



Seasonal variation of plant communities and their environments along a topographic gradient in the Iberá wetland, ancient Paraná floodplain, Argentina

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with 10 figures, 3 tables and 1 electronic appendix

Abstract: Recently, wetlands have declined worldwide due mainly to habitat loss by human activities. In order to achieve a better understanding of the impacts that are being generated on the Iberá wetland in northeastern Argentina, the objective of this study is to analyze seasonal variation of the environments present in the sandy ridges areas of this wetland. The different environments were identified and characterized according to their topography, vegetation physiognomy and dominance of species. In addition, the seasonal variation in the vegetation communities occurring in the different environments was analyzed and characterized in terms of floristic composition, abundance-cover and attributes. A thematic map of environments was generated and validated through the analysis of abundance-cover of the vegetation. Surveys were conducted seasonally, resulting in a total of 600 plots randomly selected. The percentage of dry matter, bare ground, vegetation-free water surface, vegetation height and depth of the water column were determined where appropriate. Six environments were identified: the upland areas, the temporary ponds, the upper and lower transition zones (between aquatic and terrestrial environments), the low-lying area and the “embalsados” (with aquatic-palustrine species). The environment classification suggests that the topographic gradient and associated edaphic factors would determine the presence of the different communities. The great intra-annual variation in water regime originating from seasonal precipitation in the study area produces a variety of plant communities. The patterns of plant zonation in this wetland are changed from season to season as water levels fluctuate in space and time making the system very susceptible to changes in the hydrometric level.

Keywords: Characterization of environments. Diversity. Floristic composition. Hydrometric level. Topographic gradient

Introduction

Wetlands are ecosystems characterized by high values of productivity and biodiversity, which are similar to those found in rainforests (KUSLER et al. 1994). Wetlands play an integral role in the hydrologic cycle and provide important ecosystem services that may include flood storage, water quality, carbon storage and wildlife habitat. These areas act as a buffer during periods of high water (NRC 1995). In recent decades, wetlands have declined worldwide due mainly to habitat loss by human activities. These anthropic effects produce topographic alterations of the earth's surface and changes in plant cover type's producing major changes in composition and structure of the landscape (HAFF 2001).

The large wetlands of South America are a special case of wetlands that must be considered as macrosystems due to their areal extension, complexity and internal fluxes of sediments and salts (NEIFF et al. 1994).

In this context, the wetlands associated to the Paraná River conform one of the most important fluvial wetlands corridor of the world (NEIFF & MALVÁREZ 2004). The Iberá macrosystem basin constitutes the ancient floodplain of the Paraná River, which remained con-

nected to the river until the end of the Pleistocene (NEIFF 1999, CANZIANI et al. 2006). Due to its origin, landscape pattern, water chemistry, high species richness of plants and animals, pristine condition and biogeography location, this area is unique in America (NEIFF 2004). It is one of the most important wetlands of Argentina, covering an area of 12,300 km² and representing a major source of clean water (GÁLVEZ et al. 2003, LANCELLE 2003, NEIFF & POI DE NEIFF 2005). The former river valley became a basin of gentle slope, which retained water and further developed into a vast wetland mainly fed by precipitation (ORFEO 2005). Currently, this ecoregion comprises a complex of ecosystems dominated by palustrine wetlands (marshes and swamps). These are separated by sandy ridges (relict fluvial deposits) interconnecting rounded shallow lakes, which are linked by different watercourses of different order. There is hydrophilic vegetation with “embalsados” (beds of closely packed aquatic vegetation such as water hyacinths), marshes and swamps, floodable grasslands on sand banks and small forest islands with species of the Paranaense tropical forest (NEIFF 2004). The combination of their particular flora gives rise to a variety of natural environments (CARNEVALI 1994) sustaining high animal diversity (RABINOWITZ 1997).

Recently, different disturbed local areas related with the presence of anthropogenic activities (mainly rice farming, forestation and ranching) were identified in the borders of the wetland (CÓZAR et al. 2005). The proliferation of these activities and the need to increase the area of productive land by means of illegal construction of embankments is causing changes in the environment. These changes often alter the intrinsic dynamics of the wetland modifying the normal runoff from water (WALLER 2011). Since 90's the area has also been altered and affected by the impacts caused by the Yacyreta dam, a large hydroelectric power plant constructed only a few kilometers north to the Iberá system on the Paraná River (CANZIANI et al. 2006). Since then, the progressive filling of the reservoir, has been identified as a possible cause of the increase in the hydrometric level of the Iberá system by underground water transfer (BLANCO & PARERA 2003, NEIFF 2004, CÓZAR et al. 2005). The variations in the hydrometric level in addition to the high grazing pressure on higher areas of the topographic gradient accelerate impact processes on a large scale as the "esterización". The "esterización" refers to the advance of marsh vegetation on new flooded areas. This process affects the global water balance favoring the generation of new flooded areas covering the sandy ridges (NEIFF 2004, GIUDICE et al. 2006). The process of formation of rounded shallow lakes is called "pseudokarst" and it consists in the drag of sand particles at the water table level by an increase in energy of groundwater circulation. This creates a gap that causes the ground to sink and generate a difference in the surface where water takes longer to drain or evaporate forming round shallow lakes and temporary ponds. The consequence is the loss of upland areas and landscape heterogeneity that leads to reduced biodiversity and loss of habitat for food, shelter and nesting of several wildlife species (CLT 2006).

The objective of this study is to analyze the seasonal variation of the habitat mosaic and plant communities present in the higher areas of this wetland through: 1) the identification and characterization of different environments in the sandy ridges and 2) the analysis of seasonal variation in floristic composition, abundance-cover and attributes of the plant communities occurring in different environments.

Study area

The study was conducted in the Park Guayaibí (28°00 S 57°18W), a former livestock farm located to the north of central Iberá Macrosystem, in Los Campos District (CARNEVALI 2003), Corrientes province, Argentina. It covers an area of about 550 ha corresponding to a sandy ridge bordered by marshes. The sandy ridge includes five rounded shallow lakes of pseudokarstic origin (CLT 2006; Fig. 1). The landscape is dominated by a "paja colorada" grassland, mainly represented by *Andropogon lat-*

eralis, *Axonopus fissifolius* and *Rhynchospora barrosiana* (CARNEVALI 2003). The rounded shallow lakes have a well-defined surface area, and contain water almost permanently. Vegetation cover depends on their degree of evolution and size. There are floating soils ("embalsados") in the center of the shallow lakes, formed by the accumulation of organic matter resulting from the imbalance between decomposition rate and macrophyte production. The area corresponds to a private ecological reserve under low grazing pressure, where grassland areas are subject to low-intensity burns during autumn and winter (DI FRANCESCANTONIO 2009).

As previously mentioned, currently the Iberá basin is not connected to the Paraná River (NEIFF 1999). Is mainly fed by rain and drains south-west to the Paraná River via the Corriente River. Water level fluctuations are dominated by the local climate. Seasonal water level variability is lower in the northern waterbodies and increases toward the southern water bodies (GÁLVEZ et al. 2003). Climate is subtropical-humid, with hydric and thermal seasonality. Rainfall occurs in all seasons but it is heavier in spring (September 21 to December 20) and summer (December 21 to March 20). Annual average rainfall is around 1700 mm (NEIFF & POI DE NEIFF 2005). In summer, average and maximum temperatures are 27 °C and 44 °C respectively and in winter, average temperature is 16 °C, with the historical record of minimum temperature over the past 50 years being -2 °C.

Methods

Classification of environments and field survey

A preliminary identification of the different water bodies and habitats in the study area was made based on topographic characteristics and vegetation attributes (vegetation cover and height), through the interpretation of aerial photographs (1:20000 scale) and satellite imagery (Landsat and Google Earth 2011). Data were imported into a Geographic Information System (ArcView 3.2) to generate a thematic map of environments. Results were further validated in the field.

On the sandy ridge, seasonal randomly plots of vegetation were carried out in proportion to the area of each environment type. During the censuses, abundance of present species (cover) was estimated with the Braun-Blanquet scale with modifications (MUELLER-DOMBOIS & ELLENBERG 1974). The percentages of organic matter, bare ground and free water, vegetation height and water depth were estimated when required. Plots of 1 x 1 m were used when there was dominance of a single herb layer and plots of 5 x 5 m otherwise. One hundred and fifty censuses were conducted seasonally, resulting in a total of 600 censuses. The surveys were carried out at the end of each season (summer: from March 1 to 20; au-

tumn: from June 1 to 20; winter: from September 1 to 20; spring: November 20 to December 15).

