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Regeneration of riparian forests of the Brazilian Pantanal under flood and fire influence



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ABSTRACT

Flood and fire are considered ecological filters and can shape the structure of plant communities in tropical wetlands and floodable savannas, especially on regeneration. However, in systems exposed to recurrent flood and fire, there is little information on the vegetation effects and implications for management. To test the effects of fire on flood-prone riparian forests of the Brazilian Pantanal, we analyzed how natural flood and fire can interact and influence species composition, abundance, and richness of the woody regeneration. This neotropical savanna wetland is subjected to annual and predictable flood pulses and to occasional wildfires. We established 106 plots $(2 \times 5 \text{ m})$ within the riparian forest of the Paraguay River in burned (recurrent) and unburned areas from 2001 to 2011 (verified on satellite images). We compared the plot topography with historic data of river levels from Ladário gauge in the same period. We sampled all trees, shrubs, and lianas from 0.3 to 2.5 m high. Flood in plots varied from 38 (higher areas) to 98 (lower areas) days year⁻¹. Our results show that variation in flood duration and occurrence of fire interact in a synergistic manner to reduce stem numbers on regeneration and modify species composition and distribution. Species richness differed in relation to flood duration, but not to fire. All growth forms had low number of exclusive species in both unburned and burned sites. Our results have implications for wetland management. The natural flooding regime is responsible for the diversity of habitats and species. Changes of the hydrology due to land management or climatic changes may result in changes of fire regime with consequences for the analyzed vegetation patterns and ecosystem functions. This neotropical savanna wetland system is stable and resilient as long as its natural patterns and periodicities of flooding and wildfires are maintained. Our results point to the necessity to analyze the interacting effects of selective environmental forces in order to be able to preserve the form and functions of the huge wetlands of the Pantanal.

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1. Introduction

Disturbances such as flood and fire can act as biological filters during the process of regeneration (Gentry, 1991a). The ecological roles of flood and fire are important in tropical savanna wetlands, where the riparian woody vegetation is shaped by regularly occurring floods and occasional wildfires (Pettit and Naiman, 2007). Plant community composition and structure is a function of position within the drainage network and additional disturbances such as fire (Swanson et al., 1988; Agee, 1993; Naiman et al., 1998). However, the interaction of both flood and fire does not have to be entirely destructive. For example, North American coastal redwood forests are disturbed by both flooding and fire, but these factors generate growth conditions that support the largest trees in the world (Naiman et al., 1998). Flooding is deleterious for nonadapted woody species (Hook, 1984; Kozlowski, 1984; Kozlowski

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and Pallardy, 2002), but trees growing in wetlands exposed to periodic and predictable flooding develop adaptations, such as the formation of lenticels, aerenchyma, and adventitious roots (Parolin et al., 2004), suberization of the roots to protect against radial oxygen loss (De Simone et al., 2002, 2003), and photosynthetic activity under water (Schlüter et al., 1993). These adaptive responses expressed by plants submitted to hypoxia or anoxia (Drew et al., 1981; Lobo and Joly, 1995; Scatena and Menezes, 1996) enable woody species to cope with flood, and to undergo vigorous growth and physiological activities despite flooding (Parolin, 2009; Parolin and Wittmann, 2010).

Depending on their respective sets of adaptations, species are restricted to specific areas with a determined pattern of flooding, sedimentation, and soil texture, leading to clear vegetation zonation along the flooding gradient (Parolin et al., 2004; Wittmann et al., 2008, 2010). The same is true to a certain extent with fire, where plants are adapted to survive frequent fire regimes, e.g., by possessing thick bark, fire-resistant seeds, or root crowns that sprout (Dwire and Kauffman, 2003; Heinl et al., 2007a; Ricklefs, 2003). This resistance also depends on the fire behavior (i.e., return interval, intensity, and severity), the types of fuels from arboreal and herbaceous components, leaf moisture (Agee et al., 2002), canopy closure, height of canopy base (Lyons-Tinsley and Peterson, 2012), and accumulated fuel load due to flood frequency (Cronk and Fennessy, 2001; Heinl et al., 2007b; Mitsch et al., 2010).

