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Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil

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Abstract

A phytosociological study was conducted in a riparian forest of the Rio Paraguai near Corumbá and Ladário in the state of Mato Grosso do Sul, Brazil. The topographic distribution of species was correlated with durations of the river's seasonal floodings and the cumulative time of flooding between 1974 and 1995. One hundred and eight contiguous 10×10 m plots were systematically established. All individuals with more than 15 cm of girth at breast height (gbh = 1.3 m) were sampled. A total of 695 individuals distributed among 37 species, 35 genera and 23 families were found. The Shannon index (H') for species diversity was 2.7. The highest importance value (IV) was found for *Inga vera* ssp. *affinis*, followed by *Triplaris gardneriana*, *Ocotea diospyrifolia*, *Crataeva tapia* and *Vochysia divergens*. The plots were classified into two groups according to their distance from the margin, applying Ward's method of classification and principal coordinate analysis (PCO) on the same Bray Curtis distance matrix. The topical environments were divided into four bands by Two-Way Indicator Species Analysis (TWINSPAN), and the species were also grouped into four groups. Flooding in these groups ranged from regular inundation in all 23 years of the historical series of the Ladário gauge to sporadic flooding for a maximum of 2 consecutive years.

Keywords: Flooding; Riparian forest; Topographic distribution; Pantanal; Rio paraguai; Community structure

Introduction

Seasonal inundation can produce many effects on plant communities. It can decrease the growth rate of trees (Worbes, 1985), change the metabolism of woody species (Joly, 1994) and influence the morphology of individuals and the richness, structure, and distribution of species and communities (Junk, 1996).

Many researchers have focused studies on the distribution and organization of vegetation in riparian zones. In these ecosystems, variations in topography, landform and soils have strong effects on species composition, distribution and structure both in tropical (Campbell et al., 1992; Oliveira-Filho et al., 1994b) and temperate environments (e.g. Metzler and Damman, 1985; Nakamura et al., 1997; Pabst and Spies, 1998). Furthermore, river dynamics can also determine

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patterns of succession and distribution of species (Puhakka and Kalliola, 1995; Schnitzler, 1997).

The Pantanal is an over 140,000 km^2 quaternary floodplain, which originated from the sinking of the region of the high Rio Paraguai basin. It is located in central South America, mainly in Brazil, with some extensions into Paraguay and Bolivia (BRASIL, 1982). The Brazilian Pantanal has many kinds of woody vegetation that are subjected to inundation. Most of them are monodominant (e.g. acurizal, dominated by *Attalea phaleratta* Mart. ex Spreng.; cambarazal, dominated by *Vochysia divergens* Pohl and carandazal, dominated by *Copernicia alba* Morong). Other plant communities include forests with several co-dominant species (Pott, 1994). The riparian forest, which occurs along the main rivers and secondary channels, is the main kind of forest vegetation subjected to regular flooding in the Pantanal.

Studies on the structure and species composition of riparian forests in the Pantanal are rare (i.e. Guarin-Neto et al., 1996; Veloso, 1947). Most of the surveys on woody plant communities in this region focus on non-flooded or partially flooded vegetation like cerradões (a savannah-like vegetation type) and semi-deciduous forests (e.g. Dubs, 1994, Prance and Schaller, 1982; Ratter et al., 1988; Salis, 2000; Salis et al., 1999; Soares, 1997). Recent studies explore the relations between inundation and structure and distribution of species in the Pantanal (e.g. Adámoli and Pott, 1999; Damasceno-Junior et al., 1999; Nunes Da Cunha and Junk, 1999; Prado et al., 1994; Pinder and Rosso, 1998; Zeilhofer and Schessl, 1999), but none of them describes the length and frequency of flooding in woody vegetation areas, and they do not show in detail in a single place the woody sub-communities delimitated by topographic position and inundation regime.

In Corumbá and places nearby, there is a great range of riparian forests along the Rio Paraguai. This river supports the largest areas of flooded riparian forests in the Pantanal. The aim of this study was to describe the tree community structure of the Rio Paraguai riparian forest and to investigate the relationships of structure between the topographic distribution of species and the timing of floods.

