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# EFFECT OF FIRE ON THE SOIL SEED BANK OF NEOTROPICAL GRASSLANDS IN THE PANTANAL WETLAND

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**Abstract:** Research reports have suggested that the soil seed banks can have seedling recruitment favoured by fire, especially in grassy plant communities prone to this environmental factor. We examine effects of fire on the soil seed bank of grasslands in the Neotropical wetland Pantanal (hyperseasonal savanna). Our hypothesis was of negative effect, given the contrasting traits associated to seed-seedling tolerance to fire or flooding in addition to the strength of flood as the main ecological driver in floodable areas. Soil samples were collected before and immediately after a prescribed burn in floodable savanna grasslands, at different depths (2 cm layers down to the 10 cm depth), plus litter. The soil samples were taken to a greenhouse for censuses of seedling emergence, to assess the species composition of the seed bank. We recorded a density of 7404 seeds/m$^2$ and 49 morphospecies, mostly aquatic plants (63%). Among the analysed ecological parameters, the species richness and composition did not change significantly between the pre and post-fire conditions; yet the abundance was significantly lower only in the first 2 cm layer of the burned soil. Both abundance and richness decrease with soil depth. This apparent fire tolerance of the soil seed bank of floodable savanna grasslands is here proposed as a clue to understand fire as another ecological driver, as well as flood, but further long-term studies are needed.

**Keywords:** aquatic macrophytes; plant ecology; prescribed fire; reproductive strategy; soil depth.

## INTRODUCTION

The regeneration capacity of the vegetation after disturbance is what ensures its permanence over time and for many vegetation types the soil seed bank can be the major supplier of new recruits (Hölzel & Otte 2001, Jalili *et al.* 2003, Jankowska-Błaszczuk & Grubb 2006), especially in post-fire scenarios (Keeley & Fotheringham 2000). Fire can also exert negative effects on the soil seed stock, causing a reduction of its abundance (Lipoma *et al.* 2018) and its number of species (Izhaki *et al.* 2000, Leal *et al.* 2006, Melo *et al.* 2007). Such effect is strongly associated with depth: the closer to the surface, the greater will be the effects caused by fire (Baskin & Baskin 2001, Cochrane

2003, Tesfaye *et al.* 2004). It is possible, though it seems less frequent, that a positive effect of fire could occur on the soil seed bank, because fire creates favourable conditions for germination of seeds of some species, *e.g.* by breaking dormancy of some hard coated seeds or increasing light source in dense vegetations (Parker & Kelly 1989, Kwiatkowska-Falinska *et al.* 2014, Zirondi *et al.* 2019) and stimulates flowering of many species, as has been observed in herbs and shrubs in savanna ecosystems (Coutinho 1990, Zirondi *et al.* 2019). Thus, what to expect from the effect of fire on the soil seed bank in an ecosystem where flood figures as its main driver? The Pantanal in South America is a wetland that combines flood and fire. It can be understood as a hyperseasonal savanna (Nunes-da-Cunha & Junk 2015) subjected to the flood pulse (*sensu* Junk *et al.* 1989) as its main driver (Junk *et al.* 2015). This results in a switch between wet and dry phases, the latter with fire events (Cardoso *et al.* 2000).

The concept of a mosaic of vegetation types is well applied to the Pantanal, with plant cover varying from forest to grassland and aquatic macrophytes (Nunes-da-Cunha & Junk 2015, Miranda *et al.* 2018). The Pantanal belongs to the "fluctuating water level wetlands", with low amplitude flood pulse (Junk *et al.* 2006) and circa 60% of its landscape is covered by grassy vegetation (Silva & Abdon 1998, Miranda *et al.* 2018), widely utilized as natural pasture for beef cattle (Resende & Galdino 2001). Due to the typical lignification of biomass accumulated in tropical savanna grasslands during the growing season (Ratnam *et al.* 2011), the grasses become less palatable and digestible, the reason why cattle prefer them in the regrowth phase. Coarse grass pastures are burned to ensure some productivity of the herd, what aggravates the occurrence of human-caused fire in the Pantanal (Cardoso *et al.* 2000, Junk & Nunes-da-Cunha 2012). The fire may potentiate the invasion by exotic species (Brooks *et al.* 2004) and this risk should be especially considered in the Pantanal, where many pastures of African grass *Urochloa humidicola* (Poaceae) are established.