Samples of plant species present in the study area were collected, dried and finally stored in a herbarium cabinet until further identification. The specimens collected were deposited in the herbarium of the Faculty of Exact and Natural Sciences of the Buenos Aires University (BAFC), Buenos Aires, Argentina. Nomenclature of the taxa follows ZULOAGA & MORRONE (1999).

Data analysis

To analyze abundance of species and floristic changes in different environments and seasons, average values were used to perform a cluster (or conglomerate) analysis with the Ward's clustering method and the Bray–Curtis coefficient of similarity. Multivariate Variance Analysis (MANOVA) was used to test for differences among the environments in each season. The dependent variables were species abundance, dry matter percentage, bare ground percentage, free water percentage, vegetation height and water depth. The Pillai's test was selected because it is more robust to violations of assumptions. The Hotelling's test with Bonferroni correction was used for multiple comparisons (OLSON 1976, JOHNSON & FIELD 1993). When MANOVA showed significant differences, a Discriminant Analysis (DA) was performed to determine which variables better discriminated between groups.

Assumptions of normality and homoscedasticity were tested with the Shapiro-Wilk W-test and the test for homogeneity of covariance matrices. The data that did not meet the assumptions of normality and variance homoscedasticity were square-root transformed.

For each type of environment, (pooling data from all seasons) total species richness (number of species, S) was estimated, vegetation diversity was determined using the Shannon-Wiener H index, and the Evenness (degree of uniformity of the relative abundance of species-E) was calculated as $E = H'/\ln S$ (MAGURRAN 1991). Subsequently, MANOVA and a Discriminant Analysis were used to test for significant differences in these variables among environments and to determine which of them accounted for these differences.

To estimate sampling efficiency in the different environments, a species-accumulation curve (Mao Tau function) was calculated from the observed species richness (COLWELL et al. 2004) with 95% confidence intervals, using the program EstimateS 7.5 (COLWELL 2005).

Results

Identification and characterization of different environments

A total of 144 species of vascular plants were recorded in the study area, belonging to 95 genera and 46 families (Appendix A). The most represented families were Cyperaceae (16.5%), Poaceae (15.1%), Asteraceae (10.8%) and Fabaceae (6.5%). 99% of the collected species were native.

The environments on the sandy ridge were identified *a priori* as upland areas (UA), ecotone (EC), low-lying area (LA) and temporary ponds (TP) (Fig. 1). UA are the most represented environment. In the rounded shallow lakes, two areas can be clearly distinguished along the topographic gradient: an ecotone (EC) and a low-lying area (LA). In the ecotone between the terrestrial and aquatic palustrine environments, there are two transition zones at different heights; during the rainy season (spring-summer), the upper one (UTZ) is occasionally waterlogged whereas the lower one (LTZ) is permanently waterlogged. In the low-lying area (LA) there are floating soils ("embalsados", EMB) and limnetic areas with aquatic palustrine vegetation (APV). Some temporary ponds (TP) filled with water only during periods of prolonged and heavy rainfalls are also present on the sandy ridge. Fig. 2 shows a profile of the different environments.

The conglomerate analysis (Fig. 3) revealed three major groups: Group A including the upland areas (UA), Group B including the ecotones (UTZ and LTZ) and temporary ponds (TL) and Group C including the low-lying areas (LA). In turn, group B is composed of three subgroups determined by seasonal variations in climate and hydrologic conditions rather than by topography. A constancy table for representative species of these groups is presented in Table 1.

MANOVA showed significant differences in species composition among environments for all seasons (summer: Pillai's trace = 3.95, $p < 0.0001$; autumn: Pillai's trace = 3.73, $p < 0.0001$; winter: Pillai's trace = 3.82, $p < 0.0001$ and spring: Pillai's trace = 3.82, $p < 0.0001$). In summer all the environments showed significant differences, while no significant differences were found between TP and LTZ in autumn and between TP and HTZ in winter.

The environments in terms of floristic composition and vegetation physiognomy are described as follows:

UA. In the UA two types of grasslands are found: (1) a tall grassland dominated by *Andropogon lateralis*, a cespitose perennial grass of 30–70 cm tall at the vegetative stage and up to 160 cm tall at anthesis, with *Rhynchospora barrosiana*, *R. emaciata*, *Centella asiatica* and *Eragrostis bahiensis* as accompanying species; and (2) a short grassland (mean height: 10 cm; up to 20 cm at the vegetative stage) characterized by creeping stoloniferous species, with *Axonopus fissifolius*, *Paspalum pumi-*

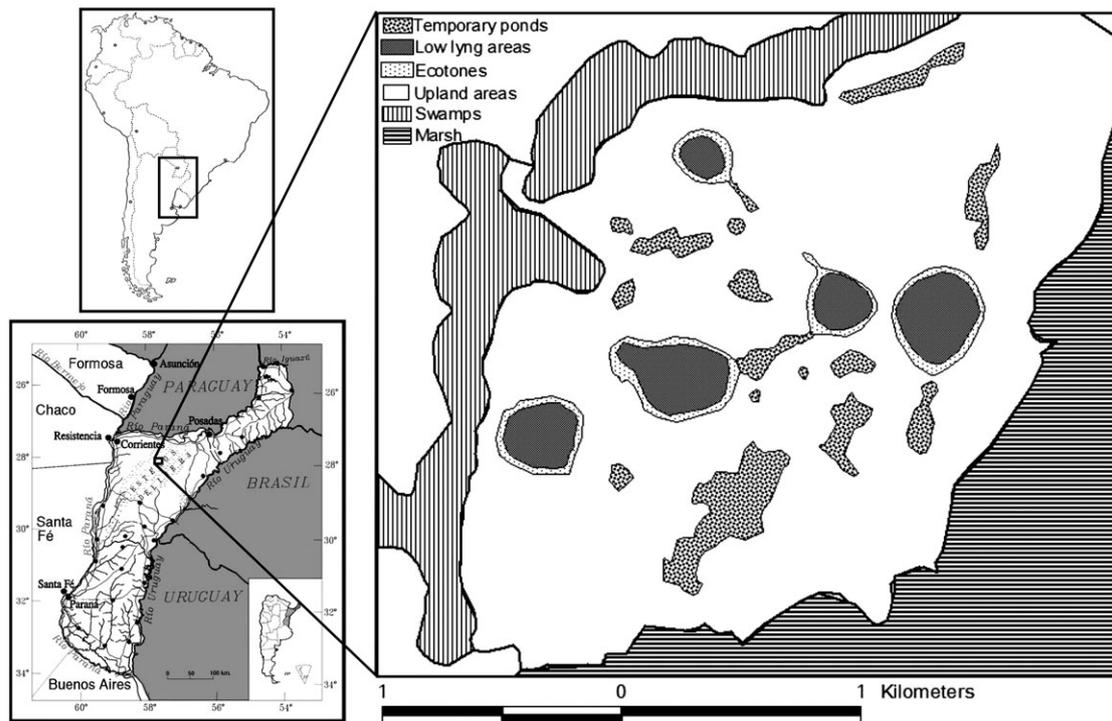


Fig. 1. Study area ($28^{\circ}00'S$ $57^{\circ}18'W$) located to the north of central Iberá Macrosystem. Thematic map of environments based on the interpretation of aerial photographs (1:20000 scale) and satellite imagery (Landsat), with further field validation.

