



# Effects of *Urochloa humidicola* on Plant Diversity in Native Grasslands in a Neotropical Wetland

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**Abstract** Studies on species invasion in wetlands are fundamental to understanding the consequences of the introduction of exotic plants, which are often utilized in grasslands. The loss of native plant diversity is of increasing concern. We evaluated the effect of *Urochloa humidicola* on floristic similarity between native and cultivated grasslands and the differences in spatial distributions between species. To analyze the effect of seasonality, we collected samples at the end of flood and dry periods. In native grasslands and another area cultivated with *U. humidicola*, samples were collected at three elevations (bottom; intermediate; and top). We identified 90 species and observed a high similarity between the cultivated and native grassland during the flood period; both grasslands exhibited significant differences during the drought period. This difference was due to an increased presence of grasses, mainly *U. humidicola*, in the cultivated grassland. Increased similarity between bottom and intermediate elevations was

due to an increased proportion of aquatic macrophytes. In contrast, the top elevation differed due to the contribution of terrestrial species. We conclude that the native and cultivated grasslands exhibit differences in vegetation composition and are primarily structured by seasonal flooding, and small variations in elevation promote zonation within the plant community.

**Keywords** Exotic species · Flood · Floristic similarity · Plant invasion · Vegetation dynamics

## Introduction

The Pantanal wetland is a region strongly ruled by hydrology. The seasonal flood is the major ecological phenomenon in this region; therefore, this land is categorized as a seasonal wetland subject to flood pulses (Junk et al. 1989). Extended flood duration is an adverse condition that cannot be overcome by many terrestrial vascular plants (Scarano 1998). Variation in elevation produces permanent and/or periodically flooded zones (Arieira and Nunes da Cunha 2006), that influence the presence and abundance of species, which are distributed along flood gradients and vary according to their tolerance to flooding and drought (Nunes da Cunha and Junk 2001).

Natural grasslands comprise the largest part of the Pantanal flood plain, which is typically utilized for cattle ranching. Several herbaceous plant communities and numerous forage species coexist (Allem and Valls 1987). The low productivity of native grasslands has caused an increase in cultivated grasses, mainly *Urochloa humidicola* (Rendle) Morrone & Zuloaga (Pott and Pott 2004). *Urochloa humidicola* is flood tolerant because of its numerous adventitious roots that become evident during periods of excessive flooding (Mattos et al. 2005).

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The introduction of these species is a threat to local biodiversity and can lead to the exclusion of native species (Clavero and García-Berthou 2005). Considering the important role of macrophytes in the conservation of wetland biodiversity and ecosystems, the introduction of *Urochloa* species is of concern given their rapid spread in the Neotropics (Michelan et al. 2010).

Temporary flooding in tropical grasslands is common due to excessive water from rainy periods or poor drainage (Dias-Filho 2002). Plants survive water stress via tolerance mechanisms that induce metabolic and morphological adaptations (Crawford 1993). In general, the damage to plants varies according to the frequency, duration and depth of the flood (Anderson 1974). Floods in the Pantanal are recurrent due to seasonal rains and/or river overflow; however, native species exhibit similar responses to water stress due to recurrent flooding as well as flooding from unpredictable events (Arieira and Nunes da Cunha 2006).

The process of flooding reflects in local plant diversity and, in this case, plant metacommunities can become more susceptible to invasion by exotic species (Sharma and Panu 2014). The combination of environmental factors with some kind of disturbance are patterns which determine richness of native and exotic species in a time-space scale (Mack et al. 2000; Shea and Chesson 2002). Therefore, flooding and dispersal and the seed bank of exotic species can affect the distribution of native plants in large scales (Fenner and Thompson 2005; Lilley and Vellend 2009), whereas initial competition and habitat preference influence small-scale distribution (Davies et al. 2005). Deleterious effects of competition on native plants are enhanced after disturbance, which may potentially lead to changes in ecosystem function (Mack et al. 2000; Pimentel et al. 2000).

The introduction of an alien aggressive flood-tolerant plant species into wetlands is of great concern because it may become invasive and so interfere with native communities (Zedler and Kercher 2004). Given that flooding has an important role in the Pantanal, and that extensive areas of grassland are being invaded by species of *Urochloa*, it is fundamentally important to understand the impact of invasive grasses in this wetland and how they can affect the native plant community. Therefore, the objective of our study was to evaluate the influence of grasslands cultivated with *U. humidicola* compared to native grasslands after the flood and drought periods in the Pantanal, and to determine the influence of topography on the spatial distribution of species.

We tested the following hypotheses: 1. The introduction of *U. humidicola* is limited by flooding and the increased colonization of adapted native species. 2. The characteristic seasonal variation of the Pantanal results in increased homogeneity in modified grassland during the rainy period. 3. Plant cover trends can be observed at topographic levels,

demonstrating that flood depth can limit the establishment of certain species according to the ground level.