Materials and methods

Study area

The study site was located on the right bank of the Rio Paraguai downstream from the Rabicho ranch between 19° 01′12″–19° 01′16″ S and 57° 27′ 01″–57° 26′ 44″W in the Pantanal of the Rio Paraguai subregion, municipality of Corumbá, Mato Grosso do Sul State, Brazil (Fig. 1).

The topography of the site is very flat, with a slope less than 2 cm km^{-1} from north to south, the same direction that the Rio Paraguai flows. In this area, the river has numerous secondary channels, meanders, oxbow lakes, islands and a large area of seasonally flooded fields. The total inundation area of the Rio Paraguai has varied from nearly 4000 to 16,000 km^2 between low and high water seasons during the last 95 years (Hamilton et al. 1996). The riparian forests are mainly located in convex parts of meanders, where sets of narrow riverbanks are deposited during the floods.

According to BRASIL (1982), the prevailing soils in the study area are eutrophic, clayey to moderately clayey. On the riverbank there is a sandy horizon on the superficial layer followed by a clay horizon, which is thicker on the higher parts and thinner toward the rear.

This area, like all of the Pantanal, has a distinct wet and dry season, a dry winter and rainy summer (Awa according to the Köppen system) with a mean annual precipitation of 1070 mm (Soriano, 1997). In this area, the Rio Paraguai has a unimodal flood pulse. The flooding peak is reached in the dry season, with the lowest level occurring in the rainy months (Fig. 2). This occurs because the local inundation depends on the rains of the upper basin, whose peak flows take about 3 months to reach the study area. During normal flood periods only higher riverbanks escape inundation, and in major floods, the entire floodplain is inundated.

This region is delimitated by hills reaching peaks of 1065 m. These uplands support a variety of plant communities. Semi-deciduous and deciduous forests are the predominant types. In flooded places, there are riparian forests along the Rio Paraguai, seasonally flooded grasslands and aquatic vegetation in the lagoons and water channels (Bortolotto et al., 1999). The riparian forest varies from evergreen to alluvial semi-deciduous forest, where some deciduous floristic elements are more abundant (Damasceno-Junior, 1997) and is classified as "Floresta estacional semidecidual aluvial" by the Brazilian system of vegetation classification (IBGE, 1992).

Data collection and analysis

A set of 108 contiguous 10 × 10 m plots was systematically established to sample all locations of the riverbank (Fig. 1). The plots were placed in blocks spaced at 1 or 2 m intervals in order to avoid overlapping due to irregularities in the natural edge. The rear, where another riverbank joined the study area, was avoided. All individuals with stems or at least one branch of 15 cm or more of girth at breast height (1.3 m above the ground level) were sampled, including palms.