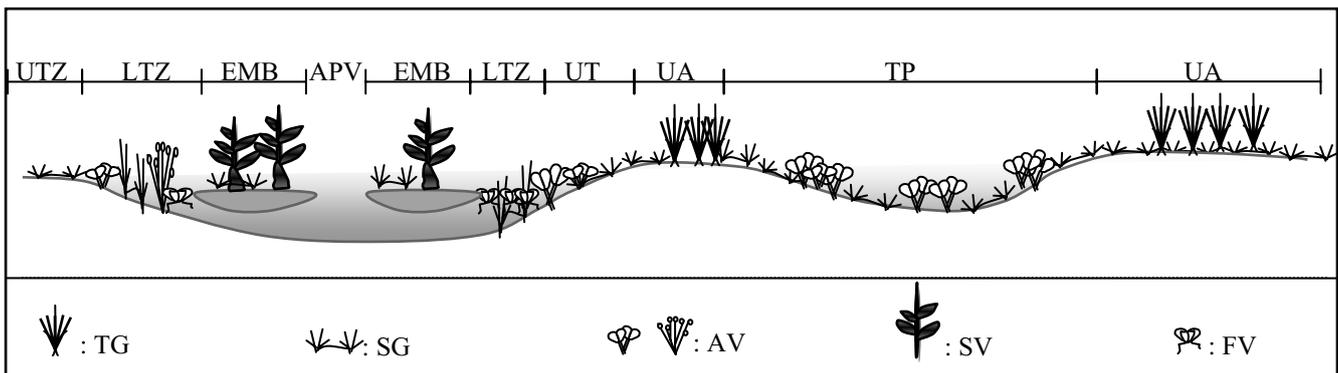


Fig. 2. Schematic profile of the environments and vegetation in the study area ($28^{\circ}00'S$ $57^{\circ}18'W$). UTZ: Upper transition zone; LTZ: lower transition zone; EMB: “embalsado”; APV: vegetation-free limnetic areas with aquatic palustrine vegetation; UA: upland area; TP: temporary pond. TG: tall grasses; SG: short grasses; AV: bottom-rooted aquatic vegetation; SV: shrubby vegetation; FV: floating vegetation. Marshes and swamps are not included.

lum and *P. alnum* as dominant species and *C. asiatica* and *Panicum schwackeanum* as accompanying species. Both grasslands show an annual bare ground cover of 4%.

TP. The marked fluctuation in the water level determines the floristic composition of this environment, from terrestrial to aquatic-palustrine species. The most abundant terrestrial species (up to 10 cm tall) are *Paspalum pumilum*, *R. barrosiana*, *C. asiatica* and *A. fissifolius*. The aquatic-palustrine environment is dominated by *Hedyotis salzmannii*, *Polygonum punctatum*, *Eleo-*

charis minima, *Luziola peruviana* and *Pontederia subovata*. This environment shows an annual bare ground cover of 9%.

UTZ. The UTZ is characterized by the presence of plants up to 15 cm tall, such as *Paspalum pumilum*, *H. salzmannii*, *E. minima* and *Hydrocotyle verticillata* as dominant species and *L. peruviana*, *C. asiatica* and *A. fissifolius* as accompanying species.

APV. The APV is dominated by *L. peruviana*, *Nymphoides indica* and *Hydrolea spinosa*. *Hedyotis salzmannii*, *Polygonum punctatum* and *Eichhornia crassipes* are

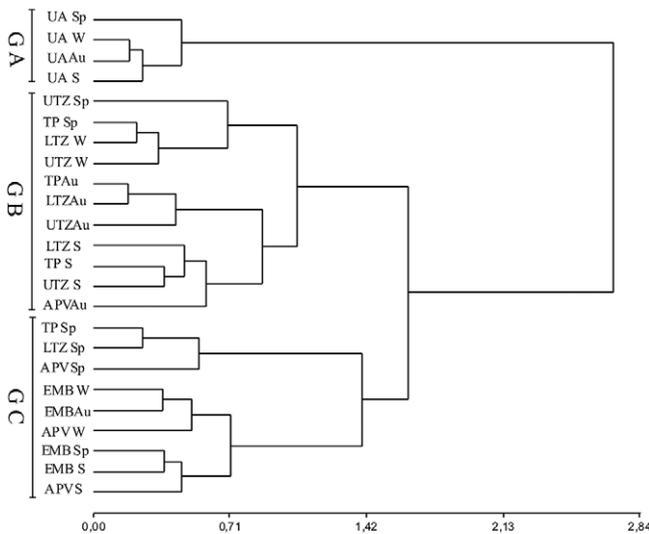


Fig. 3. Results of the Conglomerate Analysis for average cover-abundance of species obtained from each environment in each season. UA: upland area; UTZ: upper transition zone; LTZ: lower transition zone; APV: limnetic areas; EMB: “embalsado”; TP: Temporary pond. Sp: spring; S: summer; Au: autumn; W: winter; Ward’s clustering method and Bray–Curtis distance. Cophenetic correlation coefficient = 0.75.

the accompanying species. During the rainy season it shows 36% of vegetation-free water surface and a mean water column depth of 1.5 m. In the driest season this environment shows 52% of waterlogged, vegetation-free soil.

LTZ. This environment is dominated by *Pontederia subovata*, *L. peruviana* and *Polygonum punctatum*, with *Eleocharis viridans* and *H. salzmannii* as accompanying species. During the rainy season, only 10% of the water surface is free of floating vegetation and water depth ranges between 10 and 45 cm. When there is no water and the percentages of bare ground and dry matter are 10% and 65% respectively, the height of *P. punctatum* is 15–30 cm and the remaining vegetation is up to 10 cm tall.

EMB. This environment is codominated by *L. peruviana*, *Hydrolea spinosa*, *Hedyotis salzmannii* and *Eleocharis minima*, with *Hydrocotyle verticillata*, *N. indica*, *Xiris jupicai* and *Cephalanthus glabratus* as accompanying species. It has a mean bare ground of 11%. Three vegetation strata can be recognized: upper intermediate and lower. *C. glabratus* is in the upper stratum (< 200 cm); *Eupatorium laetevirens*, *Hydrolea spinosa* and *Ludwigia* spp. are in the intermediate stratum (15–60 cm); short graminoid and broadleaf species dominate the lower stratum (< 15 cm).

Table 2 summarizes the most distinctive features of the habitats and plant communities.

Table 1. Constancy table for representative species of groups obtained in the cluster analysis (A, B and C). DM: dry matter; WV: without vegetation.

Group	Family	Scientific name	Proportion
A		DM	26.419
	Poaceae	<i>Andropogon lateralis</i>	12.289
	Poaceae	<i>Axonopus fissifolius</i>	11.361
	Cyperaceae	<i>Rhynchospora barrosiana</i>	10.666
	Poaceae	<i>Paspalum pumilum</i>	9.857
	Cyperaceae	<i>Rhynchospora emaciata</i>	6.479
	Apiaceae	<i>Centella asiatica</i>	4.365
	Poaceae	<i>Paspalum alnum</i>	4.229
		WV	2.621
	Poaceae	<i>Panicum schwackeanum</i>	1.485
B		DM	38.396
		WV	35.525
	Pontederiaceae	<i>Pontederia subovata</i>	28.206
	Rubiaceae	<i>Hedyotis salzmannii</i>	22.028
	Poaceae	<i>Luziola peruviana</i>	20.22
	Cyperaceae	<i>Eleocharis minima</i>	19.599
	Polygonaceae	<i>Polygonum punctatum</i>	16.673
	Poaceae	<i>Paspalum pumilum</i>	15.775
	Apiaceae	<i>Hydrocotyle verticillata</i>	11.117
	Apiaceae	<i>Centella asiatica</i>	8.14
C	Poaceae	<i>Axonopus fissifolius</i>	7.128
	Menyanthaceae	<i>Nymphoides indica</i>	7.037
	Cyperaceae	<i>Rhynchospora barrosiana</i>	6.925
	Poaceae	<i>Panicum dichotomiflorum</i>	4.828
	Cyperaceae	<i>Eleocharis sellowiana</i>	4.626
	Pontederiaceae	<i>Pontederia subovata</i>	24.86
		WV	20.678
	Poaceae	<i>Luziola peruviana</i>	17.664
	Hydroleaceae	<i>Hydrolea spinosa</i> var. <i>paraguayensis</i>	17.206
	Rubiaceae	<i>Hedyotis salzmannii</i>	13.911
C	Cyperaceae	<i>Eleocharis minima</i>	11.616
	Rubiaceae	<i>Cephalanthus glabratus</i>	8.999
		DM	8.623
	Salviniaceae	<i>Salvinia biloba</i>	7.179
	Asteraceae	<i>Eupatorium laetevirens</i>	6.879
	Apiaceae	<i>Hydrocotyle verticillata</i>	6.397
	Poaceae	<i>Panicum schwackeanum</i>	6.267
	Menyanthaceae	<i>Nymphoides indica</i>	6.119
	Xyridaceae	<i>Xyris jupicai</i>	5.462
	Cyperaceae	<i>Eleocharis sellowiana</i>	4.761

Table 2. Main distinctive features of the environments in the study area. EU: Environmental Units; UA: upland area; TP: temporary pond; UTZ: upper transition zone; LTZ: lower transition zone; EMB: “embalsado”; APV: vegetation-free limnetic areas with aquatic palustrine vegetation.

