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Original Paper

Flood and fire affect the soil seed bank of riparian forest in the Pantanal wetland

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Abstract

Flood and fire can harm plants but they can have survival strategies, such as the seed bank. We aimed to determine the influence of fire and flood on the richness, abundance and diversity of the seed bank. Sampling was carried out in October/2013, year of prolonged drought, and October/2014, year of a heavy flood, in ten areas along the Paraguay River. The areas were selected in satellite images, five with old burn (2010, three years before sampling) and five with recent burn (2013, three months before sampling). In each area, we marked a 20 m long transect with ten 20 × 20 cm quadrats where we collected 5 cm deep topsoil samples, five with and five without litter. Seed bank richness and abundance were determined by seedling emergence. Old burn areas presented greater abundance than recent burn. The drier year presented greater abundance, richness and diversity than flood year. Removal of litter reduced the richness only in the wetter year. There was no difference in richness in the drier year. The removal of the litter did not affect the abundance and diversity. Interaction between fire and flood did not affect richness, abundance and diversity of the seed bank.

Key words: Diaspores; Fabaceae; floodable forest; neotropical wetland; plant ecology.

Resumo

Espécies vegetais sujeitas a Inundação e fogo podem manifestar estratégias de sobrevivência como o banco de sementes do solo. Pretendemos determinar a influência de fogo e inundação na riqueza, abundância e diversidade do banco de sementes. Realizamos amostragens em um ano mais seco (outubro/2013) e em um de maior inundação (outubro/2014), em dez áreas ao longo do rio Paraguai. Selecionamos 5 áreas com históricos de fogo antigo (2010, 4 anos antes da amostragem) e 5 recente (2013, 1 ano antes da amostragem). Nas áreas, marcamos transectos de 20 m, nos quais coletamos 10 amostras de solo (20 × 20 × 5 cm), cinco com e cinco sem serrapilheira. Composição e abundância do banco de sementes foram estimadas por meio de emergência de plântulas. Áreas de fogo antigo apresentaram maior abundância que áreas de fogo recente. O ano de seca apresentou maiores abundância e riqueza do que o de inundação. A remoção da serrapilheira reduziu a riqueza no ano de inundação. Não houve diferença em riqueza no ano seco. A abundância nas amostras com e sem serrapilheira foram similares. A interação entre fogo e inundação não afetou a abundancia, riqueza e diversidade do banco de sementes.

Palavras-chave: diásporos; Fabaceae; floresta inundável; àreas úmidas; ecologia vegetal.

Introduction

The soil seed bank is a strategy to ensure the vegetation regeneration after a disturbance, or seasonal events such as fire (Santana *et al.* 2010) and flood (Hölzel & Otte 2004). Annual and pluriannual fluctuations of floods determine plant recruitment and influence dispersal and the distribution of seeds in the soil (Brock & Rogers

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1998). Water dispersed seeds come mixed with plant debris, in great part from aquatic plants that germinate during floods (Bao *et al*. 2017). This accumulated organic debris, associated with aquatic macrophyte dieback, can capture and trap dispersing seeds (Ruprecht & Szabó 2012), potentially increasing local seed bank abundance and richness (Bao *et al*. 2018). Flood also acts as a trigger for the seedling emergence of annual species, rapidly withdrawing seeds from the bank and reducing its richness and abundance (Souza *et al.* 2016). It is expected that in years of lesser flood and in flood-free areas, germination and seedling emergence would be lower, so maintaining higher richness and abundance of seeds in the soil (Brock *et al*. 2003). However, there are few pieces of evidence of differences of seed bank richness and abundance between dry and flooded years.

Fire is another factor that influences the structure and diversity of the vegetation (Oliveira *et al.* 2014). The buildup of biomass, either from aquatic plants at flood or from terrestrial plants grown post-flood, is fuel for a wildfire. Depending on intensity, fire can act overcoming the seed dormancy (Santana *et al.* 2013) and removal of plant cover (Moreira & Pausas 2012), increasing light and so promoting seedling recruitment from the seed bank (Keeley *et al.* 2011). If intervals between the burning of aerial vegetation exceed the longevity of seeds in the soil, they can lose viability before fire generated gaps could favour germination (Keith & Bradstock 1994). Longer seed longevity causes lower fluctuation of the seed bank than short-lived species (Brock & Rogers 1998). Thus, the exclusion of fire for a long period can increase the richness and abundance of the seed bank up to some degree, due to lack of gaps for germination.

In the Pantanal, fire and flood are considered extreme seasonal events which temporarily (intra-annual and interannual) and spatially modify the structure and species richness of the vegetation. These two factors can interact in determining the vegetation composition. Fire events can be restricted when the flood is more intense, allowing more flood tolerant and less fire-tolerant species to become established. To the contrary, when flood intensity is lower, the occurrence of fire can reach high proportions, eliminating less tolerant species (Arruda *et al.* 2016). For that reason, our study had the objectives to assess the abundance, richness and diversity of the riparian forest seed bank in a stretch of the Paraguay River, Pantanal wetland, Corumbá, Mato Grosso do Sul, and to verify if fire and flood can interfere in the abundance, species richness and diversity of the soil seed bank. Therefore, we tried to answer the following questions: 1) Do inundation and fire history influence abundance, richness and diversity of the soil seed bank? 2) Are there differences in abundance, richness and diversity between soil with litter and without litter?