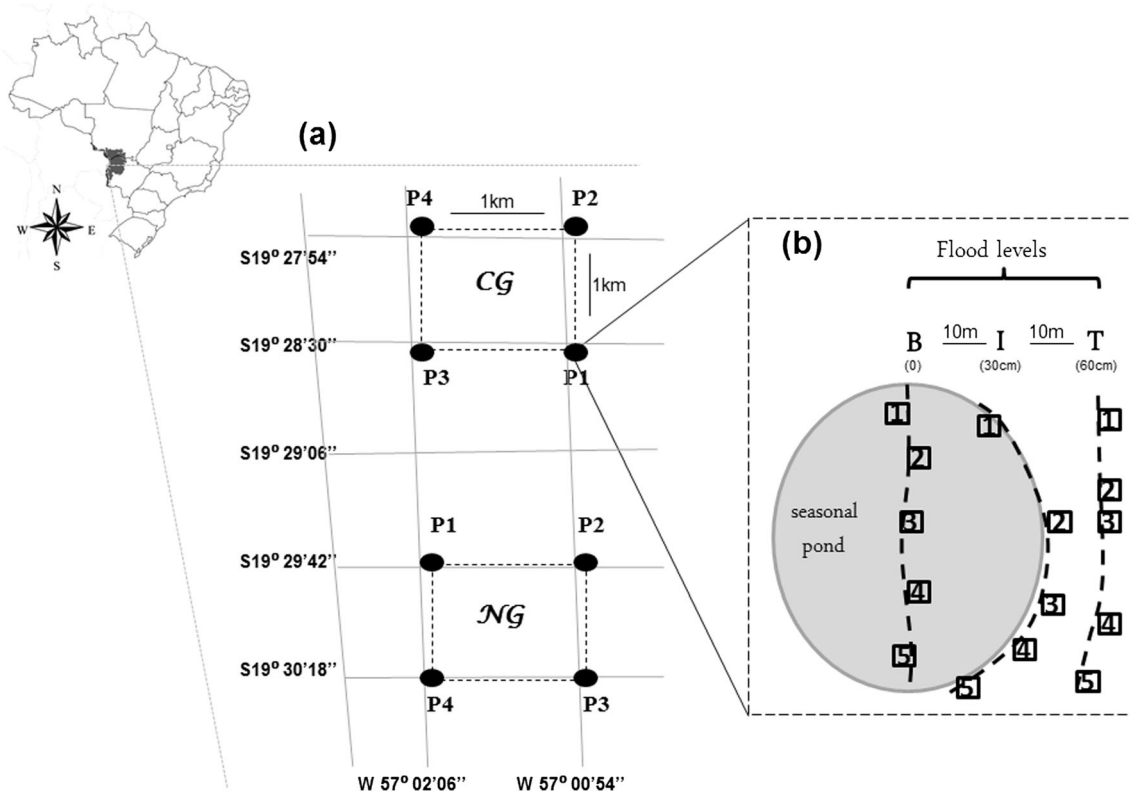
## Material and Methods

The Brazilian Pantanal wetland exhibits a sub-humid tropical climate with a mean annual temperature of 26 °C and a mean annual rainfall of 1100 mm (Allem and Valls 1987). The study area is located in the sub-region of the Abobral in the Pantanal wetland in Mato Grosso do Sul, Brazil. This area is characterized by the presence of grassland areas that undergo a period of flooding (Silva and Abdon 1998). Although the entire plain is flooded, various places are flooded for longer periods than others; these differences in flooding time vary according to elevation. These native grasslands are traditionally utilized as pastures and were partially replaced by cultivated grassland using the exotic *Urochloa humidicola* (Rendle) Morrone & Zuloaga (Poaceae). This species was first introduced 15 years ago.

To analyze the effect of the seasonal flood pulse on the plant species cover in native grassland and cultivated *U. humidicola* areas, we collected samples at the end of a flooding period (late June 2011) and at the end of a drought period (early October 2011). To analyze the influence of exotic *U. humidicola* on the structure of native vegetation under grazing pressure, samples were collected from two grassland areas, 1 Km<sup>2</sup> each, that were utilized for grazing. These grasslands were classified as native grassland and cultivated grassland with *U. humidicola* which are hereafter referred to as NG and CG, respectively. For each grassland area, we chose four seasonally flooded areas (P1, P2, P3 and P4) that were 1 Km apart (Fig. 1a). To evaluate how small differences in elevation affect the distribution of species, we collected samples in each area at the following three ground levels: B, bottom (longer flood duration); I, intermediate; and T, top (shorter flood duration) (Fig. 1b). The group levels were separated by approximately 30 cm vertically and approximately 10 m horizontally.

In the field, during both flooding and dry periods, the plant cover was estimated in a delineated area of 0.50×0.50 m. At each flood level, we sampled 5 replicates distributed according to a table of random numbers from 0 to 50 m (Fig. 1b; cf. Goodman et al. 2011). Each quadrat was subdivided into 4 equal quadrants, and data were obtained by visual estimate by the same individual observer.

Specimens from all species were collected and subsequently incorporated in the Herbarium CGMS at the Universidade Federal de Mato Grosso do Sul. The species were identified using specialized literature (e.g., Pott and Pott 1994, 2000). Individuals were named according to the plant list of Pantanal (Pott and Pott 1999) and Flora of Brazil (Forzza et al. 2010), following the APG III – Angiosperm Phylogeny Group (2009).



**Fig. 1** Location of the study area at São Bento ranch in the Abobral sub-region of Pantanal in Mato Grosso do Sul, Brazil; **a** Representative plots in cultivated grassland (CG) and native grassland (NG) with sampling

points (P1, P2, P3 and P4); **b** Flood levels (B, bottom; I, intermediate; and T, top) in the eight sampled points

The floristic similarities between the two types of grassland (NG and CG) and the two seasons, as well as among the three flood levels were compared. The plant community data were then ordinated by non-metric multidimensional scaling (NMDS) utilizing the Bray-Curtis distance. To determine the number of NMDS solutions utilized as a dependent variable, a linear regression of the original values of the matrix of similarity was performed with the values obtained from the ordination in one, two or three solutions. The best solution was that with the highest  $r^2$  value and the lowest stress value. We performed 4 ordinations (2 for NG and 2 for CG). A simple linear regression was created to test the effects of axes 1 and 2. The species with the highest contributions in similarity were determined using the similarity percentage (SIMPER).

## Results

### Floristic Composition

The vegetation was composed of 90 species from 29 families. The CG contained 63 species; 71 species were found in the NG. Only one species was a Pteridophyte fern ally (Isoetaceae). All other species were angiosperms. Families with the greatest species representation included the Poaceae

(23 species) followed by the Cyperaceae (9); the Euphorbiaceae and Plantaginaceae families (6 each); the Rubiaceae (5); the Fabaceae, Malvaceae and Onagraceae families (4); and the Alismataceae and Asteraceae families (3). Four other families were represented by 2 species, and 16 families were represented by only one species (Table 1). Approximately 75 % of the species identified were perennial, and 25 % were annual.

The most frequently observed species included the emergent *Richardia grandiflora*, *Diodia kuntzei* and *Hyptis brevipes*. During the flood period, a greater occurrence of the Cyperaceae family was observed. In terms of frequency, *Helanthium tenellum*, *Echinodorus grandiflorus*, and the aquatic plants *Eleocharis minima* and *E. acutangula* were most common. During the dry period, grass species were more common. The greatest number of species was observed in the genus *Paspalum*. Increased coverage of *Setaria parviflora*, *Digitaria fuscescens*, *Reimarochloa brasiliensis* and *Urochloa humidicola* was also observed.