Here we tested the hypothesis that the soil seed bank of the macrohabitat flood-prone savanna grasslands in the Pantanal is fire sensitive, expecting a negative effect of burning on the soil seed stock, what would have implications on the traditional pasture management still practised in the Pantanal – considering reproductive strategy by seeds as an important one for many savanna plant species (Sarmiento & Monasterio 1983). The following considerations support the negative expectation, in spite of the savanna context of the Pantanal: a) flooding, and not fire, has been massively pointed as main ecological driver in wetlands as Pantanal (Junk *et al.* 2006, Nunes-da-Cunha & Junk 2015, Miranda *et al.* 2018); b) regarding seeds and seedlings, the traits reported to flood tolerance and fire tolerance are constrasting: as seed buoyancy and fast seedling growing towards surface, to avoid anoxia or hypoxia, have been reported to plant species in wetlands (Parolin *et al.* 2003, Jackson & Colmer 2005, Junk *et al.* 2006, Parolin & Wittmann 2010); hard coated seeds and fast root seedling growing have been related to fire-prone environments (Saboya & Borghetti 2012, Keeley *et al.* 2011, Ribeiro & Borghetti 2014, Fichino *et al.* 2016); c) fire significantly reduced the soil seed stock of one of the predominant species in a wetland investigated by Miao *et al.* (2010) while flood had positive effects on the soil seed bank of the Pantanal, incresing its abundance and richness (Oliveira *et al.* 2015, Souza *et al.* 2016), and d) there is an expressive number of aquatic macrophytes seeds stored in the Pantanal seed banks (Oliveira 2009, Bao *et al.* 2014, Oliveira *et al.* 2015, Souza *et al.* 2016).

Investigations on the soil seed bank in these grasslands of the Pantanal can improve the knowledge upon the ecology of wetlands (Fenner & Thompson 2005) and guide environment-friendly management practices (Tuffi-Santos *et al.* 2004). This study intends to contribute to both aspects, evaluating the effect of a burn on the structure of the soil seed bank, taking into consideration different soil depths. We verified two ecological parameters: quantitative (species abundance and richness) and qualitative (species composition) of the soil seed bank in grazed flood-prone savanna grasslands.

## MATERIAL AND METHODS

### *Study site*

Samplings were carried out in the Northern Pantanal, in two types of flood-prone savanna grasslands located in the proximities of the Estrada

Parque Transpantaneira (Transpantaneira Park road) between the coordinates 16°37' and 16°44' S and 56°46' and 56°49' W, ~135 m a.s.l., in Poconé municipality, Mato Grosso state, Brazil. The climate is seasonal type savanna Aw (Alvares *et al.* 2013), with dry winters and rainy summers; mean annual rainfall of 1,300 mm; more pronounced drought from June to August (winter), with monthly rainfall below 10 mm and more intense rainy period from December to February (summer), when the maximum monthly rainfall is around 250-300 mm (Nunes-da-Cunha *et al.* 2007).

In the Northern part of the Pantanal, the rainy period causes river overflow to the plain, characterizing the water rise and beginning the aquatic phase of the hydrological cycle (Wantzen *et al.* 2008). After the water rise on the floodplain, it comes the flood, period of relative stability of the water level on the plain in which macrophytes such as *Caperonia castaneifolia* (Euphorbiaceae), *Eleocharis acutangula* (Cyperaceae), *Hyptis lorentziana* (Lamiaceae), *Leersia hexandra* (Poaceae), *Sagittaria guyanensis* (Alismataceae), and species of *Nymphaea* spp. (Nymphaeaceae) develop between the tussocks of the dominant grasses. Thereafter it comes the recede, when waters run back to the river beds or evaporate. Once the water receded, begins the drought and the return of the terrestrial phase of the hydrological cycle, when grasslands in the study area are dominated by the perennial tussock grasses *Andropogon hypogynus* and *Axonopus leptostachyus* (Poales, Poaceae) which persist during both hydrological phases, terrestrial and aquatic (Schessl 1999, Rebellato & Nunes da Cunha 2005).

