of the seedlings were assessed, such as height, diameter, leaf number, and occurrence of resprouting. We also tested the effect of seedling size-classes on establishment success: small (10–39 cm) and tall (40–69 cm). Furthermore, we evaluated the response of seedlings to two flood levels at the collecting point and at the planting spot, based on the watermark (left by the flood on pegs and stem barks): low (<50 cm) and high (>50 cm). Additionally, we suppressed arthropod and mammal herbivory.

The seedlings were planted (2 × 2 m) before the flood. One month after planting, the survival was 70%, i.e., only 30% of the seedlings died owing to drought, since we watered them only in the first few days. We replaced the dead individuals. After the flood period, which lasted for 6 months in 2018, we reevaluated the seedlings for survival, height, diameter, and flood depth, and repaired wire mesh cages, and applied formicide. In the first month of flooding, ca. 83% of the seedlings survived in general. However, after the flood, we observed a drop in survival (20%); seedlings of *Inga vera* and *Psychotria carthagenensis* showed the highest survival rates (>70%). Contrary to expectation, these surviving individuals were mainly in the small size-class (10–39 cm). During the flood period, the measured morphological characteristics did not significantly differ, the growth in height and diameter being minimal, but resprouting increased by 12% in most species (Fig. 20.9c). Regarding flood level, the seedlings planted on the higher ground showed better survival, owing to the shorter time of submergence of their leaves. Regarding herbivory, leaf number was higher, while leaf area was lower in the protected treatment, i.e., the protected seedlings showed more but smaller leaves ($P = <0.005$). Herbivory was higher in control plants (>10% consumed leaf area) than fenced seedlings ($P = <0.005$). Hence, the protection against mammal herbivory showed to be efficient for planted seedling survival. As well as preserving herbivory, shelters were a key resource for fauna colonization, indicating the multifunctional property of seedling shelters in improving microhabitat structure for orb-weaver spiders (Borges et al. 2020). Compared with Mato Grosso do Sul values (Antoniazzi et al. 2016), the inputs in this experimental seedling transplantation (with the cost-effectiveness of seedling transplanted with protection against herbivory) were 61% cheaper than other tree planting techniques in the region. However, there is still room to seek new alternatives aiming to lower costs of large-scale restoration. Hence, this technique has been considered as a viable option to be used for restoring sites of the Pantanal under flooding and herbivory pressure (Rodrigues et al. 2019).

Box 20.4: Method Used to Restore Vegetation in the Pantanal: Active Restoration Via Nucleation

Considering the high regeneration potential of some regions of the Pantanal (Pott et al. 2018), nucleation is a promising tool for ecological restoration. Nuclei implantation allows for the reestablishment of the environmental connectivity and, consequently, of the gene flow, thus promoting higher stability in ecosystem dynamics. We emphasize, however, that nucleation works in areas with a high natural regeneration potential, whereas in severely degraded ones, it is slow or not interconnected, and unlikely to restore a whole landscape.

The formation of nuclei through soil translocation and artificial perches allows to a connection of degraded areas and fragments (Fig. 20.10). Especially perches promote the entrance of distant seed, and so increase local diversity. However, both techniques need enrichment with seeds or seedlings of late-successional species if their seed rain is limited or absent (Abreu 2013). In the case of the Pantanal, natural open areas are flood-prone, where recruitment from tree seed rain only succeeds for flood-tolerant species. In contrast, flood-sensitive seeds start growing in dry years or on termite/ant hills, e.g., *Hymenaea stigonocarpa*. That is why various woody species colonize road embankments.

The Anderson nuclei provide another nucleation technique that gave good results (Fig. 20.11). Planting seedlings of pioneer and secondary species at high density (0.5 m apart from each other) allows the establishment of a competitive native plant cover, which soon shades out exotic grasses. Besides, it is possible that within 6 months species are flowering and fruiting, attracting pollinators, dispersers, and predators, and reestablishing critical ecological processes (Fróes 2015). Two of the fast-growing species are *Croton urucurana* and *Trema micrantha*.

The results of soil translocation and artificial perches for Areas of Permanent Preservation in the microregion of Dourados, MS (surrounding

Fig. 20.10 Nucleation: (**a**) to (**c**) Artificial perches; (**d**) and (**f**) Soil translocation; (**g**) Soil translocation after 6 months; (**h**) Soil translocation after 2 years; (**i**) Artificial perches after 2 years (Source: Abreu 2013); (**c**) and (**h**) show young *Cecropia pachystachya*

upland of Pantanal plain), showed the existence of facilitator elements that start the secondary successional process in the degraded area. The predominance of regenerating plants of the initial and intermediate succession phases in both topsoil transfer and artificial perch treatments characterizes the potentiality of the area to continue its recomposition by favoring natural succession. From the nuclei, the formation of a progressively structured community with the highest possible diversity is expected, owing to the return of interactions between producers, consumers, and decomposers.

The efficiency of nucleation for the reestablishment of ecological processes is evident from several reports (Abreu 2013; Souza 2013; Pereira et al. 2014; Fróes 2015). However, we here mention some critical points. Although these

Fig. 20.11 Anderson nuclei: (**a**) Nucleus of nine saplings at planting – late secondary successional species in the middle, December 2013; (**b**) One month after planting; (**c**) Six months after planting; (**d**)–(**f**)) One year after planting; (**g**) Onset of fructification of *Trema micrantha* at 6 months after planting; (**g–h**) Fructification of *Aegiphila sellowiana*, 14 months after planting; (**i**) Fructification of *Croton urucurana* 7 months after planting; (**j**)–(**k**) Nuclei acting as perches (bird nest in **k**); (**l**) Fruits of *Smilax brasiliensis* from seed rain in a nucleus (Source: Fróes 2015)

techniques have low initial costs, the control of exotic grasses in nuclei must be constant and is expensive (Pereira et al. 2020). Besides, weeding has to be selective and not mechanized, to maintain the regenerating plants for the future connections between nuclei. Slashers and weed string-trimmers can damage the basal bark. Grass control also prevents accidental fires that can often be fatal wildfires, and it can be made by integrative fire management (Garcia et al. 2021).

Box 20.5: Method Used to Restore the Pantanal Vegetation: Active Restoration Via Direct Sowing

Direct sowing is a method utilized for the restoration of degraded areas owing to its practicality, low costs, and fast plant establishment compared with planting seedlings (Cole et al. 2010; Ceccon et al. 2016). Nevertheless, it has some disadvantages such as lower rates of germination and low viability of the seeds as well as high plant mortality in the initial phase (Ceccon et al. 2016; Rego and Urbanetz 2017).

We summarize a direct sowing experiment, conducted in a fenced area to exclude cattle (19°06′27,46″S, 56°44′40,43″W), in the Pantanal subregion of Nhecolândia (Rego and Urbanetz 2017), in an area considered of high resilience (see in Fig. 20.1, Box 20.5). Before sowing, harvesting ants were controlled and exotic grasses were mechanically slashed. Seeds of ten native species of trees were manually sown, the various species interspaced at distances of 3 m × 0.5 m: *Anadenanthera colubrina*, *Aspidosperma australe*, *Astronium fraxinifolium*, *Dipteryx alata*, *Hymenaea courbaril*, *H. stigonocarpa*, *Magonia pubescens*, *Astronium urundeuva*, *Sterculia apetala*, and *Vitex cymosa*, with around 80% germination in laboratory tests. However, the grasses regrew, and plant establishment at 16 months after sowing and density was very low, with just ca. 1 plant/ha of only three species. *Sterculia apetala* was the tallest (2–3 m) compared with 1.3 m of *Dipteryx alata* and *Vitex cymosa*, probably because they have rather large seeds and the seedling phase is critical (Rego and Urbanetz 2017). The conclusion was that direct sowing without further control of competing grasses is not efficient in the Pantanal (Rego and Urbanetz 2017). It shows the need of long-term projects including money for weed control.

20.7 Legislation and Future Implications

Under the Native Vegetation Protection Law (Brasil 2012), which replaced the Forest Code of 1965, the restoration area of the Area of Permanent Preservation (APP) was reduced. The new law considers an APP starting from the edge of the regular watercourse bed and not anymore as stretching over the widest seasonal bed; this reduces the riparian protection strip (Garcia et al. 2013, 2016; Soares-Filho et al. 2014). With just the changes in item 1 of article 4 of the law, there is a reduction in the restoration areas of APPs of 43% in some regions of the Atlantic Forest and 56% in the Cerrado, but can still be worse in Pantanal and Amazon (Garcia et al. 2013). Hence, the restoration projects of temporarily flooded riparian forests in some subregions of the Pantanal with a short flood period (Junk et al. 2006; Arruda et al. 2016) do fit within these new zones narrowed by the law. Submitting the plants in these areas to hypoxia, caused by the low O_2 pressure (Keeley 1979), can jeopardize the effectiveness of the ecological restoration there, mainly with respect to the flood non-tolerant species. That creates a selective effect on the species composition during a variable period, dependent on the topography adjacent to the water body, and will allow the survival of the most tolerant plants only (Metzger et al. 1998; Capon 2005).

Regarding the Pantanal, there is not yet a law concerning a policy of specific environmental management, restoration, and conservation. The State of Mato Grosso, with Law 8,830/2008, established the policy of management and protection of Upper Paraguay. In 2015, the State of Mato Grosso do Sul established Decree 14,273, known as CAR Pantanal, which modifies the Native Vegetation Protection Law (Brasil 2012), restricting economic activities on the Pantanal floodplain. This decree requests the preservation of 50% of the arboreal vegetation and 40% of native grassland in a private property in the Pantanal. It grants the rural owners the sale or exchange of areas to compensate for missing legal reserves elsewhere, as long as those belong to the same biome. Hence, a need arose to uniformize the environmental legislation for the Pantanal in both states. Particularly, there is no law to uniformize Legal Reserve size in the Pantanal, as it occurs in other biomes, and if LR increased to 80%, it would reduce the soil nutrient replacement costs by 10% saving USD$ 1.1 million per year (Guerra et al. 2020b).