In floodable savannas, the ecotone belt with riparian vegetation contains trees that are tolerant of flood and fire (Pettit and Naiman, 2007). Species growth and dominance are determined by the local situation, the available propagles, i.e., the soil seed bank (Bradshaw, 1984; Harper, 1967, 1982, 1988; Whittaker, 1953). Some studies have found that the structure of these communities is closely related to the frequency and intensity of flood and fire (Bendix and Cowell, 2010; Pettit and Naiman, 2007), and to species responses conditioned by phenology, ability to resprout, seed germination, seedling development, and the competitive effects of other species (Pettit and Naiman, 2007). The interaction of environmental factors determines a gradient of species composition and distribution (Bradshaw, 1984; Cronk and Fennessy, 2001; Harper, 1967, 1982; Whittaker, 1953).

The role of fire in the flooded forests of the South American Pantanal has not been studied to date. The Pantanal is a pristine environment with a very regular flood pulse (Junk et al., 1989) and less frequent natural wildfires (Macedo et al., 2009). Human presence is low and landscape changes due to human influence are still essentially negligible in many parts of the Pantanal. The Paraguay River has fringing riparian vegetation that is subjected to periodic floods. Plant species are distributed according to gradients of topography, flood, and its duration (Damasceno-Junior et al., 2005). Heavy floods regulate species distribution; tree mortality is greater in years when localized floods occur on higher, less frequently flooded levees (Damasceno-Junior et al., 2004). The role of fire in these flooded forests has not been studied to date. Our objective is to verify if fire and inundation can interact to determine variations in richness, density, and composition of woody species regeneration in riparian forests of the Paraguay River. We expect that fire acts together with flood in a non-destructive but selective way, resulting in modification of species composition, species density, and richness of the riparian forests.

2. Materials and methods

2.1. Study area

We collected data in the riparian forests of the Paraguay River, approximately 14 km upriver from the town of Corumbá (18°57′54.70′′S and 57°39′23.53″W; 18°52′36.99′′S and 57°40′3.75″W) (Fig. 1). The climate in the region is tropical megathermic with dry winters and rainy summers (November–March), and a mean annual rainfall of 1070 mm. The mean annual temperature is 21.0–30.6 °C, and mean relative annual humidity is 76.8% (Soriano, 1997). The predominant soils in the region are gleysoils with textures from medium to heavy clay, and eutrophic or dystrophic and aluminic character (Fernandes et al., 2007).

Annual floods and occasional wildfires occur in the study area. The Pantanal floodplain is subjected to a regular flood pulse (Adámoli, 1982; Junk et al., 1989). The water from rain at the Paraguay River headwaters takes three months to reach Corumbá, and the river reaches its maximum level in the middle of the dry season (Fig. 2). Local rains occur in the months when the river is at low level, hindering the occurrence of fire events (Fig. 2). Wildfires occur primarily in the driest years, generally when the high water levels remain below 4 m on the hydrometric gauge at Ladário, the threshold of overflow to the floodplain. The grasslands adjacent to the riparian forests accumulate large amounts of dry biomass that can serve as fuel for wildfires (Galdino and Clarke, 1997; Macedo et al., 2009). Recent years with highest incidences of wildfires were 2001, 2005, and 2009 (Fig. 3). The riparian vegetation of the Paraguay River is composed primarily of species such as Inga vera, Vochysia divergens, Cecropia pachystachya, and Ocotea diospyrifolia. The canopy varies from 6 to 12 m high with some emergent individuals of Handroanthus heptaphyllus (Damasceno-Junior et al., 2005).

