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ORIGINAL ARTICLE

Abiotic factors drive the structure of aquatic plant assemblages in riverine habitats of the Brazilian "Pantanal"

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Abstract The "Pantanal" wetland is one of the largest centers of diversity of aquatic macrophytes of Brazil. The objective of this work was to present a checklist of aquatic macrophytes, and to investigate structure and patterns of occurrence regarding physico-chemical parameters, at Amolar, in the Paraguay River sub-region, in the mid-western "Pantanal" wetland, Corumbá (MS). No previous aquatic plant study has been carried out there so far. The study was conducted in June 2009 in 391 plots (0.5 × 0.5 m). We recorded 65 species of aquatic macrophytes, from 49 genera and 27 families. The richest families were Fabaceae, Poaceae, Convolvulaceae, Onagraceae, and Lentibulariaceae. The most representative life forms were emergent and free floating, comprising the most frequent species: *Hymenachne amplexicaulis* (Rudge) Nees, *Salvinia auriculata* Aubl., *Ricciocarpos natans* (L.) Corda, *Lemna aequinoctialis* Welw. and *Azolla filiculoides* Lam. presented the highest relative cover, as well as the highest importance value, followed by *S. auriculata*. The structure of the community of aquatic macrophytes presents relation with physico-chemical variables, chiefly depth: many species occurred exclusively in shallow areas and others in deep zones. The life forms partially explain the species zonation of macrophytes in relation to depth.

Keywords Conductivity · Dissolved solids · pH · Phytosociology · Wetland

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Introduction

Aquatic macrophytes are plants visible to the naked eye, which at some point in their life cycle are completely or partially submerged or floating in freshwater (Cook 1996). The importance of aquatic macrophytes and their role in the dynamics of ecosystems are widely discussed in the literature, for their high primary production (Junk and Piedade 1993) and importance in nutrient cycling (Thomaz and Cunha 2010). These plants contribute to maintain animal diversity, which utilize aquatic macrophytes as feeding grounds (Gross et al. 2001; Casatti et al. 2003; Pelicice and Agostinho 2006) and shelter and refuge (Martín et al. 2005; Agostinho et al. 2007). Macrophytes also have importance for their direct contributions for human societies, providing food, biomass, and building materials (Pott and Pott 2000). By virtue of ecosystemic services and economic importance, the number of studies on aquatic macrophytes in the Neotropical zone has increased in the last decades (Padial et al. 2008). However, inventories are still scarce for many regions (Ferreira et al. 2011) and are pre-requisites for conservation policies (Pressey and Adam 1995; Ferreira et al. 2011).

Macrophytes are organisms with low mobility and cannot avoid any combination of flow, nutrient availability, and other physical and chemical characteristics that influence their survival in aquatic systems (Pereira et al. 2012). Richness and structure of aquatic macrophyte communities are affected by a series of physico-chemical characteristics of the aquatic environments, including depth, pH, conductivity, alkalinity, dissolved oxygen, and total suspended solids (Pott and Pott 2003; Bornette and Puijalon 2011; Pereira et al. 2012; Pulido et al. 2015). In counterpart, aquatic macrophytes also modify physico-chemical properties of the aquatic environments (Vermaat et al. 2000; Madsen et al. 2001; Marion and Paillisson 2002).

The "Pantanal" is the largest complex of wetlands of the world, a continuous sedimentary plain of ca. 138.000 km^2 (Silva and Abdon 1998). As a floodable region, it favors the development of many aquatic plants, being indicated as one of the four centers of diversity of aquatic macrophytes of Brazil (Pedralli 1992). Up to now, 308 species were recorded in the Brazilian "Pantanal" (Pott et al. 2012). With such characteristics and for being a relatively pristine environment, it gives opportunities to study variations in structure of macrophyte communities in relation to environmental characteristics in tropical wetlands.

In this study, we verified how the composition and phytosociological structure of assemblages of aquatic macrophytes in the sub-region of the Paraguay River, in the "Pantanal" wetland (Corumbá, MS), can vary by function of water physico-chemical parameters. Our hypothesis is that the diverse species may respond differently to changes in some physico-chemical factors, due to differences in anatomy, physiology, requirements, or strategies for obtaining resources.

Materials and methods

Study area – The study area is located near the residual hilly range of Amolar, in the Paraguay River sub-region, in the mid-western border of the "Pantanal" wetland, Corumbá, Mato Grosso do Sul (MS), between the geographic coordinates 18°00′18″S 57°30′28″W and 18°02′18″S 57°27′07″W (Fig. 1). The climate is marked by dry winter and rainy summer, with mean annual rainfall of 1070 mm and mean temperature of 25.1 °C (Soriano 1997). The flood peak is reached during the dry season, with low fluviometric levels during the rainy season, since the local high level of the Paraguay River and connected water bodies depends on delayed flow from the headwaters (Damasceno-Junior et al. 2004). The level of the Paraguay River reached 4.36 m in June 26th on the Brazilian Navy gauge at Ladário, which was considered an average flood (Soares et al. 2010).