During drought, due to the edaphoclimatic and vegetational characteristics of the region, the Pantanal is subject to frequent fire (Cardoso *et al.* 2003, Soriano *et al.* 2015). In the annual flood pulse, flooding is monomodal and predictable (Junk *et al.* 1989), however, there are marked multiannual oscillations, with exceptionally dry years, what aggravates fire as an additional stress on this system, and exceptionally wet years, widening the reach and duration of the flooding (Junk *et al.* 2006).

### *The landscape*

The flood-prone savanna grasslands possess grassy matrix and variable density of shrubby-arboreal elements, which can be absent then called "campo limpo" (Nunes-da-Cunha *et al.* 2007). We sampled the soil seed bank in grasslands with and without woody elements. The first type, open savanna grassland, locally known as "campo de rabo-de-burro", is an herbaceous community on clayey soils and dominated by tussock grasses such as *A. hypogynus*, *A. leptostachyus* and *Paspalum* sp. (Schessl 1999). The aquatic phase lasts from February to June and the water column can reach 1.5 m high. In the second type, a savanna grassland with scattered trees [in this case *Tabebuia aurea* (Lamiales, Bignoniaceae)], the herbaceous matrix is composed of a variety of grasses, during the terrestrial phase predominating *A. hypogynus*, *A. leptostachyus*, *Paspalum lenticulare* and *P. plicatulum* (Poales, Poaceae). The maximum recorded water column during the flood is 0.8 m, and the aquatic phase normally lasts from March to May.

### *Sampling design and procedures*

In November 2007, terrestrial phase of the hydrological cycle, a prescribed fire was set in an area encompassing both types of grasslands, where we collected twelve soil samples, six immediately before the burn (control) and six a day after the burn. The samples were equally distributed between both types of grasslands, those from the post-fire were taken at 50 cm far from the samples of the pre-burn condition, forming pairs. Between pairs, the minimum sampling distance was 30 m along a transect.

Each soil sample was collected within a 24 x 24 cm frame and in 2 cm layers until reaching the depth of 10 cm, composing six layers per sampling point, with litter being taken as a layer plus five soil layers up to 10 cm deep in the soil. The litter was collected with a soft brush. The collected material was sieved (mesh 8 mm), eliminating roots and rhizomes. Next, the samples were spread into 25 x 12 x 5 cm plastic trays, over a substrate of washed sand (1 cm). The trays were placed at random in the greenhouse and the control of contamination was made with 8 trays containing only sand. The set (72 + 8) received natural light and daily irrigation, to keep the soil moist.

Seedling emergence was daily monitored and the census was carried out every fortnight, for six months. At the end of the third month, the soil was revolved to allow possible new germination. At the end of the fourth month, the trays were submerged, simulating a flood condition, a procedure to verify the emergence of aquatic plants.

The seedlings were assorted by morphotype, counted and removed from the trays and some of each morphotype were transplanted to individual pots to follow the phenophases. This allowed identification of the species by comparison with vouchers of the Herbário Central of the Universidade Federal do Mato Grosso and collaboration of experts. Species names and aquatic species classification were checked both on websites Flora do Brasil 2020 em construção (http://floradobrasil.jbrj.gov.br/) and Plantas Aquáticas do Brasil (https://sites.icb.ufmg.br/plantasaquaticasbrasil/index.htm).

### *Statistical analyses*

Species abundance, richness and composition were the ecological parameters utilized to verify if there is an effect of fire on the soil seed bank and the depth of its reach. Abundance is defined as the number of individuals emerged from the samples, richness as the number of species and composition as the identity of these species as well as the amounts recorded for each one.

Generalized linear models were developed separately for two quantitative ecological parameters, seed abundance and species richness, considering the individual effects of the treatment (fire x control) and of soil depth, plus their interaction. The models followed linear scale response with normal distribution and the estimates were made by maximum likelihood. Pairwise comparisons were made by the minimum significant difference.