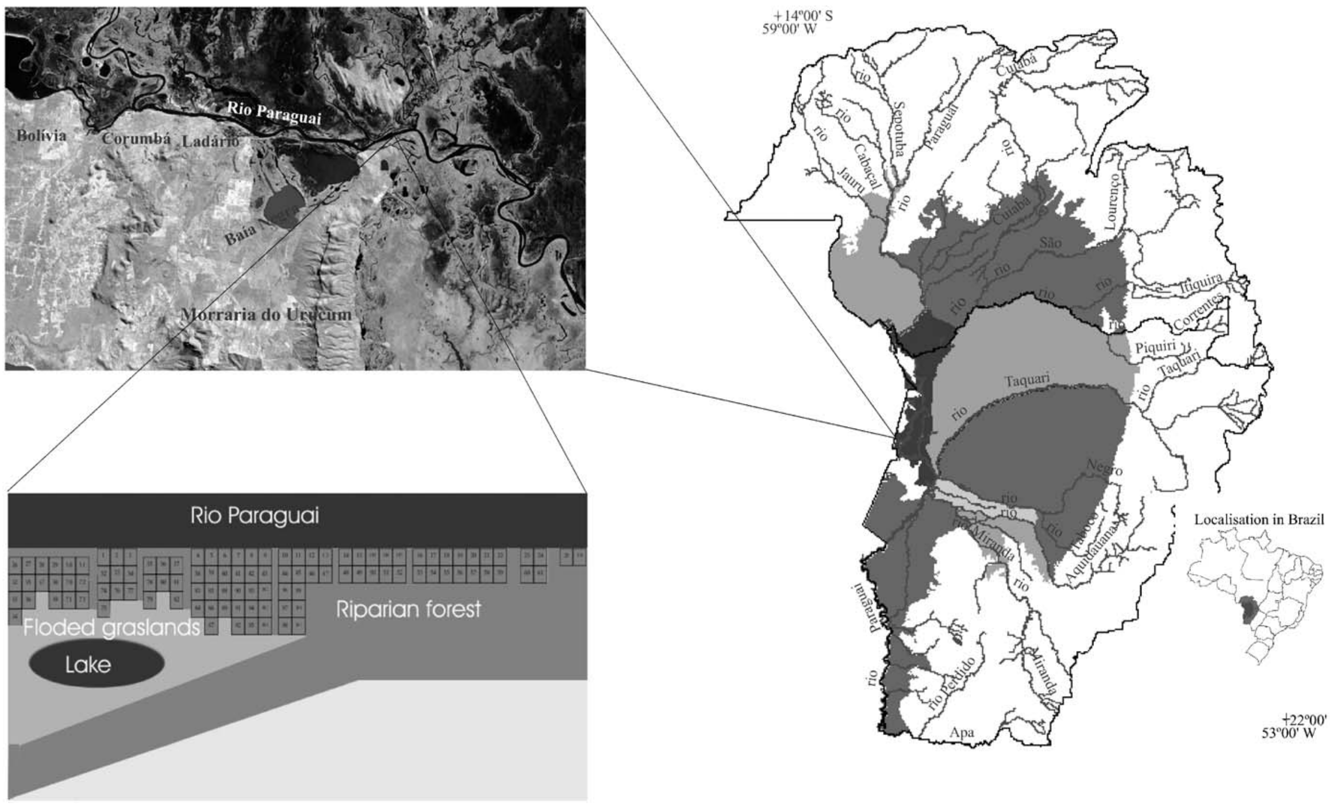

Fig. 1. Location of the study area and the set of plots in the Alto Paraguai basin, Brazilian Pantanal, according to the Pantanal subdivision made by Adámoli (1982) and modified by Silva and Abdon (1998). On the map, the gray area is the floodplain and the darkest is the Pantanal of the Paraguai sub-region. The picture is a thematic Landsat image of the region (band 4, 5 and 6 converted into gray scale).

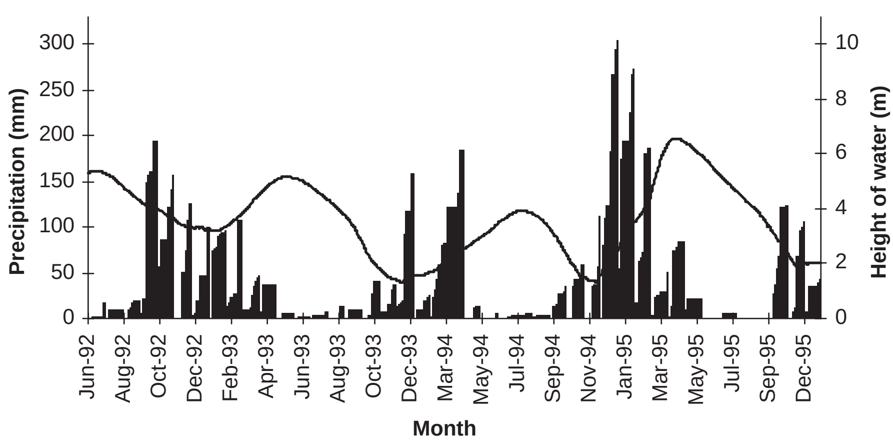

Fig. 2. Daily levels of the Rio Paraguai in Ladario (line) and monthly accumulated precipitation (bars) in Corumbá between June 1992 and December 1995. Data provided by the Brazilian Navy and Air Force, respectively.