### Relation Between Cultivated and Native Grasslands

At the end of the flooding season, there was higher similarity between grasslands. CG achieved 22.3 % similarity among species. During the same time period, NG exhibited 20.5 %

**Table 1** Species present in native and cultivated grasslands based on flood gradients (B, bottom; I, intermediate; T, top) under seasonal variation (flooding and drought seasons) in the Abobral sub-region of the Pantanal wetland in Mato Grosso do Sul, Brazil

FAMILY/SPECIES	Life Cycle	Flooding						Drought					
		Native			Cultivated			Native			Cultivated		
		B	I	T	B	I	T	B	I	T	B	I	T
<b>ACANTHACEAE</b>													
<i>Justicia laevilinguis</i> (Nees) Lindau	perennial									X			
<b>ALISMATACEAE</b>													
<i>Helanthium tenellum</i> (Martins) Britton	perennial	X	X	X	X		X						
<i>Echinodorus glaucus</i> Rataj	perennial		X										
<i>E. grandiflorus</i> (Cham. & Schldl.) Micheli	perennial	X	X	X	X	X	X	X	X		X	X	
<b>AMARANTHACEAE</b>													
<i>Pfaffia glomerata</i> (Spreng.) Pedersen	perennial										X		
<b>APIACEAE</b>													
<i>Eryngium ciliatum</i> Cham. & Schldl.	perennial			X					X				
<b>APOCYNACEAE</b>													
<i>Metastelma berterianum</i> (Spreng.) Decne.	annual							X	X				
<b>ASTERACEAE</b>													
<i>Praxelis clematidea</i> R.M. King & H. Rob.	annual								X	X		X	
<i>Sphagnetocola brachycarpa</i> (Baker) Pruski	perennial		X			X	X	X	X	X	X	X	
<i>Stilpnopappus pantanalensis</i> H. Rob.	perennial							X		X		X	
<b>COMMELINACEAE</b>													
<i>Commelina erecta</i> L.	perennial		X	X									
<b>CONVOLVULACEAE</b>													
<i>Aniseia martinicensis</i> (Jacq.) Choisy	perennial										X	X	
<i>Ipomoea subrevoluta</i> Choisy	perennial										X	X	
<b>CYPERACEAE</b>													
<i>Cyperus cornelii-ostenii</i> Kük.	perennial			X			X						
<i>C. haspan</i> L.	Perennial	X	X		X	X	X						
<i>C. surinamensi</i> Rottb.	perennial		X	X			X		X	X	X	X	
<i>Eleocharis acutangula</i> (Roxb.) Schult.	perennial	X	X		X	X	X	X	X		X	X	
<i>E. filiculmis</i> Kunth	perennial											X	
<i>E. minima</i> Kunth	perennial	X	X	X	X	X	X				X		
<i>Killingia brevifolia</i> Rottb.	perennial		X	X			X	X	X	X			
<i>Lipocarpha micrantha</i> (Vahl) G.C. Tucker	perennial			X									
<i>Schoenoplectiella supina</i> (L.) Lye	perennial			X									
<b>EUPHORBIACEAE</b>													
<i>Caperonia castaneifolia</i> (L.) A. St.-Hil.	perennial								X	X	X	X	
<i>C. palustris</i> (L.) A. St.-Hil.	annual	X											
<i>Croton glandulosus</i> L.	annual										X	X	
<i>C. trinitatis</i> Millsp.	annual	X		X			X	X	X	X	X	X	
<i>Euphorbia thymifolia</i> L.	annual						X	X	X	X	X	X	
<i>Microstachys hispida</i> (Mart.) Govaerts	perennial			X	X		X			X	X	X	
<b>HELIOTROPIACEAE</b>													
<i>Euploca filiformis</i> (Lehm.) J.I.M. Melo & Semir	annual							X	X				
<b>HYDROLEACEAE</b>													
<i>Hydrolea spinosa</i> L.	perennial				X						X	X	
<b>ISOETACEAE</b>													
<i>Isoetes pedersenii</i> H.P. Fuchs ex Hickey	perennial			X			X						
<b>LAMIACEAE</b>													
<i>Hyptis brevipes</i> Poit.	annual	X	X	X		X	X	X	X	X		X	
<i>H. lorentziana</i> O. Hoffm.	annual	X	X		X			X			X		
<b>LEGUMINOSAE</b>													
<i>Chamaecrista serpens</i> (L.) Greene	perennial										X	X	
<i>Discolobium pulchellum</i> Benth.	perennial							X					
<i>Mimosa pigra</i> L.	perennial								X				