To test possible effect of fire on the qualitative component (species composition) of the soil seed bank, aiming at the determination of clustering *a posteriori*, we performed a non-metric multidimensional scaling (NMDS) with two dimensions, followed by non-parametric analysis of similarity (ANOSIM) for determination of the probability value. Initially and in exploratory character, the scaling was composed of all samples and detected species. Next, the best shape was chosen considering only the layers 1 and 2 and excluding the species with occurrence in just one sample. All analyses followed the recommended by Legendre & Legendre (2012) and were performed in the software R, with the package vegan (Oksanen *et al.* 2018), functions *metaMDS* and *anosim*.

## RESULTS

No seedling was detected in the control trays, assuring the decontamination of the substrate and of the greenhouse. In total, we recorded 5118 emerged seedlings, what is equivalent to the minimum density of 7404 seeds/m$^2$. More than half of them (57.5 %) arose from samples before the fire. We found a richness of 49 morphospecies, 42 being identified to the species level (Table 1), resulting in approximately 70 species/m$^2$. Eleven morphospecies are exclusive, 8 being of the post-fire condition and 3 of the pre-fire condition. The fern *Pityrogramma calomelanos* (Polypodiales, Pteridaceae), which had an emergence of 897 individuals, was not accounted among the shown seedling numbers because we did not intend to include spores.

The general trend was that richness and abundance decreased according to the soil depth (Figure 1). The fire had a significant effect in the abundance of seeds only on the first soil layer ($p = 0.012$) (Figure 1a), but did not have such an effect on the distribution of richness of the soil seed bank (Figure 1b). We did not record effects of fire on species composition (Figure 2), not even when comparing soil layer to layer.

Among 49 morphospecies, 31 are aquatic plants (Table 1). Two species corresponded to approximately half of the emerged seedlings in either burned soil and the control: *Cyperus haspan* (Poales, Cyperaceae) and *Rotala mexicana* (Myrtales, Lythraceae). Only seven species encompass 80% of the emerged seedlings from both burned and unburned treatments, adding to the two aforementioned species: *Steinchisma laxum* (Poales, Poaceae), *Bacopa australis* (Lamiales, Plantaginaceae), *Setaria parviflora* (Poales, Poaceae), *Fimbristylis dichotoma* (Poales, Cyperaceae) and *Scoparia montevidensis* (Lamiales, Plantaginaceae).

## DISCUSSION

The litter does not appear as an important compartment for the supply of recruits of flood-prone savanna grasslands. The reserve is mostly in the more superficial soil layer (0-2 cm), the largest quantity and variety of seeds, what agrees with reports on various other vegetation types (Fenner & Thompson 2005): the soil layer where the seedlings

**Table 1.** Soil seed bank composition according to soil depth and fire occurrence in flood prone savanna grasslands in the Northern Pantanal (Poconé municipality, Mato Grosso state, Brazil). Asterisks indicate aquatic plant species.