The circumferences of all branches in individuals that ramified below 1.3 m were noted. Then, the basal areas were calculated separately, and the sum of these measures was considered as one individual. For density calculations, each individual was considered as one, independent of its number of branches. Tree heights were estimated by comparing each with a measuring pole of known length. The trees and shrubs were permanently labelled with a numbered aluminium tag. Voucher specimens of the different species were collected, dried and deposited in the Herbarium of Universidade Federal de Mato Grosso do Sul (COR), with duplicates sent to Universidade Estadual de Campinas (UEC) and Embrapa

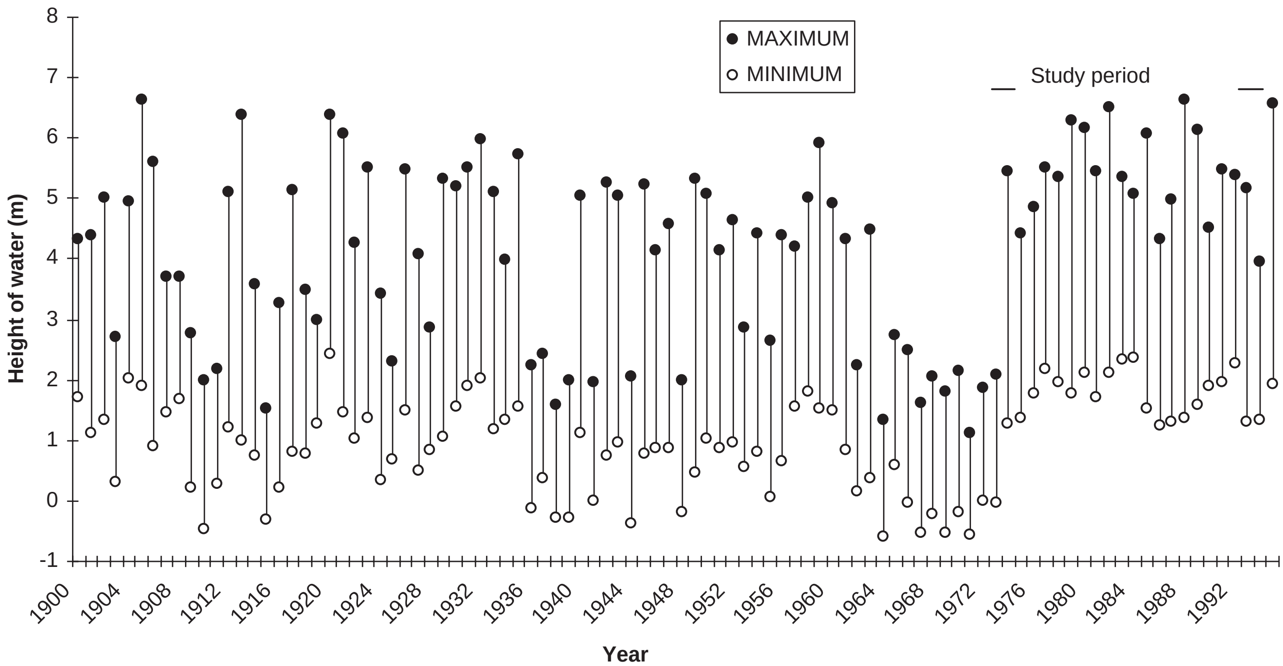

Fig. 3. Annual maximum (full circle) and minimum (empty circle) levels of the Rio Paraguai on the Ladario gauge, 1900–1995, showing the chosen period for this survey, Mato Grosso do Sul State, Brazil. Zero is at 83 m above sea level. Data from the Brazilian Navy.

(CPAP). The species were identified by comparison with other specimens deposited in these herbaria. When this was not possible, plants were sent to specialists.

To verify the horizontal distribution of species, a classification and ordination of the plots according to species groups was performed. To classify the plots, a matrix of density of stems per species by plot was used. The plots were classified using the Bray Curtis distance, clustered using Ward's method, and ordered using the principal coordinate analysis (PCO) ordination method with correction for negative eigenvalues (Legendre and Anderson, 1999). Bray Curtis distance was used because it is sensitive to density differences. The analyses were performed using the programs FITOPAC, version 1.0 (Shepherd 1994), and DistPCoA (Legendre and Anderson, 1998).

