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Do Aquatic Macrophytes Limit the Invasion Potential of Exotic Species in Pantanal Grasslands?

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Abstract

Natural disturbances have the potential to limit exotic species invasions. The exotic grass, *Urochloa humidicola*, has high propagation potential following seasonal flooding, but, flooding tends to reduce the cover. Neither the potential for *U. humidicola* form a seed bank for recruitment following seasonal flooding, nor the mechanism responsible for reducing adult plant cover during floods is currently known. The soil seed bank of a *U. humidicola* was sampled for 2 years. To examine the potential role of competition with aquatic macrophytes in reducing its cover during floods, cuttings of *U. humidicola* were flooded in tanks in presence and absence of aquatic macrophytes for 3 months. Seedling density of *U. humidicola* was higher post-flood (245 seedlings/m^{-2}) than the post-dry (130 seedlings/m^{-2}). Germination occurred throughout the year, with highest seedling densities at the five to 7 months following soil collection. Competition with aquatic plants significantly increased mortality (c. 70%) of inundated *U. humidicola*. Our findings suggest that the survival potential of *U. humidicola* under flood is high, but is limited by shading of aquatic macrophytes. Nonetheless, its seed bank germinates throughout the year, though delayed by flooding. Control of invasive species in grasslands of the Pantanal depend on natural hydrological and biological drives.

Keywords Aquatic plants · Flood tolerance · Seed bank · Wetland

Introduction

The introduction of exotic plants can alter the structure, composition, and function of ecosystems (Olden and Poff 2003; Hejda et al. 2009; Clarke et al. 2013). Wet ecosystems, can be highly vulnerable to invasion, because they comprise the largest portion of a floodplain (Pott and Silva 2015) and, these areas become suitable for pasture use, leading to increased introduction of exotic plant seeds (Pott and Ratter 2011). Hydrologically connected habitats and aquatic corridors for short and long distance seed dispersal promote the spread of highly prolific seed producers (Middleton 2003; Capon and Brock 2006; Brock 2011). The spread of exotic seeds and the formation of persistent seed banks is a threat to the diversity of

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wetlands worldwide (Andrew et al. 2015; Hejda et al. 2015; Rodríguez and Brisson 2015; Deane et al. 2016).

In many areas, exotic grasses are introduced to wetlands for pasture (Yarwood et al. 2016). The recurrent use of these grasses can make them evolutionarily tolerant to seasonal disturbances (Clarke et al. 2013), such as flooding. When introduced, they often respond rapidly to the seasonal event and become dominant." (Gallardo et al. 2015; Wang et al. 2015), due to morphological characteristics, such as fast dispersal, growth, colonization and propagation rates (Rojas and Zedles 2015; Galatowitsch et al. 2016). Ultimately, exotic grasses in high densities can reduce local plant diversity by inhibiting germination and outcompeting the native plant community (Hejda and Pysek 2006).

In the Brazilian Pantanal wetland, the African grass *Urochloa humidicola* (Rendle) Morrone & Zuloaga has been introduced to natural grasslands in the last 20 years. This species was chosen for its high productivity relative to native grasses and for its flood tolerance, attributed to its numerous adventitious roots (Dias-Filho and Carvalho 2000; Mattos et al. 2005). Flooding in the Pantanal is annual and predictable, in the southern region between April and August (Hamilton et al. 1996; Pott and Silva 2015). When the water recedes, in spite of its flood tolerance, the percent coverage of *U. humidicola* has been reduces to ca. 20% (Bao et al. 2015), the causes of such reduction are, as yet, unknown, as it is not known whether *U. humidicola* has a seed bank capable of germinating, being that its main source of colonization of the genus *Urochloa* is by the bud bank and regrowth (Fidelis et al. 2014).

In grasslands, when a dominant species reaches its optimal strategy of colonization in a seasonal habitat, it tends to survive and reproduce more in some years and less in others. This will vary according to the competition potential of neighboring species (Venable 1989). Given its relatively high flood tolerance, we predict that *U. humidicola* can be limited by competition with aquatic macrophytes. Most of these species of aquatic macrophytes show high germination rates during floods (Bao et al. 2017), with fast colonization and growth rates (Pieterse and Murphy 1990), associated with their specific adaptations to flood events (Lopes et al. 2016). The high density of aquatic macrophytes may be instrumental in regulating the growth and abundance of exotic species (Urban et al. 2006).