The great challenge of the new Pantanal Law is to create rules that generate employment and income in the region and, at the same time, do not damage the environment while meeting the demands of producers and environmentalists in the Pantanal. Science can support public policies related to restoration (Garcia et al. 2019; Tomas et al. 2018, and Tomas et al. 2019). Vegetation loss in the Pantanal forms a geographical arc, very similar to what was observed in the Amazon, from the plateau toward the lowland (Guerra et al. 2020c). This “arc of vegetation loss” in the border areas of the Pantanal coincides with the most intensely used and least resilient areas (see least resilient areas in Fig. 20.1). Therefore, if priority is given only to natural regeneration based on restoration costs, all restoration responsibility will be upon the shoulders of the traditional lowland ranchers whose land is more resilient, dispensing restoration liability from agribusiness that without proper environmental planning can be a significant degradation driver. Moreover, an Environmental Compliance Program (PRA) at the state level can be a crucial legal instrument to control, to reward, to facilitate, and to promote these remarks for the best match between compliance with the law and best socio-environmental gains. Meanwhile, the given examples can be useful for planning, implementing, and monitoring ecological restoration in the Pantanal.

Acknowledgments This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brazil (CAPES) – Finance Code 001, the University of Mato Grosso do Sul, and the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). We thank to teams of ongoing restoration projects in Pantanal: the “Strategic and participative restoration in Pantanal: “Baía Negra” protected area” (LEI/UFMS and ECOA financed by GEF- Terrestre (grant number: 055/2020); and Luan Santana, SOS Pantanal, as well as all companies (EDP) and individuals for financial support to the “Pantanal Call Movement”. LCG thanks to L’Oréal-UNESCO-the Brazilian Academy of Sciences (ABC) for the “For Women in Science” award.

References

Abdon MDM, Silva JSV, Marselhas ID et al (2007) Desmatamento no bioma Pantanal até o ano 2002: relações com a fitofisionomia e limites municipais. R Bras Cart 59(1):17–24

Abreu TSS (2013) Dinâmica florestal e aplicação de técnicas nucleadoras para restauração ecológica em área de preservação permanente da Fazenda Experimental da Universidade Federal da Grande Dourados, MS. Dissertation, Universidade Federal da Grande Dourados

Alday JG, Pallavicini Y, Marrs RH et al (2011) Functional groups and dispersal strategies as guides for predicting vegetation dynamics on reclaimed mines. Plant Ecol 212:1759–1775

Allen EB, Brown JS, Allen MF (2001) Restoration of animal, plant and microbial diversity. Encycl Biodv 5:185–202

Antoniazzi L, Sartorelli P, Costa K et al (2016) Restauração florestal em cadeias agropecuárias para adequação ao código florestal: análise econômica de oito estados brasileiros. Agroicone, INPUT, Brasil

Arruda GMT, Calbo MER (2004) Efeitos da inundação no crescimento, trocas gasosas e porosidade radicular da carnaúba (*Copernicia prunifera* (Mill.) H.E. Moore). Acta Bot Bras 18:219–224

Arruda WS, Oldeland J, Paranhos Filho AC et al (2016) Inundation and fire shape the structure of riparian forests in the Pantanal, Brazil. PLoS One 11(6):e0156825

Barral MP, Benayas JMR, Meli P et al (2015) Quantifying the impacts of ecological restoration on biodiversity and ecosystem services in agroecosystems: a global meta-analysis. Agric Ecosyst Environ 202:223–231

Bogarín MRA, Reis LK, Laura VA, Pott AG, Szabo JK, Garcia LC (In Prep) Morphological and phenological strategies for flooding tolerance in Cerrado and Pantanal trees: implications for restoration under a new legislation

Borges FLG, Oliveira MR, Reis LK, Garcia LC (2020) Screens and webs: multifunctional seedling shelters contribute to Araneae restoration. Ecol Eng 158:106026

Bradshaw AD (1996) Underlying principles of restoration. Can J Fish Aquat 53:3–9

Brancalion PHS, Garcia LC, Loyola R et al (2016) A critical analysis of the native vegetation protection law of Brazil (2012): updates and ongoing initiatives. Nat Conserv 14:1–15

Brasil. Lei n.° 12.651, de 25 de maio de 2012. Dispõe sobre a proteção da vegetação nativa; altera as Leis n.°s 6.938, de 31 de agosto de 1981, 9.393, de 19 de dezembro de 1996, e 11.428, de 22 de dezembro de 2006; revoga as Leis n.°s 4.771, de 15 de setembro de 1965, e 7.754, de 14 de abril de 1989, e a Medida Provisória n.° 2.166–67, de 24 de agosto de 2001; e dá outras providências. Diário Oficial [da] República Federativa do Brasil, Brasília, DF, 149(102):1–8. Seção 1. In: http://pesquisa.in.gov.br/imprensa/jsp/visualiza/index.jsp?data=28/05/2012&jornal=1&pagina=1&totalArquivos=168

Calegari L, Martins SV, Busato LC et al (2011) Seedling production of native tree species in nurseries via rescue of young plants. Rev Árvore 35(1):41–50

Capon SJ (2005) Flood variability and spatial variation in plant community composition and structure on a large arid floodplain. J Arid Environ 60:283–302

Cardoso EL, Salis SM, Crispim SMA et al (2017) Regeneração natural de áreas utilizadas como roça no Pantanal da Nhecolândia. Bol Pesq Desenvolv Embrapa Pantanal 134:1–20

Ceccon E, Gonzalez EJ, Martorell C (2016) Is direct seeding a biologically viable strategy for restoring forest ecosystems? Evidence from a meta-analysis. Land Degrad Dev 27:511–520

Cherry JA, Ramseur GS, Sparks EL et al (2015) Testing Sea level rise impacts in tidal wetlands: a novel in situ approach. Methods Ecol Evol 6(12):1443–1451

Cole RJ, Holl KD, Keene CL et al (2010) Direct seeding of late-successional trees to restore tropical montane forest. For Ecol Manag 261:1590–1597

Colmer TD, Voesenek LACJ (2009) Flooding tolerance: suites of plant traits in variable environments. Funct Plant Biol 36:665–681

Coutinho LM (2006) O conceito de bioma. Acta Bot Bras 20(1):13–23

Crawford RMM (1992) Oxygen availability as an ecological limit to plan distribution. Adv Ecol Res 23:93–185

Donatti CI, Galetti M, Pizo MA et al (2007) Living in the land of ghosts: fruit traits and the importance of large mammals as seed dispersers in the Pantanal, Brazil. In: Dennis AJ et al (eds) Seed dispersal: theory and its application in a changing world. Cabi Publishing, Cambridge, pp p104–p123

Dong X, Hengjie Z, Haiting J et al (2013) Ecological restoration of degraded wetlands in China. J Resour Ecol 4(1):63–69

Drew MMC (1997) Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Physiol Plant Mol Biol 48:223–250

Fattorini M, Halle S (2004) The dynamic environmental filter model: how do filtering effects change in assembling communities after disturbance. In: Temperton VM et al (eds) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, pp 96–114

Fróes CQ (2015) Técnica de restauração ecológica aplicada à Área de Preservação Permanente no sul do Mato Grosso do Sul. Dissertation, Universidade Federal da Grande Dourados

Garcia LC, Barros FV, Lemos Filho JP (2009) Fructification phenology as an important tool in the recovery of iron mining areas in Minas Gerais, Brazil. Braz J Biol 69:887–893

Garcia LC, Santos JSD, Matsumoto M et al (2013) Restoration challenges and opportunities for increasing landscape connectivity under the new Brazilian forest act. Nat Conserv 11:181–185

Garcia LC, Hobbs RJ, Santos FAM et al (2014) Flower and fruit availability along a forest restoration gradient. Biotropica 46:114–123

Garcia LC, Cianciaruso MV, Ribeiro DB et al (2015) Flower functional trait responses to restoration time. Appl Veg Sci 18:402–412

Garcia LC, Ellovitch MF, Rodrigues RR et al (2016) Análise científica e jurídica das mudanças no Código Florestal, a recente Lei de Proteção da Vegetação Nativa. Abeco, UFMS, Rio de Janeiro

Garcia LC, Chaves RB, Calmon M et al (2019) Políticas públicas e governança. In: Crouzeilles R et al (eds) Relatório temático sobre restauração de paisagens e ecossistemas. Plataforma Brasileira de Biodiversidade Serviços Ecossistêmicos (BPBES). e Instituto Internacional para Sustentabilidade (IIS), Rio de Janeiro, pp 14–19

Garcia LC, Szabo JK, Roque FO, Pereira AMM, Nunes da Cunha C, Damasceno-Júnior GA, Morato RG, Tomas WM, Libonati R, Ribeiro DB (2021) Record-breaking wildfires in the world's largest continuous tropical wetland: Integrative fire management is urgently needed for both biodiversity and humans. Journal of Environmental Management 293112870-10.1016/j.jenvman.2021.112870

Grace JB, Ford MA (1996) The potential impact of herbivores on the susceptibility of the marsh plant *Sagittaria lancifolia* to saltwater intrusion in coastal wetlands. Estuaries 19:13–20

Guerra A, Reis LK, Borges FLG, Ojeda PTA, Pineda DAM, Miranda CO, Laurance SG, Garcia LC (2020a) Ecological restoration in Brazilian biomes: identifying advances and gaps. For Ecol Manag 458:117802

Guerra A, Oliveira PTS, Roque FO, Rosa IMD, Ochoa-Quintero JM, Guariento RD, Colman CB, Dib V, Maioli V, Strassburg B, Garcia LC (2020b) The importance of Legal Reserves for protecting the Pantanal biome and preventing agricultural losses. J Environ Manag 260:110128

Guerra A, Roque F, Garcia LC, Ochoa-Quintero JM, Oliveira PT, Guariento RD, Rosa I (2020c) Drivers and projections of vegetation loss in the Pantanal and neighboring ecosystems. Land Use Policy 91:104388

He Q, Silliman BR (2015) Biogeographic consequences of nutrient enrichment for plant-herbivore interactions in coastal wetlands. Ecol Lett 18:462–471

Hobbs RJ, Norton DA (2004) Ecological filters, thresholds, and gradients in resistance to ecosystem reassembly. In: Temperton VM et al (eds) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, pp 72–95

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? For Ecol Manag 261:1558–1563

Joly CA, Crawford RMM (1982) Variation in tolerance and metabolic responses to flooding in some tropical trees. J Exp Bot 33:799–809

Jørgensen D (2015) Ecological restoration as objective, target, and tool in international biodiversity policy. Ecol Soc 20(4):43

Junk WJ, Cunha CND, Wantzen KM et al (2006) Biodiversity and its conservation in the Pantanal of Mato Grosso. Brazil Aquatic Sci 68:278–309

Keeley JE (1979) Population differentiation along a flood frequency gradient: physiological adaptations to flooding in *Nyssa sylvatica*. Ecol Monogr 49:89–108