Material and methods

Study area

The study was carried out on both margins of a stretch of the riparian forest of the Paraguay River, between the coordinates 19º31’23.97”S 57º6’1.9”W and 19º41’38”S 56º59’56.4”W (Fig.1), in the municipality of Corumbá, Mato Grosso do Sul, Brazil. This floodplain has sandy-loamy to clayey Gleysol, eutrophic or dystrophic and aluminic, characteristic of lowlands under constant or periodical floods (Fernandes *et al.* 2007).

According to Köppen’s classification, the climate of Corumbá is Awa, *i.e.*, tropical megathermic (mean temperature of the coolest month >18 °C), seasonal, with dry winter and rainy summer, with mean annual rainfall of 1100 mm, average annual temperature of 21–31 ºC, and mean annual relative humidity of 76.8% (Soriano 1997). Paradoxically, local flood time is not related to the local rainy season, but with rains on the headwaters of the Upper Paraguay Basin, with three months lag because the waters flow slowly downstream, since the Pantanal is very flat, with an N-S declivity of only 2.5 cm/km (Brasil 1979). Thereby, flooding on the plain occurs in the dry season, so extending the period of soil moisture, allowing Amazonian trees to occur in the riparian forest (Damasceno-Junior *et al.* 2004; Arruda *et al.* 2016). However, in drier years the river does not overflow, when its level stays below 4 m (daily recorded by the Navy fluviometric station at Ladário, close to the study area), and fire may occur due to the buildup of dry organic matter in the adjacent grasslands (Hamilton *et al.* 1996).

Data collection

To choose the sampling areas we utilized Landsat 5 images obtained from the Instituto Nacional de Pesquisas Espaciais (INPE). We consulted the flood records of the last five years, to detect when the Paraguay River was low and thus fire could reach the riparian forest, the chosen years being 2010 and 2013. Next, we inspected the satellite images for signs (black) of burned areas in the driest months of those years. We marked and

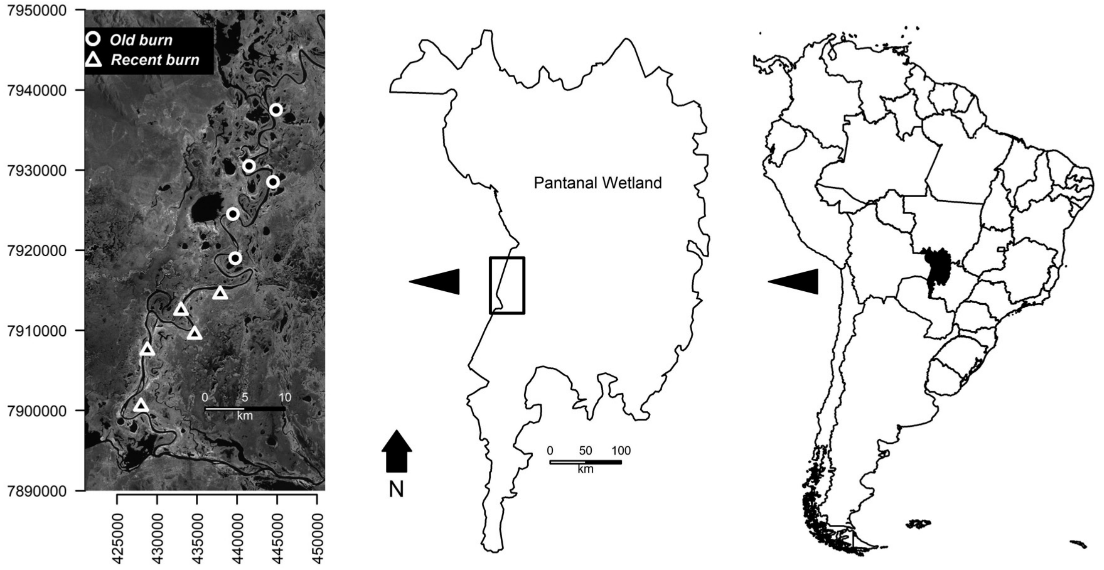

Figure 1 – Location of the studied region showing areas of recent and old burn in riparian forest of the Paraguay River, Pantanal wetland, Brazil.

georeferenced five areas of old burn (2010, three years before sampling) and five of recent burn (2013, three months before sampling), totalling 10 sampling areas along a stretch of the Paraguay River (Fig. 1).

In each sampling area we marked a 20 m long transect and at 5 m intervals we took two paired soil samples (five including litter and five without it), *i.e.*, 10 samples per transect, adding to 50 samples of old burn and 50 of the recent burn, total of 100. The sample was a 20 × 20 cm slice of 5 cm topsoil. The samplings were performed in two hydrologic conditions, the first in October 2013 (year of prolonged drought) and the second in October 2014 (year of a heavy flood). The second fieldwork had been planned for May 2014, but the area was flooded until October when it became possible to collect soil.