We aim to examine how native grasslands of the Pantanal persist years after the introduction of exotic species in areas where the flood conditions favor seed dispersal of invasive species. We assessed the role of competition with aquatic macrophytes in reducing cover of *U. humidicola* during flooded conditions. Secondly, we carried out a field study to examine whether *U. humidicola* forms a seed bank and, if so, the optimal seasonality for emergence. We hypothesized that: (i) *U. humidicola* cover would be reduced in presence of native aquatic macrophytes due to competition for light; and (ii) *U. humidicola* forms a seed bank, which germinates throughout the year, with highest germination at the end of flood. This could be an effective adaptive strategy for *U. humidicola,* as the end of the flood is characterized by relatively stable environmental conditions and the absence of competitors (e.g., aquatic macrophytes).

Methods

Study Area

Seed bank samples were collected in a seasonally flooded grassland (19°29′27.3"S; 57°01′55.9"W) in the Pantanal wetland (Central-West Brazil, Fig. 1). The climate is sub-humid tropical, with an average annual temperature of 26 °C (Allem and Valls 1987) and mean annual rainfall of 1100 mm. The grassland is flooded annually in the summer (between April and August); from both local rain and river overflow (Silva and Abdon 1998). The natural grasslands of the Pantanal have been subject to cattle ranching for over 200 years (Pott and Silva 2015). In the absence of grazing, tall tussock grasses return and shade out existing short grasses (Pott and Silva 2015) and low herbs (Pott and Ratter 2011). The existing grassland species are able to withstand moderate grazing and trampling (Pott and Ratter 2011). Commercial seeds of *Urochloa humidicola* have been sown at Fazenda São Bento in the last 20 years, while the native vegetation has been plowed and the shrubs cleared. In the study area, *U. humidicola* was sown with *Pennisetum typhoides* two years before our first sampling, when the short-lived grass (annual species) had already died.

Sampling

To evaluate of the seed bank of *U. humidicola*, top soil samples were collected twice at the end of the dry season: October/2013 and 2014 (2013D, 2014D) and twice at the end of the flood period: July/2014 and 2015 (2014F, 2015F), when the water level can vary from 0.30 to 1.50 m deep (data from research station Base de Estudos do Pantanal (UFMS), 2013–2015; Fig. S1a). Four seasonally flooded areas (with ponds in the flood period) with cultivated pasture were sampled (**pond 1** 19°29′23.3"S; 57°01′51.6"W, **pond 2** 19°29′25.3"S; 57°01′19.9"W, **pond 3** 19°28′39.8"S; 57°02′14.2"W and **pond 4** 19°28′06.0"S; 57°02′00.5"W; Fig. 1).

The Pantanal floodplain, because of differences in relief, forms several seasonal ponds (Pott and Silva 2015), which present variation in the vegetation structure (Bao et al. 2015). To achieve greater amplitude of variation of seed capture, we collected soil samples along three contour lines (i.e., transects), representing relative elevation differences of low, mid, and high (Fig. S1b). In each area (seasonal pond), we collected soil samples randomly (using a table of random numbers from 1 to 50 m).