King SL, Sharitz RR, Groninger JW et al (2009) The ecology, restoration, and management of southeastern floodplain ecosystems: a synthesis. Wetlands 29:624–634

Kirmer A, Tischew S, Ozinga WA et al (2008) Importance of regional species pools and functional traits in colonisation processes: predicting re-colonisation after large-scale destruction of ecosystems. J Appl Ecol 45:1523–1530

Kozlowski TT (1984) Plant responses to flooding of soil. Bio Sci 34:162–167

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiol Monogr 1(1):1–29

Kozlowski TT (2002) Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands 22:550–561

Labadz JC, Butcher DP, Sinnott D (2002) Wetlands and still waters. In: Perrow MR et al (eds) Handbook of ecological restoration. Cambridge University Press, Cambridge, pp 106–132

LaGrange T (2010) Wetland program plan for Nebraska. Nebraska Game and Parks Commission, Lincoln, 65 p

Letícia Koutchin, Reis Angélica, Guerra Maria Luciana Zequim, Colado Felipe Luís Gomes, Borges Maxwell da Rosa, Oliveira Evânia Xavier, Gondim Thomaz Ricardo Favreto, Sinani Natalia, Guerin Letícia Couto, Garcia (2019) Which spatial arrangement of green manure is able to reduce herbivory and invasion of exotic grasses in native species?. Ecological Applications 29(8) 10.1002/eap.2000

Libonati R, Sander LA, Peres LF, DaCamara CC, Garcia LC (2020) Rescue Brazil's burning Pantanal wetlands. Nature 588:217–220

Lobo PC, Joly CA (1998) Tolerance to hypoxia and anoxia in neotropical tree species. Oecol Bras 4:137–156

Lori AJR, Lee FA (2005) Effects of managed impoundments and herbivory on wetland plant production and stand structure. Wetlands 25(1):38–50

Marques MCM, Joly CA (2000) Germinação e crescimento de *Calophyllum brasiliense* (Clusiaceae), uma espécie típica de florestas inundadas. Acta Bot Bras 14:113–120

Martins PI, Belém LBC, Szabo JK, Libonati R, Garcia LC (in Press) Prioritising areas for wildfire prevention and post-fire restoration in the Brazilian Pantanal. Ecological Engineering

Meli P, Benayas JMR, Balvanera P et al (2014) Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: a meta-analysis. PLoS One 9(4):e93507

Metzger JP, Goldenberg R, Bernacci LC (1998) Diversidade e estrutura de fragmentos de mata de várzea e de mata mesófila semidecídua submontana do rio Jacaré-Pepira (SP). Braz J Bot 21:321–330

Moreno-Mateos D, Power ME, Comín FA et al (2012) Structural and functional loss in restored wetland ecosystems. PLoS Biol 10(1):e1001247

Nunes AP, Ticianeli FAT, Tomas WM (2006) Aves ameaçadas ocorrentes no Pantanal. Doc Embr Pant 83:1–47

Nuttle T (2007) Evaluation of restoration practice based on environmental filters. Restor Ecol 15(2):330–333

Okamoto JM (1998) Ecofisiologia da germinação e do metabolismo respiratório de quatro espécies do gênero *Inga* Mill. (Mimosaceae) submetidas à hipoxia e anoxia. Dissertation, Universidade Estadual de Campinas

Oliveira MT, Damasceno-Junior GA, Pott A, et al (2014) Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence. Forest Ecol Manag 331:256–263

Oliveira AKDM, Gualtieri SCJ (2017) Trocas gasosas e grau de tolerância ao estresse hídrico induzido em plantas jovens de *Tabebuia aurea* (Paratudo) submetidas a alagamento. Ciênc Florest 27:181–191

Oliveira ASD, Ferreira CS, Graciano-Ribeiro D et al (2015) Anatomical and morphological modifications in response to flooding by six Cerrado tree species. Acta Bot Bras 29:478–488

Paranhos Filho AC, Moreira ES, Oliveira AKMD et al (2014) Analysis of land cover changes using remote sensing between 2003 and 2010 in the Pantanal region. Eng Sanit Ambient 19:69–76

Parolin P, Junk WJ (2002) The effect of submergence on seed germination in trees from Amazonian floodplains. Bol Mus Para Emílio Goeldi Sér Bot 18:1–9

Pereira ZV, Ribeiro JF, Ogata R et al (2014) Semeadura direta mecanizada na recuperação de Reserva Legal com diversificação de espécies do bioma Cerrado do Distrito Federal. Cad Agroecol 9(4):1–11

Pereira ZV, Sangalli A, Padovan MP, Lobtchenko JCP (2020) Ecological restoration in a permanent preservation area in the state of Mato Grosso do Sul. Brazil J Anim Environ Res 3(4):4394–4407

Periotto NA, Tundisi JG (2013) Ecosystem services of UHE Carlos Botelho (Lobo/Broa): a new approach for management and planning of dams multiple-uses. Braz J Biol 73(3):471–482

Pfadenhauer J, Grootjans A (2009) Wetland restoration in Central Europe: aims and methods. Appl Veg Sci 2(1):95–106

Pott A, Oliveira AKM, Damasceno-Junior GA et al (2011) Plant diversity of the Pantanal wetland. Braz J Biol 71:265–273

Pott A, Garcia LC, Pereira ZV et al (2018) Potencial de regeneração natural da vegetação do Pantanal. Ministério do Meio Ambiente, p 6

Pregelli, DR, Albuquerque L, Gouveia J et al (2008) Recuperação de nascentes em área de Cerrado, Embrapa Gado de Corte, Campo Grande, Brasil. In IX Simpósio Nacional do Cerrado e II Simpósio Internacional Savanas Tropicais, Brasília, DF. In:simposio.cpac.embrapa.br/simposio_pc210/fichas/00578_trab1_ficha.pdf

Ramsar (2015) Wetlands: a global disappearing act. Fact sheet 3, February de 2015. https://www.ramsar.org/sites/default/files/documents/library/factsheet3_global_disappearing_act_0.pdf

Rebellato L, Cunha CND (2005) Efeito do "fluxo sazonal mínimo da inundação" sobre a composição e estrutura de um campo inundável no Pantanal de Poconé, MT, Brasil. Acta Bot Bras 19(4):789–799

Rego NH, Urbanetz C (2017) Potencial do uso da semeadura direta para a recomposição florestal no Pantanal da Nhecolândia, MS. Cir Téc Embr Pant 117:1–6

Reis LK, Guerra A, Colado MLZ, Borges FLG, Oliveira MR, Godim EX, Siani TRF, Guerin N, Garcia LC (2019) Which spatial arrangement of green manure is able to reduce herbivory and invasion of exotic grasses in native species? Ecological Applications 29: 1–24.

Reis LK, Damasceno-Junior GA, Battaglia L, Garcia LC (2021) Can transplanting seedlings with protection against herbivory be a cost-effective restoration strategy for seasonally flooded environments? For Ecol Manag 483:118742

Resende EK (2008) Pulso de inundação: processo ecológico essencial à vida no Pantanal. Doc Embr Pant 94:1–16

Rey-Benayas JM, Newton AC, Diaz A et al (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1124

Rezende CE, Kahn JR, Passareli L et al (2015) An economic valuation of mangrove restoration in Brazil. Ecol Econ 1(20):296–302

Rodrigues MA, Paoli AAS, Barbosa JM et al (2010) Evaluation of seed rain in areas of Restinga with different regeneration stages. Rev Árvore 34(5):814–824

Rodrigues RR, Jakovac CC, Moraes LF, Vieira D, Sampaio AB, Ganade G, Garcia LC, Overbeck GE (2019) Capítulo 5: Práticas de restauração nos diferentes biomas brasileiros. In: Crouzeilles R, Rodrigues RR, Strassburg BBN (eds) BPBES/IIS: Relatório Temático sobre Restauração de Paisagens e Ecossistemas. Editora Cubo, São Carlos, pp 32–37. https://www.bpbes.net.br/wp-content/uploads/2019/10/Relatorio_Restauracao_VF.pdf

Roque FO, Ochoa-Quintero J, Ribeiro DB et al (2016) Upland habitat loss as a threat to Pantanal wetlands. Conserv Biol 30(5):1131–1134

Rovai AS, Barufi JB, Pagliosa PR et al (2013) Photosynthetic performance of restored and natural mangroves under different environmental constraints. Environ Pollut 181:233–241

SER – Society for Ecological Restoration International Science and Working Policy Group, Washington DC (2014) The SER International Primer on Ecological Restoration. http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration

Soares VC, Scremin-Dias E, Daibes LF, Damasceno-Junior GA, Pott A, Lima LB (2021) Fire has little to no effect on the enhancement of germination, but buried seeds may survive in a Neotropical wetland. Flora 278:151801

Soares-Filho B, Rajão R, Macedo M et al (2014) Cracking Brazil's forest code. Science 344:363–364

Souza RP (2013) Semeadura direta de espécies florestais nativas, como alternativa de restauração ecológica para a região de Dourados, estado do Mato Grosso do Sul. Dissertation, Universidade Federal da Grande Dourados

Souza EB, Ferreira FA, Pott A (2016) Effects of flooding and its temporal variation on seedling recruitment from the soil seed bank of a Neotropical floodplain. Acta Bot Bras 30:560–568

Tomas WM, Cáceres NC, Nunes AP et al (2010) Mammals in the Pantanal wetland, Brazil. In: Junk WJ et al (eds) The pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft Publishers, Sofia-Moscow, pp 563–595

Tomas WM, Garcia LC, Roque FO et al (2018) Análise dos conceitos de "mesma identidade ecológica", "equivalência ecológica" e "offsetting" para compensação de Reserva Legal. DocEmbr Pant 159:1–30

Tomas et al (2019) Sustainability agenda for the Pantanal wetland: perspectives on a collaborative interface for science, policy, and decision-making. Trop Conserv Sci 12:1–29

Viani RAG, Brancalion PHS, Rodrigues RR (2012) Leaf area reduction and transplant timing for the use of seedlings from understorey in forest restoration. Rev Árvore 36(2):331–339

Vogt J, Lin Y, Pranchai A et al (2014) The importance of conspecific facilitation during recruitment and regeneration: a case study in degraded mangroves. Bas Appl Ecol 15(8):651–660

Zamith LR, Scarano FR (2010) Restoration of a coastal swamp forest in Southeast Brazil. Wetl Ecol Manag 18(4):435–448

Zedler JB (2000) Progress in trends restore ecology. Trends Ecol Evol 15(10):402–407