Collection and data analysis – Data were collected during June 2009, at the peak of flood. On a small motor boat, we sampled 391 plots of 0.5 × 0.5 m, distributed along 50 transactions from the distal edge of the aquatic vegetation toward the margin of the oxbow lake, branch or river. The length of the transect and the number of plots varied depending on the width of the macrophyte bank. In each sampling unit, we identified the occurring species, estimated their percentages of cover and measured depth (cm), dissolved oxygen, pH, conductivity (+mV), and total suspended solids (mg L^{-1}), utilizing a multiparameter water quality checker (Horiba) (Table 1).

Botanical material was collected, pressed, dried, labeled, and stored in the Herbarium CGMS of the Universidade Federal do Mato Grosso do Sul (except *Galactia paraguariensis* Chodat & Hassl. stored in the Herbarium of EMBRAPA Pantanal—CPAP). Plant identification was based on Pott and Pott (2000), updated in accordance with APG III (2009) and the Brazilian plant list (Forzza et al. 2010). Life forms of the species were classified into emergent, amphibious, free floating, rooted floating, rooted submerse, free submerse, and epiphyte, according to Irgang et al. (1984) and Pedralli et al. (1985).

The community structure was analyzed through calculation of absolute and relative frequency and dominance, as well as importance value (IV), which is the sum of the frequency and relative coverage (total sum 200), applying formulae and concepts given by Damasceno-Junior and Pott (2011). To determine sampling effort, we utilized species—accumulation curve, and to estimate local richness, we applied the non-parametric Jackknife 1 index after 1000 aleatorizations of data, utilizing the software EstimateS (Colwell 2009). We choose to use the proportion of species cover as a measure of abundance by Damasceno-Junior and Pott (2011).

To verify how species composition and abundance relate with water depth and physico-chemical parameters, we performed a Canonical Correspondence Analysis (CCA). Tests were carried out using the function envfit vegan package, which calculates by 999 permutations the significance relationship between environmental variables and axes (Oksanen et al. 2016). Due to the high number of species, we represented in the graphic those that presented higher correlation with the variables analyzed. To verify if and how these variables (depth, dissolved oxygen, pH, conductivity, and total suspended solids) influence cover of different life forms, we made an initial multiple regression. Then, for selection of the simplest and most parsimonious model supported by the data, we utilized the approach of selection of models based on the theory of information criteria (Burnham and Anderson 2002). The Akaike information criterion (AIC) is a tool widely utilized for selection of models in ecology (Johnson and Omland 2004). To detail the relation between the species and depth, we made a direct ordination (CA) considering the frequency of occurrence. All analyses were performed in R language (R Core Team 2013), using Vegan and Car packages.