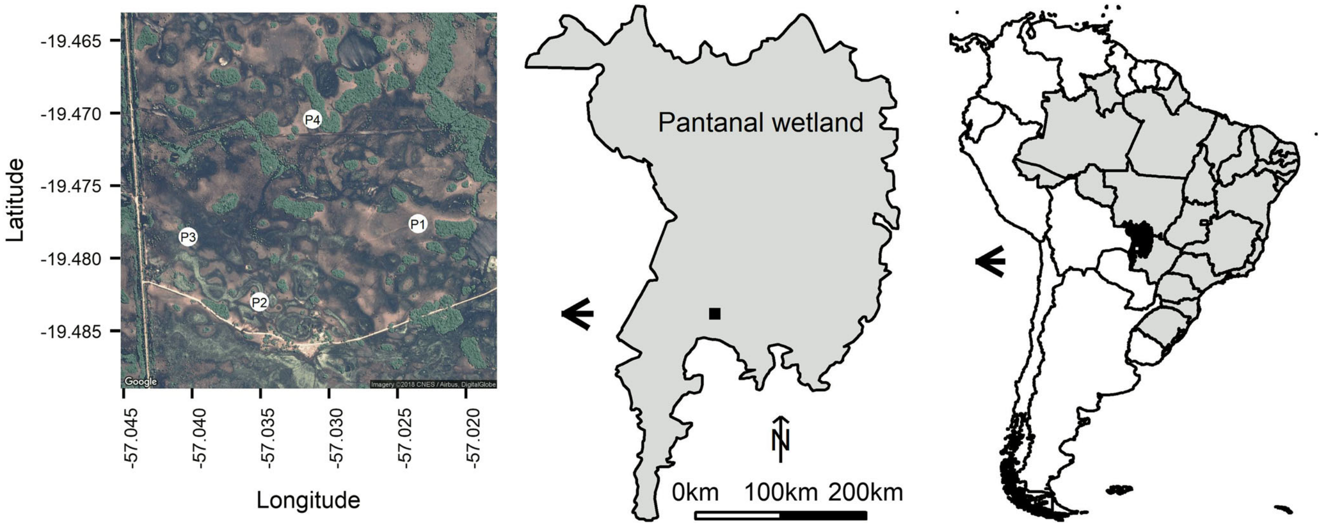

Fig. 1 Study area located in the Center-West of Brazil, in the Pantanal of Mato Grosso do Sul, with four seasonal ponds (P1, P2, P3 and P4), distributed in a grassland cultivated with *U. humidicola* at Fazenda São Bento. Below is the State Park Road; at the top, the green forest of the Abobral river gallery; small dark green spots are forest islets on the brown pastures. (Source of the image: "Fazenda São Bento", Pantanal South (19°29′27.3 ″S; 57°01′55.9″ W) Google Earth (accessed November 15, 2017))

Transects were marked during the flood season, observing the water level, one in the lowest zone, in the middle of the pond = low (ca. 60 cm deep), one at the pond edge = mid (ca. 30 cm deep) and one in the higher zone, on the external part = high (ca. 1 cm deep), (e.g. Bao et al. 2014, 2015, 2017). We collected five soil samples per transect, a total of 15 samples per seasonal pond and 60 samples per seasonal period (flood and dry). A slide of soil was collected inside 0.20 × 0.20 m frame, 3 cm deep (e.g. Bao et al. 2014, 2017). The samples were kept in plastic bags and transported to the greenhouse.

Evaluation of the Seed Bank

The seed bank was evaluated using the seedling emergence method (Thompson et al. 1997) in the greenhouse. The soil samples were spread into plastic trays (30 cm × 20 cm × 10 cm) over a 3 cm layer of sterilized sand, under ambient temperature. An automatic sprinkler irrigated the greenhouse twice a day and the trays were perforated to avoid waterlogging and were rotated weekly. The seedlings were counted weekly and removed to avoid competition with new seedlings (Thompson et al. 1997). As the objective was to evaluate the *U. humidicola* seed bank, only the grass seedlings were counted. Seedlings of other species were removed from the trays. To evaluate the persistence of the seed bank in the post-dry and post-flood seasons, samples were collected post-dry/ 2013 and 2014 (September) and post-flood / 2014 and 2015 (July). Seedling emergence was evaluated for 12 months to examine peak emergence times and potential delays in seed bank emergence.

Effect of Aquatic Macrophytes on Survivorship of *U. humidicola* in Flooded Conditions

To examine the effect of competition with native aquatic macrophytes on cover of *U. humidicola* two treatments were established: presence and absence of aquatic macrophytes. The experiment had three tanks per treatment with enough water to submerge the cuttings of *U. humidicola* (ca. 0.90 m tall). The tanks were under full sun, only covered with mosquito screen. We submerged five trays with five cuttings each for a total of 25 cuttings per tank (Fig. S2a). *U. humidicola* plants were collected from seedlings removed from the seed bank study, and transplanted into trays for this study. The tanks without aquatic macrophytes was the control treatment. In the treatment with aquatic macrophytes, five trays with seedlings of *Sagittaria guayanensis*, *Limnocharis flava*, *Hydrocleys parviflora* and *Pontederia subovata* were added to the tanks (Fig. S2b). These species were chosen for being abundant in the Pantanal and for having floating leaves.

In each tank with aquatic macrophytes, a cover of ca. 70% was standardized (based on a pilot test we established that 70% is the minimum value to begin to have an effect on the occurrence of *U. humidicola*). The experiment was carried out for 3 months, representing the average time the grassland remains flooded annually (data collected at ranch Fazenda São Bento, 2013–2015). Mortality of individual grasses was considered when the aerial parts were dead (cf. Baruch 1994). It is noteworthy that there was no direct competition for resources other than light between *U. humidicola* and the macrophytes, since they were planted in separate trays.

Data Analysis

All analyses were conducted in R environment (R Core Team 2016). The survival of *U. humidicola* was estimated in both treatments using the Kaplan-Meier non-parametric estimator (Kaplan and Meier 1958), using the survfit function and the survival curves were compared with log rank test (Harrington and Fleming 1982), applying the survdiff function of the survival package (Therneau 2015). The log-rank test calculates a value of *chi*-square (χ^2) for all events in each group. The sum of these values was used to generate a value $\chi^2$of comparison between the two curves.