Zedler JB, Kercher S (2005) Wetland resources: status, trends, ecosystem services, and restorability. Ann Rev Environ Resour 30:39–74

Zelarayán ML, Celentano D, Oliveira EC et al (2015) Impacto da degradação sobre o estoque total de carbono de florestas ripárias na Amazônia Oriental, Brasil. Acta Amaz 45(3):271–282

Zhang YZ, Wang X (2001) A review of ecological restoration studies on natural wetland. Acta Ecol Sin 21(2):309–314

Chapter 21
Monetary Value of the Ecosystem Services of the Pantanal and Its Surroundings: First Approximations and Perspectives

Fábio Padilha Bolzan, Guellity Marcel Fonseca Pereira, Walfrido Moraes Tomas, Reinaldo Lourival, José Sabino, Franco Leandro Souza, Francisco Valente-Neto, Rafael Morais Chiaravalloti, Letícia Couto Garcia, Angélica Guerra, Rafaela Danielli Nicola, Áurea da Silva Garcia, Julio Francisco Alves Fernandes, Cyntia Cavalcante Santos, Mayara Camila Scur, Paula Isla Martins, Cassio Bernardino, and Fabio de Oliveira Roque

21.1 Introduction

The valuation of multiple ecosystem services (ES) provided by nature and the development of public policies to maintain those services that sustain life on the planet (https://www.millenniumassessment.org; http://www.teebweb.org; https://

F. P. Bolzan (✉) · G. M. F. Pereira · F. L. Souza · F. Valente-Neto · L. C. Garcia · A. Guerra
Bioscience Institute, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil

W. M. Tomas
Wildlife Laboratory, Embrapa Pantanal, Corumbá, MS, Brazil

R. Lourival
Nature and Culture International, Brasilia, DF, Brazil

J. Sabino
Universidade Anhanguera-Uniderp, Campo Grande, MS, Brazil

R. M. Chiaravalloti
IPE – Institute of Ecological Research, Nazaré Paulista, SP, Brazil

R. D. Nicola · Á. da Silva Garcia · J. F. A. Fernandes · C. C. Santos · M. C. Scur
Wetlands International Brazil & Mupan – Women in Action for the Pantanal,
Campo Grande, MS, Brazil

P. I. Martins · C. Bernardino
World Wildlife Fund – WWF Brazil, Campo Grande, MS, Brazil

F. de Oliveira Roque
Bioscience Institute, Federal University of Mato Grosso do Sul, Campo Grande, MS, Brazil

Centre for Tropical Environmental and Sustainability Science (TESS), James Cook
University, Cairns, QLD, Australia

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6_21

www.ipbes.net; https://www.bpbes.net.br) are among the most important challenges facing sustainable development. In recent decades, discussion of this issue has mostly focused on ES monetization (Costanza et al. 1997; Wilson and Carpenter 1999; de Groot et al. 2002; Gómez-Baggethun and Ruiz-Pérez 2011). Although ES economic valuation has been performed in many parts of the planet, there are still many regions and ecosystems for which such approaches are underdeveloped, and others where local scales and particularities have not been properly considered (Tammi et al. 2017).

ES monetization, commoditization, and valuation have been shown to be powerful tools for the development of public and private policies focused on ecosystem management and conservation (Tallis and Polasky 2009; Kumar et al. 2013; Alkemade et al. 2014; Trischler and Charles 2019). The description of the monetary value of stocks, demands, and flows of ecosystem functions at different spatial and temporal scales simplifies the communication on ES importance and opens dialogue opportunities between government, environmental entities, society, and market. However, a substantial effort is required to transform such ecological estimates into public policies and effective management plans (Costanza et al. 2017).

21.2 Value of Natural Wetlands

Wetlands occupy 3% of the global surface area, but constitute 43.5% of the global provision of ES. Inland, coastal, nearshore, and marine wetlands sustain and generate a wide range of ES. The monetary value of ES (Davidson et al. 2019) goes beyond the considerable diversity of plants and animals they contain; it includes regulation, provision, and cultural services that directly affect society in general. For instance, carbon storage and sequestration contribute significantly to climate regulation (Kayranli et al. 2010), playing an important role in mitigating the effects of climate change (https://www.millenniumassessment.org), as well as controlling the regional dynamics of nutrients, the biochemical and hydrological cycles so essential to fisheries and food security (Bullock and Acreman 2003; Reddy and DeLaune 2008; Huygens et al. 2013; Sueltenfuss and Cooper 2019).

The seminal study of Costanza et al. (1997) provided the first estimate of the global monetary value of the direct benefits provided by wetlands in terms of ecosystem services (US$ 14 trillion/year), later updated to US$ 50.7 trillion/year based on more detailed mapping tools (Costanza et al. 2014). De Groot et al. (2012) provided a more refined value for ES offered by inland wetlands, based on 168 studies, reaching a value of US$ 25,682 per ha/year. More recently, Davidson et al. (2019) estimated the global value of wetland ES as US$ 47.4 trillion/year using new information and a revised coastal and inland wetland classification.

As might be expected, the monetary valuation of ES varies as a function of the methodologies, criteria, and types of ecosystem services measured. Establishment of a standard approach to all kinds of wetlands is a challenge owing to their high environmental heterogeneity. For this reason, measuring specific services as indicators for particular areas is an appropriate method to support the development of regional public policy strategies (Trischler and Charles 2019).

21.3 The Pantanal and Its Surroundings

The Pantanal is considered one of the most important ES hotspots in the world, occupying 179,300 km^2, and located in the center of South America (Tomas et al. 2019). This wetland lies within the central portion of the Upper Paraguay River Basin (UPRB) and receives contributions from the various sub-basins draining the upland savannas of central Brazil, Bolivia, and Paraguay. Around 80% of Pantanal native vegetation remains, while some 60% of its Cerrado-covered plateaus have been converted to pasture and croplands (Roque et al. 2016). This ecosystem houses healthy populations of endangered species, such as jaguar (*Panthera onca*), giant otter (*Pteronura brasiliensis*), marsh deer (*Blastocerus dichotomus*), and hyacinth macaws (*Anodorhynchus hyacinthinus*) (Tomas et al. 2011; Cavalcanti et al. 2012; Tomas et al. 2015). The Pantanal is a highly dynamic sedimentary floodplain macroecosystem influenced by an annual flood pulse caused by the Paraguay River and its tributaries, and regional geomorphological characteristics (Junk 1993; Junk 1999; Kleidorfer et al. 2009; Alho and Sabino 2012). The spatial and temporal heterogeneity of the landscape provides many types of ES as goods for human well-being, including a highly diversified flora, fauna, and habitat types (biodiversity); food, freshwater, and pastureland (provisioning); climate stability and flood control (regulation); and scenic beauty, recreation, and spiritual and cultural diversity (sociocultural) (Seidl and Moraes 2000; Sandifer et al. 2015).

Costanza et al. (1997) estimated the value of Pantanal's environmental services at US$ 10,000 per ha/year. However, their evaluation did not consider the heterogeneity of this wetland system, comprising distinct subregions (Da Silva et al. 1998). Seidl and Moraes (2000) estimated the value of ES in the Nhecolandia Pantanal subregion at 15.5 billion dollars per year, resulting in a per hectare value that is 50% lower than calculations of Costanza et al. (1997). Seidl and Moraes's study was the first regional study guided and focused on data collected from the Pantanal River Basin to provide a detailed ES analysis, using water supply and disturbance regulation as the main services and benefits identified.

In this chapter, we aim to update the monetary valuation of ES for the Pantanal and Upper Paraguay River Basin (UPRB) based on recent available data including ecosystem maps and detailed land cover classifications, and therefore stimulate further discussions and development of valuation processes. We included the UPRB as an integrated unit in our analysis because of the tight functional, ecological, social, and economical interdependency between Pantanal wetlands and Cerrado uplands (Hamilton 2002; Junk et al. 2011).

21.4 Estimating the Pantanal and UPRB ES Monetary Value

We used the mean unit values from de Groot et al. (2012) and Costanza et al. (2014) to extrapolate estimated values for each land cover type (e.g., grassland, forest, freshwater) in the Pantanal and Upper Paraguay River Basin in Brazil. We regionalized the evaluation using MapBiomas Collection 2.3 datasets (http://mapbiomas.org) to calculate the total area of the different ecosystems and land-use types in the Pantanal and on the surrounding plateaus (corresponding to the UPRB).

Based on the map of wetlands, woodland ecosystems (savannas and forests), grasslands, and freshwater (Fig. 21.1), we attributed the values proposed by De Groot et al. (2012) to the following ecosystem services: provision services, regulating services, habitat services, and cultural services. Hence, we considered these as ES provided by the natural ecosystems. In the case of landscapes modified by anthropic activities (cattle production and crops), we calculated the net margin value per hectare using the most recent available databases (de Oliveira et al. 2016; Richetti et al. 2017), and we considered these as ES provided by anthropogenic activities.

21.5 First Approximation of the UPRB ES Monetary Value

Our exercise resulted in a total value of US$ 95 billion/year for the UPRB (US$ 2639.99 per ha/year) of which US$ 59 billion (US$ 3932.05 per ha/year) being from the Pantanal floodplain (~62%) and US$ 36 billion (US$ 1712.60/ha/year) from the surrounding plateaus (~38%) (Table 21.1). In terms of average per hectare per year, we find US$ 2639.99 from the UPRB, US$ 3932.05 from the Pantanal, and US$ 1712.60 from surrounding plateaus (Table 21.1). When we consider only anthropogenic activities, ~89% of the total net value is from the plateau (US$ 484 of 53 million/year), being the average per hectare per year of US$ 43.21 from the plateau and US$ 20.83 from the Pantanal. On the other hand, if we consider the ES provided by the natural ecosystems, the plateaus provide a value of US$ 35 billion/year (~32%) and the Pantanal of US$ 59 billion/year (~68%) (Table 21.1) On average, per hectare per year for ES, we have US$ 3650.49 from the plateau and US$ 4735.76 from the Pantanal.