2.2. Data collection

Our study was carried out in the riparian forest of the Paraguay River, Pantanal, Corumbá, MS, between October and November 2011. We sampled 14 areas of the riparian forest that had fire incidence three times in the decade from 2001 to 2011 (in 2001, 2005, and 2009) as determined by Landsat-5 satellite images provided online by the Instituto Nacional de Pesquisas Espaciais (INPE). Using the same satellite images, we selected 14 areas of the riparian forest for sampling that had been free of fire since at least 2001. Therefore, the study included a total of 28 areas sampled. We established 28 transects in these areas, with one transect per area. Transects were established perpendicular to the river, extending from the margin to the border with flooded grasslands. The strip of the riparian forest varied from 10 to 50 m. Subsequently, we established 2–7 plots of 2×5 m in each transect, depending on the width of the strip of riparian forest, with one plot each 5 m. This sampling was always performed in a way to encompass from the highest to the lowest topographic positions of each area along the transect. Because of the topographic heterogeneity within each transect we considered the single plots as sampling units. For each plot, we recorded the height of the water mark left by the last flood on the trunk of the closest tree with the same topographic position. Because of the proximity of these areas with the Ladário gauge and the flat topography (2 cm km^{-1}) , the water-mark height of each plot was converted into topographic position with respect to the zero of Ladário gauge (see Damasceno-Junior et al., 2005). This was done by subtracting the maximum value registered for the river on the gauge in 2011 by the value of the water-mark height on trunks recorded for each plot. This conversion was calculated because Ladário gauge has a long series of data for Paraguay River levels that has been collected daily since 1900, which serves as a good reference for inundation patterns. This conversion renders these data suitable as a reference to understand possible influence of flood duration on regeneration. The period used for this study was from 2001 until 2011.

In each plot, we sampled all individuals of woody plants and lianas with height between 0.3 and 2.5 m, except herbaceous species.



Fig. 1. Localization of the study area in the upper Paraguay basin. The dark area corresponds to the Pantanal wetland floodplain (map adapted from Silva and Abdon, 1998). The zoomed river map shows the unburned (black) and burned (white) sampled areas of the riparian forest of the Paraguay River, Corumbá, MS, Brazil.





Fig. 3. Maximum and minimum water levels of the Paraguay River in meters (m) at Ladário gauge from 2001 to 2011. Data provided by the Brazilian Navy. The dashed line shows the approximate threshold for the Paraguay River overflowing; arrows indicate the years with low-level inundation when the studied fire events occurred.

Fig. 2. Mean monthly rainfall (mm) and water level of the Paraguay River (m) at Ladário; data average from 2001 to 2011. Data provided by the Brazilian Navy and by the Brazilian National Institute of Meteorology (BDMEP–INMET).

The height of each individual was measured. Plant material was collected and herborized in the field. We also collected botanical material (fertile branches) of adult individuals to facilitate plant identification and to prepare exsiccatae for the Herbarium CGMS. Identification of seedlings and young individuals was performed by comparing these materials with herbarium specimens.

2.3. Data analysis

To verify if floristic composition and abundance of individuals per species vary among plots under different flood levels and different fire histories, we utilized a permutational multivariate analysis of variance (PERMANOVA) using the Adonis function in vegan package in R platform (R Development Core Team, 2013). We used a Bray–Curtis distance as measure of dissimilarity in species composition; the significance of difference among compared communities was obtained using 999 permutations. To verify if flood and fire occurrence interact to influence the richness and density of individuals, we performed a generalized linear model (GLM). The distributions of density and richness were verified using the fitdistrplus package in R platform (R Development Core Team, 2013). The models and interactions were tested using the function glm in R platform (R Development Core Team, 2013). For richness, the family used was Poisson; for density the family used was negative binomial. We tested the interaction of fire and inundation (topographic level of each plot with respect to the zero of Ladário gauge) on the number of species and number of individuals per plot. Fire history groups (unburned *versus* burned) were defined as factor and river level was used as covariate. Graphical presentations of these analyzes were generated using the package visreg (R Development Core Team, 2013).

3. Results

We recorded 50 species in the sampled areas that were distributed in 30 families and 44 genera; 25 were liana species, 17 were trees, 7 were shrubs, and one palm (Table 1). The most abundant



Fig. 4. Most abundant species in burned (B) and unburned (U) areas in the riparian forest of the Paraguay River, Corumbá, MS, Brazil.

species in unburned areas were Tabernaemontana siphilitica, Paullinia spicata, Myrcia splendens, I. vera, Dolichandra ungis-cati, Albizia inundata, Anemopaegma flavum, and Odontocarya tamoides

Table 1

Tree, shrub and liana species of young individuals recorded in unburned (U) and burned (B) areas of riparian forest of the Paraguay River, MS, Brazil.