The collected soil samples were kept in labelled plastic bags and taken to the greenhouse at the Universidade Federal de Mato Grosso do Sul. We spread the soil over a 2 cm layer of washed and seed free sand into labelled plastic trays of 6.5 × 19.5 × 31 cm, perforated for drainage, randomly placed and weekly rotated on benches in a screened greenhouse (50% shade), under room temperature and irrigated twice a day by automatic sprinklers. The species composition and abundance of the soil seed bank were estimated by the seedling emergence method, whereby germinated seeds were counted, identified and removed to avoid competition with new seedlings (Boedeltje *et al.* 2002). We recorded the number of emerged seedlings in the trays at seven-day intervals. For the year of drought we made 15 counts and for the wetter year, 13. Emerged seedlings were identified and counted per species, then removed. Species identification was occasionally only possible during flowering. Some yet unidentified species were transplanted to pots for later identification and then added to the records. For identification, we used field guides of local flora (*e.g.*, Pott & Pott 1994, 2000) and experience of the authors.

Analysis of data

To test the effect of hydrologic condition and of fire history we utilized generalized linear models (GLM), with the function glm() in the R statistical programming language, version 3.4.0 (R Core Team 2017). We chose GLMs because our data did not fit into a normal distribution. Species richness and abundance data fit a Poisson distribution, but due to the overdispersion of data, we applied a Quasi-GLM model to correct the standard errors (Zuur *et al.* 2009). We calculated Shannon diversity for each sample using the diversity() function of the vegan package (Oksanen 2017). We tested the effect of fire and flood, on the Shannon diversity with GLM with a Gaussian distribution and log link function. The influence of flood (year of drought and year of heavy flood) and fire condition (old and recent burn) on richness abundance and Shannon diversity was analyzed in a bifactorial model with interaction between fire and flood conditions. The influence of litter on richness, abundance and Shannon diversity was analyzed separately for each flood condition.

Results

In the soil seed bank in a stretch of the riparian forest of the Paraguay River, we recorded 7195 emerged seedlings, distributed in 24 families, 53 genera and 61 species (Tab. 1). The families with highest species richness were Fabaceae (eight species), Cyperaceae and Poaceae (seven species), Euphorbiaceae and Onagraceae (five species), adding to 53% of the identified species. The families Asteraceae and Malvaceae (three species), Convolvulaceae, Lamiaceae, Polygonaceae and Plantaginaceae (two species) represented 7.3% of species. The others had a single species each, however, Urticaceae stood out for the high abundance of *Cecropia pachystachya* Trécul.

The most abundant genera were *Cecropia, Cyperus, Ludwigia, Hymenachne, Borreria* and *Randia*, expressing 68.5% of the total of species recorded in the seed bank, and the main species were *Cyperus haspan* L. (11%), *Cecropia pachystachya* (10%), *Borreria quadrifaria* E.L. Cabral (10%), *Ludwigia decurrens* Walter (9.5%) and *Randia armata* (Sw.) DC. (9%). Herbs were strongly dominant in both years, as we recorded 3,113 seedlings in 2013 (dry), and 3,029 in 2014 (flood), a total of 6,142, corresponding to 86% of the seedlings identified in the seed bank.

Other growth habits were also recorded, such as vines, shrubs and subshrubs. We recorded eight liana species, with 143 seedlings emerged from the seed bank, the most abundant being *Canavalia mattogrossensis* (Barb.Rodr.) Malme (40 seedlings), *Rhynchosia minima* (L.) DC. (37) and *Mikania micrantha* Kunth (31). Shrubs were represented by eight species and a total of 771 seedlings, corresponding to 11% of all seedlings, the most abundant species being *R. armata* (684)

Table 1 – List of species and their total abundances (TA) and habits (H) present in the soil seed bank of areas with different fire histories (OB - old burn and RB - recent burn), in presence (P) and absence (A) of litter in dry and flood years, in riparian forest of the Paraguay River, Pantanal wetland, Corumbá, Mato Grosso do Sul, Brazil.

			Dry year				**Flood year**			
Family/Species			**RB**		**OB**		**RB**		**OB**	
	TA	H	P	A	P	A	P	A	P	A
Amaranthaceae										
Pfaffia glomerata (Spreng.) Pedersen	1	Herb	0	0	1	0	0	0	0	0
Asteraceae										
Aspilia latissima Malme	12	Herb	0	0	6	3	0	0	3	0
Melanthera latifolia (Gardn.) Cabrera	36	Herb	6	2	0	2	10	8	0	8
Mikania micrantha Kunth	31	Liana	3	5	10	2	6	3	1	1
Boraginaceae										
Euploca procumbens (Mill.) Diane & Hilger	17	Herb	0	0	3	10	0	0	2	2
Heliotropium indicum L.	10	Herb	0	0	2	2	2	0	2	2
Convolvulaceae										
Ipomoea chiliantha Hallier f.	7	Liana	0	0	4	0	0	0	3	0
Ipomoea tenera Meissn.	8	Liana	3	3	0	0	1	1	0	0
Cucurbitaceae										
Cyclanthera hystrix (Gillies) Arn.	12	Liana	0	3	3	3	0	2	0	1
Cyperaceae										
Cyperus haspan L.	769	Herb	89	51	119	135	350	10	10	5
Cyperus surinamensis Rottb.	366	Herb	83	51	71	102	10	20	19	10