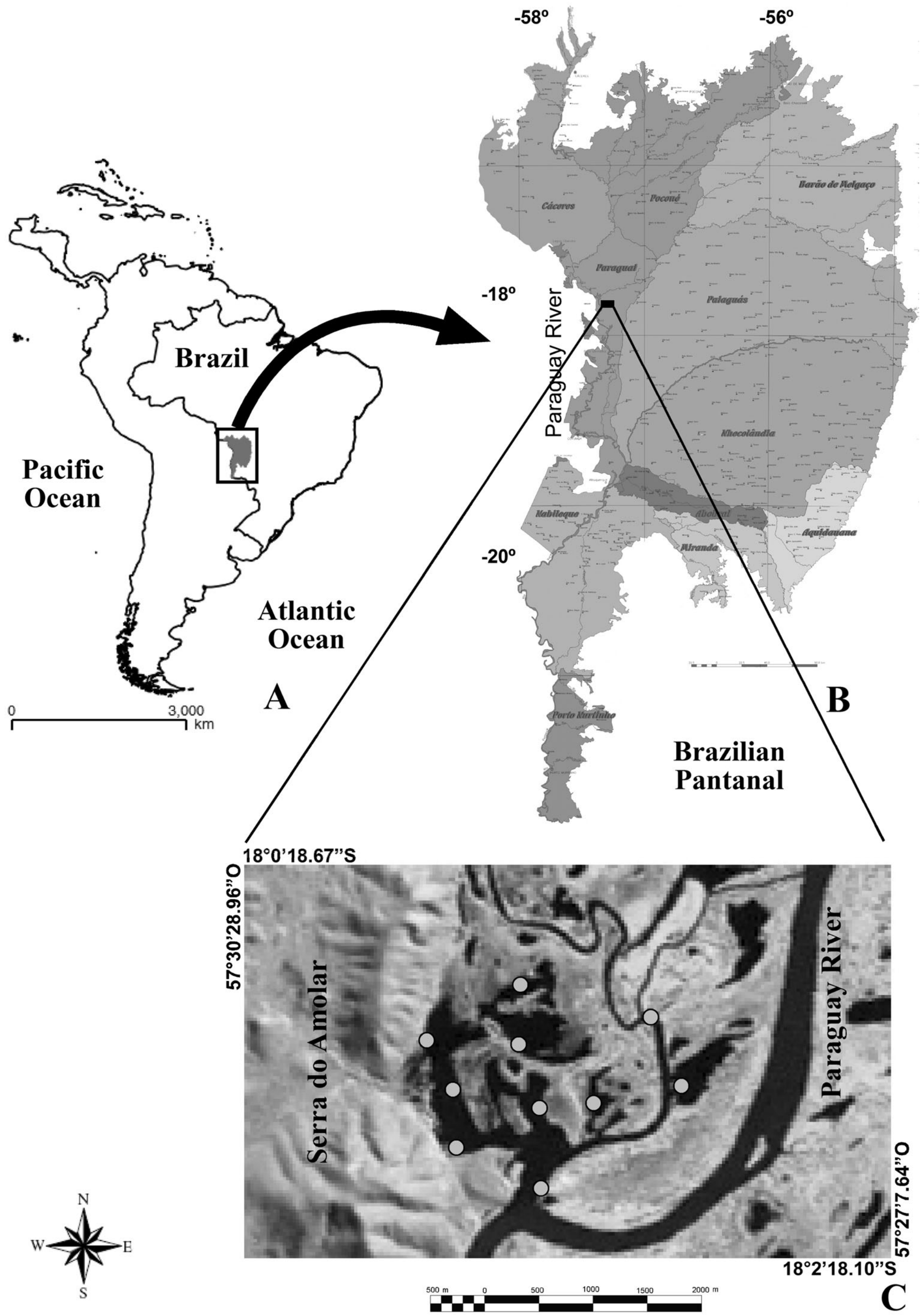

Fig. 1 Study area at Amolar, in the Paraguay River sub-region, in the "Pantanal" wetland, Corumbá, MS: **a** Localization of the Brazilian "Pantanal" in South America, **b** Sub-regions of the "Pantanal", modified from Embrapa Pantanal (2009), **c** Sampling sites on satellite image (INPE 2009). *Each point* represents the approximate location of a set of five transects

Results

We recorded 27 families, 49 genera and 65 species of aquatic macrophytes, being one Marchantiophyta, four Monylophyta, and all the other species were Angiosperms (Table 2). The richest family was Fabaceae (12 species), followed by Poaceae (8), Convolvulaceae (5), Onagraceae (5), and Lentibulariaceae (4). Fifteen families were represented by a single species. The richest genera were *Ludwigia* (5 species), *Ipomoea* (4), and *Utricularia* (4).

The rarefaction curve showed a rapid increase of the number of species with increased sampling area, presenting a lower slope on the last sampling points (Fig. 2), which indicates a possible approximation to the real number of species, estimated by Jackknife 1 as 71 species. This way, 91.5% of the recorded species were estimated for the area.

Table 1 Explanatory variables investigated, with mean, minimum, and maximum values

Environmental variables	Unit	Mean	Min	Max
Depth	cm	214	25	324
Conductivity	$\mu S\ cm^{-1}$	51.7	46.4	55.8
Suspended solids	$mg\ L^{-1}$	26	23.1	27.5
pH		6.1	6	6.4
O_2	$mg\ L^{-1}$	1	0.9	1.16

We recorded all life forms proposed by Irgang et al. (1984), the emergent form being the most representative with 36 species (55.4% of the total). Next occurred free floating (13), rooted floating (7), free submerged (4), amphibious (3), epiphyte, and rooted submerged (one species each) (Table 2). The most frequent species were the free floating *Salvinia auriculata* Aubl. (44% of the total of plots), *Ricciocarpos natans* (L.) Corda (32.4%), *Lemna aequinoctialis* Welw. (26.8%), *Azolla filiculoides* Lam. (24.5%), *Eichhornia crassipes* (Mart.) Solms (23.8%), *Ludwigia helminthorrhiza* (Mart.) H. Hara (21.7%), and the rooted floating *Hymenachne amplexicaulis* (Rudge) Nees (32.2%) (Fig. 3; Table 2). The other species occurred in less than 20% of the plots, and 17 species occurred in less than 1% of the sampling units, such as *Hydrocotyle ranunculoides* L.f., *Ipomoea subrevoluta* Choisy, *Ludwigia sedoides* (Humb. & Bonpl.) H. Hara, *Rhynchanthera novemnervia* DC. and *Commelina schomburgkiana* Klotzch *ex* Seub. (Fig. 3).

Hymenachne amplexicaulis was the species with the largest relative cover (RC: 11.6%), followed by *E. crassipes* (10.6%), *Oxycaryum cubense* (Poepp. & Kunth) Lye (8.3%), *E. azurea* (8.1%), and *Paspalum repens* Berg. (6.9%). The remaining species presented RC below 6%, while 47 species had cover below 1%, including frequent species but with small size, such as *R. natans* and *L. aequinoctialis.* Regarding importance value (IV), we highlight *H. amplexicaulis* (18.9), *E. crassipes* (15.9), and *S. auriculata* (15.5) (Fig. 3). These species represented less than 5% of the total species richness, and however, accounted for more than 50% of the IV. More than 50% of the species had an IV less than 1 (Table 2).

The structure of the assemblage of aquatic macrophytes was best represented in two dimensions by CCA that explained 57% of the variation (Fig. 4). Axis 1 explained 34.57% of the variation and the axis 2 explained 23.17%. The species composition was significantly correlated with the environmental variables, axis 1 being more related with depth ($r^2 = 0.63$, $P < 0.001$) and axis 2 more related with the other physico-chemical parameters ($r^2 = 0.26$, $P < 0.001$). Species such as *Oryza glumaepatula* Steud. *S. auriculata,* and *L. helminthorrhiza* occurred in waters with higher conductivity and pH, and more dissolved solids. Some species such as *E. crassipes*, *E. azurea*, *Victoria amazonica* (Poepp.) Sowerby and *Pistia stratiotes* L. occurred in waters with low values of conductivity, pH, dissolved O_2, and dissolved solids, in oxbow lakes. The environments in transition with flooded forests also exhibited lower conductivity, O_2, and suspended solids.