| Family | Scientific name | Habit | U | В |
|--|---|--------|--------|--------|
| Amaranthaceae Pfaffia glomerata (Spreng.) Pedersen | | Shrub | Х | х |
| Apocynaceae | Blepharodon cf. pictum (Vahl) W.D. Stevens | Liana | Х | - |
| | Indet. | Liana | Х | - |
| | Prestonia coalita (Vell.) Woodson | Liana | Х | Х |
| | Rhabdadenia madida (Vell.) Miers | Liana | Х | Х |
| | Tabernaemontana siphilitica (L. f.) Leeuwenb. | Shrub | Х | Х |
| Arecaceae | Bactris glaucescens Drude | Palm | Х | х |
| Bignoniaceae | Adenocalvmma bracteatum (Cham.) DC. | Liana | - | х |
| C | Anemopaegma flavum Morong | Liana | Х | х |
| | Dolichandra unguis-cati (L.) L.G. Lohmann | Liana | Х | х |
| | Bignonia corymbosa (Vent.) L.G. Lohmann | Liana | Х | Х |
| Capparaceae | Crateva tapia L. | Tree | Х | - |
| Celastraceae | Hippocratea volubilis L. | Liana | - | х |
| Clusiaceae | Garcinia brasiliensis Mart. | Tree | _ | X |
| Combretaceae | Combretum lanceolatum Pohl ex Eichler | Liana | х | X |
| Convolvulaceae | Inomoea carnea laca | Shrub | x | - |
| convolvalaceae | Inomoea ruhens Choisy | Liana | - | х |
| | Merremia umbellata (L.) Hallier f | Liana | х | - |
| Funhorbiaceae | Indet | Liana | x | _ |
| Fabaceae | Cassia grandis I f | Tree | x | _ |
| Tubuccuc | Senna pendula (Humb & Bonnl ex Willd) H S. Irwin & Barneby | Shruh | x | _ |
| | Senegalia martiusiana (Steud.) Seigler & Fhinger | Tree | - | x |
| | Albizia inundata (Mart.) Barneby & IW. Crimes | Tree | v | X |
| | Inga yora Willd | Тгор | X | X |
| | ngu veru wind. Bergeronia sericea Micheli | Tree | X | ~ |
| | Camptosama naraguariansa (Chodat & Hassl.) Hassl | Liana | x v | - |
| | Dterocernus michelii Britton | Trop | A V | - v |
| Lauracoao | Ocoteg diagnurifolia (Maico) Mag | Tree | A V | × × |
| Lauraceae | Struchnes methorressensis S. Moore | Liana | A V | ^ |
| Logalilaceae | Nindenmuella etamosa (Griech) M.B. Anderson | Lidild | A V | - |
| Maluageae | Niedenzuella stannea (Griseb.) W.R. Anderson | Lidiid | X | X |
| Malvaceae | Bylineria maninijolia Benili. | Lidlid | X | X |
| Memorea | Carologia ramionaes (DC.) Milers | Lidild | Λ | A V |
| Moraceae | Soroceu sprucei ssp. suxicoiu (Hassi.) C.C. Berg | Thee | - | X |
| Myrtaceae | Eugenia egensis DC. | Shirub | X | X |
| | Eugenia pseudoverticiliata S. Moore | Tree | X | X |
| | Eugenia sp. | lfee | - | X |
| D | Myrcia splendens (Sw.) DC. | Shrub | Х | X |
| Passifioraceae | Passifiora joetiaa L. | Liana | - | X |
| D 1 | Passiflora gibertii N.E. Br. | Liana | - | X |
| Polygonaceae | Coccoloba alagoensis Wedd. | Iree | X | X |
| | Triplaris americana L. | Tree | X | X |
| | Triplaris gardneriana Wedd. | Tree | X | Х |
| Rubiaceae | Genipa americana L. | Tree | Х | Х |
| | Rudgea myrsinifolia Benth. | Shrub | - | Х |
| Sapindaceae | Paullinia pinnata L. | Liana | Х | - |
| _ | Paulima spicata Benth. | Liana | Х | Х |
| Sapotaceae | Pouteria glomerata (Miq.) Radlk. | Tree | Х | Х |
| Salicaceae | Casearia aculeata Jacq. | Shrub | Х | Х |
| Smilacaceae | Smilax sp. | Liana | - | Х |
| Vitaceae | Cissus verticillata (L.) Nicolson & C.E. Jarvis | Liana | - | Х |



Fig. 5. Comparison of growth forms occurring exclusively in unburned, burned or in both, sites in the riparian forest of the Paraguay River, Corumbá, MS, Brazil.