			Dry year				Flood year			
Family/Species			**RB**		**OB**		**RB**		**OB**	
	TA	H	P	A	P	A	P	A	P	A
Eleocharis minima Kunth	13	Herb	0	7	0	0	6	0	0	0
Eleocharis plicarhachis (Griseb.) Svens.	9	Herb	0	6	0	0	0	0	3	0
Fimbristylis dichotoma (L.) Vahl	21	Herb	0	2	0	5	0	7	7	0
Lipocarpha micrantha (Vahl) G.C. Tucher	44	Herb	0	0	0	0	10	10	12	12
Rhynchospora corymbosa (L.) Britton	5	Herb	1	1	0	0	3	0	0	0
Euphorbiaceae										
Astraea lobata (L.) Klotzsch	23	Herb	5	4	5	3	3	1	1	1
Caperonia castaneifolia (L.) A. St.-Hil.	2	Herb	1	0	0	0	0	0	1	0
Croton trinitatis Millsp.	34	Herb	8	3	8	2	5	5	1	2
Dalechampia scandens L.	4	Liana	3	0	0	0	0	1	0	0
Euphorbia thymifolia L.	8	Herb	0	0	0	0	0	5	3	0
Fabaceae										
Aeschynomene sensitiva Sw.	2	Herb	1	0	0	0	1	0	0	0
Bauhinia bauhinioides (Mart.) Macbr.	1	Shrub	0	0	0	1	0	0	0	0
Canavalia mattogrossensis (Rodr.) Malme	4	Liana	1	0	0	0	1	1	1	0
Mimosa adenocarpa Benth.	28	Shrub	3	2	2	11	3	3	2	2
Neptunia plena (L.) Benth.	26	Herb	3	2	2	15	1	1	1	1
Rhynchosia minima (L.) DC.	37	Liana	15	0	12	10	0	0	0	0
Sesbania exasperata Kunth	5	Shrub	5	0	0	0	0	0	0	0
Vigna longifolia (Benth.) Verdc.	7	Herb	2	0	0	0	5	0	0	0
Lamiaceae										
Hyptis brevipes Poit.	136	Herb	10	10	10	3	50	50	0	3
Hyptis suaveolens(L.) Poit.	26	Herb	0	0	5	5	0	0	8	8
Lythraceae										
Rotala ramosior (L.) Koehne	69	Herb	0	0	30	0	0	0	39	0
Malvaceae										
Byttneria divaricata Benth.	21	Shrub	5	0	0	6	6	0	0	4
Melochia arenosa Benth.	24	Subshrub	2	2	2	2	2	0	10	4
Pavonia laeteviren R.E. Fr.	22	Shrub	0	0	12	3	0	0	0	7
Melastomataceae										
Rhynchanthera novemnervia DC.	3	Herb	0	0	1	0	0	0	1	1
Onagraceae										
Ludwigia decurrens Walter	729	Herb	31	27	408	100	41	41	39	42
Ludwigia grandiflora (Michx.) Greuter & Burdet	162	Herb	20	20	20	20	10	30	20	22
Ludwigia leptocarpa (Nutt.) H. Hara	88	Herb	7	3	6	10	1	0	31	30
Ludwigia octovalvis (Jacq.) P.H. Raven	108	Herb	1	30	12	30	33	2	2	1
Ludwigia tomentosa (Cambess.) H. Hara	7	Shrub	1	0	5	1	0	0	0	0
Plantaginaceae										
Bacopa australis V.C. Souza	22	Herb	22	0	0	0	0	0	0	0