To test the temporal variation of germination from the seed bank, seedling density after emergence from the seed bank was evaluated for 12 months ($n = 40$) at the end of the dry period and flood, months that presented germination = 0 were disregarded. We also analyzed the seasonal and annual differences in seed bank density ($n = 60$).

For the seasonal and annual differences in seed bank density, we used generalized linear models (GLM) with Tweedie distribution (Smyth and Jørgensen 2002). We chose the use of GLM and not GAM because we have only one categorical predictive variable. We know that GAMMS can be used when there are continuous and categorical predictive variables together, which does not fit our data. Models with this distribution are indicated for continuous positive data with many zeros (Dunn and Smyth 2005). To deal with the intrinsic temporal dependence between the months in temporal variation of germination, we addict the samples as random factor in a generalized linear mixed model (GLMM) with the same Tweedie distribution. We implemented these analyzes with the statmod (Giner and Smyth 2016) and lme4 (Bates et al. 2015) packages. The results of the models of observation times and seasonal variation were submitted to pairwise multiple comparison of least-squares means with Bonferroni p-adjustment using the lsmeans package (Lenth 2016).

Results

Effect of Aquatic Macrophytes on Survivorship of *U. humidicola* in Flooded Conditions

Urochloa humidicola showed a high flood tolerance, in the control treatment, but the presence of aquatic macrophytes resulted in aerial mortality of ca. 70% of cuttings. The proportion of survivors at week-3 in both treatments was high (0.99 absence) and (0.96 presence). Survival rate declined gradually over time such that by week-9 only 8.6% survived in the presence of aquatic macrophytes, while 88% survived in their absence (Fig. 2).

Based on the difference between the survival curves, mortality was significantly different between treatments ($\chi^2 = 44.2$; $p < 0.001$), with higher mortality in the presence of macrophytes (Table 1). The proportion of survivors at the end of the experiment was 85% in absence and 33% in presence of aquatic macrophytes (Table 1). This finding indicates high survivorship of *U. humidicola* after 12 weeks of continuous flooding, and that survivorship is significantly reduced by ~70% cover of aquatic macrophytes.

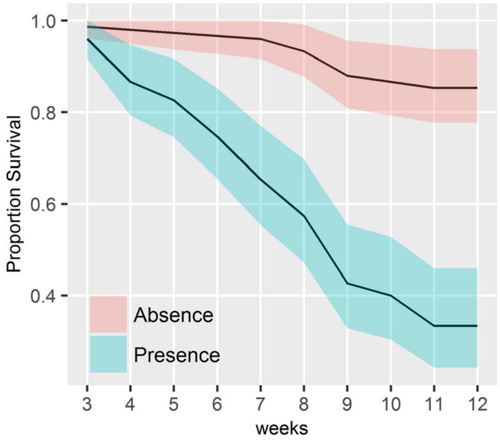

Fig. 2 Kaplan-Meier survival curves and confidence intervals of *Urochloa humidicola* seedlings under flooding in treatments with presence and absence of aquatic macrophytes from the Pantanal seasonally flooded grassland. Shaded areas represent 95% confidence intervals

Evaluation of the Seed Bank of *U. humidicola*

Seeds of *U. humidicola* germinated from the seed bank in both seasons (post-flood and post-dry) in all years of sampling. The total density of germinated seeds in post-flood season (245 seedlings/m^2) was nearly twice as high as that in post-dry season (130 seedlings/m^2). There was no difference between the same periods (dry vs dry; flood vs flood). Data for 2013D showed the lowest germinated seed density when compared to post-flood periods: 2013D vs 2014F (z-ratio = 3, 55, $p = 0.002$, Fig. 3) and 2013D vs 2015F (z-ratio = 3.52, $p = 0.002$, Fig. 3).

The density of *U. humidicola* seedlings increased in the first several months of the greenhouse experiment. In the 3rd month when germination began seedling density was 8 seedlings.m^{-2} (post-flood) and 5 seedlings.m^{-2} (post-dry).