EU	Vegetation physiognomy	Vegetation mean height	Dominant species	Period with water
UA	Tall grassland dominated by a tall caespitose species	30–70 cm; inflorescences \geq 150 cm	<i>Andropogon lateralis</i>	Short-term waterlogging during prolonged or intense rainfalls, or during heavy floods
	Short grassland dominated by creeping stoloniferous species	5–15 cm; inflorescences \leq 30 cm	<i>Axonopus fissifolius</i> , <i>Paspalum pumilum</i> and <i>P. alnum</i>	
TP	Aquatic-palustrine communities (spring-summer)	–	<i>Hedyotis salzmannii</i> , <i>Polygonum punctatum</i> , <i>Eleocharis minima</i> , <i>Luziola peruviana</i> and <i>Pontederia subovata</i>	During the rainy season (spring-summer)
	Terrestrial communities (autumn-winter)	Up to 40 cm in the dry season	<i>Paspalum pumilum</i> , <i>Rhynchospora barrosiana</i> , <i>Centella asiatica</i> and <i>Axonopus fissifolius</i>	
UTZ	Communities dominated by short broadleaf and graminoid species	\leq 15 cm	<i>Paspalum pumilum</i> , <i>Hedyotis salzmannii</i> , <i>Eleocharis minima</i> and <i>Hydrocotyle verticillata</i>	At different times during the rainy season (spring-summer)
LTZ	Aquatic-palustrine communities	–	<i>Pontederia subovata</i> , <i>Luziola peruviana</i> and <i>Polygonum punctatum</i>	During the rainy season (spring-summer)
EMB	Upper stratum of woody shrubs	\geq 2m	<i>Cephalanthus glabratus</i>	–
	intermediate stratum of woody and broadleaf species	15–60 cm	<i>Eupatorium laetevirens</i> , <i>Hydrolea spinosa</i> and <i>Ludwigia</i> spp.	
	lower stratum of broadleaf and graminoid species	\leq 15 cm	<i>Luziola peruviana</i> , <i>Hydrolea spinosa</i> , <i>Hedyotis salzmannii</i> and <i>Eleocharis minima</i>	
APV	Aquatic-palustrine communities	–	<i>Luziola peruviana</i> , <i>Nymphoides indica</i> , <i>Hydrolea spinosa</i> and <i>Pontederia subovata</i>	All year round; soils may be waterlogged in autumn and winter

Seasonal variation

UA. The UA show significant differences in abundance-cover among seasons (Pillai's trace = 4.10, $p < 0.0001$). The first two axes of the discriminant analysis account for 85.5% of the total variation (Fig. 4). The first axis (74%) separates spring from the other seasons, due to the presence of *Paspalum pumilum*, *Axonopus fissifolius* and *Rhynchospora barrosiana*, while the second axis (15%) separates the remaining seasons along a gradient from summer to winter. At the negative end of the gradient (summer), the discriminant species is *Aeschynomene lorentziana*, while at the positive end (winter), there is an increase in the abundance-cover of *P. pumilum*, *Borreria ocymoides* and cover of dry matter; in autumn *A. lorentziana* and *P. pumilum* show intermediate values.

TP. The TP showed significant differences in plant abundance-cover among seasons (Pillai's trace = 8.29, $p < 0.0001$). The first axis of the discriminant analysis accounts for 85.4% of the total variation. The records of winter and autumn are located at the positive end of the first axis, showing high cover of dry matter and presence

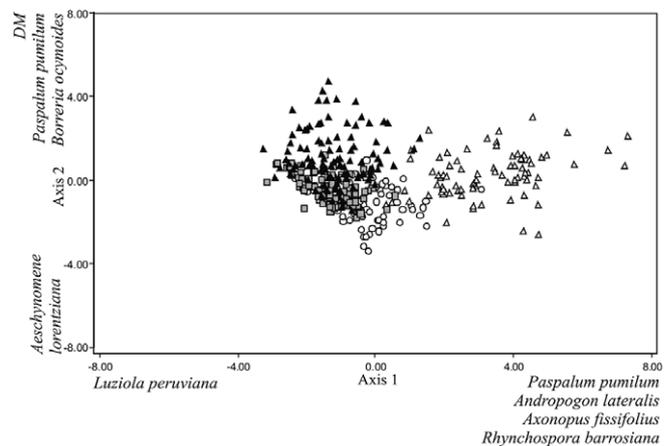


Fig. 4. Results of the Discriminant Analysis for the upland areas (UA) in the different seasons. Black triangle: winter; grey square: autumn; white circle: summer; white triangle: spring.

of *Polygonum punctatum*, *Conyza bonariensis* and *Paspalum pumilum*. The record of spring is located at the negative end of the first axis, with the presence of *Hydro-*

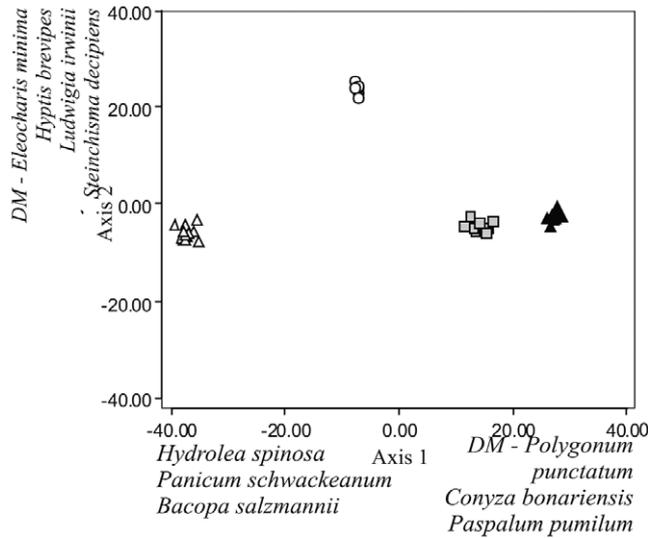


Fig. 5. Results of the Discriminant Analysis for the temporary ponds (TP) in the different seasons. Black triangle: winter; grey square: autumn; white circle: summer; white triangle: spring; DM: dry matter.

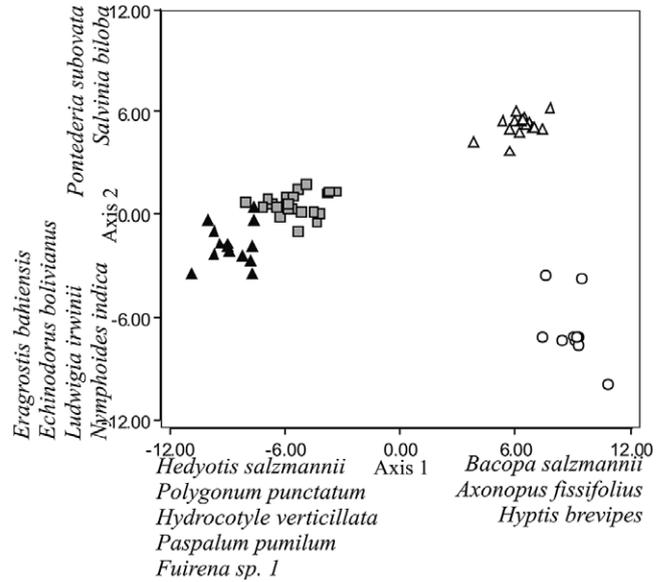


Fig. 7. Results of the Discriminant Analysis for the lower transition zones (LTZ) in the different seasons. Black triangle: winter; grey square: autumn; white circle: summer; white triangle: spring.

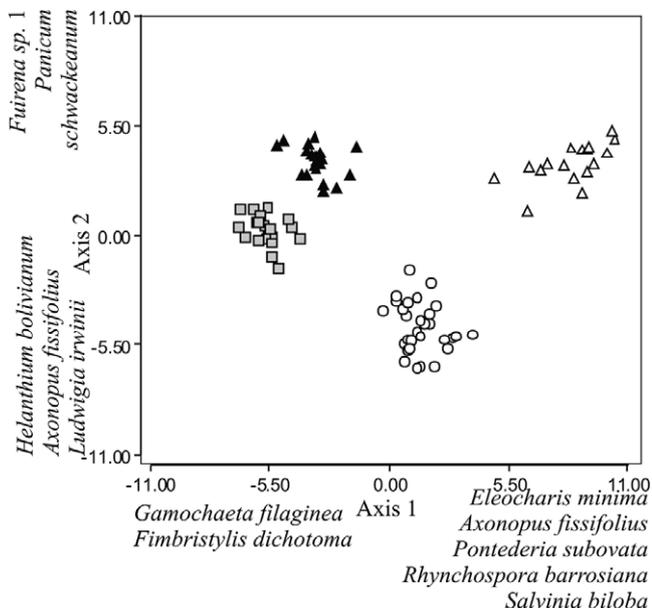


Fig. 6. Results of the Discriminant Analysis for the upper transition zones (UTZ) in the different seasons. Black triangle: winter; grey square: autumn; white circle: summer; white triangle: spring.

lea spinosa, *Panicum schwackeanum* and *Bacopa salzmannii*. The second axis explains 13% of the variation and separates summer from the rest of the seasons, with presence of *Eleocharis minima*, *Hyptis brevipes*, *Ludwigia irwinii* and *Steinchisma decipiens* (Fig. 5).