			Dry year				**Flood year**			
Family/Species			**RB**		**OB**		**RB**		**OB**	
	TA	H	P	A	P	A	P	A	P	A
Scoparia dulcis L.	14	Herb	5	0	4	4	0	0	0	1
Poaceae										
Digitaria bicornis (L.) Roem. & Schult.	148	Herb	0	100	0	20	0	0	28	0
Eragrostis rufescens Schrad. *ex* Schult.	139	Herb	20	27	38	37	0	10	3	4
Hymenachne amplexicaulis Rudge	515	Herb	100	48	41	39	50	185	30	22
Panicum dichotomiflorum Michx.	68	Herb	0	0	20	18	0	0	30	0
Paspalum repens Berg.	44	Herb	5	5	5	5	10	15	5	4
Setaria parviflora (Poir.) Kerguelen	3	Herb	1	1	0	0	1	0	0	0
Steinchisma laxum (Sw.) Zuloaga	341	Herb	50	40	50	40	20	50	50	41
Polygonaceae										
Polygonum ferrugineum Wedd.	30	Herb	5	5	5	5	3	2	3	2
Triplaris americana L.	3	Tree	3	0	0	0	0	0	0	0
Phyllanthaceae										
Phyllanthus amarus Schum. & Thon.	40	Herb	20	5	4	4	1	1	3	3
Pteridaceae										
Ceratopteris pteridoides (Hook.) Hieron.	568	Herb	0	100	100	0	230	120	18	0
Rubiaceae										
Borreria quadrifaria Cabral	760	Herb	142	100	100	215	85	63	35	20
Randia armata (Sw.) DC.	684	Shrub	200	150	0	75	75	75	0	109
Solanaceae										
Solanum nigrescens M.Martens & Galeotti	3	Herb	1	0	0	0	1	1	0	0
Sphenocleaceae										
Sphenoclea zeylanica Gaertn.	2	Herb	0	0	2	0	0	0	0	0
Urticaceae										
Cecropia pachystachya Trécul.	766	Tree	193	219	143	108	50	20	30	3
Verbenaceae										
Lippia alba (Mill.) N.E. Br. *ex* Britton & P. Wilson	3	Shrub	1	1	0	0	0	1	0	0
Vitaceae										
Cissus spinosa Cambess.	4	Liana	0	0	1	0	0	0	2	1

and we recorded only a single subshrub, *Melochia arenosa* (24). All above-cited species were found either in areas of old or recent burn.

Influence of post-fire periods and hydrological conditions

There was no interaction between the factors fire (old and recent burn) and hydrologic condition (year of drought and year of the flood). Nonetheless, separately either factor influenced the abundance and richness of the seed bank. Regarding fire history, the old burn presented greater species richness (t=3.147, $p<0.001$) (Tab. 2; Fig. 2ab) and abundance (t=2.74, $p<0.001$) (Tab. 2; Fig. 2b) when compared with the recent burn. The hydrologic condition with greater abundance was the dry year (t=4.15, $p<0.001$) (Tab. 2; Fig. 2c), with 3,790 seedlings, being 2,467 in old burn and 1,323 in the recent burn. In the year of the flood, the abundance was lower with 3,195 seedlings, 2,126 being in old burn and 1,069 in the recent burn. In regard to species richness, we also detected a significant difference between hydrologic conditions, with higher richness in the dry year (t=5,296, p<0.001) (Tab. 2; Fig. 2d). The same way, the diversity also was affected by the hydrologic conditions, with higher diversity in the dry year (t=3.19, p<0.01) (Tab 2; Fig. 3). We recorded 59 species in the dry year (44 in old burn and 46 in recent burn) and 53 in the year of the flood (44 in old burn and 40 in the recent burn).

Influence of litter

The abundance in samples with litter (3,575 seedlings) was similar to samples without litter (3,620), without significant difference in either year of drought (Tab. 3; Fig. 4a) or flood (Tab. 3; Fig. 4b). In samples with litter, we found 37 species, compared with 24 without litter. There was no difference in richness in the dry year (Tab. 3; Fig. 4c). However, richness was higher in soil with litter in the year of the flood (t=2.193; p=0.031) (Tab. 3; Fig. 4d). We did not detect significant effects of litter on species diversity.

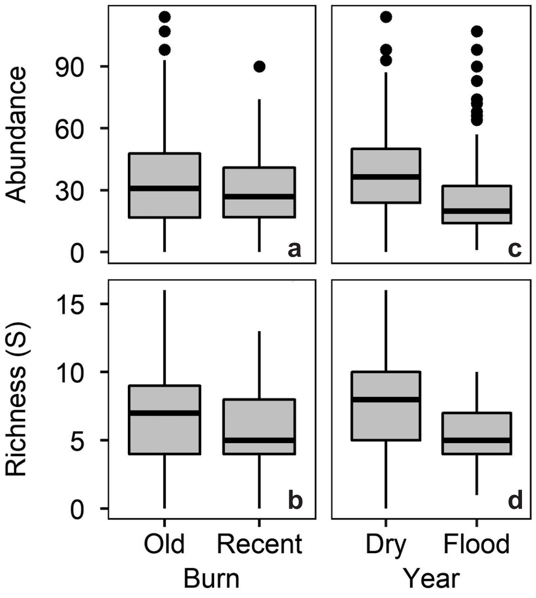

Figure 2 – Abundance (number of individuals) and species richness (S) comparing recent and old burn (a; b) and between dry and flood years (c; d), in the soil seed bank in riparian forest of the Paraguay River, Pantanal wetland, Brazil.