To verify the vertical distribution of the species, the highest water mark, left by the 1995 flooding on the trunk of each tree, was also measured. A staff gauge in the study site recorded inundation level variation over 3 months. This variation was the same as shown by the Ladário gauge used by the Brazilian Navy, which has been collecting daily data since 1900 ($r^2 = 99.85\%$, $P < 0.001$). Because of this, the water mark measurements could be transformed into topographic localization for each tree in reference to the zero level of the Ladário gauge. This was used to estimate individuals' topographic heights and the time that each one had been inundated between 1974 and 1996. This period was chosen because, after a long dry period in the 1960s, there has been a relative uniformity of yearly floods since 1974 (Fig. 3).

Since the object of this analysis was to make clear the association between species and flooding intensity and since the original plots were often quite heterogeneous with respect to flooding level, the plots were disregarded. For this analysis, bands, defined by their height above the zero level on the Ladário gauge, were the sampling units. Each 20 cm height class above the zero mark was considered to be a unit, and all species with four or more individuals were included. With these data, a matrix with the different class intervals and the number of individuals of each species in it was established. Then, a Two-Way Indicator Species Analysis (TWINSPAN -- Hill, 1979) was performed. The pseudospecies cut levels used were 0, 2, 5, 10, 20, 30 and 50, and software default settings were used for other options. The palms were excluded from this analysis because they were poorly sampled with the used inclusion criteria and, consequently, the samples obtained do not accurately represent their possible topographic distribution.

For every topographic band split by TWINSPAN analysis, the data from the Ladário gauge was used to calculate how much time it had remained inundated during the study period. The maximum number of consecutive years with and without flooding, and also the mean and standard deviation of inundated days per year (only for years with flooding) were calculated. This was possible because local rains cause little variation in flooding. Additionally, there is considerable variation between years (see Fig. 3).

The phytosociological parameters were calculated according to the methods described in Curtis and Macintosh (1951), the Shannon index was estimated using a log natural basis, and comparisons were made with other surveys that used the same basis. Calculations were made with FITOPAC software (Shepherd, 1994).

Results

Structure and species composition

A total of 695 shrubs and trees distributed among 37 species, 35 genera and 23 families were found. The richest family was Leguminosae (*sensu lato*), with seven species, followed by Polygonaceae, Myrtaceae and Euphorbiaceae, with three species each, and by Arecaceae and Rubiaceae, each with two species. The remaining 17 families were represented by only one species each (Table 1). The species/area curve indicates that a great amount of area would need to be added to the sample in order to obtain many more species; hence, this size (1.08 ha) was suitable for the purpose of this study (Fig. 4). This curve shows a logarithmic increase, in accordance with results obtained by Condit et al. (1996).

The stand density and basal area were 643.5 individuals and 18.1 $m^2 ha^{-1}$, respectively. The Shannon index was 2.7 for species, and the evenness found was 0.74 (Table 2).

Table 1. Species sampled in the riparian forest of the Rio Paraguai in Corumbá, Mato Grosso do Sul State, Brazil, with respective botanical families and growth habits