Our results clearly indicate that the ES value of the Pantanal lands is much higher than currently recognized by the market, society, policy makers, as well as decision makers. Despite this, there is no actual market value for the land, since there are neither public policies nor a market for multiple ES values. Our findings open an important window of opportunity to discuss land-use and necessary public policies for the Pantanal. The region has considerable potential to conciliate conservation and food production, including restoration programs, payments for ecological services, certifications, and environmental compensation and offsetting mechanisms. Moreover, the monetary value of ES provides an insight into the enormous

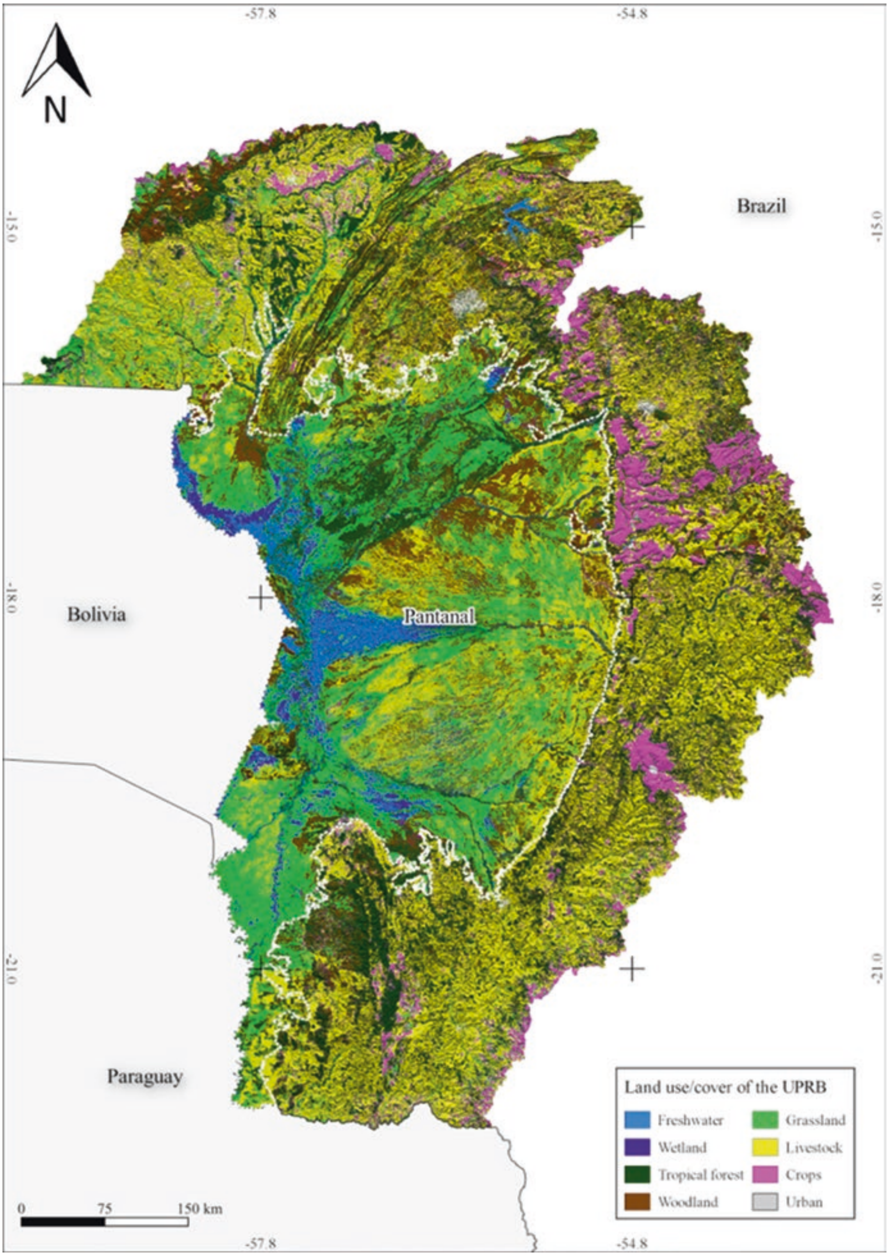


Fig. 21.1 Different ecosystems and land-use types in the Upper Paraguay River Basin (UPRB), Brazil, based on 2017 land cover maps. The white line indicates the boundary between the Pantanal floodplain and the plateau

Table 21.1 ES values and total areas of different ecosystems and land-use systems in the Pantanal floodplain and its surrounding plateaus, and for the entire Upper Paraguay River Basin (UPRB) in Brazil (i.e., Pantanal floodplain and plateaus together)

		Pantanal floodplain		Plateau		UPRB	
Ecosystems	US$/ha/year	Area(ha)	US$/year	Area(ha)	US$/year	Area(ha)	US$/year
Freshwater[a]	4267	612,979	2,615,582,844	74,704	318,761,968	687,683	2,934,344,812
Wetlands[a]	25,682	599,399	15,393,772,052	0	0	599,399	15,393,772,052
Tropical forest[a]	5264	4,766,344	25,090,033,711	5,132,841	27,019,272,760	9,899,184	52,109,306,471
Woodland[a]	1588	2,143,946	3,404,587,010	3,783,924	6,008,871,677	5,927,871	9,413,458,687
Grassland[a]	2871	4,309,942	12,373,843,396	671,824	1,928,805,670	4,981,766	14,302,649,066
Livestock[b]	20	2,528,129	50,562,588	7,963,344	159,266,885	10,491,474	209,829,473
Crops[b]	100	26,600	2,659,950	3,254,080	325,407,977	3,280,679	328,067,927
Total		**14,987,340**	**58,931,041,551**	**20,880,716**	**35,760,386,938**	**35,868,056**	**94,691,428,489**
Average (US$/ha/year)		**3932.05**		**1712.60**		**2639.99**	

[a] Natural ecosystems

[b] Anthropogenic activities

opportunity represented by economic conciliation of the Pantanal floodplain and the surrounding plateaus. A clear message emerging from our results is that the current monetary gains associated only with the agribusiness (e.g., cattle ranching, soy, maize, sugarcane, cotton, and forestry) are relatively small in comparison with the total monetary value of ecosystem services of untrammelled natural land cover (Figs. 21.2 and 21.3).

21.6 New Pieces of the Puzzle

21.6.1 Traditional Communities and Ecosystem Services

The cultural richness of the Pantanal is influenced by a mosaic of human cultures in the cross-border region between Brazil, Bolivia, and Paraguay. Indigenous populations and traditional people (*Pantaneiros*) coexist in the area, enhancing its cultural richness. The cultural interaction between *Pantaneiros*/indigenous people and natural resources occurs in a number of ways. They use Pantanal areas for fishing, as a source of clean water, for temporary settlements, to capture live bait (crabs and small fish), and to obtain diverse other natural goods. For example, the Pantaneiros use 376 species of medicinal plants, which are used against 18 illness categories (Bieski et al. 2012). A practice inherited from the Guató indigenous culture (Bortolotto and Guarim Neto 2005) is the use of the water hyacinth *Eichhornia crassipes* (Mart.) Solms (locally called “Camalote”), to make handicrafts. Ceramics produced and painted by Kadiwéu people demonstrate their ethnicity, including geometric representations of their social structure, mystic figures, and legends (Müller 2017). Besides, the black dye for this ceramic is produced from the sap of a native plant species (*Bulnesia sarmientoi*), while the Bocaiúva fruit (*Acrocomia aculeata*) is harvested to produce flour and ice cream.

Fishing is a key practice in the Pantanal for traditional communities and indigenous people, and provides both protein and income. In a survey carried out on the Paraguay River in the town of Cáceres (Mato Grosso State), only 7% of the respondents worked in agriculture, while 93% were fishermen (Ordonio et al. 2011; Arruda et al. 2014). Fifteen traditional communities have been recorded in the Brazilian part of the Pantanal wetland; they are distributed mainly along the Paraguay River. These communities are usually composed of an average of 80 fishermen, totaling 1200 traditional fishermen. This number is smaller than the total number of professional fishermen registered in the southern Pantanal alone (~2000) (Catella et al. 2014), but highlights the local importance of fishing-based incomes. The average income per fishermen is approximately US$ 300/month (Chiaravalloti 2019), with a yearly income close to US$ 4,320,000 for the 15 traditional communities, clearly indicating that this is a key activity for the local population and for the Pantanal economy.

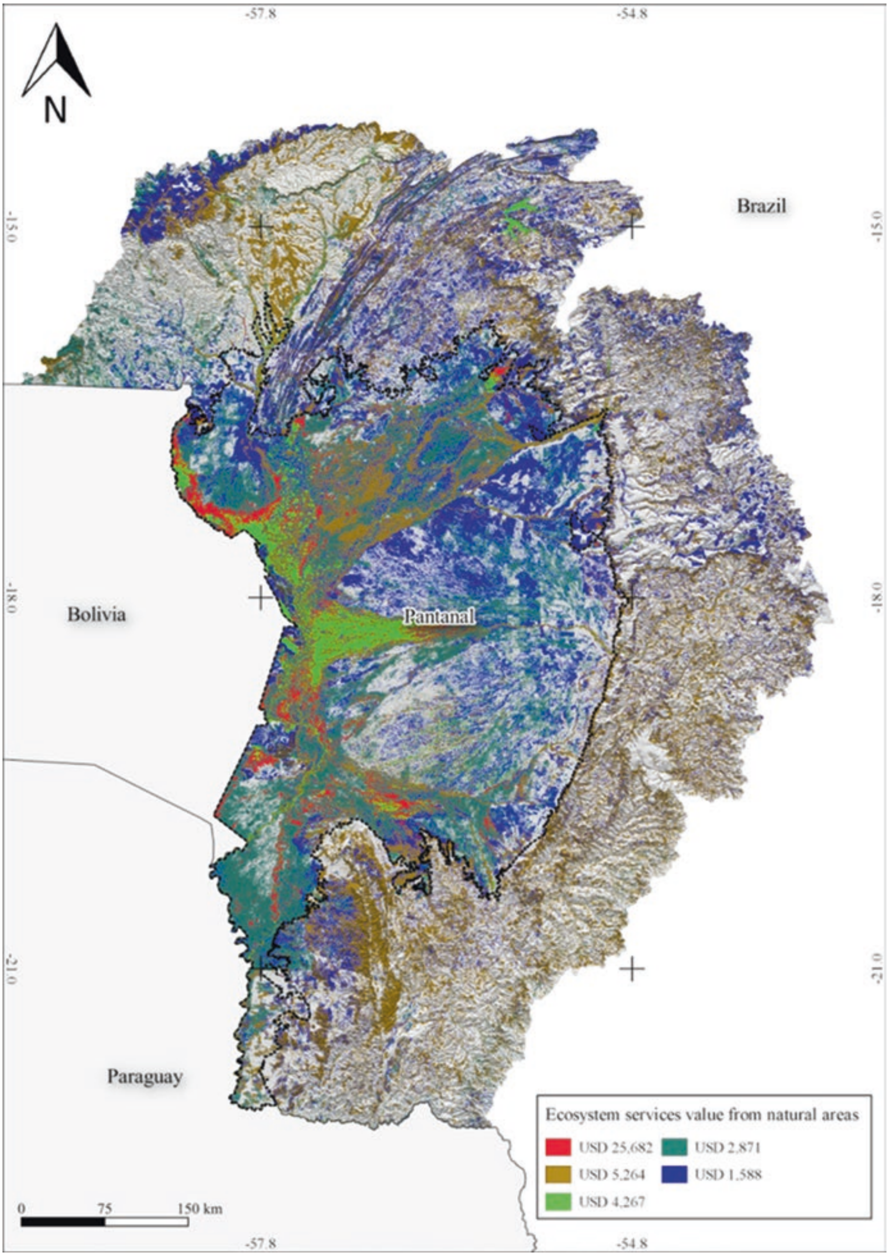


Fig. 21.2 Spatial distribution of the estimated ES values (US$/ha/year) for different natural ecosystems of the Upper Paraguay River Basin in Brazil