Table 2 – Generalized linear models to effect of flood and fire history on richness and abundance of the soil seed bank in riparian forest of the Paraguay River, Pantanal wetland, Brazil. Significant values (p<0.05) in bold.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Abundance				
(Intercept)	3.83	0.08	49.21	<0.01
Dry year	0.53	0.13	**4.15**	**<0.01**
Old burn	0.33	0.12	**2.74**	**<0.01**
Flood year:recent burn	0.36	0.19	1.95	0.05
Richness				
(Intercept)	2.13	0.05	41.68	<0.01
Dry year	0.43	0.08	**5.30**	**<0.01**
Old burn	0.24	0.08	**3.15**	**<0.01**
Flood year:recent burn	0.16	0.12	1.33	0.19
Shannon diversity				
(Intercept)	1.68	0.07	25.61	<0.01
Dry year	-0.30	0.09	**-3.19**	**<0.01**
Old burn	-0.08	0.09	-0.81	0.42
Flood year:recent fire	-0.05	0.13	-0.35	0.72

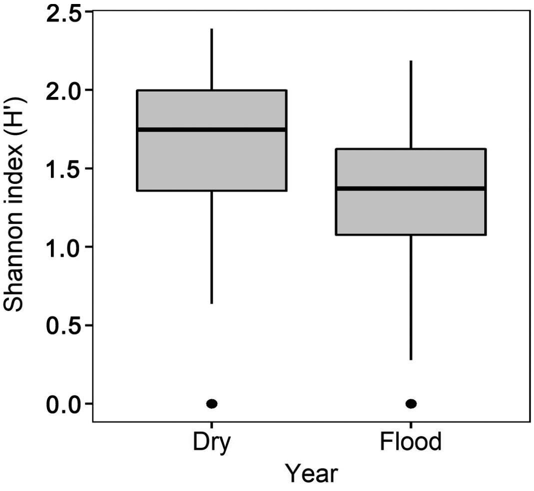

Figure 3 – Shannon diversity index (H') of soil seed bank samples between dry and flood years, in riparian forest of the Paraguay River, Pantanal wetland, Brazil.

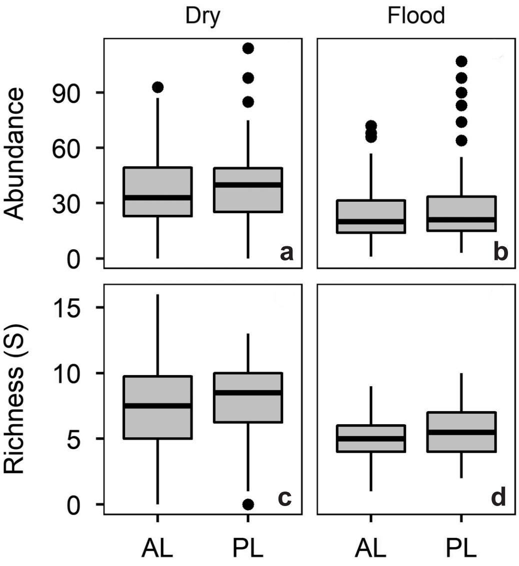

Figure 4 – Abundance (number of individuals) and species richness (number of species) comparing soil samples with presence (PL) and absence of litter (AL) in dry (a; c) and flood years (b; d), in the soil seed bank in riparian forest of the Paraguay River, Pantanal wetland, Brazil.

Discussion

We observed that interannual differences in flood and different intervals in fire history can influence abundance, diversity and species richness of the riparian forest seed bank. These factors can promote or hinder germination, cause seed death and influence spatial distribution, richness and abundance of the seed bank. The seed bank of this riparian forest revealed a very high occurrence of herbaceous species. The predominance of herbs over woody species in the seed bank was also reported by other authors (*e.g.*, Araújo *et al.* 2004; Siqueira *et al.* 2004). Such predominance is characteristic of temporally flooded areas (Leck & Simpson 1994; Souza *et al.* 2016). A great part of the herbaceous species can occur in floodable environments due to their flood tolerance or flood escape strategies such as the annual life cycle, or total flood dependence (aquatic plants) (Souza *et al*. 2016). The last two traits are less frequent in woody species, which occur in these areas due to adaptations of flood tolerance (Parolin 2009). Herbaceous species present fast colonization (Daws *et al.* 2008), high seed productivity and high capacity of dispersal. Moreover, many herbs have high seed longevity, another reason why they become more abundant in the seed bank than woody species (Middleton 2003; Brock 2011).

The most abundant species were plants of the genera *Cyperus*, *Ludwigia*, *Hymenachne*, *Borreria* and *Randia* (Tab. 1). These genera also were the main ones in seed banks in a seasonal deciduous riparian forest, Atlantic Forest and rice fields (Araújo *et al.* 2004; Mesquita *et al.* 2013), and some of these genera were also observed in seed bank in the Pantanal (Bao *et al.* 2014; Souza *et al.* 2016). *Cyperus haspan* was one of the most abundant species in the seed banks of seasonally flooded grasslands (Bao *et al.* 2014; Souza *et al.* 2016). In floodplains occur plant communities where the genera *Panicum* and *Paspalum* predominate, while on drier terraces the genera *Acacia* and *Mimosa* occur, as well as various pioneering families, such as Solanaceae and Asteraceae (Veloso *et al.* 1991). The presence of Asteraceae in the seed bank may be important for regeneration of local vegetation (Bechara *et al.* 2007). Representants of Asteraceae in the seed bank were *Aspilia latissima* Malme, *Melanthera latifolia* (Gardner) Cabrera and *M. micrantha*, all abundant pioneers in disturbed riparian vegetation (Pott & Pott 1994). The high occurrence of Fabaceae is characteristic of fire prone-areas (Andrade & Miranda 2014) since the fire has an important role in the overcoming of physical dormancy stimulating the germination of hard seeds of legumes, increasing their populations (Santana *et al.* 2010; Oliveira *et al.* 2014). In this regard, fire can increase seedling emergence and improve the regeneration of plant communities.