Table 1 Kaplan-Meier estimates of survivor of treatments compared using Log-Rank Mantel-Haenszel test

	N	n.censor	O	E	(O-E)^2/E	(O-E)^2/V
Absence	75	64	11	35.6	17	44.2
Presence	75	25	50	25.4	23.9	44.2

N total number of seedlings per treatment, *n.censor* number of survivors, *O* Observed, *E* expected, *V* variance

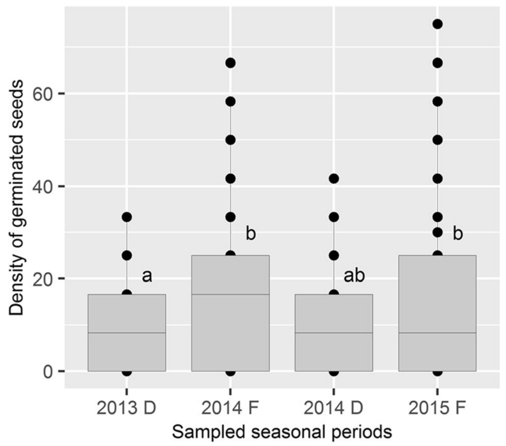

Fig. 3 Density of germinated *Urochloa humidicola* seeds in greenhouse post-dry (D) and post-flood (F) seasons from the seed bank of a Pantanal grassland wetland. Different letters indicate the significant differences between the seasonal periods calculated by pairwise multiple comparison of least-squares means ($p < 0.05$)

Table 2 Generalized Linear Mixed Models (GLMs) of germination between the months for flood and dry seasons in grassland in the Pantanal wetland

Seasons	Estimate	Std.Error	t-value	Pr(>|t|)	Lsmean
Post-dry					
5th (Intercept)	−0.125	0.620	−0.202	0.840	−0.125 ^{ab}
6th	1.521	0.462	3.291	**0.001**	1.395 ^{c}
7th	1.185	0.478	2.476	**0.013**	1.059 ^{c}
8th	0.030	0.579	0.053	0.958	−0.095 ^{ab}
9th	−0.170	0.607	−0.280	0.780	−0.295 ^{ab}
10th	−1.134	0.801	−1.415	0.157	−1.259 ^{b}
Post-flood					
3th (Intercept)	−1.782	1.026	−1.737	0.082	−1.782 ^{a}
4th	1.384	1.048	1.321	0.187	−0.398 ^{ab}
5th	3.216	0.949	3.388	**0.001**	1.434 ^{cd}
6th	3.836	0.938	4.088	**<0.001**	2.054 ^{c}
7th	3.604	0.942	3.828	**<0.001**	1.822 ^{c}
8th	2.995	0.954	3.139	**0.002**	1.214 ^{bcd}
9th	2.123	0.990	2.145	**0.032**	0.342 ^{abd}
10th	1.956	1.000	1.956	0.050	0.174 ^{abd}

Bold indicates the significant differences of GLMs ($p < 0.05$). Different letters show the significant differences between the months calculated by pairwise multiple comparison of least-squares means (lsmean; $p < 0.05$)

The greatest seed germination occurred during the 6th month regardless of whether if the samples were collected post-flood (364 seedlings.m^{-2}) or post-dry season (226 seedlings.m^{-2}). Thereafter, germination declined and the seed bank was depleted by the 11th month (Fig. 4).

Seedling density was higher 5 to 7 months post-flood than 5 to 8 months post-dry season (Table 2). These findings show that the germination peak can occur in the flood-dry interval.

Discussion

Effect of Aquatic Macrophytes on Survivorship of *U. humidicola* in Flooded Conditions

The presence of aquatic macrophytes during periods of flooding reduces the cover of *U. humidicola* by ca. 70%. Therefore, flooding indirectly influenced the cover of this exotic species by promoting competitively dominant species. This reduction was observed in the field during post-flood periods (Bao et al. 2015), when many species of aquatic and amphibious plants germinate (Pott and Silva 2015), and contribute to high seed bank richness (Bao et al. 2014; Oliveira et al. 2015; Souza et al. 2016). These native seed banks may be responsible for the control of *U. humidicola*. The high mortality of *U. humidicola* induced by floating aquatic macrophytes may be associated with decreased light and oxygen, which stress and kill many exotic species, even those with dominant characteristics (Blake and Duffy 2012). However, *U. humidicola* can survive under running water, such as seasonal streams and riparian zones, with more oxygen and less aquatic macrophytes with floating leaves, as seen in morphophysiological tests (Dias-Filho and Carvalho 2000).

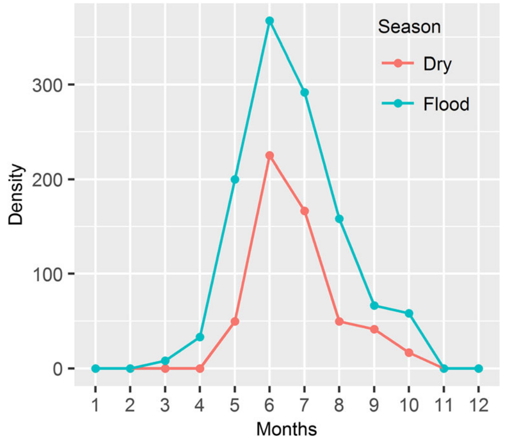

Fig. 4 Total density of germinated *Urochloa humidicola* seeds in the greenhouse over 12 months from soil seed bank collected in the flood and dry seasons in grassland in the Pantanal wetland

Our finding indicates that *U. humidicola* can be biologically controlled during floods. Because macrophytes were planted in separate containers, the pressure of competition in this case was mainly associated with competition for light rather than nutrient resources. However, habitats prone to seasonal variation present changes in the plant community every year (Middleton 2003), thereby the existence of gaps in their adaptation to environmental change can be the key to the restoration and conservation of native flora.