UTZ. The UTZ shows differences in abundance-cover among all seasons (Pillai's trace = 10.61, $p < 0.0001$). The first two axes explain 83.6% of the variation; the first axis (54%) separates winter from the rest of the seasons,

which are separated by the second axis (29.6%). The records of spring are located at the positive end of the first axis, with presence of *E. minima*, *Axonopus fissifolius*, *Pontederia subovata*, *R. barrosiana* and *Salvinia biloba*. The records of autumn are located at the negative end of the first axis, with presence of *Gamochaeta filaginea* and *Fimbristylis dichotoma*. Winter is separated from the rest of the seasons due to the presence of *Fuirena sp.* and *Panicum schwackeanum* (positive end of axis 2) while the presence or higher abundance-cover of *Helanthium bolivianum*, *A. fissifolius* and *L. irwinii* account for the separation of summer from the rest of the seasons (negative end of axis 2) (Fig. 6).

LTZ. The LTZ also shows seasonal differences (Pillai's trace = 12.84, $p < 0.0001$). The first two axes explain 84.7% of the variation. The records of autumn and winter (63.2%) are located at the negative end of the first axis, whereas those of spring and summer are distributed toward the positive values. The second axis (21.5%) separates autumn and summer from the rest of the seasons (Fig. 7). The presence of *B. salzmannii*, *A. fissifolius* and *Hyptis brevipes* separates the records of summer from the rest of the seasons, whereas the presence and higher abundance-cover of *Hedyotis salzmannii*, *Polygonum punctatum*, *Hydrocotyle verticillata*, *Paspalum pumilum* and *Fuirena sp. 1* separates the records of winter (negative values of the second axis). Spring (positive values of the second axis) is characterized by higher abundance-cover of *Pontederia subovata* and *S. biloba*.

APV. The APV exhibits seasonal variations (Pillai's trace: 34.13; $p < 0.0001$). The first two axes of the discriminant analysis account for 97.9% of the total variation (Fig. 8). The records of autumn are distributed toward

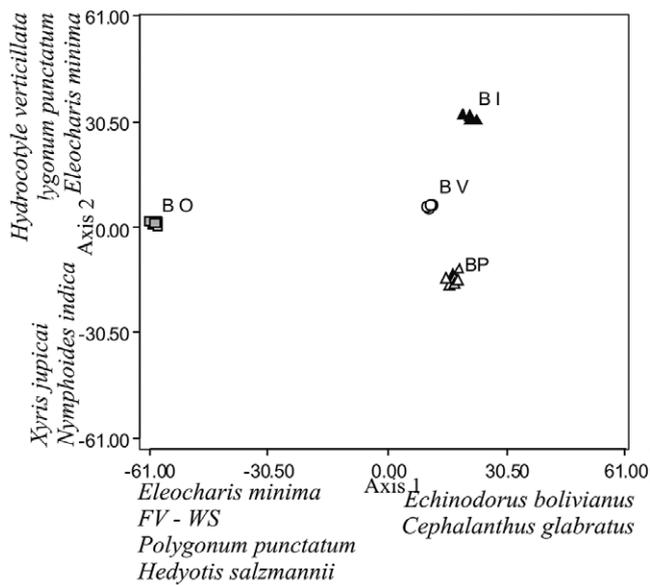


Fig. 8. Results of the Discriminant Analysis for the limnetic areas (APV) in the different seasons. Black triangle: winter; grey square: autumn; white circle: summer; white triangle: spring; FV: free vegetation; WS: waterlogged soils.

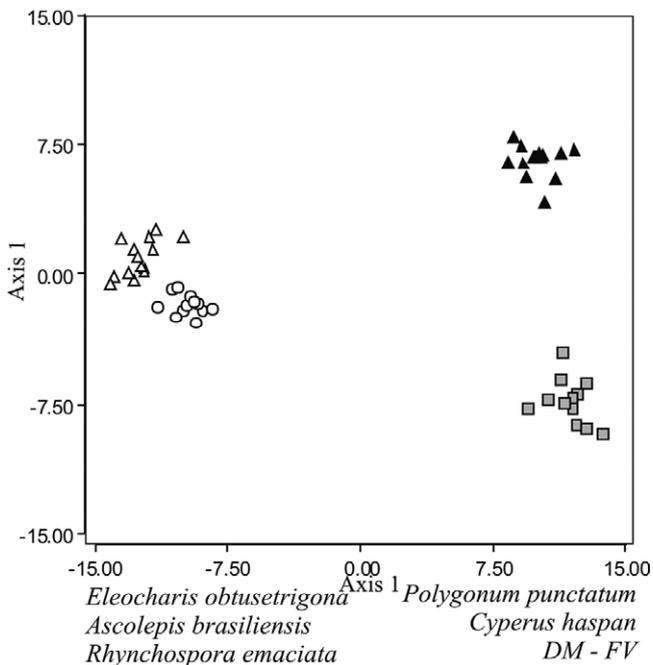


Fig. 9. Results of the Discriminant Analysis for the "embalsados" (EMB) in the different seasons. Black triangle: winter; grey square: autumn; white circle: summer; white triangle: spring; FV: free vegetation; DM: dry matter.

the negative values of the first axis (76.4%), which are characterized by high cover of bare ground, vegetation-free water surface and presence of *E. minima*, *Polygonum punctatum* and *Hedyotis salzmannii*. The presence of *Helanthium bolivianum* and *Cephalanthus glabratus* se-

parates the remaining seasons at the positive end of the first axis (21.5%). The records of winter are located at the positive end of the second axis, with presence of *Hydrocotyle verticillata*, *P. punctatum* and *E. minima*, and the records of spring are distributed toward the negative values, with higher abundance-cover of *Xyris jupicai* and *Nymphoides indica*.

EMB. Although the EMB is the most stable environment, MANOVA indicates differences among seasons (Pillai's trace: 5.90; $p < 0.0001$). The first axis of the discriminant analysis explains 76.7% of the variation (Fig. 9). The multiple comparisons revealed differences between autumn and winter and between spring and summer. The coldest seasons are separated from the others by higher cover of dry matter and bare ground, and higher abundance-cover of *Cyperus haspan* and *P. punctatum*. On the contrary, the warmest seasons are separated by higher abundance-cover of *E. obtusetrigona*, *Ascolepis brasiliensis* and *R. emaciata*.

There are differences in the analyzed attributes of the vegetation communities (total species richness, S; species diversity, H; and evenness, E) (Pillai's trace = 1.7, $p < 0.0001$). The upland and APV (UA and APV respectively) differed from the other environments (Table 3). The first two axes of the discriminant analysis account for 98.8% of the total variation. The UP differs by higher richness and lower evenness whereas the APV differs by higher evenness and diversity.

The species accumulation curve (Mao Tau function) for the environments of lowest species richness indicate that the number of plots censused seasonally was relatively adequate, except for the APV (Fig. 10). This environment is relatively homogeneous within each season but it becomes almost inaccessible during seasons when water level is high, for these reasons the number of plots censused in APV was not increased.

Values of species richness, diversity and evenness in the different environments are shown in Table 3.

Table 3. Multiple comparisons of MANOVA for species Richness (S), Diversity (H) and Evenness (E) of the different environments (Env). APV: limnetic areas; UA: upland area; LTZ: lower transition zone; TP: temporary pond; EMB: "embalsado"; UTZ: upper transition zone.

Env	S	H	E	
APV	14.5	2.14	0.8	a
UA	49.5	2.43	0.63	b
LTZ	28	2.38	0.72	c
TP	30.75	2.61	0.77	c
EMB	34.75	2.57	0.73	c
UTZ	32.5	2.73	0.79	c

Different letters (a, b, c) indicate significant differences ($p < 0.05$).