Table 3 – Generalized linear models to effect of litter on richness and abundance of the soil seed bank in riparian forest of the Paraguay River, Pantanal wetland, Brazil. Significant values (p<0.05) in bold.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
Abundance Flood year				
(Intercept)	3.2229	0.112	28.787	<0.01
Presence of litter	0.1817	0.1516	1.198	0.234
Abundance Dry year				
(Intercept)	3.60875	0.08414	42.89	<0.01
Presence of litter	0.14028	0.11503	1.219	0.226
Richness Flood year				
(Intercept)	1.57277	0.05629	27.939	<0.01
Presence of litter	0.16769	0.07648	**2.193**	**0.0307**
Richness Dry year				
(Intercept)	1.97685	0.06384	30.963	<0.01
Presence of litter	0.08238	0.08849	0.931	0.354
Shannon diversity Flood year				
(Intercept)	1.26	0.06	20.76	<2e-16
Presence of litter	0.13	0.09	1.50	0.14
Shannon diversity Dry year				
(Intercept)	1.58426	0.06987	22.673	<2e-16
Presence of litter	0.11617	0.09882	1.176	0.243

Influence of post-fire periods and hydrologic conditions

There was no influence of fire and flood interaction on abundance, species richness and diversity of the seed bank, though, when analysed separately, either effect of fire or of the flood caused differences in total abundance of the seed bank. Nevertheless, these two variables can act together as a double filter (Arruda *et al*. 2016). In areas under deeper and/or longer flood, when fire eliminates the vegetation, the next flood hinders colonization, while in less flooded forests, fire opens gaps for regeneration, thereby favouring colonization (Oliveira *et al.* 2014). Thus, the seed bank can be the main regeneration mechanism. Under fire, the temperature rise on the surface and in the topsoil can affect either negatively the seed bank, by embryo death of seeds without tegument resistance (Hanley & Lamont 2000). Some important herbaceous species in the region for being aquatic and terrestrial may not survive under fire effect (*e.g.*, *Bacopa australis*, *Ludwigia grandiflora*, *L. octovalvis* and *Rotala ramosior*). On the other hand, in some cases, the fire can affect positively, by overcoming dormancy of species with hard seeds (Keeley *et al.* 2011), as in our study, for example, *Paspalum repens*, *Mimosa adenocarpa* and *Sesbania exasperata*.

Due to the environmental filter being able to influence in two ways, removing seeds from the bank by death or germination, this may be the reason why some local species common in the standing vegetation were more abundant in the areas of recent burn. Among these, we highlighted *Cyperus haspan, Hyptis brevipes, Hymenachne amplexicaulis, Ceratopteris pteridoides, Randia armata* and *Cecropia pachystachya*. It is possible that these species were not affected by the environmental filter since the presence of high abundance in the area with recent fire occurrence indicates that they are resistant and also their germination is less influenced by fire than the other species of this study. This favours them to maintain a larger number of seeds post-fire. Among the most abundant species (with more than 100 individuals), only *Ludwigia decurrens* had a considerable difference with greater abundance in the old burn (589) than in recent burn (140) areas. This indicates that the germination of *L. decurrens* can be affected by fire (germination or death), decreasing its abundance in the recent fire areas, probably because the seeds are small and lack hard testa.

Positive effects (dormancy overcoming) can be readily observed in tree species of the Cerrado with seeds with some degree of resistance to high temperatures of fire (Coutinho 1982) and drying when compared to gallery forest trees (Ribeiro & Borghetti 2014). The pioneer shrub *Sesbania virgata* has a corky pod wherein the seeds could withstand mild fire. Although the seed bank gives certain post-fire resilience to the vegetation (Scott *et al.* 2010), large quantities of seeds can be killed during a wildfire, reducing their abundance in the soil (Blodgett *et al.* 2000), as we found in our study.

Seed abundance in areas of the recent burn was lower than the old burn. According to Whelan (1995), such difference can be related to a lower resistance of seeds under fire. Because of the Pantanal seasonality, with an aquatic phase and another terrestrial, there is the buildup of dry biomass, prone to wildfire (Junk *et al.* 1989). Herbs have short life cycles, so they can grow and set seed more readily after fire (Whelan 1995). This could explain the plant response to fire since sampling in areas of the old burn was made four years after the last fire, whereas in recent burn it was three months post-fire. Probably three years time was enough to replenish the seed bank by means of local seed rain or from adjacent areas (van der Valk & Pederson 1989).