Famíly	Scientific name	Habit
Arecaceae	*Acrocomia aculeata* (Jacq.) Lodd.	Palm
	Bactris glaucescens Drude	Palm
Bignoniaceae	*Tabebuia heptaphylla* (Vell.) Tol.	Tree
Capparaceae	*Crataeva tapia* L.	Tree
Cecropiaceae	*Cecropia pachystachya* Tréc	Tree
Chrysobalanaceae	*Couepia uiti* (Mart. & Zucc.) Bth.	Shrub
Euphorbiaceae	*Alchornea castaneifolia* (Willd.) A. Juss.	Shrub
	Alchornea discolor Poepp.	Tree
	Sapium obovatum Kl.	Tree
Flacourtiaceae	*Casearia aculeata* Jacq.	Shrub
Hippocrateaceae	*Salacia elliptica* (Mart.) Peyr.	Shrub
Lauraceae	*Ocotea diospyrifolia* (Meisn.) Mez	Tree
Leguminosae Caesalpinioideae	*Hymenaea courbaril* L. var. *stilbocarpa* (Hayne) Y.T. Lee & Langenh.	Tree
Leguminosae Mimosoideae	*Albizzia inundata* (Mart.) Barneby & J.W. Grimes	Tree
	Inga vera Willd. ssp. *affinis* (DC.) Pennington	Tree
	Zygia inaequalis (H.B.K.) Pitt.	Shrub
Leguminosae Papilionoideae	*Andira inermis* H.B.K.	Tree
	Bergeronia sericea Mich.	Shrub
	Pterocarpus michelli Brit.	Tree
Meliaceae	*Trichilia stellato-tomentosa* Kze.	Shrub
Melastomataceae	*Mouriri guianensis* Aubl.	Shrub
Moraceae	*Brosimum gaudichaudii* Tréc.	Shrub
Myrtaceae	*Eugenia egensis* DC.	Shrub
	Eugenia cf. *polystachya* Rich.	Tree
	Myrcia cf. *mollis* (H.B.K.) DC.	Shrub
Nyctaginaceae	*Neea hermaphrodita* S. Moore	Shrub
Polygonaceae	*Coccoloba* cf. *alagoensis* Wedd.	Tree
	Ruprechtia brachysepala Meisn.	Tree
	Triplaris gardneriana Wedd.	Tree
Rubiaceae	*Genipa americana* L.	Tree
	Tocoyena formosa C. & S.	Shrub
Sapindaceae	*Cupania castaneaeifolia* Mart.	Tree
Sapotaceae	*Pouteria glomerata* (Miq.) Radlk.	Tree
Sterculiaceae	*Guazuma tomentosa* H.B.K.	Shrub
Ulmaceae	*Celtis pubescens* (H.B.K.) Spreng.	Tree
Verbenaceae	*Vitex cymosa* Bert.	Tree
Vochysiaceae	*Vochysia divergens* Pohl	Tree

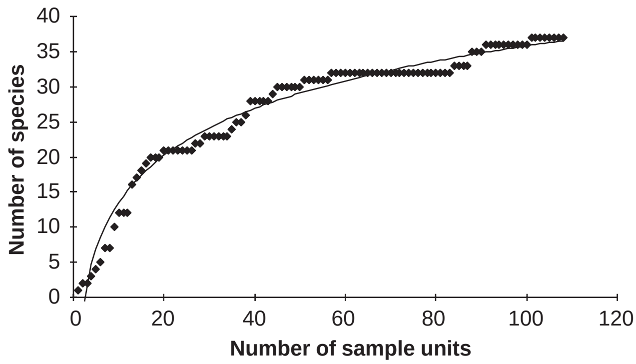

Fig. 4. Number of species found by sampled area (sample unit = 100 m^2) in the riparian forest of the Rio Paraguai, Corumbá, Mato Grosso do Sul State, Brazil. The order of sample units was obtained by random selection. The best-fit curve has the following equation: $Y = -8.79 + 22.3\ \text{Log}\,X$. ($R^2 = 96.6\%$, $P < 0.001$).

The riparian forest was relatively low, with the canopy reaching between 6 and 12 m, most often 6–8 m. In some locations, *Tabebuia heptaphylla* occurred as an emergent species. The canopy in the higher parts of the riverbank is mainly composed of *Inga vera* ssp. *affinis*, the most abundant species. Besides *Inga vera*, the canopy included *Vochysia divergens*, *Cecropia pachystachya* and *Tabebuia heptaphylla*. In these areas, the understorey had shrubs between 2 and 5 m tall: *Neea hermaphrodita*, *Alchornea discolor*, and *Myrcia* cf. *mollis* are the most common species. In the low-lying places, in the transition to flooded grasslands, *Albizia inundata* and *Triplaris gardneriana* were the predominant canopy species, with *Bactris glaucescens* being the predominant species in the 3 m layer in the understorey (Fig. 5).