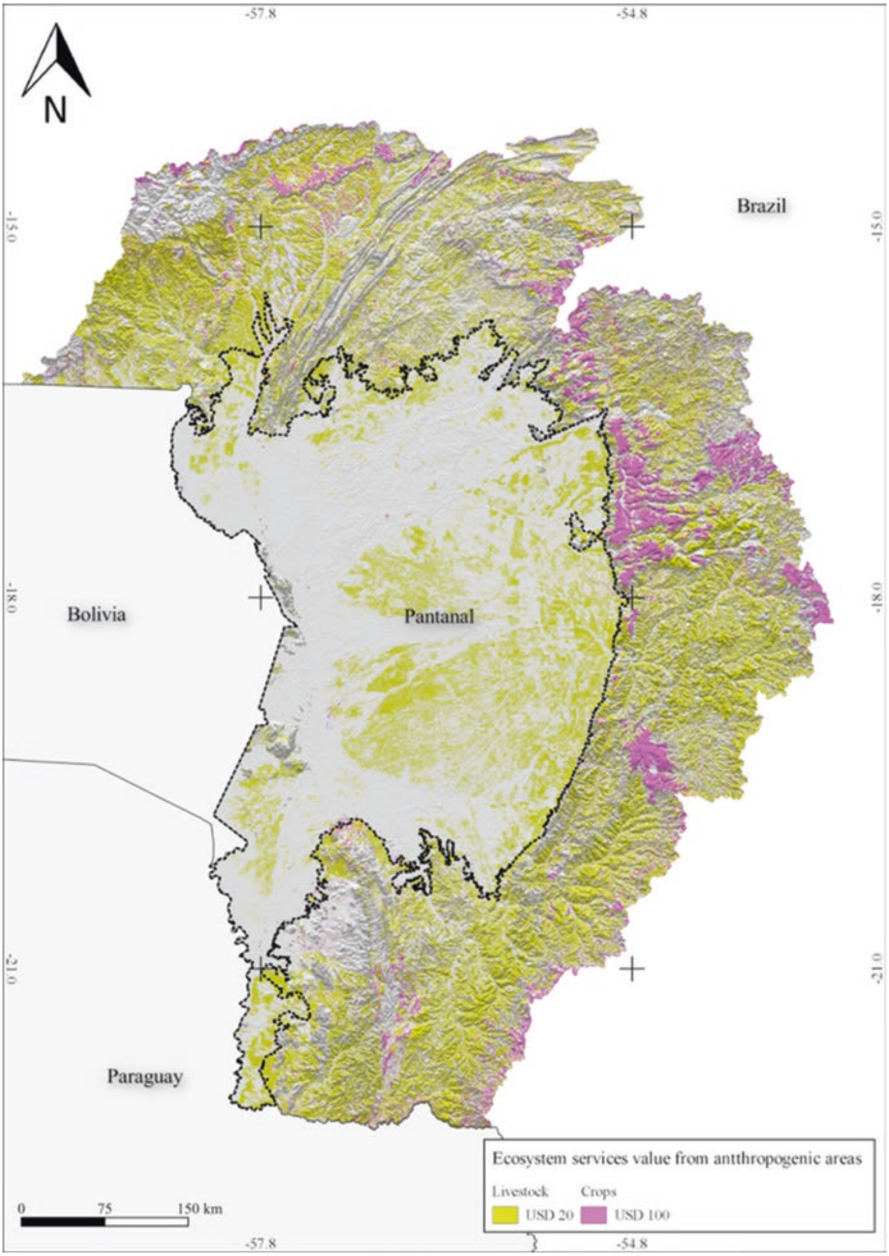


Fig. 21.3 Spatial distribution of the estimated net margin values (US$/ha/year) of anthropogenic areas of the Upper Paraguay River Basin, Brazil

The Pantanal may generate US$ 14.40 ha/year for traditional anglers, based on their yearly income (US$ 4,320,000), considering an estimated total area of 300,000 ha for the 15 traditional territories, and an area of 20,000 ha occupied by each community. However, this may be a gross underestimation of the total value. First, not all fishing-associated communities have been identified in the Pantanal and, therefore, remain to be evaluated. In addition, and perhaps most importantly, the value of the Pantanal for local people goes beyond the income generated by fishing. People place great value on locations, which their families have inhabited historically, or regions that have played an important role in their personal lives or family history (Chiaravalloti et al. 2017). Although this type of ES is difficult to valuate without specific methodologies, such as willingness to pay, it represents an important value that must be considered in any management initiative for the region. Hence, at least 300,000 ha of the Pantanal wetland, classified as part of traditional territories, should, in addition to the economic and ecological values, receive enhanced valorization owing to the intrinsic cultural and historic values for those living there.

21.6.2 Other Values

Other studies addressing animals and plants have also been relevant to the determination of Pantanal ES values, such as ecotourism (Tomas et al. 2019). Just as an example of such potential, the monetary value of the jaguar (*Panthera onca*) for ecotourism and its contribution to the local economy resulted in a value at 6.8 million dollars/year for the region of the *Encontro das Águas* State Park in the Pantanal of Mato Grosso State (Tortato et al. 2017). The values provided by jaguar ecotourism greatly exceed the losses associated with cattle predation, which has been estimated at US$ 121,500/year in a large, representative area (Tortato et al. 2017).

Recreational fishing is highly important for the Pantanal's tourism and economy. In 2016, 14,750 recreational fishermen visited the Mato Grosso do Sul UPRB (Catella et al. 2017). In the towns of Miranda and Corumbá, Mato Grosso do Sul State, this activity provided some 35–56 million dollars/year (Shrestha et al. 2002).

Fish also provide ES by regulating food chains, controlling pests, acting in the cycling of nutrients, and offering recreation opportunities (Holmlund and Hammer 1999). At the headwaters that flow into the Pantanal, there is a vigorous and growing nature-based tourism market for observing aquatic biodiversity, especially fish (Bessa et al. 2017). However, if tourist activity exceeds visitation limits, there are negative impacts on aquatic biota, such as higher stress responses and negative individual behavior (Lima et al. 2014).

In addition to wildlife contemplation and ecotourism, other activities, such as the development of productive chains to explore native plants, are also of considerable importance in developing more refined estimates for the value of regional ES. Baru nuts (locally "cumbaru" or "baru": *Dipteryx alata* Vogel – Fabaceae), for example, have considerable market value and improve the income for many communities and families (Melo 2015). The native Pantanal rice (*Oryza latifolia* and *Oryza rufipogon*) are also species that can contribute to the economic valuation of this system as a gourmet product for a niche market. These species are naturally abundant in the low-lying areas of the Pantanal impacted by long-lasting floods, can be sustainably exploited by communities, and have great appeal in sophisticated food preparation (Bertazzoni and Damasceno-Júnior 2011; see also the chapter on Monodominant Stands, Chap. 8). Other species such as the "bocaiuva" palm (*Acrocomia aculeata*), "pequi" (*Caryocar brasiliense*), "guavira" berry (*Campomanesia adamantium*), "mangaba" (*Hancornia speciosa*), "araticum" (*Annona* sp.), "laranjinha-de-pacu" (*Pouteria glomerata*), and several other non-timber products that are traditionally used in the region have been increasingly studied and contribute to aggregate value to the native flora of the Pantanal (Sinatex 2017; see the chapter on Native Food Plants, Chap. 19).

One of the major challenges for the monetization of ES based on species in the Pantanal is the spatially aggregated distribution of biodiversity, which limits the estimates to specific regions. For example, jaguars do not occur uniformly throughout the Pantanal area, while native rice stands occur only in specific zones of difficult access. Yet, seasonality limits a constant availability of native fruits and will not always be available for harvesting. In addition, recreational fishing is limited to accessible areas on large rivers. Although such ecosystem services are presumably found throughout of Pantanal floodplains, they will not be necessarily converted into commodities and monetarized. Accordingly, future approaches for more refined scenarios must prioritize the analysis of the spatial aggregated distribution of these activities.

21.7 Challenges, Opportunities, and Future

To further the development of the economic valuation of ES values of the Pantanal, it is necessary to advance the regionalization of estimates by providing tools that allow to spatialize the different ecosystem services. This more detailed approach is relevant because on a temporal scale we can fill in knowledge gaps that can further be applied in land use and its management (Xu et al. 2018; Peçanha et al. 2019).

The development of market measurement systems is an important part of the development of ecosystem services markets, involving basic regional estimates (van Maasakkers 2018). Hence, these relative values can be added to pluralistic valuation methods that reduce discrepancies and broaden the framework of articulations involving human-nature relationships, ecosystem services, and biodiversity conservation (Himes and Muraca 2018; Lienhoop and Schröter-Schlaack 2018). However, a great challenge in this approach is the lack of a market for ecosystem services at different governance scales (national, state, municipality). Initiatives such as the REDD+, carbon storage, carbon credit, biobanking, and other kinds of monetary activities based on the reduction of climate change drivers and environmental impacts glimpse opportunities, even in the international context.