Evaluation of the Seed Bank

Native and exotic species in a flooded field may exhibit different germination patterns over time because of different responses to water availability, relative to the seasonal event. In our study, the seed bank of the exotic *U. humidicola* was present in both seasonal periods, and in every year, suggesting that it forms a seed bank that can colonize following seasonal events. In addition, higher germination post-flood supports our hypothesis that the grass can germinate after the seasonal flooding, when conditions for seedling establishment become favorable.

Exotic species such as of the genus *Urochloa* have various pre-germination requirements to overcome dormancy and become permeable (Marcos Filho et al. 1987). In plant communities of wet zones, the specific requirements for breaking dormancy and for germination in some cases are favored by the environment (Capon 2007). The highest germination in the post-flood period can be due to softening of the tegument (in *Urochloa*, palea and lemma), which can break dormancy (Kozlowski 1997). Seed survival of flooding reveals the adaptative success of this exotic species in the floodable grasslands of the Pantanal. Several studies with grasses in the Pantanal show that the greatest germination is linked to the end of the flood period, such as in: *Digitaria fuscescens*, *D. horizontalis*, *Paspalum almum*, *P. plicatulum*, *Pennisetum glaucum* and *Reimarochloa acuta* (Bao et al. 2014, in the Abobral sub-region); *D. ciliaris*, *D. cuyabensis*, *Hemarthria altissima* and *Leersia hexandra* (Souza et al. 2016, in the Miranda sub-region); *Steinchisma laxum* and *Setaria parviflora* (Oliveira et al. 2015, in the Barão do Melgaço sub-region).

Germination of *U. humidicola* seeds also occurred in the post-dry period, revealing an accumulation of seeds in the soil throughout the year. Despite the formation of a seed bank during drought, seedling density was lower, but the success of colonization of *U. humidicola* in the dry period is attributed to its vegetative spread (Soares Filho, 1994). Increase of cover (ca. 46.3%) by regrowth in the dry period had already been observed (Bao et al. 2015). The high propagation potential of exotic grasses, such as *U. humidicola*, is due to its nature as strongly stoloniferous (Valle et al. 2015).

The germination of *U. humidicola* in both periods (dry and flooded) in a greenhouse indicates that this species demonstrates the power to form a seed bank capable of germinating throughout the year. When the seeds were placed under controlled conditions in greenhouse, the seeds of both periods had the highest germination between 5th, 6th and 7th months. In the field, it has been reported that there is no germination of new seedlings during flooding (Bao et al. 2015). This fact may be the key to controlling exotic species with invasive characteristics, regardless of their ability to propagate and regrow after the disturbance (Kelly and Parker 1990). In this way, we can predict that long periods of flooding in the Pantanal can act in a positive way, avoiding the germination of exotic species and favoring the native species adapted to these flood conditions.

The study of the *U. humidicola* seed bank was the first step in predicting how the native plant community will respond in natural regeneration processes during and after seasonal flooding and drought, and with this data we can predict the average *U. humidicola* seed stock in soil and the ideal period of control of the seed bank. Our hypotheses were supported, with evidence that flooding may act as a stimulus for *U. humidicola* seed germination and that germination may occur at high density over the months under suitable conditions.

This experimental study may contribute to the understanding of some points of interest that were previously not perceptible in the field. This experiment associated with field studies complements and contributes to plans for restoration and conservation of native flora. Thus, our experimental results provide an estimate of the seed density of the exotic grass present in the soil and reinforce evidence that, after extreme seasonal events, alongside its potential for repopulation, the species has a seed bank capable of germinating and colonizing these grasslands. In addition, our data reveal the flood tolerance of the species and give us information that the existence of exotic species may be limited by the timely shading of aquatic macrophytes during floods. Thus, it is possible to analyze whether a seed addition of native species during and after flooding would be sufficient to control the propagation of *U. humidicola* in the grassland.