| Species | Prior to fire | | | | | | | After fire | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | |
| **ALISMATACEAE** | | | | | | | | | | | | | | | |
| *Helianthium tenellum* (Martius) Britton | | 1 | | | | | 1 | | | | | | | | 1 |
| *Sagittaria guayanensis* Kunth* | | | | | | | | | | 1 | | 1 | | 2 | 2 |
| **BORAGINACEAE** | | | | | | | | | | | | | | | |
| *Euploca parciflora* (Mart.) J.I.M.Melo & Semir | 1 | 19 | | | | | 20 | | 14 | 26 | | 4 | 1 | 45 | 65 |
| **CYPERACEAE** | | | | | | | | | | | | | | | |
| *Cyperus haspan* L.* | 2 | 204 | 62 | 34 | 26 | 12 | 340 | 3 | 151 | 147 | 36 | 50 | 30 | 417 | 757 |
| *Eleocharis acutangula* (Roxb.) Shult.* | 1 | 26 | 6 | 6 | 7 | 9 | 55 | 1 | 13 | 13 | 2 | 3 | 1 | 33 | 88 |
| *Eleocharis* cf. *minima* Kunth* | | 2 | 18 | 7 | 7 | | 34 | | 1 | 1 | 2 | 13 | | 17 | 51 |
| *Eleocharis elegans* (Kunth) Roem. & Shult.* | | 24 | 17 | 7 | 7 | 4 | 59 | 1 | 14 | 3 | 2 | | 3 | 23 | 82 |
| *Eleocharis geniculata* (L.) Roem. & Schult.* | | 1 | 2 | 1 | | | 4 | | | 1 | | 2 | | 3 | 7 |
| *Eleocharis nudipes* (Kunth) Palla* | | 1 | 1 | 1 | | 1 | 4 | | | 3 | | | | 3 | 7 |
| *Fimbristylis dichotoma* (L.) Vahl* | 7 | 89 | 24 | 9 | 13 | 13 | 155 | 4 | 27 | 11 | 5 | 3 | 2 | 52 | 207 |
| *Rhynchospora* sp. | | 2 | 1 | 2 | 1 | 1 | 7 | | 3 | 2 | | | | 5 | 12 |
| *Scleria gaertneri* Raddi* | | | 1 | | | | 1 | | | | | | | | 1 |
| *Scleria. reticularis* Michx. Ex Willd. | 1 | 3 | | | 1 | | 5 | | 2 | | 3 | 1 | | 6 | 11 |
| **EUPHORBIACEAE** | | | | | | | | | | | | | | | |
| *Euphorbia hyssopifolia* L.* | | 19 | 1 | 1 | 1 | 1 | 23 | | 10 | 5 | 1 | 2 | 2 | 20 | 43 |
| **FABACEAE** | | | | | | | | | | | | | | | |
| *Aeschynomene* sp.* | | 1 | | | | | 1 | | | | | | | | 1 |

**Table 1.** Continued on next page...

**Table 1.** ...Continued

| Species | Prior to fire | | | | | | | After fire | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | |
| *Eriosema platycarpon* Micheli | | | | | | | | | | | 1 | | | 1 | 1 |
| **LYTHRACEAE** | | | | | | | | | | | | | | | |
| *Cuphea* sp.* | | 1 | | | | | 1 | | | | | | | | 1 |
| *Rotala mexicana* Cham. & Schltdl. | 1 | 543 | 304 | 120 | 69 | 39 | 1076 | 3 | 253 | 210 | 121 | 67 | 35 | 689 | 1765 |
| *Rotala ramosior* (L.) Koehne | | 6 | 1 | 1 | 1 | | 9 | | | | | 1 | | 1 | 10 |
| **MALVACEAE** | | | | | | | | | | | | | | | |
| *Byttneria genistella* Triana & Planch. | | | | | | | | | 1 | | 1 | | | 2 | 2 |
| *Corchorus argutus* Kunth* | | | | | | | | 1 | | | | | | 1 | 1 |
| *Pavonia angustifolia* Benth. | | | | | | 1 | 1 | | | | | | | | 1 |
| *Waltheria communis* A.St.-Hil. | | | | | | | | | 1 | | | | | 1 | 1 |
| **ONAGRACEAE** | | | | | | | | | | | | | | | |
| *Ludwigia decurrens* Walter* | | | | | | | | | | | 1 | | | 1 | 1 |
| *Ludwigia inclinata* (L.f.) M. Gómez* | 1 | 1 | | | | 1 | 3 | | 5 | 1 | | 2 | | 8 | 11 |
| *Ludwigia octovalvis* (Jacq.) P.H. Raven* | 1 | 3 | 2 | | | | 6 | 2 | | 1 | 2 | 1 | 2 | 8 | 14 |
| **PHYLLANTHACEAE** | | | | | | | | | | | | | | | |
| *Phyllanthus stipulatus* (Raf.) G.L. Webster* | 1 | 48 | 9 | 3 | 18 | 1 | 80 | 3 | 19 | 3 | 3 | 15 | 2 | 45 | 125 |
| **PLANTAGINACEAE** | | | | | | | | | | | | | | | |
| *Bacopa* aff. *verticillata* (Pennell & Gleason) Pennell* | | 7 | 6 | 1 | | | 14 | | 5 | 1 | 1 | | | 7 | 21 |
| *Bacopa australis* V.C.Souza* | 2 | 63 | 76 | 52 | 22 | 16 | 231 | 2 | 27 | 37 | 49 | 37 | 15 | 167 | 398 |
| *Bacopa reflexa* (Benth.) Edwall* | | 8 | 1 | 1 | | | 10 | | 19 | 3 | | 1 | | 23 | 33 |