**Table 1** (continued)

FAMILY/SPECIES	Life Cycle	Flooding						Drought						
		Native			Cultivated			Native			Cultivated			
		B	I	T	B	I	T	B	I	T	B	I	T	
<i>Senna aculeata</i> (Pohl ex Benth.) H.S. Irwin & Barneby	perennial											X		
LYTHRACEAE														
<i>Cuphea retrorsicapilla</i> Koehne	perennial		X	X								X		
<i>Rotala ramosior</i> (L.) Koehne	annual	X	X	X		X	X							
MALVACEAE														
<i>Melochia arenosa</i> Benth.	perennial	X							X			X		X
<i>M. simplex</i> A. St.-Hil.	perennial		X		X	X	X	X	X	X	X	X	X	X
<i>M. villosa</i> (Mill.) Fawc. & Rendle	perennial												X	X
<i>Sida rhombifolia</i> L.	perennial											X	X	X
NYMPHAEACEAE														
<i>Nymphaea gardneriana</i> Planch.	perennial				X									
ONAGRACEAE														
<i>Ludwigia grandiflora</i> (Michx.) Greuter & Burdet	perennial				X	X						X	X	
<i>L. nervosa</i> (Poir.) H. Hara	perennial											X		
<i>L. octovalvis</i> (Jacq.) P.H. Raven	annual	X	X	X	X	X	X							
<i>L. peploides</i> (Kunth) P.H. Raven	perennial	X	X											
OROBANACEAE														
<i>Agalinis glandulosa</i> (G.M.Barroso) V.C. Souza	annual								X	X				X
PHYLLANTHACEAE														
<i>Phyllanthus stipulatus</i> (Raf.) G.L. Webster	annual			X					X	X				
PLANTAGINACEAE														
<i>Angelonia salicariifolia</i> Bonpl.	perennial			X			X	X	X	X				X
<i>Bacopa australis</i> V.C. Souza	perennial		X	X		X	X							
<i>B. myriophylloides</i> Wettst.	perennial				X									
<i>B. salzmannii</i> (Benth.) Wettst. ex Edwall	perennial			X										
<i>B. stricta</i> (Schrad.) Edwall	annual		X								X			
<i>Scoparia montevidensis</i> (Spreng.) R.E. Fr.	annual								X	X				X
POACEAE														
<i>Andropogon hypogynus</i> Hack.	perennial										X			
<i>Axonopus leptostachyus</i> (Flüggé) Hitchc.	perennial			X			X		X					
<i>A. purpusii</i> (Mez) Chase	perennial			X		X			X	X		X	X	X
<i>Cynodon dactylon</i> (L.) Pers.	perennial			X				X				X	X	
<i>Digitaria bicornis</i> (Lam.) Roem. & Schult.	annual													X
<i>D. fuscescens</i> (J. Presl) Henrard	perennial							X	X	X	X			
<i>D. horizontalis</i> Willd.	perennial									X				
<i>Echinochloa polystachya</i> (Kunth) Hitchc.	perennial							X	X		X			
<i>Eragrostis articulata</i> (Schrank) Nees	annual									X				
<i>Eragrostis bahiensis</i> Schrad. ex Schult.	annual									X				
<i>Hemarthria altissima</i> (Poir.) Stapf & C.E. Hubb.	perennial							X	X		X			
<i>Leersia hexandra</i> G.C. Tucker	perennial		X		X			X	X		X			
<i>Panicum repens</i> L.	perennial													
<i>Paspalum almum</i> Chase	perennial							X			X	X	X	X
<i>P. notatum</i> Alain ex Flüggé	perennial			X		X	X							
<i>P. oteroi</i> Swallen	perennial									X				X
<i>P. plicatum</i> Michx.	perennial	X						X	X	X				X
<i>Pennisetum glaucum</i> (L.) R. Br.	perennial													X
<i>Reimarochloa acuta</i> (Flüggé) Hitchc.	perennial			X				X	X	X	X			
<i>R. brasiliensis</i> (Spreng.) Hitchc.	perennial	X	X	X	X	X		X	X	X	X	X	X	
<i>Setaria parviflora</i> (Poir.) Kerguélen	annual							X	X	X	X	X	X	X
<i>Steinchisma laxum</i> (Sw.) Zuloaga	perennial				X	X	X				X	X	X	X
<i>Urochloa humidicola</i> (Rendle) Morrone & Zuloaga	perennial				X	X	X				X	X	X	X

**Table 1** (continued)

FAMILY/SPECIES	Life Cycle	Flooding						Drought					
		Native			Cultivated			Native			Cultivated		
		B	I	T	B	I	T	B	I	T	B	I	T
POLYGALACEAE													
<i>Polygala timoutoides</i> Chodat	annual								X	X			X
POLYGOLACEAE													
<i>Polygonum punctatum</i> Elliott	perennial		X	X									
PONTEDERIACEAE													
<i>Pontederia parviflora</i> Alexander	perennial	X	X										
<i>P. subovata</i> (Seub.) Lowden	perennial				X	X	X						
PORTULACACEAE													
<i>Portulaca pilosa</i> L.	annual								X				
RUBIACEAE													
<i>Borreria eryngioides</i> Cham. & Schltld.	annual					X						X	X
<i>Diodia kuntzei</i> K. Schum.	perennial	X	X	X	X	X	X	X	X	X	X	X	X
<i>D. radula</i> (Willd. ex Roem. & Schult.) Cham. & Schltld.	perennial							X					
<i>Richardia grandiflora</i> (Cham. & Schltld.) Steud.	annual	X	X	X	X	X	X	X	X	X	X	X	X
<i>Staelia thymoides</i> Cham. & Schltld.	perennial	X	X	X	X		X			X			X
VERBENACEAE													
<i>Lippia alba</i> (Mill.) N.E. Br. ex Britton & P. Wilson	perennial			X					X	X			

species similarity (Fig. 2a). The similarity between both grasslands was maintained by the aquatic macrophytes *Eleocharis acutangula*, *E. minima*, *Pontederia subovata* and *Echinodorus grandiflorus*. Together, these species contributed to greater than 60 % of the similarity observed between NG and CG and were responsible for the observed low percentage (17.8 %) of *U. humidicola*. The high percentage of these species in the rainy season resulted in an increased similarity between both grasslands.

The exotic *U. humidicola*, which exhibited minimal cover during flooding, was observed in both CG and NG. These findings demonstrate that the flood in this case resulted in increased homogenization between native and cultivated species (Fig. 2b).

At the end of the dry period, the similarity among species in NG was increased (24.7 %) compared with CG (18.5 %). The reduced similarity in CG was due to the high percentage of *U. humidicola* (Fig. 2c). *U. humidicola* alone contributed to 46.3 % of the dissimilarity observed between the grasslands; a significant difference ( $r=0.44$ ,  $P<0.001$ ) between NG and CG was observed in the dry period (Fig. 2c).

An increase in *U. humidicola* coverage occurred during the dry period due to the limited growth of native species. In NG, we observed increased native species coverage. As native species coverage took over cultivated species, the heterogeneity of the grasslands increased in this period (Fig. 2d).