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References

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

Andrew SM, Totland O, Moe SR (2015) Spatial variation in plant species richness and diversity along human disturbance and environmental gradients in a tropical wetland. Wetlands Ecology and Management 23:395–404. https://doi.org/10.1007/s11273-014-9390-2

Bao F, Pott A, Ferreira FA, Arruda R (2014) Soil seed bank of floodable native and cultivated grassland in the Pantanal wetland: effects of flood gradient, season and species invasion. Brazilian Journal of Botany 37:239–250. https://doi.org/10.1007/s40415-014-0076-z

Bao F, Assis MA, Arruda R, Pott A (2015) Effects of *Urochloa humidicola* on plant diversity in native grasslands in a Neotropical wetland. Wetlands 35:841–850. https://doi.org/10.1007/s13157-015-0673-z

Bao F, Elsey-Quirk T, Assis MA, Pott A (2017) Seed bank of seasonally flooded grassland: experimental simulation of flood and post-flood. Aquatic Ecology 50:1–13. https://doi.org/10.1007/s10452-017-9647-y

Baruch Z (1994) Responses to drought and flooding in tropical forage grasses. Plant and Soil 164:87–96. https://doi.org/10.1007/BF00010114

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48. https://doi.org/10.18637/jss.v067.i01

Blake RE, Duffy JE (2012) Changes in biodiversity and environmental stressors influence community structure of an experimental eelgrass Zostera marina system. Marine Ecology Progress Series 470:41–54. https://doi.org/10.3354/meps10006

Brock MA (2011) Persistence of seed banks in Australian temporary wetlands. Freshwater Biolology 56:1312–1327. https://doi.org/10.1111/j.1365-2427.2010.02570.x

Capon SJ (2007) Effects of flooding on seedling emergence from the soil seed bank of a large desert floodplain. Wetlands 27:904–914. https://doi.org/10.1672/0277-5212(2007)27%5B904:EOFOSE%5D2.0.CO;2

Capon SJ, Brock MA (2006) Flooding, soil seed bank dynamics and vegetation resilience of a hydrologically variable desert floodplain. Freshwater Biolology 51:206–223. https://doi.org/10.1111/j.1365-2427.2005.01484.x

Clarke PJ, Lawes MJ, Midgley JJ, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJ (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Physiologist 197:19–35. https://doi.org/10.1111/nph.12001

Deane DC, Fordham DA, He F, Bradshaw CJA (2016) Diversity patterns of seasonal wetland plant communities mainly driven by rare terrestrial species. Biodiversity and Conservation 25:1569–1585. https://doi.org/10.1007/s10531-016-1139-1

Dias-Filho MB, Carvalho CJR (2000) Physiological and morphological responses of Brachiaria spp. to flooding. Pesquisa Agropecuária Brasileira 35:1959–1966

Dunn PK, Smyth GK (2005) Series evaluation of Tweedie exponential dispersion model densities. Statistics and Computing 15:267–280. https://doi.org/10.1007/s11222-005-4070-y

Fidelis A, Appezzato-da-Glória B, Pillar VD, Pfadenhauer J (2014) Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands. Flora 209:110–116

Galatowitsch SM, Larson DL, Larson JL (2016) Factors affecting post-control reinvasion by seed of an invasive species, *Phragmites australis*, in the Central Platte River, Nebraska. Biological Invasions 18:2505–2516. https://doi.org/10.1007/s10530-015-1048-3

Gallardo B, Clavero M, Sánchez MI, Vilà M (2015) Global ecological impacts of invasive species in aquatic ecosystems. Global Change Biology 22:151–163. https://doi.org/10.1111/gcb.13004

Giner G, Smyth GK (2016) Statmod: probability calculations for the inverse Gaussian distribution. R Journal 8:339–351

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

Harrington DP, Fleming TR (1982) A class of rank test procedures for censored survival data. Biometrika 69:553–566

Hejda M, Pysek P (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biological Conservation 132:143–152. dx.doi.org. https://doi.org/10.1016/j.biocon.2006.03.025

Hejda M, Pysek P, Jarosik V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology 97:393–403. https://doi.org/10.1111/j.1365-2745.2009.01480.x

Hejda M, Chytrý M, Pergl J, Pysek P (2015) Native-range habitats of invasive plants: are they similar to invaded-range habitats and do they differ according to the geographical direction of invasion? Diversity and Distributions 21:312–321. https://doi.org/10.1111/ddi.12269

Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. Journal American Statistic Association 53:457–481. https://doi.org/10.2307/2281868

Kelly VR, Parker VT (1990) Seed bank survival and dynamics in sprouting and nonsprouting *Arctostaphylos* species. The American Midland Naturalist 40:114–123. https://doi.org/10.2307/2426084