**Table 1.** Continued on next page...

**Table 1.** ...Continued

| Species | Prior to fire | | | | | | | After fire | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | |
| *Conobea scoparioides* (Cham. & Schltdl.) Benth.* | | 4 | 4 | | | 1 | 9 | | 3 | | 1 | 2 | 3 | 9 | 18 |
| *Scoparia montevidensis* (Spreng.) R.E.Fr. | | 43 | 15 | 10 | 7 | 8 | 83 | | 70 | 47 | 72 | 18 | 10 | 217 | 300 |
| **POACEAE** | | | | | | | | | | | | | | | |
| *Axonopus purpusii* (Mez) Chase | | 2 | | | 1 | 1 | 4 | | 5 | 3 | | | | 8 | 12 |
| *Leersia hexandra* Sw.* | 2 | 51 | 3 | 3 | 2 | 2 | 63 | 2 | 43 | 3 | 1 | 1 | | 50 | 113 |
| *Luziola fragilis* Swallen* | | 6 | 2 | | | 1 | 9 | | 2 | 3 | 2 | | 1 | 8 | 17 |
| *Panicum dichotomiflorum* Michx.* | 2 | 39 | 11 | 4 | | 1 | 57 | 2 | 9 | 5 | 1 | 7 | 1 | 25 | 82 |
| *Paspalum lenticulare* Kunth | | 10 | 1 | | | | 11 | | 1 | | | | | 1 | 12 |
| *Setaria parviflora* (Poir.) Kerghélen* | | 162 | 31 | 20 | 1 | 4 | 218 | | 32 | 29 | 3 | 8 | 4 | 76 | 294 |
| *Steinchisma laxum* (Sw.) Zuloaga* | 24 | 172 | 30 | 22 | 16 | 11 | 275 | 9 | 89 | 30 | 8 | 17 | 4 | 157 | 432 |
| Species 1 | | | | 1 | | | 1 | | | | | | | | 1 |
| **POLYGALACEAE** | | | | | | | | | | | | | | | |
| *Polygala appendiculata* Vell. | | | 1 | | | | 1 | | | 2 | | | | 2 | 3 |
| **PONTEDERIACEAE** | | | | | | | | | | | | | | | |
| *Pontederia parviflora* Alexander* | 5 | 2 | | | | | 7 | | | | | | | | 7 |
| **RUBIACEAE** | | | | | | | | | | | | | | | |
| *Borreria quadrifaria* E.L. Cabral | | | | | | | | | 1 | | | | | 1 | 1 |
| *Borreria tenella* (Kunth) Cham. & Schltdl. | | 13 | 5 | 16 | | 2 | 36 | | 12 | 2 | | 3 | 2 | 19 | 55 |
| *Diodia kuntzei* K.Schum.* | | 8 | 1 | 1 | 1 | 1 | 12 | | 4 | 2 | | 1 | | 7 | 19 |
| Species 2 | | | | | | | | | 2 | | | | | 2 | 2 |
| *Spermacoceodes* sp. | | 1 | | | | | 1 | | 1 | | 1 | | | 2 | 3 |

**Table 1.** Continued on next page...

**Table 1.** ...Continued

| Species | Prior to fire | | | | | | | After fire | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | Litter | 0-2 cm | 2-4 cm | 4-6 cm | 6-8 cm | 8-10 cm | Total | |
| **TURNERACEAE** | | | | | | | | | | | | | | | |
| *Piriqueta corumbensis* Moura | | 6 | 1 | | | | 7 | | 3 | 3 | | | | 6 | 13 |
| **INDETERMINATE** | | | | | | | | | | | | | | | |
| Species 3 | | 6 | | | 1 | 1 | 8 | 3 | 3 | | | | | 6 | 14 |
| | 51 | 1597 | 637 | 323 | 202 | 132 | 2942 | 36 | 845 | 598 | 319 | 260 | 118 | 2176 | 5118 |