(Fig. 4). The main species in burned areas were *M. splendens*, *P. spicata*, *T. siphilitica*, *Genipa americana*, *Bignonia corymbosa*, *Combretum lanceolatum*, *Eugenia egensis*, and *Prestonia coalita*. Twentysix species (52%) were common to both burned and unburned areas, and most of them occurred with large numbers of individuals. Twelve species (24%) occurred only in unburned sites; 10 species occurred with one individual and two occurred with two. Twelve species (24%) occurred only in burned areas, including primarily *Eugenia* sp. (9), *Passiflora foetida* (5), and *Garcinia brasiliensis* (4).

All growth forms occurred in both unburned and burned sites, with more lianas as a general pattern. There was always a lower number of species per growth forms restricted to either unburned or burned areas (Fig. 5).

The topographic position of the sampled plots varied from 3.77 to 4.84 m in reference to the zero level of the Ladário gauge. Thus, the highest topographic position remained inundated a mean of 38



Fig. 6. Generalized linear model for species richness of regeneration in the riparian forests of the Paraguay River, Corumbá, MS, Brazil, according to the topographic position of the burned and unburned plots in relation to the zero level of the Ladário gauge. The lower areas were inundated more days per year (*z* value = -3.1 for the elevation above the Ladário zero; *p* = 0.001; *z* value = 1.5 for fire × elevation interaction; *p* = 0.12; Pseudo *R*² = 0.10).



Fig. 7. Generalized linear model for abundance of individuals of regeneration in the riparian forests of the Paraguay River, Corumbá, MS, Brazil, according to the topographic position of the burned and unburned plots in relation to the zero level of the Ladário gauge. The lower areas were inundated more days per year (z value = -3.4 for elevation above the Ladário zero; p < 0.001; z value = 2.16 for fire × elevation interaction; p = 0.03; Pseudo $R^2 = 0.13$).

 $(sd \pm 38; min = 0; max = 96)$ days y^{-1} and the lowest topographic position remained inundated a mean of 98 (sd ± 68; min = 0; max = 172) days y^{-1} between 2001 and 2011.

The results of PERMANOVA showed differences in species composition in response to fire (F = 3.22; p = 0.001), the time of inundation (F = 2.68; p = 0.002) and in response to the interaction of both factors (F = 1.31; p = 0.012). Species such as *M. splendens*, *Paullinia pinnata*, and *Rhabdadenia madida* occurred more frequently in higher areas, while *I. vera*, *A. inundata*, and *O. tamoides* occurred more frequently in lower areas. As shown above (Table 1 and Fig. 4), we found variation in species composition and in the number of individuals in both burned and unburned areas.

There was no interaction between fire and inundation that influenced species richness in the analyzed areas; however, we found that flood level had a significant influence on species richness (Fig. 6). There were less species in areas with longer periods of inundation per year, but fire did not affect this relationship.

We found significant interaction between fire and inundation on the number of individuals found per plot on the regeneration of the riparian forests of the Paraguay River (Fig. 7). The number of individuals were lower with longer periods of inundation. With the occurrence of fire, the differences were very pronounced with more individuals in higher areas and less individuals in low lying areas.