Considering the frequency of occurrence, the direct ordination indicated that various species occurred only in shallower water (>0.25 m), in general, close to the transition with riparian floodable forests, such as *Louisiella elephantipes* (Nees ex Trin.) Zuloaga and *Melochia arenosa* Benth. and the lianas *Ipomoea rubens* choisy and *Dioclea burkartii.* R.H. Maxwell. The same way, we recorded species which only occurred in greater depths (<3.24 m), as the case of *E. azurea, V. amazonica,* and *Marsilea crotophora* D.M. Johnson. Exclusively in intermediate depths, we found *Ceratopteris pteridoides* (Hook.), *Utricularia foliosa* L. and *Sesbania exasperata* Kunth. Various species were recorded either in shallow waters or in deep ones, the case of *E. crassipes, L. aequinoctialis, Vigna lasiocarpa* (Mart. ex Benth.) Verdc. *H. amplexicaulis*, among others (Figs. 4, 5).

The combination of variables selected for the best models AIC explaining individual species occurrence differed among life forms. The RC of amphibious and rooted submerged species was not explained by any of the analyzed parameters. Emergent species were negatively related with depth and conductivity, and positively with total dissolved solids. The RC of epiphytes was positively influenced by depth and pH, but negatively by conductivity and total dissolved solids. The free floating species had their RC positively influenced by depth, total suspended solids, and O_2, and negatively by conductivity and pH (Table 3).

Discussion

Our survey with 65 species showed that richness of aquatic macrophytes at Amolar is equivalent or superior to that recorded in other areas in this floodplain and corresponding to 21.1% of the 308 species cataloged in the Brazilian "Pantanal" (Pott et al. 2012). In other surveys in areas under influence of the Paraguay River, 57–59 species were recorded (Catian et al. 2012; Cunha et al. 2012). However, in the northernmost regions, Silva and Carniello (2007) found 82 species in the sub-region of Cáceres, and Pott et al. (2011) recorded 135 species at 17 sampling sites in the National Park of Pantanal and nearby private preserves. One could expect that the sampled area could be even richer, once the region has a great variety of habitats such

Table 2 List of species of aquatic macrophytes at Amolar, in the Paraguay River sub-region, "Pantanal" wetland, Corumbá, MS, life forms, relative frequency (RF), relative cover (RC), and importance value (IV)

Family/species	Life form	Voucher	RF	RC	IV
Marchantiophyta (Bryophyta)					
Ricciaceae					
Ricciocarpos natans (L.) Corda	Free floating	27,136	7.34	1.19	8.53
Monylophyta					
Marsileaceae					
Marsilea crotophora D.M. Johnson	Rooted floating	27,115	2.31	2.87	5.18
Pteridaceae					
Ceratopteris pteridoides (Hook.) Hieron	Free floating	28,476	0.92	0.50	1.42
Salviniaceae					
Azolla filiculoides Lam.	Free floating	36,099	5.55	3.25	8.79
Salvinia auriculata Aubl.	Free floating	25,093	9.94	5.56	15.50
Magnoliophyta (Angiospermae)					
Acanthaceae					
Justicia laevilinguis (Nees) Lind.	Emergent	27,091	0.35	0.21	0.56
Apocynaceae					
Rhabdadenia madida (Vell.) Miers	Emergent	27,093	1.04	0.60	1.64
Araceae					
Lemna aequinoctialis Welw.	Free floating	27,249	6.07	0.32	6.39
Pistia stratiotes L.	Free floating	27,241	0.29	0.08	0.37
Wolffiella welwitschii (Hegelm.) Monod	Free floating	48,030	2.95	0.12	3.07
Araliaceae					
Hydrocotyle ranunculoides L.f.	Free floating	28,480	0.06	0.00	0.06
Asteraceae					
Aspilia latissima Malme	Emergent	27,095	0.12	0.21	0.33
Enydra radicans (Willd.) Lack	Emergent	27,096	0.17	0.09	0.26
Combretaceae					
Combretum lanceolatum Pohl *ex* Eichler	Emergent	27,098	0.12	0.18	0.29
Commelinaceae					
Commelina schomburgkiana Klotzch *ex* Seub.	Emergent	28,492	0.12	0.07	0.19
Convolvulaceae					
Aniseia martinicensis (Jacq.) Choisy	Emergent	27,099	0.29	0.13	0.42
Ipomoea carnea ssp. *fistulosa* (Mart. *ex* Choisy) D.F. Austin	Emergent	27,101	0.40	1.07	1.47
Ipomoea chiliantha Hallier f.	Emergent	27,267	0.23	0.25	0.48
Ipomoea rubens Choisy	Emergent	27,102	0.52	0.99	1.51
Ipomoea subrevoluta Choisy	Emergent	27,103	0.06	0.04	0.10
Cucurbitaceae					
Cayaponia podantha Cogn.	Emergent	29,026	0.29	0.10	0.39
Cyperaceae					
Oxycaryum cubense (Poepp. & Kunth) Lye	Epiphyte	25,099	3.87	8.32	12.19
Scleria lacustris C. Wright	Emergent	47,983	0.46	0.16	0.62
Euphorbiaceae					
Caperonia castaneifolia (L.) A. St.-Hil.	Emergent	28,493	0.40	0.22	0.63
Fabaceae					
Aeschynomene rudis Benth.	Emergent	25,094	0.81	0.74	1.55
Aeschynomene sensitiva Sw.	Emergent	27,109	0.17	0.04	0.21
Bauhinia corniculata Benth.	Amphibious	27,268	0.29	0.24	0.53
Dioclea burkartii R.H. Maxwell	Emergent	25,095	0.29	0.65	0.94