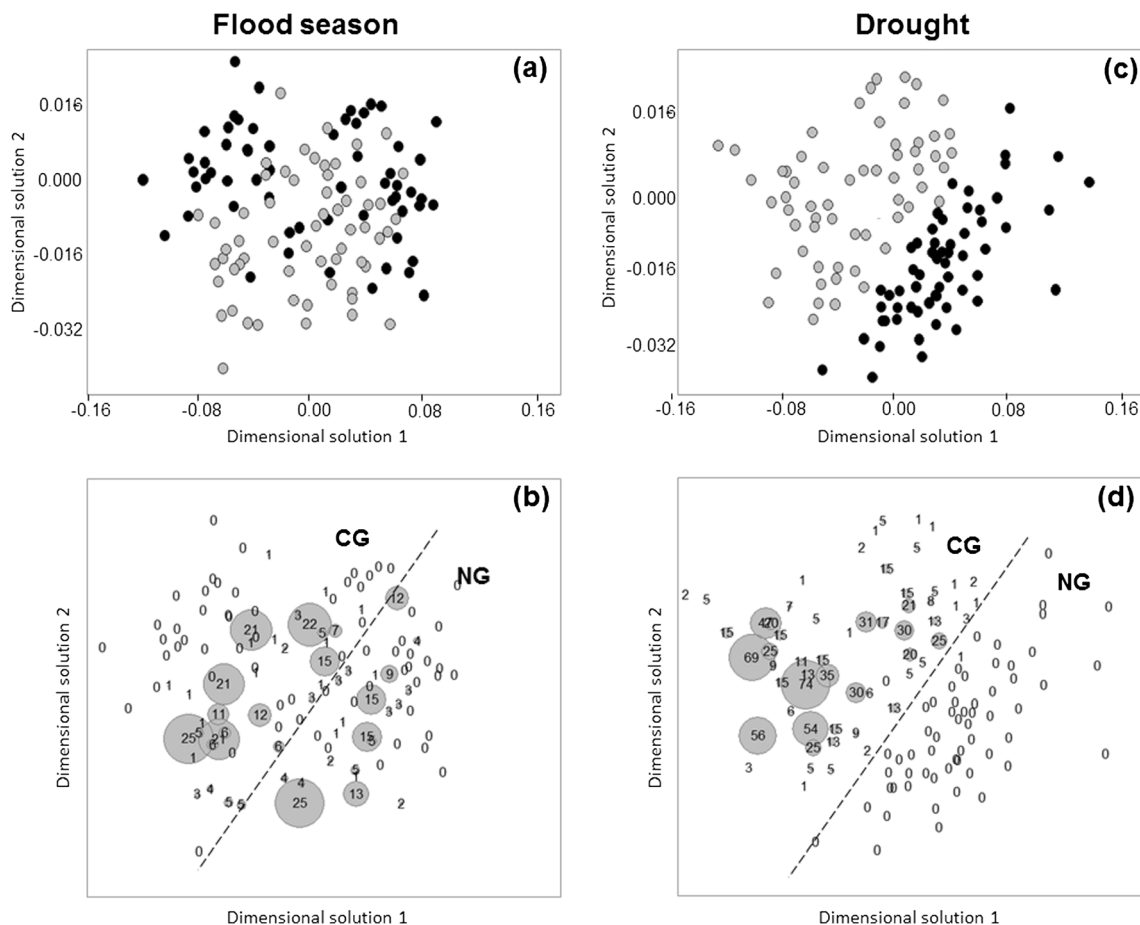
By comparing the rainy and dry periods, we observed differences in vegetation structure and composition that were independent of the grassland type. During the rainy season,

an increase in species similarity (19.6 %) was observed; more than 50 % of similarity in this period was attributed to *Eleocharis acutangula* (21.2 %), *E. minima* (21.0 %) and *Pontederia subovata* (19.7 %).

During the drought period, species similarity decreased (17.3 %). A reduction in the proportion of aquatic macrophytes provided room for terrestrial species such as *Richardia grandiflora* (27.6 %), *Reimarochloa brasiliensis* (18.7 %) and *U. humidicola* (12.3 %), which demonstrated the greatest similarity during this period. These species contributed to the difference observed between the seasons. Seasonality affects species in a manner that follows a pattern of distribution dependent on flood and drought, thereby forming two groups of distinct species (Fig. 3).

### Effect of Flood Levels on the Spatial Distribution of Species

The greatest similarity among species was observed at the I elevation (16.3 %); the lowest similarities were observed at the T (16.1 %) and B levels (14.5 %). The emergent *R. grandiflora* demonstrated the greatest contribution towards similarity (34.4 %), with increased representation at the T level; contributions to B and I were high for *P. subovata* (17.9 %) and *E. acutangula* (16.9 %), respectively. Furthermore, the stoloniferous Rubiaceae *R. grandiflora* and *Diodia kuntzei* were the only species identified at all levels in both grasslands and during both seasons.



**Fig. 2** Ordination by nonmetric multidimensional scaling (NMDS) of the similarity between species (Bray-Curtis index), as calculated from the vegetation cover of each species in relation to seasonality and the type of grassland; **a** the effect of the flood season on cultivated (●) and native grasslands (○); **b** NMDS diagram illustrating the effect of the flood

season on the distribution of *U. humidicola* in cultivated grassland (CG) and native grassland (NG); **c** the effect of the dry season on cultivated (●) and native grasslands (○); **d** the effect of the dry season on the distribution of *U. humidicola* in CG and NG

Some perennial species were exclusive to a given elevation. For example, *Hyptis lorentziana*, *Discolobium pulchellum*, *Nymphaea gardneriana* and *Ludwigia nervosa* were exclusively observed on the B level. The legume *Mimosa pigra* was exclusively observed on the I level. The sedges *Cyperus cornelii-ostenii* and *Schoenoplectiella supina* and the fern ally *Isoetes pedersenii* were exclusively identified on the T level (Table 1).

The largest difference in species community composition observed between elevation treatment levels occurred between T and B (91.7 %); the species that provided the greatest contributions to this difference included *R. grandiflora* (8.9 %), *P. subovata* (6.2 %), *R. brasiliensis* (6.2 %), *E. minima* (5.5 %) and *U. humidicola* (5.5 %). The smallest difference in species similarity occurred between relief levels B and I (85.2 %), where *R. brasiliensis* (11.4 %), *E. acutangula* (10 %), *P. subovata* (9.3 %) and *U. humidicola* (6.2 %) contributed to 50 % of the difference.