Large-scale implementation of payments for environmental services (PES) is unlikely in the Pantanal in the short term, owing to the low level of environmental awareness among decision makers and low levels of financial support (Schulz et al. 2015). Moreover, major threats to the Pantanal plain come from upland agribusiness (Roque et al. 2016). Another key challenge is the strong socioeconomic inequality between inhabitants of the Pantanal lowlands and wealthy farmers of the plateau, so that potential suppliers of ecosystem services would face very high opportunity costs to participate in PES schemes. These opportunity costs are related to the privatization of some property rights required for ES exchange initiation, marketization to create opportunities to recover costs, introduction of ES policies or laws, and market facilitation needed to introduce financial or technical resources involving NGOs, universities, and other actors to support the market arrangement (Kolinjivadi et al. 2017).

Such challenges not only apply to PES but also are valid for any conservation strategy related to ES monetary valuation in the Pantanal, because its lands are mostly private. Hence, we believe that PES, or any kind of financial incentives for conservation, should not be considered a panacea, but instead as part of a pluralized valuation approach that includes environmental, social, and cultural values. In addition, financial incentives for conservation should be followed by education and communication programs with the aim of improving the level of environmental awareness among decision makers and stakeholders. It is important to note that, despite the challenges to large-scale PES implementation, there are many successful local initiatives that can be scaled up in the coming years, such as the Project *Fazenda Pantaneira Sustentável* (Santos et al. 2017), coordinated by Embrapa-Pantanal, and the "Manancial Vivo" Program (MVP) (Pagiola et al. 2013), which is a partnership between the National Water Agency (ANA) and the municipality of Campo Grande, Mato Grosso do Sul State. The MVP provides funds to farmers who conserve the soil, protect native vegetation, and restore degraded areas in the Guariroba River Basin (Sone et al. 2019). This protected environmental area is the main water supply for Campo Grande. Besides runoff reduction, there were increases in base flow, while soil erosion was reduced by 25% between 2012 and 2016 in the Guariroba River Basin (Sone et al. 2019). The MVP still reaches few farmers, but the results show the importance of applying conservation practices at the farm level to improve water quantity and quality.

An integrated framework and a more refined analysis of ecological services in the UPBR will not only contribute to achieving a more realistic understanding of the social and economic dynamics of the region but will also contribute to a better integration of views from the various stakeholders and actors. Monetization methods suffer a lot of criticism but, while it may be imperfect, has the advantage of providing valuable information on ecosystem services. Together with social and ecological approaches, stakeholders can use ES monetization to help decision-making

(Pascual et al. 2017; Díaz et al. 2018). We believe that a spatially explicit demonstration of the monetary dimension of ecological services will contribute to improve the dialogue between actors (landowners, decision makers, policy makers, investors, conservationists, general society) concerning political solutions capable of reconciliating the often conflicting demands of agribusiness and biodiversity conservation in the Pantanal over the long term. In summary, the monetary dimension of ecosystem services should be part of the Pantanal's agenda (Tomas et al. 2019).

Finally, we emphasize that estimates of ecosystem services in the Pantanal are not the same as pricing. In fact, we have shown another value for the biome, as our ES value estimates have underscored the natural potential of this ecosystem to improve local well-being. In addition to other regional approaches, this type of estimation can narrow the link between ES and the context of land use and natural area management, providing appropriate information on the economic development and conservation policies for the Pantanal.

References

Alho CJR, Sabino J (2012) Seasonal Pantanal flood pulse: implications for biodiversity conservation – a review. Oecologia Aust 16:958–978. https://doi.org/10.4257/oeco.2012.1604.17

Alkemade R, Burkhard B, Crossman ND, Nedkov S, Petz K (2014) Quantifying ecosystem services and indicators for science, policy and practice. Ecol Indic 37:161–162. https://doi.org/10.1016/j.ecolind.2013.11.014

Bertazzoni EC, Damasceno-Júnior GA (2011) Aspectos da biologia e fenologia de Oryza latifolia Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Bot Brasilica 25:476–786. https://doi.org/10.1590/S0102-33062011000200023

Bessa E, Silva F, Sabino J (2017) Impacts of fish tourism. In: Ecotourism's promise and peril. Springer International Publishing, Cham, pp 59–72

Bieski IGC, Rios Santos F, de Oliveira RM, Espinosa MM, Macedo M, Albuquerque UP, de Oliveira Martins DT (2012) Ethnopharmacology of medicinal plants of the Pantanal region (Mato Grosso, Brazil). Evidence Based Complement Altern Med 2012:1–36. https://doi.org/10.1155/2012/272749

Bortolotto IM, Guarim Neto G (2005) O uso do camalote, Eichhornia crassipes (Mart.) Solms, Pontederiaceae, para confecção de artesanato no Distrito de Albuquerque, Corumbá, MS, Brasil. Acta Bot Brasilica 19:331–337. https://doi.org/10.1590/S0102-33062005000200016

Bullock A, Acreman M (2003) The role of wetlands in the hydrological cycle. Hydrol Earth Syst Sci 7:358–389. https://doi.org/10.5194/hess-7-358-2003

Catella AC, Albuquerque SP, de Campos FLR, dos Santos DC (2014) Sistema de Controle da Pesca de Mato Grosso do Sul SCPESCA/MS – 20 – 2013

Catella AC, de Campos FLR, Albuquerque SP (2017) Sistema de Controle da Pesca de Mato Grosso do Sul – SCPESCA/MS 23 – 2016. Corumbá

Cavalcanti SMC, De Azevedo FCC, Tomás WM, Boulhosa RLP, Crawshaw PG (2012) Jaguar in Brazil the status of the jaguar in the Pantanal. Cat News:29–34

Chiaravalloti R (2019) The displacement of insufficiently "traditional" communities: local fisheries in the Pantanal. Conserv Soc 17:173. https://doi.org/10.4103/cs.cs_18_58

Chiaravalloti RM, Homewood K, Erikson K (2017) Sustainability and land tenure: who owns the floodplain in the Pantanal, Brazil? Land Use Policy 64:511–524. https://doi.org/10.1016/j.landusepol.2017.03.005

Costanza R, D'Arge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, van den Belt M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260. https://doi.org/10.1038/387253a0

Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. Glob Environ Chang 26:152–158. https://doi.org/10.1016/j.gloenvcha.2014.04.002

Costanza R, de Groot R, Braat L, Kubiszewski I, Fioramonti L, Sutton P, Farber S, Grasso M (2017) Twenty years of ecosystem services: how far have we come and how far do we still need to go? Ecosyst Serv 28:1–16. https://doi.org/10.1016/j.ecoser.2017.09.008

Da Silva JDSV, De Moura AM, Boock A, Da Silva MP (1998) Fitofisionomias dominantes em parte das sub-regiões do nabileque e miranda, sul do pantanal. Pesqui Agropecu Bras 33:1713–1719

Davidson NC, Van Dam AA, Finlayson CM, McInnes RJ (2019) Worth of wetlands: revised global monetary values of coastal and inland wetland ecosystem services. Mar Freshw Res. https://doi.org/10.1071/MF18391

de Arruda SBS, da Andrade LNPS, de Souza CA, da Cruz JS, dos Leandro GRS (2014) Socioeconomic characteristics of the riparians on the Paraguay River, the city of Cáceres, Pantanal - Brazil. Geogr em Questão 7:162–177

de Groot RS, Wilson MA, Boumans RM (2002) A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecol Econ 41:393–408. https://doi.org/10.1016/S0921-8009(02)00089-7

de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, Christie M, Crossman N, Ghermandi A, Hein L, Hussain S, Kumar P, McVittie A, Portela R, Rodriguez LC, ten Brink P, van Beukering P (2012) Global estimates of the value of ecosystems and their services in monetary units. Ecosyst Serv 1:50–61. https://doi.org/10.1016/j.ecoser.2012.07.005

de Melo SABX (2015) Sustentabilidade socioeconomica e ambiental da cadeia produtiva do Cumbaru (Dipteryx alata Vogel) em Poconé/MT. Universidade Estadual de Mato Grosso, Bioma Pantanal

de Oliveira LOF, de Abreu UGP, Dias FRT, Fernandes FA, Nogueira É, Silva JCB da (2016) Estimativa da População de Bovinos no Pantanal por meio de Modelos Matemáticos e Índices Tradicionais. Corumbá

Díaz S, Pascual U, Stenseke M, Martín-López B, Watson RT, Molnár Z, Hill R, Chan KMA, Baste IA, Brauman KA, Polasky S, Church A, Lonsdale M, Larigauderie A, Leadley PW, van Oudenhoven APE, van der Plaat F, Schröter M, Lavorel S, Aumeeruddy-Thomas Y, Bukvareva E, Davies K, Demissew S, Erpul G, Failler P, Guerra CA, Hewitt CL, Keune H, Lindley S, Shirayama Y (2018) Assessing nature's contributions to people. Science (80-) 359:270–272. https://doi.org/10.1126/science.aap8826

Gómez-Baggethun E, Ruiz-Pérez M (2011) Economic valuation and the commodification of ecosystem services. Prog Phys Geogr Earth Environ 35:613–628. https://doi.org/10.1177/0309133311421708

Hamilton SK (2002) Human impacts on hydrology in the pantanal wetland of South America. Water Sci Technol 45:35–44. https://doi.org/10.1007/s00105-007-1453-3

Himes A, Muraca B (2018) Relational values: the key to pluralistic valuation of ecosystem services. Curr Opin Environ Sustain 35:1–7. https://doi.org/10.1016/j.cosust.2018.09.005

Holmlund CM, Hammer M (1999) Ecosystem services generated by fish populations. Ecol Econ 200:253–268

Huygens D, Trimmer M, Rütting T, Müller C, Heppell CM, Lansdown K, Boeckx P (2013) Biogeochemical nitrogen cycling in wetland ecosystems: Nitrogen-15 isotope techniques. In: Methods in biogeochemistry of wetlands. John Wiley & Sons, Ltd, pp 553–591. https://doi.org/10.2136/sssabookser10

Junk WJ (1993) Wetlands of tropical South America. In: Wetlands of the world: inventory, ecology and management volume I. Springer, Dordrecht, pp 679–739

Junk WJ (1999) The flood pulse concept of large rivers: learning from the tropics. River Syst 11:261–280. https://doi.org/10.1127/lr/11/1999/261

Junk WJ, da Silva CJ, Nunes da Cunha C (2011) The Pantanal: ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Pensoft

Kayranli B, Scholz M, Mustafa A, Hedmark Å (2010) Carbon storage and fluxes within freshwater wetlands: a critical review. Wetlands 30:111–124. https://doi.org/10.1007/s13157-009-0003-4

Kleidorfer M, Möderl M, Fach S, Rauch W (2009) Optimization of measurement campaigns for calibration of a conceptual sewer model. Water Sci Technol 59:1523–1530. https://doi.org/10.2166/wst.2009.154