Table 2 continued

Family/species	Life form	Voucher	RF	RC	IV
Galactia paraguariensis Chodat & Hassl.	Emergent	13,067	0.06	0.02	0.08
Mimosa pellita Humb. & Bonpl. *ex* Willd.	Emergent	27,111	0.92	0.67	1.60
Mimosa polycarpa Kunth	Amphibious	27,260	0.06	0.06	0.12
Neptunia plena (L.) Benth.	Free floating	27,112	0.06	0.10	0.16
Senna pendula (Humb. & Bonpl. *ex* Willd.) H.S. Irwin & Barneby	Emergent	27,114	0.23	0.09	0.32
Sesbania exasperata Kunth	Emergent	27,277	0.52	0.43	0.95
Vigna lasiocarpa (Mart. *ex* Benth.) Verdc.	Emergent	51,833	4.45	2.61	7.05
Vigna longifolia (Benth.) Verdc.	Emergent	51,834	0.12	0.06	0.18
Hydrocharitaceae					
Limnobium laevigatum (Humb. & Bonpl. *ex* Willd.) Heine	Free floating	27,236	0.23	0.12	0.36
Lentibulariaceae					
Utricularia breviscapa Wright *ex* Griseb.	Free submerged	27,240	0.75	0.27	1.02
Utricularia foliosa L.	Free submerged	25,097	1.62	0.93	2.55
Utricularia gibba L.	Free submerged	28,489	2.14	0.25	2.39
Utricularia hydrocarpa Vahl	Free submerged	27239	0.12	0.02	0.14
Malvaceae					
Byttneria rhamnifolia Benth.	Amphibious	27,269	0.06	0.03	0.09
Melochia arenosa Benth.	Emergent	27,138	0.58	0.30	0.88
Melastomataceae					
Rhynchanthera novemnervia DC.	Emergent	27,117	0.06	0.15	0.21
Nymphaeaceae					
Victoria amazonica (Poepp.) Sowerby	Rooted floating	51,806	0.46	2.28	2.74
Onagraceae					
Ludwigia grandiflora (Michx.) Zardini	Emergent	27,118	1.33	0.61	1.94
Ludwigia helminthorrhiza (Mart.) H. Hara	Free floating	27,119	4.91	5.73	10.64
Ludwigia inclinata (L.f.) P.H. Raven	Rooted submerged	25,096	0.23	0.09	0.32
Ludwigia leptocarpa (Nutt.) H. Hara	Emergent	27,120	0.69	0.48	1.18
Ludwigia sedoides (Humb. & Bonpl.) H. Hara	Rooted floating	25,085	0.06	0.02	0.08
Phyllanthaceae					
Phyllanthus fluitans Muell. Arg.	Free floating	27,272	0.40	0.15	0.56
Poaceae					
Hymenachne amplexicaulis (Rudge) Nees	Rooted floating	27,125	7.28	11.60	18.88
Leersia hexandra Sw.	Emergent	27,263	2.31	1.91	4.22
*Louisiella elephantipes (*Nees *ex* Trin.) Zuloaga	Emergent	27,129	0.12	0.08	0.20
Oryza glumaepatula Steud.	Emergent	27,233	3.00	5.29	8.30
Oryza latifolia Desv.	Emergent	27,127	2.31	2.31	4.62
Panicum dichotomiflorum Michx.	Emergent	27,128	0.46	0.39	0.86
Paspalum repens Berg.	Rooted floating	27,131	4.45	6.92	11.37
Streptostachys mertensii (Roth) Zuloaga & Morrone	Emergente	27,234	0.12	0.04	0.15
Polygonaceae					
Polygonum acuminatum Kunth	Emergent	27,132	1.39	2.57	3.96
Polygonum ferrugineum Wedd.	Emergent	27,133	0.23	0.27	0.50
Pontederiaceae					
Eichhornia azurea (Sw.) Kunth	Rooted floating	28,465	2.89	8.11	11.00
Eichhornia crassipes (Mart.) Solms	Free floating	27,135	5.37	10.58	15.95
Pontederia rotundifolia L.f.	Rooted floating	25,098	3.64	5.36	9.00
Vitaceae					
Cissus spinosa Cambess.	Emergent	27,260	0.98	0.87	1.85