By grouping species, we found a high correlation between the B and I levels that is independent of the grassland type and

the occurrence of flooding. Given that T does not resemble the other levels, a separate group is formed (Fig. 3).

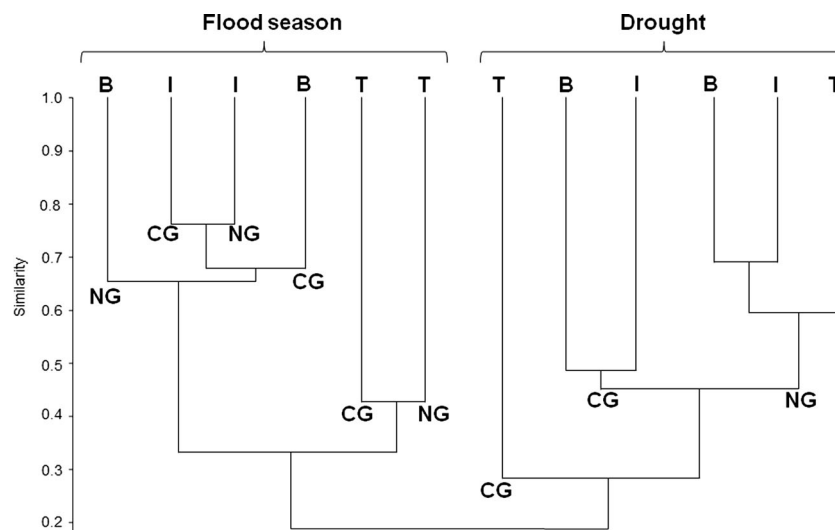
## Discussion

### Floristic Composition

Our study describes differences in the floristic diversity and the structural characteristics of the vegetation noted between CG and NG; these differences are dictated by the flood pulse. All of the species listed in this text are present on the list of Pantanal plants (Pott and Pott 1999) and plants of the Brazilian flora (Forzza et al. 2010).

The occurrence of grasses and sedges is common in seasonally flooded open habitats such as grasslands (Ladeua and Ellison 1999). The observed species composition is in agreement with previous studies elsewhere in the region (e.g., Pagotto et al. 2011). Grasses and legumes represent the greatest number of species in the Pantanal (Pott and Pott

**Fig. 3** Grouping of species based on similarity (Bray-Curtis index) in the two grasslands (cultivated grassland (CG) and native grassland (NG)) within the flood levels (B, bottom; I, intermediate; T, top). Distinct groups were formed by the seasonality effect (flood and drought seasons)



1999), e.g., *Paspalum* spp. *Axonopus purpusii*, *Reimarochla acuta* and *R. brasiliensis* (Valls 1994). Legumes are frequently present under certain types of disturbances, such as flooding and grazing (Allem and Valls 1987). Additionally, the high cover of *Richardia grandiflora*, *Cynodon dactylon* and *Hyptis brevipes* reflects excessive grazing and increased trampling and harrowing (Pott and Pott 1994). *Isoetes pedersenii* was the single Pteridophyte species sampled in this field; plants in this genus commonly appear in seasonally flooded areas (Choi et al. 2008).

### Relationships Between Cultivated and Native Grasslands

Many emergent exotic species are capable of outcompeting native vegetation due to fast growth (Cronk and Fennessy 2001). We observed homogenization and heterogenization between NG and CG that could be explained by seasonal variation. Although flooding reduces the *U. humidicola* coverage in CG compared to the dry period, this plant soon resumes its dominance due to its adventitious roots (Mattos et al. 2005) that suppress native species (Bennett et al. 2012).

Although *U. humidicola* presented in some patches during flooding in NG, it did not succeed during the dry period. Such plants must pass through filters of adaptability, meeting the necessary conditions to germinate and compete with native plants for success and colonization (Lambers et al. 1998). In this case, native species exhibit greater adaptability to seasonal variation. Furthermore, the low cover of *U. humidicola* in the NG may be an example of increased local diversity inhibiting exotic invasion (MacArthur and Wilson 1967; D'Antonio and Vitousek 1992). The seasonal flood, which forms temporary ponds and creates a difficult habitat for the adaptation of exotic species (Junk et al. 2006), is another factor that may inhibit exotic invasion in the NG.

Increased species richness was observed in NG compared with CG; this observation was likely due to the increased coverage of *U. humidicola* in CG, which may limit the germination of other species. Furthermore, *U. humidicola* is allelopathic (Souza Filho et al. 2005). A single dominant invasive species can exert competitive pressure, reducing spatial heterogeneity (McGranaham et al. 2012).

The differences observed in vegetation structure between flooding and dry periods are due to the similarity of some species. Even though the flooding period only lasted 2 weeks on the T level and 2 months on the B level, the structure and composition of the vegetation was modified. The aquatic plants that were abundant during flooding, such as *Bacopa*, *Cyperus*, *Echinodorus*, *Eleocharis*, *Ludwigia* and *Nymphaea* species, were replaced by numerous pioneer and emergent grasses during the dry period. In secondary succession, which encompasses the replacement of species after any disturbance affecting the existing vegetation, the composition and density of species determine the plant community structure (Gleason 1926).

### Effect of Flood Levels on the Spatial Distribution of Species

As expected, the different types of hydrological regimes and topographies reveal a plant community with high selectivity within flood levels. With regard to grasslands, either flood or drought periods offer harsh conditions for plant establishment. The topographic variation in areas under seasonal floods promotes a pattern of species zonation in the structure of plant communities (Cattanio et al. 2002). The response to post-flood events, such as drought, is also equally important in seasonal habitats (Bunker and Carson 2005). Due to undeveloped root systems, drought conditions can be more stressful and deadly to young plants than older plants. Given this



disparity, intolerant species can be excluded from the community (Lieberman and Li 1992).

We observed a lower number of species in the B level during the rainy period. This observation was likely due to an excess of dead matter that was deposited as the water receded. However, species richness at the B level was increased in the dry period. This occurs in areas flooded for longer periods, as such areas receive a greater number of carried seeds (Pagotto et al. 2011). Seed build-up varies according to income (through dispersal) and output (Luken 1990). Both situations vary widely year round, and succession is likely regulated by seasonal patterns of seed income (Young et al. 1987). Such patterns result in variations in abundance, species richness and vegetation composition (Pagotto et al. 2011).