We found only two arboreal species, *Triplaris americana* and *C. pachystachya*. *Cecropia* spp. need light to germinate, thereby found in gaps, being indicators of secondary vegetation in forest zones (Parolin *et al.* 2002; Batista *et al.* 2008). In the riparian forest of the Paraguay River, *C. pachystachya* is an indicator of burned riverine woods (Oliveira *et al.* 2014), being dispersed by bats and birds (Pott & Pott 1994). This tree lacks fire resistance mechanism, but it rapidly colonizes gaps left by fire (Godoi & Takaki 2004), though it may resprout (Oliveira *et al.* 2014). *Triplaris americana* is anemochorous, thereby it easily reaches available gaps, which makes it abundant in riparian forests and floodable forest islets (Pott & Pott 1994). With respect to the recorded shrubs, their diaspores can float, particularly the corky pod of *S. virgata*, while *R. armata* is ornitochorous (Pott & Pott 1994).

Like fire, the flood can stimulate or inhibit germination of the seed bank. Our study revealed lower abundance, species richness and diversity of seeds in the soil in the year of flood compared with the drier year. Some studies indicate that continuous flood can inhibit the germination of most terrestrial and amphibious species, and only enhances germination of aquatic plants (Boedeltje *et al.* 2002). Furthermore, a prolonged flood can cause seed death (Baskin & Baskin 2014), what could explain our results. Yet, other studies show that seasonal floods function as a trigger for germination, increasing post-flood recruitment from the seed bank and reducing abundance and species richness of seeds in the soil (Leck 1989; Jutila 2001; Hölzel & Otte 2004; Souza *et al.* 2016). For some species, the nutrient buildup due to sedimentation and decomposition and, consequently, more nitrate and other factors, such as light requirement and anoxy, seem to be important mechanisms to overcome dormancy soon after water drawdown (Jutila 2001; Baskin & Baskin 2014). In this case, the lower abundance and species richness can reveal that the duration and intensity of flood were sufficient to affect the seed bank.

Either factor, flood or fire, are directly related with reduction of the seed rain, because of top kill of most species and diminished seed set, thereby reducing abundance in the seed bank. Nevertheless, in the Pantanal floodplain, the regeneration of the vegetation can improve by enhanced germination induced by flood, especially for annual herbs (Souza *et al.* 2016). It is evident that this riparian forest, prone to flood and fire, presents high abundance and species richness reflected by the seed bank. This indicates that there is a stock of seeds present in the soil capable to regenerate the vegetation, giving it resilience, independently on disturbance.

Influence of litter

In this study, the manual removal of litter in the flood year reduced species richness. Litter can represent a natural trap for seeds, especially in disturbed areas, accumulating more seeds than bare soil (Ruprecht & Szabó 2012). In the Pantanal, during the flood occurs fast growth of aquatic plants, their aerial parts die post-flood and this organic layer builds upon the ground, providing substrate where seeds can increase their deposition (Middleton 2003). Furthermore, the litter can exert an important role in the protection of seeds against predation, but it can inhibit germination for restricting light entrance (Facelli & Pickett 1991), allowing light dependent seeds (*e.g.*, *C. pachystachya*) to remain for longer in the litter. In our study, litter removal in flood year excludes several species but the abundance is not altered.

Extreme seasonal events in the Pantanal are recurrent and predictable, and many species depend on these factors to become established. During a flood year, there is increased production of organic debris plus litter, but in a dry year, such fuel can produce intense wildfire. Although our results do not clarify if there is interaction between the factors, we found that fire and flood are explicative of the abundance and species richness of seedlings emerged from the seed bank of riparian forest in the Pantanal. In these ecological systems, where more than one extreme seasonal event shapes the plant community, the strategies of germination and establishment of the species are distinct, and the ecological traits of some species can indicate adaptative strategies.

The plant species found near water bodies (river) have adaptations to disturbances, such as dispersal by water and wind, for fast recovery post-fire (Dwire & Kauffman 2003). However, we did not have a control treatment without fire, though such status would be hard to find in the Pantanal, except in river isles. The riparian forests of the Pantanal are considered to be shaped by and adapted to periodic wildfires (Arruda *et al.* 2016). Overall, we consider fire and flood as determinant factors in this riparian forest structure, since our results suggest that it presents high abundance and species richness of seeds, revealing that the seed bank contributes to the initial regeneration after extreme seasonal events. This is the first report on riparian forest seed bank in the Pantanal wetland. Therefore, these remote areas of difficult access should be further investigated, particularly the processes that influence the dynamics and maintenance of the plant species composition and diversity of riparian forests.

We conclude that fire and flood affect the seed bank richness, abundance and diversity, it can influence the seasonal regeneration and thus, the structure of the plant community. In areas with recent burn, there is less seed abundance because fire can act by killing plants, thereby reducing production of seeds, or benefiting them by overcoming dormancy (especially in legumes), decreasing seed in the soil. In addition, fire decreases the litter layer, and thus hinders to accumulate seeds, because they are more exposed to predation. Abundance and species richness is lower in the flood year than in the drier year. Flooding and fire can reduce the seed bank by death or by improving the germination of some species. The fire and flood interaction do not affect the abundance and species richness of the soil seed bank.

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