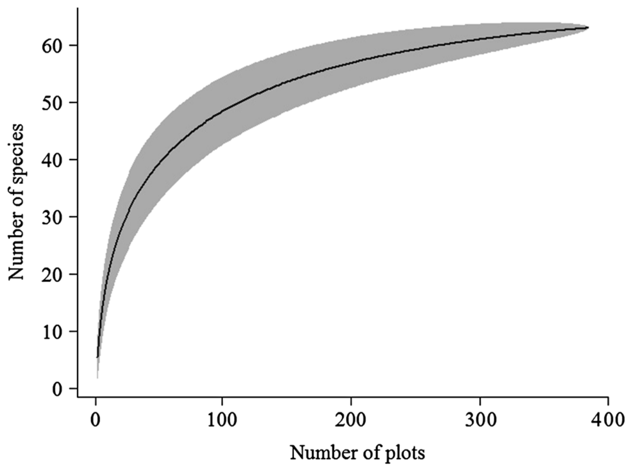

Fig. 2 Species—accumulation curve, representing the sampling effort for the aquatic macrophytes recorded at Amolar, in the Paraguay River sub-region, "Pantanal" wetland, Corumbá, MS. *Gray area* represents the standard deviation from 1000 permutations

as floodable grasslands under less direct action of the river current and other areas closer to the river bed. Both types of habitats vary much in depth, which provides great variability of habitats and niches that can be occupied by macrophytes.

Fabaceae, Poaceae, and Onagraceae were also recorded as some of the richest families of the macrophytes in other studies in other areas of the "Pantanal" (Rocha et al. 2007; Silva and Carniello 2007; Pivari et al. 2008; Cunha et al. 2012), being pointed out by Pott et al. (2011) as some of the most representative among the aquatic macrophytes of the "Pantanal" plain. Considering life forms, the highest richness of emergent species corroborates Pott and Pott (2000), although the recorded proportion of free floating species was much higher in our work. The number of amphibious plants was much lower, which can be the result of the sampled habitats, with plots distributed perpendicularly to the river bed. Yet, in turbid waters, if the nutrient level is sufficient for plant growth, assemblages of macrophytes are dominated by species with floating leaves or floating species (Bornette and Puijalon 2011). Submerged life forms comprise a lower percentage in communities of turbid waters in the "Pantanal", once they only thrive where light is enough for photosynthesis (Castro and Garcia 1996).

Hymenachne amplexicaulis, species with the highest IV at Amolar, is a C_3 grass of aggressive growth, being considered a noxious weed of flooded areas in several countries where it was introduced, such as USA and Australia (Csurhes et al. 1999). *Eichhornia crassipes*, *E. azurea,* and *O. cubense* can be considered weeds in reservoirs and waterways elsewhere (Gopal and Sharma 1981; Tanaka et al. 2002; Bryson et al. 2008), due to their highly efficient vegetative propagation systems for fast colonization and consequent high dominance (high IV).

The species composition of aquatic plants was correlated with the analyzed physico-chemical parameters, chiefly depth. Pott et al. (1989) already reported such zonation of aquatic macrophytes in the "Pantanal", which seems more striking on shores of water bodies (emerse soil/water interface), since small differences in depth in this zone shall represent large microecological variations for the plants. Life forms explain, at least partially, the correlation of aquatic macrophytes with depth. Shallow habitats were mostly occupied by emergent species, while the deepest were covered by rooted floating plants. In still waters or trapped by rooted plants, some small free floating species such as *Wolffiella welwitschii* (Hegelm.) Monod *L. aequinoctialis*, *S. auriculata*, *A. filiculoides,* and *R. natans*

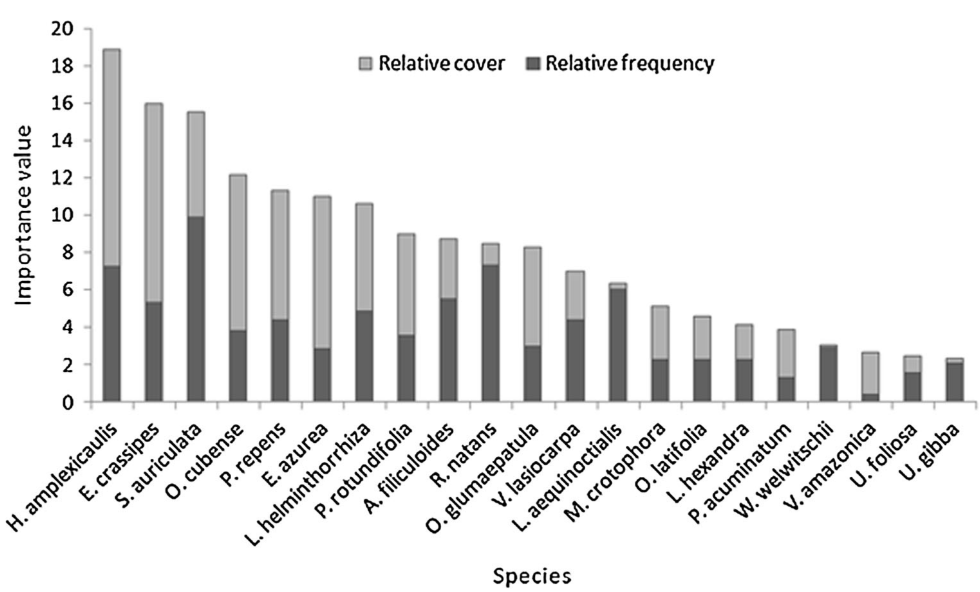

Fig. 3 Relative cover (RC), relative frequency (RF), and importance value (full bar) of the most frequent species of the assemblage of aquatic macrophytes at Amolar, in the Paraguay River sub-region, "Pantanal" wetland, Corumbá, MS