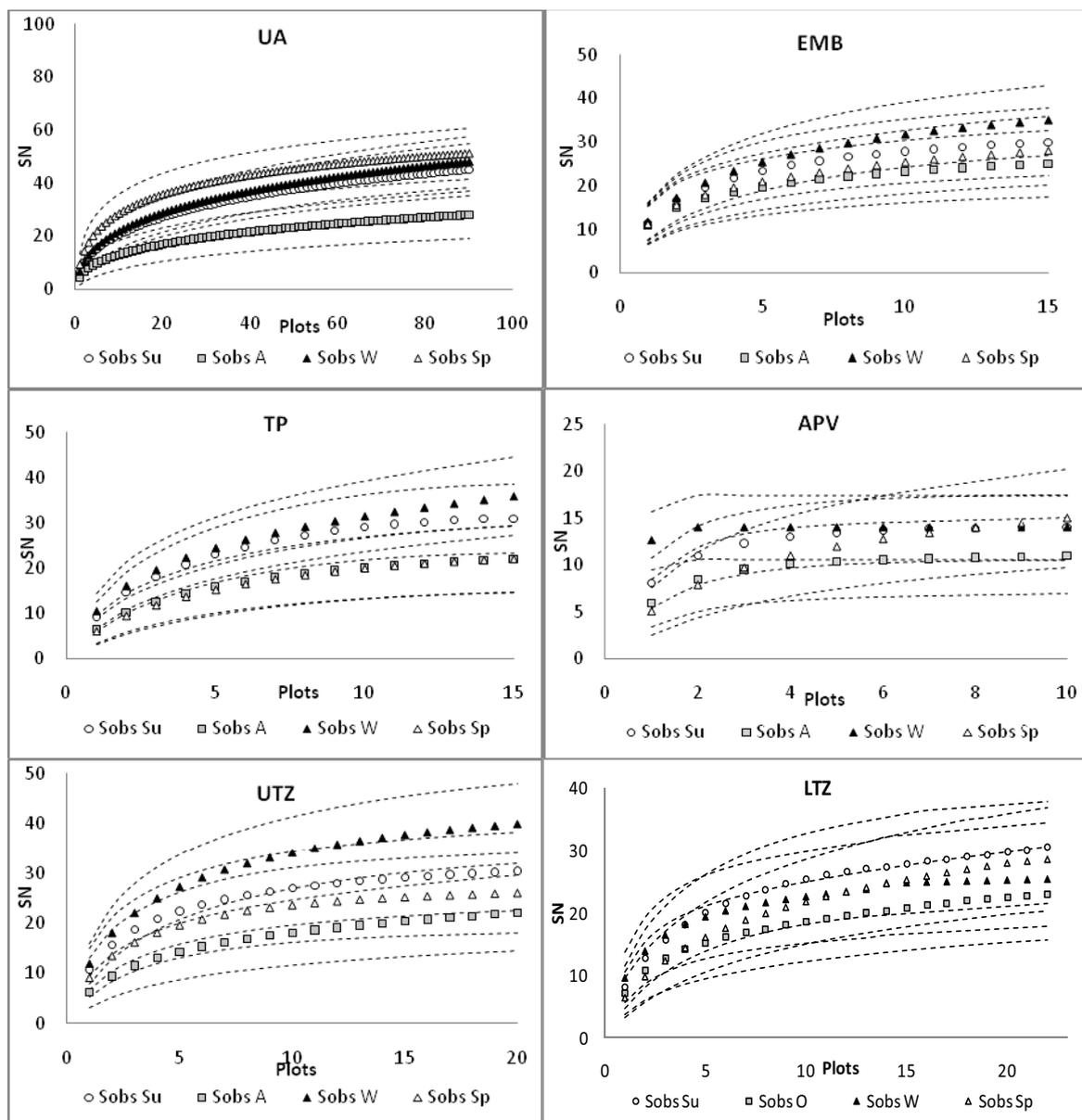


Fig. 10. Species-accumulation curve for the vegetation in each environment present on a sandy ridge in the Iberá Macrosystem (Corrientes). Surveys were performed between spring 2007 and winter 2008. Dotted lines are the 95% confidence intervals. Sp: spring; Su: summer; A: autumn; W: winter; UA: upland area; UTZ: upper transition zone; LTZ: lower transition zone; APV: limnetic areas with aquatic palustrine vegetation; EMB: “embalsado”; TP: Temporary pond.

Discussion

While multiple factors are undoubtedly important in determining the presence of a particular vegetation type at a given spatial location in a diverse and dynamic landscape, our results show that seasonal hydrological processes and the topography have a major influence on plant cover types and species combinations. Our results support the concept that many vegetation communities in wetlands are on hydrological gradients (ARMENTANO et al. 2006, OLMSTED & ARMENTANO 1997, TODD et al. 2010) and that the change in vegetation in response to hydrologic fluctuation

can be relatively rapid (i.e. season). Water regime is a major determinant of plant community development and patterns of plant zonation in wetlands. It can be described by the depth, duration, frequency, rate of filling and drying, timing and predictability of flooded and dry phases in a wetland (BUNN et al. 1997). In our study the large intra-annual variation in water regime produce a variety of plant communities. The patterns of plant zonation in this wetland are changed from season to season as water levels fluctuate in space and time making the system very susceptible to changes in the hydrometric level. This spatio-temporal variation in plant communities in

response to the flooding regime has been observed in the Venezuelan plains (RIAL 2001, 2004, 2006), in the Amazonas (JUNK 1984), in the Pantanal of Brazil (PINDER & ROSSO 1998, ZEILHOFER & SCHESSL 1999), in the Paraná Basin (NEIFF 1986, THOMAZ et al. 2009), and also in other non American floodplain systems like those referred by GOPAL (1990) in India.

In addition, at local level, there are impacts caused by livestock activities. The natural pastures are modified by grazing (selective foraging) and also by the burning produced by the farmers to encourage regrowth of grasses, thus causing variations in the vegetation composition and physiognomy (LATERRA 2003, OVERBECK et al. 2007, OVERBECK & PFADENHAUER 2007).

The high species richness may be related to intrinsic factors of the wetland such as environmental diversity and heterogeneity, which are determined by the topography and the local hydrological dynamics (hydromorphism) (NEIFF 1999, NEIFF 2001, NEIFF & MALVAREZ 2004); and the moderate levels of disturbance that increase species richness (CONNELL 1978, GUO 1996, POLLOCK et al. 1998), which is highest at intermediate values of biomass in both wetlands and grasslands (TILMAN 1982, RODRIGUEZ et al. 1987, HUSTON 1994, CORNWELL & GRUBB 2003). In this study, most of the dominant species were perennial, in accordance with that reported for other grasslands subjected to moderate levels of disturbance (LATERRA 2003, MADANES et al. 2007). The increase in species richness coincided with decreasing hydroperiod, or increasing topographic elevation, this was also observed in the Brazilian Pantanal (PINDER & ROSSO 1998).

Poaceae, Cyperaceae, Fabaceae and Asteraceae were the dominant families in the area, which is in agreement with the composition described for grasslands on sandy ridges in the central region of the Iberá Macrosystem (ARBO & TRESSENS 2002, CARNEVALLI 2003, NEIFF 2004). The most representative families in number of species are largely the same for both the Paraná floodplain and the Pantanal ecosystems (THOMAZ et al. 2009, ALVES FERREIRA et al. 2011). Most of the species in the environments were native, possibly because the study area was surrounded by marshes contributing to a relative isolation. The fact that it was located on a private reserve with low levels of anthropogenic disturbance, low cattle density and restrictions on the movement of cattle from other locations may have prevented the introduction of non-native species. In addition, controlled burns implemented in the Park would have favored native over exotic species (DI FRANCESCANTONIO 2009).

The results of the Conglomerate Analysis (major groups A, B and C) coincide with those of the MANOVA. The comparison of the transition zones (UTZ, LTZ) and the temporary ponds (TP) yielded no significant differences in abundance-cover when autumn, winter and spring were considered. This variable was more

similar among environments within a season than among seasons within an environment. In conclusion, many of the habitats characterized in this wetland system showed higher quality and quantity variations (composition and abundance, respectively) in the plant communities over time than when compared with other environments (other vegetation communities) at a single point in time.