Kozlowski TT (1997) Responses of woody plants to flooding and salinity. Tree Physiology Monography 1:1–29. https://doi.org/10.1093/treephys/17.7.490

Lenth RV (2016) Least-squares means: the R package lsmeans. Journal of Statistical Software 69:1–33. https://doi.org/10.18637/jss.v069.i01

Lopes A, Parolin P, Piedade MTF (2016) Morphological and physiological traits of aquatic macrophytes respond to water chemistry in the Amazon Basin: an example of the genus *Montrichardia* Crueg (Araceae). Hydrobiologia 766:1–15. https://doi.org/10.1007/s10750-015-2431-x

Marcos Filho J, Cícero SM, Silva WR (1987) Avaliação da qualidade das sementes. Piracicaba: FEALQ. 230 p

Mattos JLS, Gomide JÁ, Huaman CAM (2005) Crescimento de espécies do gênero Brachiaria sob alagamento em casa de vegetação. Revista Brasileira de Zoologia 34:10–16. https://doi.org/10.1590/S1516-35982005000300007

Middleton BA (2003) Soil seed banks and the potential restoration of forested wetland after farming. Journal of Applied Ecology 40:1025–1034. https://doi.org/10.1111/j.1365-2664.2003.00866.x

Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. The American Naturalist 162:442–460. https://doi.org/10.1086/378212

Oliveira PC, Torezan JM, Nunes da Cunha C (2015) Effects of flooding on the spatial distribuition of soil seed and spore banks of native grasslands of the Pantanal wetland. Acta Botânica Brasílica 29:400–407. https://doi.org/10.1590/0102-33062015abb0027

Pieterse AH, Murphy KJ (1990) Aquatic weeds. The ecology and management of nuisance aquatic vegetation. Oxford Science Publications, Oxford

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

Pott A, Silva JSV (2015) Terrestrial and aquatic vegetation diversity of the Pantanal wetland. In: Bergier I, Assine ML (eds) Dynamics of the Pantanal wetland in South America. The Handbook of Environmental Chemistry, vol 37, pp 111–131. https://doi.org/10.1007/6982015352

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. Accessed 5 Oct 2016

Rodríguez M, Brisson J (2015) Pollutant removal efficiency of native versus exotic common reed (*Phragmites australis*) in North American treatment wetlands. Ecological Engineering 74:364–370. https://doi.org/10.1016/j.ecoleng.2014.11.005

Rojas IM, Zedles JB (2015) An invasive exotic grass reduced sedge meadow species richness by half. Wetlands Ecology and Management 23:649–663

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

Smyth G, Jørgensen B (2002) Fitting Tweedie's compound poisson model to insurance claims data: dispersion modelling. ASTIN Bulletin 32:143–157

Soares Filho C.V. Recomendações de Espécies e Variedades de Brachiaria para diferentes condições, 1994. In: Anais XI Simpósio Sobre Manejo de Pastagem. Piracicaba - SP: FEALQ, pp 25–48

Souza EB, Ferreira FA, Pott A (2016) Effects of flooding and its temporal variation on seedling recruitment from the soil seed bank of a

Neotropical floodplain. Acta Botânica Brasílica 31:64–75. https://doi.org/10.1590/0102-33062016abb0202

Therneau T (2015) A Package for Survival Analysis in S. version 2.38 https://CRAN.R-project.org/package=survival. Accessed 5 Oct 2016

Thompson K, Bakker JP, Bekker RM (1997) The soil seed banks of North West Europe: methodology, density and longevity. University Press, Cambridge, p 288p

Urban RA, Titus JE, Zhu WX (2006) An invasive macrophyte alters sediment chemistry due to suppression of a native isoetid. Oecologia 148: 455–463. https://doi.org/10.1007/s00442-006-0393-4

Valle CB, Jank L, Resende RMS (2015) O melhoramento de forrageiras tropicais no Brasil. Ceres 56:1–4

Venable DL (1989) Modeling the evolutionary ecology of seed banks. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press, London, pp 67–88

Wang W, Wang C, Sardans J, Tong C, Jia R, Zeng C, Penuelas J (2015) Flood regime affects soil stoichiometry and the distribution of the invasive plants in subtropical estuarine wetlands in China. Catena 128:144–154. https://doi.org/10.1016/j.catena.2015.01.017

Yarwood SA, Baldwin AH, Gonzalez MM, Buyer JS (2016) Archaeal rhizosphere communities differ between the native and invasive lineages of the wetland plant *Phragmites australis* (common reed) in a Chesapeake Bay subestuary. Biological Invasions 18:2717–2728. https://doi.org/10.1007/s10530-016-1144-z