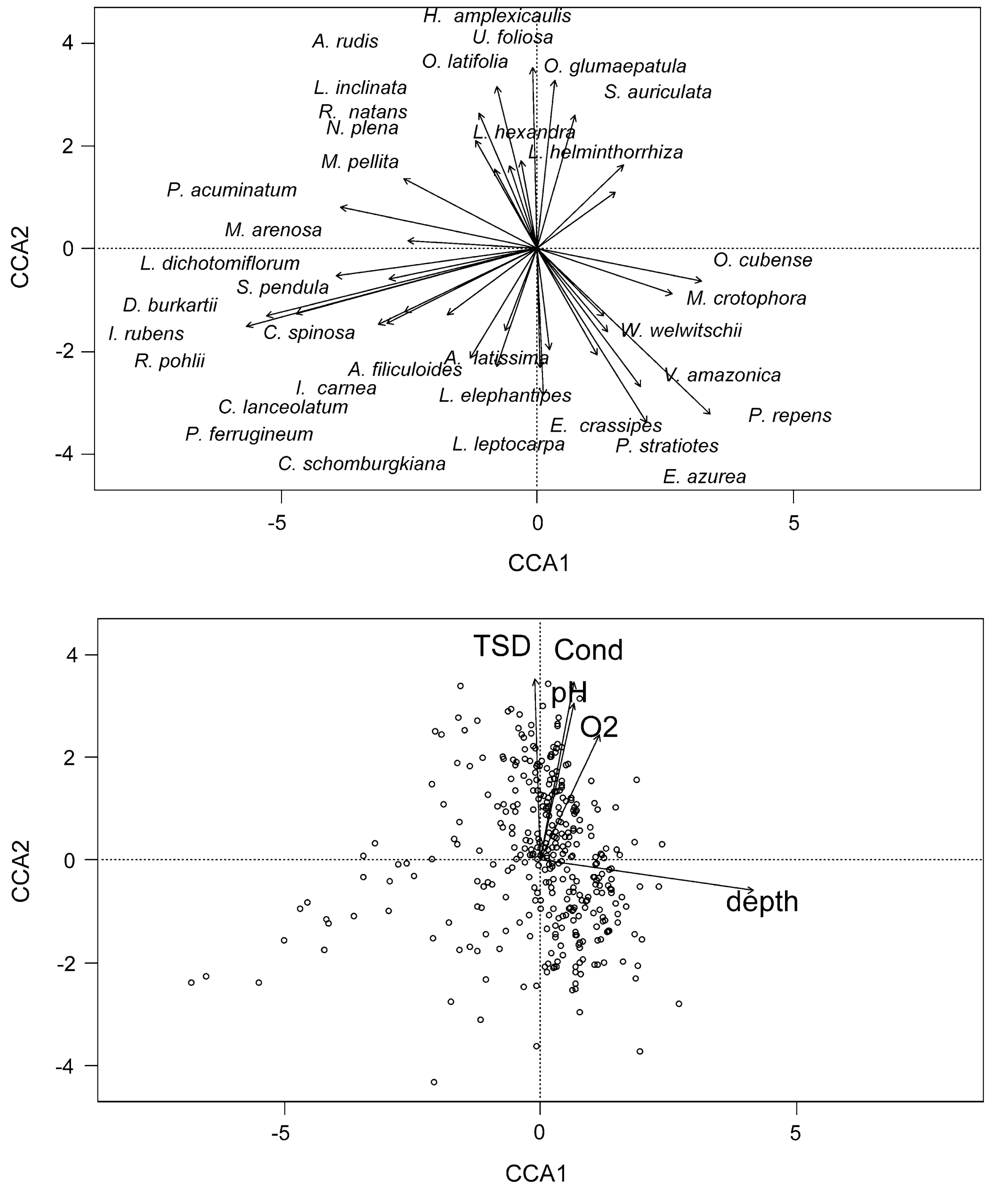

Fig. 4 Canonical Correspondence Analysis (CCA), axis 1 ($\lambda_1 = 0, 34$) and axis 2 ($\lambda_2 = 0, 23$) showing the distribution of species and of the analyzed environmental variables: pH, TSD (total dissolved solids), Cond (conductivity), dissolved oxygen (O_2) and depth at Amolar, sub-region of Paraguay River, "Pantanal" wetland, Corumbá, MS

occur in all depths, suggesting that this life form is not related with the soil in any of the life phases of the individual.

The species cover is explained by different combinations of physico-chemical parameters, suggesting the existence of various optimal ranges and individual responses, as reflex of their structural and physiological adaptations. Conductivity was the most relevant chemical variable to predict cover of most life forms, except amphibious and rooted submerged. Conductivity combined with pH determines the availability of carbon (Pulido et al. 2015), which is essential for growth and the main element of the plant sustaining system. The modes of carbon use differ among taxonomic groups and also between species with same growth form (Spence and Maberly 1985; Vestergaard and Sand-Jensen 2000). Particle and nutrient resuspension can potentially limit light penetration into the water (Madsen et al. 2001) and subsequently hinder plant growth and recruitment (Barko et al. 1986; Schwarz and Hawes 1997). On the other hand, it can favor sediment and nutrient accumulation (Anderson and Kalff 1988), and consequently species growth (Lehmann et al. 1997), especially of free floating species, as these cannot absorb nutrients from the substrate.