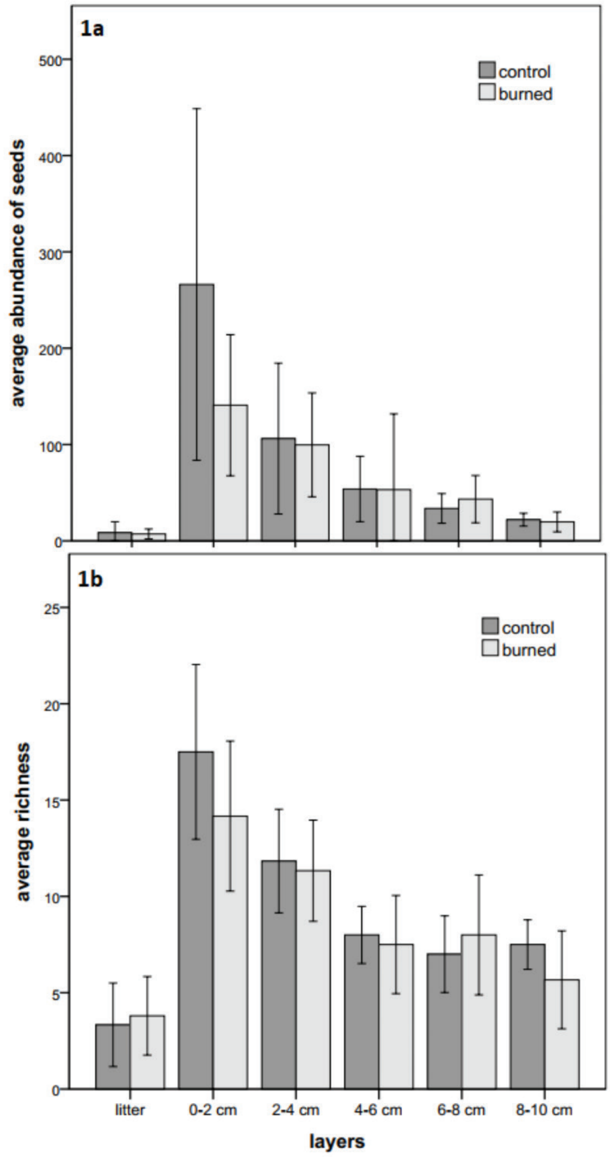


**Figure 1.** Soil seed bank ecological parameters according to soil depth obtained by seedling emergence method in a greenhouse. Soil samples came from unburned (control) and burned sites from flood-prone savanna grasslands in the Pantanal wetland. a) Abundance; b) Richness. Rods represent 95% of confidence interval.

are most recruited is the same that most receives diaspores. According to our finding, fire acts exactly with higher intensity on this compartment closest to the surface, hindering the size of the soil seed stock, but not its composition – when analysed in terms of community. It is necessary to highlight that all ecological analyses at the community level can conceal important effects over each species. This reduction in the number of available propagules can hinder the seed-dependent regeneration of the vegetation. However, such effect can be attenuated

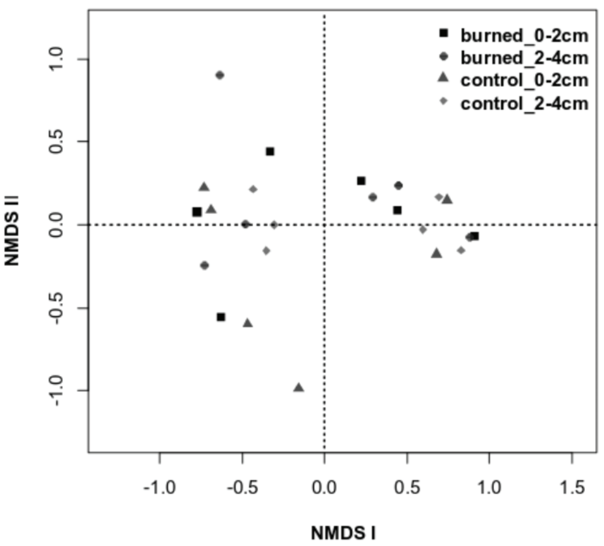


**Figure 2.** Non-metric multidimensional scaling (NMDS) ordination reflecting species composition of soil seed banks from flood-prone savanna grasslands in the Pantanal wetland, Brazil. Soil samples were taken before (control) and after prescribed fire (burned). This NMDS takes in account samples from two first layers: 0-2 and 2-4 cm depth.