4. Discussion

Flood and fire can be considered as biological filters in the Brazilian Pantanal, which act together primarily by regulating the number of individuals and composition of species in the riparian areas (Table 2). The fire acts as a biological filter during the dry season killing plants with different intensity which depends on the kind of fuel (Agee et al., 2002) and position of woody debris (Pettit and Naiman, 2007). The inundation is associated with microtopography, which is responsible for more or less inundation along the year. The regeneration of the analyzed riparian forests responded to the interaction between flood and fire in terms of reduced density of the regenerating young individuals and changes in species composition. Stem density was reduced especially with increasing flooding depth, i.e., patches that are flooded for longer periods presented the lowest numbers of individuals. Based on the topographic position, these habitats remain flooded between 38 days year⁻¹ on the highest ground levels and 98 days on the

| Table 2 | |
|--|----|
| Impact of flood and fire on several parameters analyzed in the present study | ί. |

| Parameter/ intensity | Impact of | | | | |
|------------------------------|--|--|---|--|--|
| | Flood | Fire | Interaction | | |
| Intensity | High, annual and more predictable in lower areas | High, unpredictable | Positive, fires only occur in years with low inundation or in months with low precipitation and lower water level | | |
| Density (number of stems) | High, reduced density with flooding | High, reduced density with burning | Positive, fire reduces density with flooding but increase without | | |
| Diversity of growth forms | Low, flood does not reduce diversity | Low, fire does not reduce diversity | Not detected | | |
| Species richness | High, reduced species richness with long flooding | Low, fire does not reduce richness | Not detected | | |
| Species composition | High, different species along the flooding gradient | High, different species composition/ proportion due to fire | Positive, inundation select with species can grow up after fire | | |

lowest sites. The longer the flood duration, the lower was the stem density, because flooding restricts the survival of trees and shrubs in these habitats (Damasceno-Junior et al., 2005; Piedade et al., 2010; Van Andel, 2003; Wittmann et al., 2008). On the higher parts of the levee, fire eliminates trees, shrubs, and lianas, and opens gaps (Heinl et al., 2007a). In the absence of floods and during less inundation, the gaps are occupied by regenerated life forms. In the lower areas, border with floodable grasslands, the inundation is more predictable and occurs every year. The lower areas are also more prone to catch fire, once it originates in the grasslands. Moreover, floods in these areas are responsible for the elimination of a greater number of the colonizing individuals. Thus, in the higher parts of the levee, fire creates space for the regeneration of all life forms. On the other hand, in the low-level areas, fire eliminates individuals and floods prevent colonization, creating an interaction between both factors acting as a double filter. Therefore, fire and flood are acting in synergy, restricting the number of individuals that could be recruited in areas where both factors occur.

Although the environmental conditions impose restrictions on growth and survival of many plant species, the adapted species found here allow for a high functional diversity. Functional groups, represented by the diversity of growth forms (trees, lianas and shrubs), were similar in all flooded positions and in burned and non-burned areas (Fig. 4), indicating that they were unaffected by flood or fire. However, species richness was affected by flood height and not by fire. No significant influence of fire on species richness could be documented in the analyzed areas. The number of exclusive species in each area was the same. Moreover, we noticed substitution of species in fewer individuals in burned areas, with no impact on the richness. Several shade-intolerant species were favored by open canopies and the gaps created by the fire. Thus, the fire events were not severe enough to restrict species occurrence and diversity. Our data support the finding that the reduction of competition for local resources enabled by a fast fire favors multiplication of some species (Silva and Batalha, 2008).

Many species in our study were sensitive to flood in different degrees. The Pantanal wetland forests comprise species, which immigrate from the adjacent Amazonian, Cerrado, and Chaco vegetation (Adámoli, 1982; Nunes-da-Cunha et al., 2007), where preadaptations to standing water occur. However, especially in the initial developmental phase when the plants are more susceptible to environmental pressures such as flood, this single factor becomes a limitation for many species. Only submerged plants with special adaptations such as the ability to photosynthesize under water (Parolin, 2009) may colonize the lowest-lying sites, which are waterlogged or submerged until 6 months a year.

The species distribution along the flooding gradient was closely linked to flood tolerance and to the action of fire (Table 2). Due to clear zonation, some plant species in this environment occur only on specific sites with particular flood duration. Their occurrence in turn is an indicator of specific flood events at those sites. However, their distribution in relation to fire events indicates the substitution of less frequent species with the more frequent ones, and the rise in number of the following species: *P. spicata, C. lanceolatum, G. americana* and *M. splendens*.