The scarcity of studies in various sub-regions of the "Pantanal", the human pressure on this ecosystem, and the importance of these plants for the dynamics of aquatic ecosystems show the importance of this work, since surveys and ecological assessments on this plant group are indispensable to understand diversity of the wetland. Our

Fig. 5 Distribution of the main species of aquatic macrophytes in relation to water depth (zonation) at Amolar, in the Paraguay River sub-region, "Pantanal" wetland, Corumbá, MS

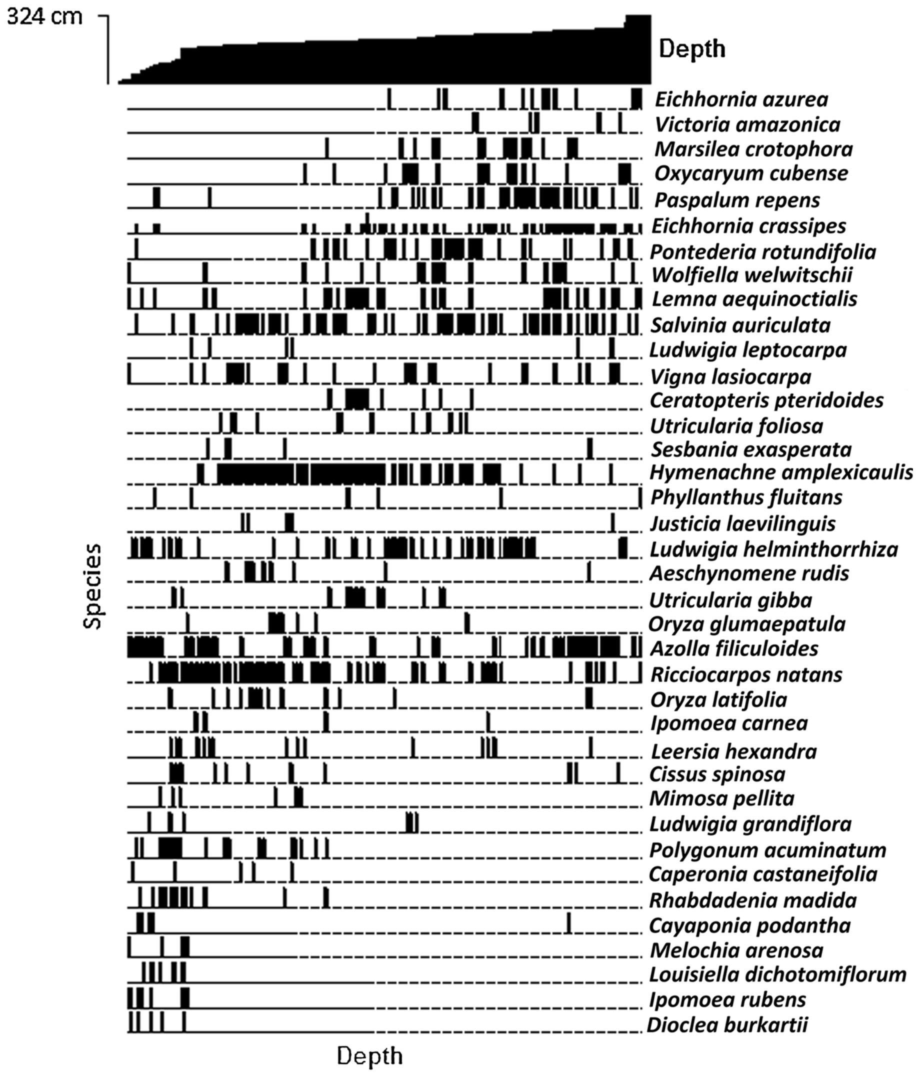

Table 3 Models selected by the Akaike's information criterion (AIC) to explain cover of different life forms, considering depth, dissolved oxygen (DO), temperature, conductivity, total suspended solids (TSS), and pH

Life form	Model	ΔAIC	R^2	F	P
Amphibious	−13.33 intercept				
Emergent	131.77 intercept −0.159 depth −4.55 conductivity +6.22 TSS	3.33	0.2695	19.57	$P < 0.001$
Epiphytes	841.53 intercept +0.25 depth +463.73 DO—4.39 conductivity −182.00 pH	1.97	0.439	12.19	$P < 0.001$
Rooted floating	460.48 intercept +0.11 depth −4.34 conductivity +8.94 TSS −72.96 pH	1.84	0.155	11.41	$P < 0.001$
Free floating	−392.85 intercept +116.31 DO −4.089 conductivity +3.03 TSS +69.45 pH	2.47	0.14	10.48	$P < 0.001$
Rooted submerged	5.5 intercept				
Free submerged	8.12 intercept +430.19 DO −8.14 conductivity	3.06	0.276	8.243	$P < 0.001$

results indicate the importance of water physical and chemical characteristics in the macrophyte community composition and the potential role of this community as a bioindicator. Considering that the "Pantanal" is exposed to several problems, such as land use of the watershed and silting, the present study can help to foresee the response of different species or life forms to different human impacts or global changes and, so, help managing entities to make decisions on conservation, management, and restoration.

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