over time (Miao *et al.* 2010) because of a progressive reposition of seeds brought in by water flow in wetlands (Dawson *et al.* 2016), so the bank is not depleted. Nonetheless, investigations on the long-term impact of fire on the soil seed stock of the Pantanal have not even started yet. In flood-free vegetation, for example, such negative effect can last for at least three years (Lipoma *et al.* 2018). Yet regarding the temporal reach of the studies, even the seasonal variations only recently started to be investigated (Bao *et al.* 2014, Souza *et al.* 2016).

Among the dominant species in the vegetation established at sampling time, only the grass *P. lenticulare* was recorded, however, its abundance corresponds to less than 0.25%. The lack of correspondence between the above-ground vegetation and the seed bank was also verified by other studies, *e.g.*, in agroecosystems in Spain (López-Mariño *et al.* 2000), in different vegetation types of a protected area in Iran (Jalili *et al.* 2003) and in seasonal semideciduous forest in Brazil (Melo *et al.* 2007). This can be related to the maintenance of transient seed banks by the predominant grasses and to the seasonal fluctuation of the bank (Thompson *et al.* 1997), not detected by sampling in a single episode.

The number of species of the soil seed bank (*i.e.*, species richness) and their composition did not change by the applied fire under the conditions of the test, countering the initial expectation of negative effect also on these ecological parameters. The absence of significant effects on both species richness and composition, to the contrary of the reported by other studies (Leal *et al.* 2006, Melo *et al.* 2007, Ikeda *et al.* 2008), can be attributed to some practical aspects of fire (Parker & Kelly 1989, Cardoso *et al.* 2000): in this case fire occurred in the middle of November, within the allowed period and after the first rains. Perhaps in the high dry season (from June to September) the fire effect would be stronger, although it was not tested here.

We can consider the absence of significant effects on a community majorly constituted of aquatic plants as a clue to rise for discussion that fire is an ecological driver as important as flood, the latter extensively proven as such (Junk *et al.* 2006, Nunes da Cunha & Junk 2015). Fire and flood as main drivers reinforce the understanding of the Pantanal as a hyperseasonal savanna. In this regard, it is worth to remind that flood as an annual and predictable regime is quite recent in the evolutive history of the Pantanal, having been established since less than 2,000 years ago (Assine & Soares 2004). If before the establishment of the present flooding regime the Pantanal corresponded mainly to flood-free savanna as yet in most of its surroundings (Brazilian Cerrado) - what is deduced from the floristic similarity of both systems (Pott & Pott 1994, Costa *et al.* 2010, Pott *et al.* 2011) - hence we can suppose, based on paleobotany for central Brazil (Ledru *et al.* 1998), that fire is a much older agent in this landscape than flood (Assine & Soares 2004), influencing the vegetation even before the occurrences of modern anthropic fire (*i.e.*, related to >200 years cattle ranching). Ancient fire and modern fire would have driven this vegetation which soil seed stock does not respond with notable changes in composition under the effect of a single burn, although this relationship remains to be further investigated. Another intriguing question arose from this work: what seed traits would be related to both fire and flooding tolerance?

Regarding the adoption of fire as pasture management tool in floodable grasslands of the Pantanal, it is safe to recognize that only long-term studies can clarify the consequences of this agent for the vegetation, endorsing or not the use of burning. Considering fire effects, we do not have yet for wetlands, nor for hyperseasonal savannas, the same degree of knowledge available for the Cerrado or other savannas (Ratnam *et al.* 2011, Veldman *et al.* 2015).

The soil seed bank of the studied grasslands is composed essentially of aquatic species, and does not contain dominant above-ground vegetation species during the sampling period, according to our punctual study. The composition and richness of the seed bank showed to be tolerant of a single burn, except seed abundance in the compartment closest to the soil surface. Long term-studies are suggested to assess the impacts of pasture management with fire on the vegetation dynamics.

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