Our data showed that, except for density and nearly half of the species, regeneration of the riparian forests after fire events was different from the regeneration in the unburned areas. However, the main species remained the same along the inundation gradient with differences in abundance. Moreover, the interaction between the fire and flood events modified the composition of species. This shows the high resilience of the community in relation to these disturbances. High ecological plasticity of the local species and high robustness of the seed bank might account for this. Preliminary surveys showed no difference in the composition of the seed bank between burned and unburned forest of the Paraguay River (Fernando Alves Ferreira, pers. comm.). One of the main aspects of this interaction is the resprouting capacity, which is an important adaptation in the riparian habitats during fire events, facilitating recolonization (Dwire and Kauffman, 2003). The riparian forests responded to the interaction between flood and fire in terms of selection towards species which easily resprout. This has been documented for other Savanna ecosystems around the world (Higgins et al., 2000; Bellingham and Sparrow, 2000), and is typical for a highly dynamic system where resilience and fast regrowth are among the most important characteristics for plant survival. We observed that some of the most abundant species in both burned and unburned areas showed a high resprouting capacity. This favors colonization and fast regeneration despite flooding and fire in these habitats. In other words, both fire and flood are factors of disturbance that favor species with the capacity of resprouting through basal ramification or by shooting from rhizomes, such as observed in the palm species, Bactris glaucescens. The main differences in the number of individuals can be attributed to these species, which can occupy the habitat subjected to inundation soon after a fire event.

The action of fire on the riparian zones influencing plant communities (Jackson and Sullivan, 2009) can be an important element in modeling their ecological characteristics (Pettit and Naiman, 2007). *I. vera* and *A. inundata* are species resistant to over 200 days of flood a year (Damasceno-Junior et al., 2005). *I. vera* is the most abundant riparian forest species of the Paraguay River, even in burned areas, as fire does not reach the canopy and cannot kill adult plants. Seedlings of *Pouteria glomerata*, an abundant tree species in the riparian forests in the Pantanal (Pott and Pott, 1994), tolerate up to 6 months of submersion (Maurenza et al., 2009). However, their abundance was low in burned plots and young individuals of this species seemed not to survive fire.

In burned areas, we found many individuals of *G. americana*. It is an initial secondary tree (Lorenzi, 2002), which is fire sensitive

(Pott and Pott, 1994). The large number of saplings in the post fire plots originated from seeds. The species is flood tolerant (Andrade et al., 1999), but seedling growth is reduced with longer periods of flooding.

Where flooding was short and wildfires occurred, the presence of lianas was favored. This agrees with the finding that disturbed and/or fragmented areas show an increased abundance of pioneers and lianas (Laurance et al., 2011; Schnitzer et al., 2004) that adapt and tolerate environmental changes (Gentry, 1991b). The occupation strategies of pioneers and lianas are related to the stage of forest regeneration (Schnitzer and Bongers, 2002). This is also true in areas under longer periods of flooding and after wildfires. Some species dominated in these situations, such as the lianas *C. lanceolatum, A. flavum*, and *O. tamoides*. These species can be favored by resprouting after fire (Pott and Pott, 1994).

To conclude, identifying the adaptive strategies of plants and their responses to highly selective environmental pressures is the basis for understanding their distribution and ecological needs for survival and regeneration. This knowledge is crucial for formulating management options, sustainable use of the environment, and conservation of tropical wetlands and savannas. Our results from the riverine forests of the Pantanal may be representative of similar ecosystems where regular flood and wildfires interact in environments that are characterized by high species diversity. Waterlogging and submergence, however, are not deleterious to the species that have adapted and this allows for a large diversity of species.

Our findings have implications for management of these wetland environments. The importance of flood for species richness, composition, and distribution was highlighted by our data. The natural flood regime is responsible for the diversity of habitats and species. Fire is not that deleterious and its interaction with inundation plays an important role in the regulation of the composition and abundance of individuals in these riparian forests. However, an increase in fire frequency and intensity due to land use and climate changes may yield a different picture. Our study indicates that this riparian forest is generally resilient as long as its natural patterns and periodicities of flooding and wildfires are preserved. Given the heavy impact expected from increased human pressure, land use changes, and increased severity of floods and fires related to climate changes (Clark, 2007; Asner et al., 2009), our results point to the necessity to analyze the interacting effects of selective environmental forces in order to preserve the form and function of the huge wetlands of the Pantanal.

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