The high similarity observed between the B and I levels is common in periodically flooded areas. This similarity is attributed to the emergent plants *Hyptis brevipes*, *Reimarochloa brasiliensis* and *Richardia grandiflora* and the aquatic amphibious species *Diodia kuntzei*, *Echinodorus grandiflorus*, *Eleocharis acutangula*, *E. minima*, *Ludwigia octovalvis* and *Melochia simplex* (Pott and Pott 1994, 2000). Sedges are frequently observed in grasslands after a flood period (Crispim et al. 2002). The diversity of aquatic plants associated with flood pulses favor the development of macrophytes with various life forms (Junk et al. 1989).

Differences observed in the T level were attributed to the diversity of grass species identified in the grassland. Such diversity is characteristic of a dry habitat with little or no flooding (Allem and Valls 1987; Crispim et al. 2002; Gasparino et al. 2006; Schessl 1999).

A lack of oxygen and an increase in the concentration of phytotoxic components in flooded soils hinder both root growth and the physiological functions of plants (Mendelssohn et al. 1981). These conditions select for various types of plant metabolism (Joly 1994). Consequently, we hypothesize that small variations in topography exert large effects on plant community structure under flood conditions. A striking characteristic in wetlands is the distribution of plants in well-defined zones (Spence 1982). Alterations in water levels can create conditions that reduce or eliminate the possibility of seed production, germination and establishment (Barret et al. 1993).

The seasonal effects function as a filter at different topographic levels, favoring the establishment and development of native species due to enhanced adaptation. However, *U. humidicola* relies on vegetative propagation, which is more efficient than seed germination. Because CG presents with a history of planting, this exotic grass becomes dominant. The richness of exotic species is considerably increased in all spatial scales in grasslands with an overgrazing history (Altesor et al. 2006), whereas the richness of native species is reduced. Nevertheless, flood delays the establishment of

*U. humidicola*. If the propagation mechanism of this plant eventually fails, native diversity is restored. The abundance of seeds and seedlings suggests that the seed bank plays an efficient role in the regeneration of diversity (Bao et al. 2014).

Although diversity is temporarily lost in natural grasslands that are subject to disturbance via the introduction of an exotic species and/or flooding, these areas are recolonized with a high proportion of emergent species and native grasses. These native plants regenerate quickly, mainly due to local richness and abundance. In accordance with our hypotheses, as well as the seasonal cycle, the variation between the characteristic flooding and dry periods in the Pantanal wetland acts as a determining factor to increase the similarity between native and cultivated grasslands. The variation in topography reveals a community structured within each level, which varies with flooding.

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## References

- Allem AC, Valls JFM (1987) Recursos forrageiros nativos do Pantanal Mato-grossense. Brasília, Embrapa-Cenargen. Documentos 8
- Altesor A, Pineiro G, Lezama F, Jackson RB, Sarasola M (2006) Ecosystem changes associated with grazing in subhumid South American grassland. *J Veg Sci* 17:323–332. doi:10.1111/j.1654-1103.2006.tb02452.x
- Anderson ER (1974) The reaction of seven *Cenchrus ciliaris* L. cultivars to flooding. *Trop Grasslands* 8:33–39
- Apg III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot J Linn Soc* 161:105–121. doi:10.1111/j.1095-8339.2009.00996.x
- Arieira J, Nunes da Cunha CN (2006) Fitossociologia de uma floresta inundável monodominante de *Vochysia divergens* Pohl (Vochysiaceae), no Pantanal Norte, MT, Brasil. *Acta Bot Bras* 20: 569–580. doi:10.1590/S0102-33062006000300007
- 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. *Braz J Bot* 37:239–250. doi:10.1007/s40415-014-0076-z
- Barret SCH, Eckert CG, Husband BC (1993) Evolutionary processes in aquatic plant populations. *Aquat Bot* 44:105–145
- Bennett JR, Dunwiddie PW, Giblin DE, Arcese P (2012) Native versus exotic community patterns across three scales: roles of competition, environment and incomplete invasion. *Evol Syst* 14:381–392. doi: 10.1016/j.ppees.2012.10.001
- Bunker DE, Carson WP (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. *J Ecol* 93:794–806. doi:10.1111/j.1365-2745.2005.01019.x
- Cattanio JH, Anderson AB, Carvalho MS (2002) Floristic composition and topographic variation in a tidal floodplain forest in the Amazon Estuary. *Braz J Bot* 25:419–430
- Choi HK, Jung J, KIM C (2008) Two new species of *Isoetes* (Isoetaceae) from Jeju Island, South Korea. *J Plant Biol* 51:354–358