These results, together with the classification of the environments, suggest that the different communities would be determined by the topographic gradient and associated edaphic factors. These would also affect species richness, evenness and diversity as suggested by the fact that the environments subjected to substantial variation in the water level showed similar values of these variables. Moreover, species richness, evenness and diversity seemed to increase with increasing fluctuations, which is consistent with the intermediate disturbance hypothesis (CONNELL 1978, GUO 1996, POLLOCK et al. 1998). On the other hand, the uplands, with low variation in the water level and subjected to occasional short periods of waterlogging, showed high species richness and low evenness. This was due to the dominance of *Andropogon lateralis* and the presence of several isolated species with low cover in the grassland. Finally, the APV, which is filled with water during almost the entire year showed higher evenness and lower diversity and richness compared to the other environments. A low species richness has been reported from lowlands in the Paraná River Delta (QUINTANA et al. 2002) and in natural communities in the Lower Delta, characterized by being simple and dominated by a few species (KANDUS et al. 2003).

Notwithstanding the marked seasonal differences in the composition, abundance and cover of the different species among environments, values were more similar between spring and summer and between autumn and winter, probably due to seasonal variations in water level and temperature in the study area. This is in agreement with NEIFF (2004), who stated that the dynamics of water was the factor most affecting these variables, despite the importance of other disturbs such as fire and grazing in terms of both frequency and intensity.

The composition, abundance and physiognomy of vegetation are important in studies of habitat use and habitat selection by both domestic animals and wildlife because they determine the structural characteristics of the habitat (ROTENBERRY & WIENS 1980). In addition, these variables may be useful to infer the availability of resources such as food, breeding sites and shelter from predators (HILDÉN 1965, WIENS 1992).

The floristic composition of grasslands is a parameter of foraging quality which determines the grazing responses, together with grassland management, dry matter yield and environmental factors (ROYO PALLARES & GOLDFARB 1999, PIZZIO et al. 2000, SAMPEDRO et al. 2004). Based on species composition and cover, grasslands in the uplands may provide a high amount of forage supply.

The most representative species in the uplands, *A. lateralis* and the short *Axonopus fissifolius*, *Paspalum alnum*, *P. pumilum* and *Rhynchospora barrosiana* found in the grasslands, have been described as soft grasses of high grazing value present throughout the year (HOYOS & LASCANO 1988, PÉREGO 2002, PIZZIO & FERNANDEZ 2003, SAMPEDRO et al. 2004, ARBÓ & TRESSENS 2002). The low and high transition zones also harbor species of high grazing value, such as *P. pumilum* and *A. fissifolius* – occurring in the uplands – and the palustrine species *Eleocharis minima*, *Luziola peruviana* (VEGA ORDUZCOMO & STEVENSON 2007) and *Hydrocotyle verticillata* (VELÁQUEZ 1994).

Advances in the “esterización” process would involve a decrease in plant species richness and a decrease in the production areas, and moreover, the loss of habitats of many species of wildlife. This study provides information for studies on habitat use and selection by commercially important species like the capybara (*Hydrochoerus hydrochaeris*) or threatened with extinction like the marsh deer (*Blastocercus dichotomus*). Moreover, it is an indispensable tool for the management of protected areas in the region. Knowledge of the spatial and temporal variability of these wetland environments obtained in our study is a baseline that allows evaluating future changes in response to anthropogenic modifications as well as the ecosystem response to global climate change in one of the most important wetlands in South America.

Acknowledgements: The authors would like to thank Conservation Land Trust and Sr. Salvador Sotelo and his family for their help and support during this study. Research was partially funded by grant X-481 (UBACyT) from the University of Buenos Aires. We also thank Dra. María Gabriela López (Instituto de Botánica del Nordeste, Corrientes, Argentina) and Dr. Diego Salariato (Instituto Darwinion, San Isidro, Argentina) for their assistance in the identification of samples of *Bulbostylis* and *Axonopus* respectively.

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Electronic appendix

Appendix A. Mean cover percentage for species of vascular plants in the study area (28°00 S 57°18W) between November 2006 and October 2008. Esteros del Iberá, Corrientes, Argentina.

Appendix data associated with this article can be found in the online version at www.schweizerbart.de/journals/phyto

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Appendix A. Mean cover percentage for species of vascular plants in the study area (28°00 S 57°18W) between November 2006 and October 2008. Esteros del Iberá, Corrientes, Argentina. S: status; UA: upland area; APV: limnetic areas; EMB: “embalsado”; UTZ: upper transition zone; LTZ: lower transition zone; TP: Temporary ponds; S: status; N: native; E: endemic; Ad: adventive; r: rare; DM: dry matter; WV: without vegetation.

Family	Species	S	APV	EMB	UTZ	LTZ	TP	UA
Acanthaceae	<i>Justicia laevilinguis</i>	N	0.13			0.192		
Alismataceae	<i>Helanthium bolivianum</i>	N	2.004	1.154	2.313	0.806	0.377	0.019
	<i>Sagittaria rhombifolia</i>	N		0.392				
Amaranthaceae	<i>Alternanthera philoxeroides</i>	E		0.09				
Apiaceae	<i>Centella asiatica</i>	N		<0.001	4.208	0.967	2.965	4.365
	<i>Eryngium elegans</i>	N						0.06
	<i>Eryngium sanguisorba</i>	N					0.052	0.029
	<i>Hydrocotyle ranunculoides</i>	N		1.412				
Asteraceae	<i>Hydrocotyle verticillata</i>	N	2.252	4.145	7.333	2.291	1.493	0.167
	<i>Baccharis articulata</i>	N			0.002			
	<i>Chrysolaena cognata</i>	N						r
	<i>Chrysolaena flexuosa</i>	N			0.03	0.677	0.005	0.066
	<i>Conyza aff. bonariensis</i>	N	0.117		0.155	0.079	0.125	0.0007
	<i>Erechtites hieracifolius</i>	Ad	0.039	0.017	0.028		0.0003	
	<i>Eupatorium candolleianum</i>	E						r
	<i>Eupatorium laetevirens</i>	N	2.592	4.287	0.117	0.508	0.392	0.009
	<i>Eupatorium macrocephalum</i>	N		0.401	0.019			0.021
	<i>Eupatorium subhastatum</i>	E						0.0003
	<i>Facelis aff. retusa</i>	E			<0.001			
	<i>Gamochaeta filaginea</i>	E			0.203	0.004	0.081	0.01
	<i>Mikania periplocifolia</i>	N	0.913	0.762	0.003	0.03		
	<i>Orthopappus angustifolius</i>	N						0.031
	<i>Pterocaulon angustifolium</i>	N						r
	<i>Pterocaulon polystachyum</i>	E				0.105		
<i>Vernonia cognata</i>	N						r	
<i>Vernonia flexuosa</i>	E						r	
Boraginaceae	<i>Heliotropium</i> sp1		0.25	0.798	0.097	0.085	0.065	
Callitrichaceae	Aff. <i>Callitriche deflexa</i>	N				0.007		
Campanulaceae	<i>Lobelia hederacea</i>	N					0.008	0.229
Cyperaceae	Aff. <i>Oxycaryum cubense</i>	N		0.0001		0.105		
	<i>Ascolepis brasiliensis</i>	N		0.223				
	<i>Bulbostylis capillaris</i>	N					r	
	Cyperaceae X		0.43	0.119		0.008		
	Cyperaceae Y							r

