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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 × 5 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.

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 non-adapted 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.