- Clavero M, Garcí'A-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20:110. doi:10.1016/j.tree.2005.01.003
- Crawford DMM (1993) Oxygen availability as an ecological limit to plant distribution. *Adv Ecol Res* 23:93–185
- Crispim SMA, Santos AS, Chalita LVAS, Fernandes AHBM, Silva MP (2002) Variação sazonal na frequência e composição botânica em área de máxima inundação, Pantanal-MS, Brasil. *Arch Zootec* 51:149–160
- Cronk JK, Fennessy MS (2001) *Wetland Plants: Biology and Ecology*. Lewis Publishers, 384pp
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86:1602–1610. doi:10.1890/04-1196
- Dias-Filho MB (2002) Tolerance to flooding in five *Brachiaria brizantha* accessions. *Pesq Agrop Brasileira* 37:439–447. doi:10.1590/S0100-204X2002000400003
- Fenner M, Thompson K (2005) *The ecology of seeds*. Cambridge University Press, Cambridge
- Forzza RC, Leitman PM, Costa AF, Carvalho Jr. AA, Peixoto AL, Walter BMT, Bicudo C, Zappi D, Costa DP, Lleras E, Martinelli G, Lima HC, Prado J, Stehmann JR, Baumgratz JFA, Pirani JR, Sylvestre L, Maia LC, Lohmann LG, Queiroz LP, Silveira M, Coelho MN, Mamede MC, Bastos MNC, Morim MP, Barbosa MR, Menezes M, Hopkins M, Secco R, Cavalcanti TB, Souza VC (2010) Introdução In Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/2012>. Accessed 10 Jun 2014
- Gasparino D, Malavasi UC, Malavasi MM, Souza I (2006) Quantificação do banco de sementes sob diferentes usos do solo em área de domínio ciliar. *Rev Árvore* 30:1–9
- Gleason HA (1926) The individualistic concept of plant association. *Bull Torrey Bot Club* 53:7–26
- Goodman AM, Ganf GG, Maier HR, Dandy GC (2011) The effect of inundation and salinity on the germination of seed banks from wetlands in South Australia. *Aquat Bot* 94:102–106. doi:10.1016/j.aquabot.2010.11.003
- Joly CA (1994) Flooding tolerance: a reinterpretation of Crawford's metabolic theory. *Proceedings of the Royal Society of Edinburgh*, 102p
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in River-Floodplain-Systems. *Can Spec Publ Fish Aquat Sci* 106:110–127
- Junk WJ, Nunes da Cunha C, Wantzen KM, Petermann P, Strussmann C, Marques MI, Adis J (2006) Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat Sci* 68:278–309. doi:10.1007/s00027-006-0851-4
- Ladeua SL, Ellison AM (1999) Seed bank composition of a northeastern U.S. tussock. *Wetlands* 19:255–261
- Lambers H, Chapin FS III, Pons TL (1998) *Plant Physiological Ecology*, 1st edn. Springer, New York, pp 1–9pp
- Lieberman D, Li M (1992) Seedling recruitment patterns in a tropical dry forest in Ghana. *J Veg Sci* 3:375–382. doi:10.2307/3235763
- Lilley PL, Vellend M (2009) Negative native-exotic diversity relationship in oak savannas explained by human influence and climate. *Oikos* 118:1373–1382. doi:10.1111/j.1600-0706.2009.17503.x
- Luken JO (1990) Directing ecological succession. Chapman and Hall, London, 91 pp
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton, 421 pp
- Macgranahan DA, Engle DM, Wilsey BJ, Fuhlendorf SD, Miller JR, Debinski DM (2012) Grazing and an invasive grass confound spatial pattern of exotic and native grassland plant species richness. *Basic Appl Ecol* 13:654–662. doi:10.1016/j.baec.2012.09.011
- Mack RN, Simberloff D, Lonsdale WM et al (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710. doi:10.1890/1051-0761(2000)010
- Mattos JLS, Gomide JA, Huaman CAM (2005) Crescimento de espécies do gênero *Brachiaria* sob alagamento em casa de vegetação. *Rev Bras Zootec* 34:765–773
- Mendelssohn IA, Mckee KL, Patrick WH (1981) Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* 214:439–441
- Michelan TS, Thomaz SM, Mormul RP, Carvalho P (2010) Effects of an exotic invasive macrophyte (tropical signalgrass) on native plant community composition, species richness and functional diversity. *Freshw Biol* 55:1315–1326. doi:10.1111/j.1365-2427.2009.0
- Nunes da Cunha C, Junk WJ (2001) Distribution of woody plant communities along the flood gradient in the Pantanal of Poconé, Mato Grosso, Brazil. *Int J Ecol Environ Sci* 27:63–70
- Pagotto MA, Silveira RML, Nunes da Cunha C, Fantini-Cruz I (2011) Distribution of herbaceous species in the soil seed bank of a flood seasonality area, Northern Pantanal, Brazil. *Int Rev Hydrobiol* 96:149–163. doi:10.1002/iroh.201111315
- Pimentel D, Lach L, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50:53–55
- Pott A, Pott VJ (1994) *Plantas do Pantanal*. Brasília, Embrapa
- Pott A, Pott VJ (1999) Flora do Pantanal-Listagem atual de fanerógamas. In II Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal. Manejo e Conservação, Embrapa Pantanal, Corumbá, p.298–325
- Pott VJ, Pott A (2000) *Plantas aquáticas do Pantanal*. Brasília, EMBRAPA
- Pott A, Pott VJ (2004) Features and conservation of the Brazilian Pantanal wetland. *Wetl Ecol Manag* 12:547–522. doi:10.1007/s11273-005-1754-1
- Scarano FRA (1998) Comparison of dispersal, germination and establishment of woody plants subjected to distinct flooding regimes in Brazilian flood-prone forests and estuarine vegetation. In: Scarano FRA, Franco AC (eds.). *Ecophysiological strategies of xerophytic and amphibious plants in the Neotropics*. Series Oecologia Brasiliensis v. IV. Rio de Janeiro, Brasil: PPGE-UFRJ, 177–193 pp
- Schessl M (1999) Floristic composition and structure of floodplain vegetation in the Northern Pantanal of Mato Grosso, Brazil. *Phyton* 39:303–336
- Sharma T, Panu U (2014) A simplified model for predicting drought magnitudes: a case of streamflow droughts in Canadian Prairies. *Water Resour Manag* 28:1597–1611. doi:10.1007/s11269-014-0568-4
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176. doi:10.1016/S0169-5347(02)02495-3
- Silva JSV, Abdon MM (1998) Delimitação do Pantanal Brasileiro e suas sub-regiões. *Pesq Agrop Brasileira* 33:1703–1711
- Souza Filho APS, Pereira AAG, Bayma JC (2005) Aleloquímico produzido pela gramínea forrageira *Brachiaria humidicola*. *Planta Daninha* 23:25–32. doi:10.1590/S0100-83582005000100004
- Spence DH (1982) The zonation of plants in freshwater lakes. *Adv Ecol Res* 12:37–125
- Valls JFM (1994) O espectro taxonômico das gramíneas do Pantanal. In: *Utilización y manejo de pastizales*. Ed. Puignau, J.P. Uruguay, Montevideo, IICA-PROCISUR, n.40. 227–237 pp
- Young KR, Ewel JJ, Brown BJ (1987) Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71:157–173
- Zedler JB, Kercher S (2004) Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. *Crit Rev Plant Sci* 23:431–452