Kolinjivadi V, Van Hecken G, Rodríguez de Francisco JC, Pelenc J, Kosoy N (2017) As a lock to a key? Why science is more than just an instrument to pay for nature's services. Curr Opin Environ Sustain 26–27:1–6. https://doi.org/10.1016/j.cosust.2016.12.004

Kumar P, Esen SE, Yashiro M (2013) Linking ecosystem services to strategic environmental assessment in development policies. Environ Impact Assess Rev 40:75–81. https://doi.org/10.1016/j.eiar.2013.01.002

Lienhoop N, Schröter-Schlaack C (2018) Involving multiple actors in ecosystem service governance: exploring the role of stated preference valuation. Ecosyst Serv 34:181–188. https://doi.org/10.1016/j.ecoser.2018.08.009

Lima AC, Assis J, Sayanda D, Sabino J, Oliveira RF (2014) Impact of ecotourism on the fish fauna of Bonito region (Mato Grosso do Sul state, Brazil): ecological, behavioural and physiological measures. Neotrop Ichthyol 12:133–143. https://doi.org/10.1590/S1679-62252014000100014

Müller AM (2017) Arte Kadiwéu: processos de produção. Universidade de Coimbra

Ordonio D, Bezerra S, Torres De Oliveira H (2011) Impactos Socioambientais no Rio Paraguai, Cáceres, Mato Grosso, Brasil - Percepção dos Pescadores da Colônia Z-2 Social and environmental impacts in the Paraguai River Cáceres, Mato Grosso, Brazil-fishermen's perceptions of the Colony z-2. Ciência e Educ 17:957–973

Pagiola S, von Glehn HC, Taffarello D (2013) Experiências de pagamentos por serviços ambientais no Brasil. Centro de Referência em Educação Ambiental, São Paulo

Pascual U, Balvanera P, Díaz S, Pataki G, Roth E, Stenseke M, Watson RT, Başak Dessane E, Islar M, Kelemen E, Maris V, Quaas M, Subramanian SM, Wittmer H, Adlan A, Ahn SE, Al-Hafedh YS, Amankwah E, Asah ST, Berry P, Bilgin A, Breslow SJ, Bullock C, Cáceres D, Daly-Hassen H, Figueroa E, Golden CD, Gómez-Baggethun E, González-Jiménez D, Houdet J, Keune H, Kumar R, Ma K, May PH, Mead A, O'Farrell P, Pandit R, Pengue W, Pichis-Madruga R, Popa F, Preston S, Pacheco-Balanza D, Saarikoski H, Strassburg BB, van den Belt M, Verma M, Wickson F, Yagi N (2017) Valuing nature's contributions to people: the IPBES approach. Curr Opin Environ Sustain 26–27:7–16. https://doi.org/10.1016/j.cosust.2016.12.006

Peçanha R, Ferraz D, Silva J, Mattos R (2019) Marco Referencial em Serviços Ecossistêmicos, 1a edição. Embrapa Solos, Brasilia

Reddy KR, DeLaune RD (2008) Biogeochemistry of wetlands, 1st edn. CRC Press, Boca Raton

Richetti A, Garcia RA, da Ferreira LEAG (2017) Mapeamento da economia agrícola de Mato Grosso do Sul – MEA/MS. Campo Grande

Roque FO, Ochoa-Quintero J, Ribeiro DB, Sugai LSM, Costa-Pereira R, Lourival R, Bino G (2016) Upland habitat loss as a threat to Pantanal wetlands. Conserv Biol 30:1131–1134. https://doi.org/10.1111/cobi.12713

Sandifer PA, Sutton-Grier AE, Ward BP (2015) Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: opportunities to enhance health and biodiversity conservation. Ecosyst Serv 12:1–15. https://doi.org/10.1016/j.ecoser.2014.12.007

Santos SA, de Lima HP, Massruhá SMFS, de Abreu UGP, Tomás WM, Salis SM, Cardoso EL, de Oliveira MD, Soares MTS, dos Santos A, de Oliveira LOF, Calheiros DF, Crispim SMA, Soriano BMA, Amâncio COG, Nunes AP, Pellegrin LA (2017) A fuzzy logic-based tool to assess beef cattle ranching sustainability in complex environmental systems. J Environ Manag 198:95–106. https://doi.org/10.1016/j.jenvman.2017.04.076

Schulz C, Ioris AAR, Martin-Ortega J, Glenk K (2015) Prospects for payments for ecosystem Services in the Brazilian Pantanal: a scenario analysis. J Environ Dev 24:26–53. https://doi.org/10.1177/1070496514548580

Seidl AF, Moraes AS (2000) Global valuation of ecosystem services: application to the Pantanal da Nhecolandia, Brazil. Ecol Econ 33:1–6. https://doi.org/10.1016/S0921-8009(99)00146-9

Shrestha RK, Seidl AF, Moraes AS (2002) Value of recreational fishing in the Brazilian Pantanal: a travel cost analysis using count data models. Ecol Econ 42:289–299. https://doi.org/10.1016/S0921-8009(02)00106-4

Sinatex (2017) Anais do II Simpósio de Frutos Nativos e Exóticos. 173

Sone JS, Gesualdo GC, Zamboni PAP, Vieira NOM, Mattos TS, Carvalho GA, Rodrigues DBB, Alves Sobrinho T, Oliveira PTS (2019) Water provisioning improvement through payment for ecosystem services. Sci Total Environ 655:1197–1206. https://doi.org/10.1016/j.scitotenv.2018.11.319

Sueltenfuss JP, Cooper DJ (2019) A new approach for hydrologic performance standards in wetland mitigation. J Environ Manag 231:1154–1163. https://doi.org/10.1016/j.jenvman.2018.11.001

Tallis H, Polasky S (2009) Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Ann N Y Acad Sci 1162:265–283. https://doi.org/10.1111/j.1749-6632.2009.04152.x

Tammi I, Mustajärvi K, Rasinmäki J (2017) Integrating spatial valuation of ecosystem services into regional planning and development. Ecosyst Serv. https://doi.org/10.1016/j.ecoser.2016.11.008

Tomas W, Cáceres N, Nunes A, Fischer E, Mourão G, Campos Z (2011) Mammals in the Pantanal wetland, Brazil. In: Junk WJ, da Silva CJ, da Cunha CN, Wantzen KM (eds), The Pantanal ecology, biodiversity and sustainable management of a large neotropical seasonal wetland, Pensoft, pp 563–595

Tomas WM, Camilo AR, Ribas C, Leuchtenberger C, Borges PAL, Mourão G, Pellegrin LA (2015) Distribution and status of giant otter (Pteronura brasiliensis) in the Pantanal wetland, Brazil. Lat Am J Aquat Mamm 10:107. https://doi.org/10.5597/lajam00202

Tomas WM, de Oliveira RF, Morato RG, Medici PE, Chiaravalloti RM, Tortato FR, Penha JMF, Izzo TJ, Garcia LC, Lourival RFF, Girard P, Albuquerque NR, Almeida-Gomes M, da Andrade MHS, Araujo FAS, Araujo AC, De Arruda EC, Assunção VA, Battirola LD, Benites M, Bolzan FP, Boock JC, Bortolotto IM, da Brasil MS, Camilo AR, Campos Z, Carniello MA, Catella AC, Cheida CC, Crawshaw PG, Crispim SMA, GAD J, Desbiez ALJ, Dias FA, Eaton DP, Faggioni GP, Farinaccio MA, Fernandes JFA, Ferreira VL, Fischer EA, Fragoso CE, Freitas GO, Galvani F, Garcia AS, Garcia CM, Graciolli G, Guariento RD, Guedes NMR, Guerra A, Herrera HM, Hoogesteijn R, Ikeda SC, Juliano RS, Kantek DLZK, Keuroghlian A, ACR L, ALR L, Landeiro VL, Laps RR, Layme V, Leimgruber P, Rocha FL, Mamede S, DKS M, Marques MI, Mateus LAF, Moraes RN, Moreira TA, Mourão GM, Nicola RD, Nogueira DG, Nunes AP, da Nunes da Cunha C, Oliveira MD, Oliveira MR, Paggi GM, Pellegrin AO, Pereira GMF, Peres IAHFS, Pinho JB, Pinto JOP, Pott A, Provete DB, dos Reis VDA, dos Reis LK, Renaud P-C, Ribeiro DB, Rossetto OC, Sabino J, Rumiz D, Salis SM, Santana DJ, Santos SA, Sartori ÂL, Sato M, Schuchmann K, Scremin-Dias E, GHF S, Severo-Neto F, Sigrist MR, Silva A, Silva CJ, Siqueira AL, Soriano BMA, Sousa LM, Souza FL, Strussmann C, Sugai LSM, Tocantins N, Urbanetz C, Valente-Neto F, Viana DP, Yanosky A, Junk WJ (2019) Sustainability agenda for the Pantanal wetland: perspectives on a collaborative Interface for science, policy, and decision-making. Trop Conserv Sci 12:1–30. https://doi.org/10.1177/1940082919872634

Tortato FR, Izzo TJ, Hoogesteijn R, Peres CA (2017) The numbers of the beast: valuation of jaguar (Panthera onca) tourism and cattle depredation in the Brazilian Pantanal. Glob Ecol Conserv 11:106–114. https://doi.org/10.1016/j.gecco.2017.05.003

Trischler J, Charles M (2019) The application of a service ecosystems Lens to public policy analysis and design: exploring the Frontiers. J Public Policy Mark 38:19–35. https://doi.org/10.1177/0743915618818566

van Maasakkers M (2018) What role does planning have in the creation of ecosystem service markets? Evidence from two cases in Oregon. J Plan Educ Res:1–14. https://doi.org/10.1177/0739456X18773502

Wilson MA, Carpenter SR (1999) Economic valuation of freshwater ecosystem services in the United States: 1971-1997. Ecol Appl 9:772–783. https://doi.org/10.1890/1051-0761(1999)009[0772:EVOFES]2.0.CO;2

Xu X, Jiang B, Tan Y, Costanza R, Yang G (2018) Lake-wetland ecosystem services modeling and valuation: Progress, gaps and future directions. Ecosyst Serv 33:19–28. https://doi.org/10.1016/j.ecoser.2018.08.001

Index

G. A. Damasceno-Junior, A. Pott (eds.), *Flora and Vegetation of the Pantanal Wetland*, Plant and Vegetation 18, https://doi.org/10.1007/978-3-030-83375-6