	Cyperaceae Z							r
	<i>Cyperus aggregatus</i> var. <i>aggregatus</i>	N			0.0001			
	<i>Cyperus haspa</i> var. <i>haspan</i>	N	0.399	0.258	0.024	0.371	0.096	<0.001
	<i>Eleocharis filiculmis</i>	N	0.13	0.154	0.808	0.074		
	<i>Eleocharis minima</i>	N	2.98	8.636	10.155	4.166	5.278	0.481
	<i>Eleocharis obtusetrigona</i>	N		0.177	0.148	0.077	0.047	
	<i>Eleocharis sellowiana</i>	N	1.711	3.05	3.416	0.51	0.7	0.238
	<i>Eleocharis viridans</i>	E	1.543		0.191	1.801	0.94	
	<i>Fimbristylis dichotoma</i>	Ad			0.101	0.097	0.079	0.195
	<i>Fuirena robusta</i>	N		r				
	<i>Fuirena</i> sp1.		0.24	0.099	0.745	0.195	0.96	0.171
	<i>Fuirena</i> sp2.			0.066				
	<i>Kyllinga odorata</i>	N						0.214
	<i>Kyllinga vaginata</i>	N			r			
	<i>Lipocarpa humboldtiana</i>	N						<0.001
	<i>Rhynchospora barrosiana</i>	N		0.006	3.869	0.253	2.803	10.666
	<i>Rhynchospora emaciata</i>	N	0.133	0.241	0.473	0.086	0.405	6.479
	<i>Scleria distans</i>	N		0.406				0.973
Droseraceae	<i>Drosera brevifolia</i>	N						0.007
Eriocaulaceae	<i>Eriocaulon magnum</i>	E	0.692	1.084				
	<i>Syngonanthus caulescens</i>	N	0.056	0.793			0.035	0.0003
Euphorbiaceae	<i>Caperonia castaneifolia</i>	N					0.047	
	<i>Euphorbia papillosa</i>	N						0.041
Fabaceae	<i>Aeschynomene falcata</i>	N						0.078
	<i>Aeschynomene lorentziana</i>	N						0.028
	<i>Aeschynomene montevidensis</i>	N	0.009	0.156		0.033		
	<i>Arachis correntina</i>	E						0.037
	<i>Chamaecrista rotundifolia</i>	N		0.005				0.087
	<i>Desmodium barbatum</i>	N						0.596
	<i>Indigofera asperifolia</i>	N						0.022
	<i>Stylosanthes guianensis</i> var. <i>subviscosa</i>							0.008
	<i>Zornia gemella</i>	N						0.042
Hydrocharitaceae	<i>Limnobium laevigatum</i>	N	r					
Hydroleaceae	<i>Hydrolea spinosa</i> var. <i>paraguayensis</i>	N	6.549	10.657	2.641	1.19	0.683	0.02
Hypoxidaceae	<i>Hypoxis decumbens</i> L.	N						0.075
Iridaceae	<i>Sisyrinchium micranthum</i>	N						0.189
	<i>Sisyrinchium</i> sp				r			
Juncaceae	<i>Juncus microcephalus</i>	N		0.429	0.452	0.576	1.208	0.022
Lamiaceae	<i>Hyptis brevipes</i>	N	1.556	0.046	1.508	0.218	1.945	0.345
Lentibulariaceae	<i>Utricularia gibba</i>	N	0.02	0.008				
Limnocharitaceae	<i>Hydrocleys nymphoides</i>	N	0.332					
Lythraceae	<i>Cuphea carthagenensis</i>	N			<0.001			0.021

Marsileaceae	<i>Regnellidium diphyllum</i>	E		0.171		0.082		
Mayacaceae	<i>Mayaca fluviatilis</i>	N	1.64	0.6	0.179	0.338	1.56	
Melastomataceae	<i>Acisanthera alsinaefolia</i>	N		0.039	0.359	0.103	0.113	0.33
	<i>Tibouchina gracilis</i>	N						0.527
Menyanthaceae	<i>Nymphoides indica</i>	N	3.292	2.827	2.38	2.424	2.233	0.049
Molluginaceae	<i>Glinus radiatus</i>	N				0.042	0.172	
Onagraceae	<i>Ludwigia grandiflora</i>	N	0.83	0.574	0.793	1.023	1.323	0.024
	<i>Ludwigia irwinii</i>	N	0.104	0.082	0.324	0.087	0.279	0.016
	<i>Ludwigia leptocarpa</i>	N	0.0004	0.056	0.004	0.063	0.01	
	<i>Ludwigia peploides</i>	N	0.3	1.284				
	<i>Ludwigia sericea</i>	N	0.656	0.117	0.23	0.201	0.186	0.0348
	<i>Oenothera</i> sp.				0.006			
Ophioglossaceae	<i>Ophioglossum ellipticum</i>	N			0.404		0.198	0.378
Orchidaceae	<i>Habenaria</i> aff. <i>repens</i>	N		0.056				
Orobanchaceae	<i>Buchnera longifolia</i>	N						r
Phyllanthaceae	<i>Phyllanthus stipulatus</i>	N						0.006
Plantaginaceae	<i>Bacopa dubia</i>	N						<0.001
	<i>Bacopa salzmannii</i>	N	1.278	2.379	2.564	0.265	0.701	0.021
	<i>Estemodia</i> sp.				0.045	0.019	0.102	
	<i>Gratiola peruviana</i>	N			0.156	0.685	1.127	0.022
	<i>Scoparia dulcis</i>	N		0.034	0.767	0.794	0.566	0.043
	<i>Scoparia montevidensis</i>	N						0.033
Poaceae	<i>Andropogon lateralis</i>	N		0.01	0.106		0.005	12.29
	<i>Andropogon selloanus</i>	N						0.407
	<i>Anthaenantia lanata</i>	N						r
	<i>Axonopus fissifolius</i>	N	0.001		4.901	0.529	1.698	11.36
	<i>Digitaria eriostachya</i>	N						r
	<i>Eragrostis bahiensis</i>	N		0.078	0.181	0.126	0.028	0.626
	<i>Eragrostis hypnoides</i>	N	0.242		0.077	2.405	0.815	
	<i>Imperata brasiliensis</i>	N	0.264					
	<i>Luziola peruviana</i>	N	7.935	9.729	4.909	8.535	6.776	0.063
	<i>Panicum</i> aff. <i>pedersenii</i>	E		0.102		0.033		
	<i>Panicum dichotomiflorum</i>	N			1.368	2.096	1.364	0.518
	<i>Panicum schwackeanum</i>	N	0.735	5.532	0.867		0.759	1.485
	<i>Panicum stoloniferum</i>	N					0.492	0.027
	<i>Paspalum acuminatum</i>	N			0.027			
	<i>Paspalum almum</i>	N			0.292	0.006	0.082	4.229
	<i>Paspalum nicorae</i>	E						0.007
	<i>Paspalum notatum</i>	N						0.062
	<i>Paspalum pumilum</i>	N	0.0004	0.209	9.69	2.57	3.515	9.857
	<i>Paspalum</i> sp.1				0.016		0.031	0.199
	<i>Setaria parviflora</i>	N						0.192
	<i>Steinchisma decipiens</i>	N			0.093		0.055	0.508
	<i>Steinchisma laxa</i>	N						r
Polygalaceae	<i>Polygala leptocaulis</i>	N						r
	<i>Polygala longicaulis</i>	N						0.0002

	<i>Polygala molluginifolia</i>	N						0.0005
	<i>Polygala timoutoides</i>	N			0.003		0.005	0.0701
	<i>Polygonum meisnerianum</i>	N						r
	<i>Polygonum punctatum</i>	N	1.444	2.777	1.019	7.809	7.845	0.0009
Pontederiaceae	<i>Pontederia subovata</i>	N	24.413	0.447	2.909	15.192	10.105	0.017
Primulaceae	<i>Centunculus minimus</i>	Ad			0.075		0.035	0.0002
Ranunculaceae	<i>Ranunculus bonariensis</i>	N		0.048	0.053		0.647	
Rubiaceae	<i>Borreria ocymoides</i>	N			0.14		0.066	0.008
	<i>Cephalanthus glabratus</i>	N	5.11	3.889		0.082		
	<i>Diodia kuntzei</i>	N			0.096	0.006		0.037
	<i>Hedyotis salzmannii</i> synonymous to <i>Oldenlandia salzmannii</i>	N	4.231	9.68	7.076	5.227	9.725	0.7
Salviniaceae	<i>Salvinia biloba</i>	N	6.677	0.502	0.213	1.938	1.206	
Solanaceae	<i>Solanum americanum.</i>	N						
	<i>Solanum reflexum</i>	N		0.703		<0.001	0.0001	
Sterculiaceae	<i>Melochia villosa</i> var. <i>tomentosa</i>	N				0.121		
Thelypteridaceae	<i>Thelypteris interrupta</i>	N		0.037				
Verbenaceae	<i>Lippia</i> sp.							0.0004
	<i>Lippia turnerifolia</i>	N			r			
Xyridaceae	<i>Xyris guaranitica</i>	N						0.009
	<i>Xyris jupicai</i>	N	1.137	4.325	0.323		0.158	0.228
	Dicotyledonea 1							0.0001
	Dicotyledonea 2							0.0001
	Dicotyledonea 3			0.095				
	Dicotyledonea 4		1.087					
	WV		11.379	9.299	8.659	14.456	12.41	2.621
	DM		5.278	3.345	8.912	17.102	12.382	26.419