Inga vera ssp. *affinis* reached the highest values in all phytosociological parameters. This species, and other nine (*Triplaris gardneriana*, *Ocotea diospyrifolia*, *Crataeva tapia*, *Vochysia divergens*, *Cecropia pachystachya*, *Eugenia* cf. *polystachya*, *Tabebuia heptaphylla*, *Myrcia* cf. *mollis* and *Albizia inundata*), totalled 77.4% of the importance value (IV). The remaining 27 species accounted for 22.6% of the IV (Table 3).

The species appeared to have different space occupation strategies and growth features. Some occurred in greater number and smaller basal area, such as *Triplaris gardneriana*, *Ocotea diospyrifolia* and *Crataeva tapia*. Other species had a lower number of individuals but greater basal area, e.g. *Hymenaea courbaril* and *Tabebuia heptaphylla*. For *Vochysia divergens*, both basal area and number of individuals were high. Only four species (10.8%) occurred with only one individual and three others (8.1%) with two individuals.

Horizontal distribution of species

The survey plots were divided into two main clusters, with small differences in some plots between methods (Figs. 6–8). The first four axes in PCO ordination explain 31.9% of the total variation. In the first group, only plots near the river margin on the higher parts of the riverbank were split. In the second group, some plots near the margin were also separated by the method, but most of the plots were located in the transition to flooded grasslands (border plots). These two environments are typically subjected to different water regimes because of the riverbank's topographic configuration (Figs. 5 and 8).

For the two groups, *Cupania castaneifolia* and *Tabebuia heptaphylla* occurred exclusively on the riverbank near the edge plots group, while *Zygia inaequalis*, *Ruprechtia brachysepala* and *Alchornea castaneifolia* occurred exclusively in the other group.

Three of the most important species in the IV occurred with the greatest number of individuals in the high riverbank plots. *Inga vera* occurred with 186 and 40 individuals in each of the two groups, and *Vochysia divergens* with 28:3. On the other hand, in the low-lying plots, *Triplaris gardneriana* (5:65), *Albizia inundata* (1:18), *Crataeva tapia* (4:46), *Eugenia polystachya* (6:15), and *Coccoloba* cf. *alagoensis* (2:10) predominated.

Topographic distribution of species and inundation

Individuals on the riverbank were between the 3.2 and 6.6 m topographic positions on the Ladário staff gauge (Fig. 9). For the chosen inclusion criteria they occurred mainly between 3.8 and 5.8 m.

The TWINSPAN analysis performed on 27 species with four or more individuals according to their topographic position, divided the species into four blocks (Table 4). The first, (A), was composed of species that apparently do not tolerate flooding (*Celtis pubescens*, *Gazuma ulmifolia*, *Tocoyena formosa* and *Trichilia stelato-tomentosa*). These species occurred only in the medium-high and high environments that remained non-inundated during most of the 23 years under analysis (Table 4, Fig. 10). The second block, (B), consists of species that are relatively indifferent to topographic position, although two (*Cecropia pachystachya* and *Casearia aculeata*) tend to be absent in the lower sites (Table 4). The third block, (C), is composed of nine species that occurred in medium to medium-high environments. In this block, for almost all species, only a few individuals occurred at each interval. Some are understorey shade-tolerant species (*Neea hermaphrodita*, *Coccoloba* cf. *alagoensis*, *Myrcia* cf. *mollis* and *Bactris glaucescens*), and others are canopy species (*Vitex*

Table 2. Comparison of sampling methods and summary of results obtained in studies of forest vegetation in the Pantanal, seasonally flooded várzea of the Amazon and riparian forests in Mato Grosso do Sul/Paraná State, Brazil

Source	Location/forest type	Total density (Indiv./ha)	Basal area ($m^2 ha^{-1}$)	Shannon (LN)	No. of species	Sample size (ha)	Criteria for inclusion (gbh cm)
This study	Riparian Forest, Rio Paraguai-MS	643.5 (386)	18.1(17.1)	2.7 (2.1)	37 (29)	1.08	⩾15 (⩾31)
Souza et al. (1997)	Riparian Forest, Rio Paraná-MS	2,046	25.05	2.93	42	0.33	⩾15
	Riparian Forest- island, Rio Paraná-MS	2,214	35.60	1.3	11	0.42	⩾15
	Transition Riparian forest/mountain semi-deciduous forest Rio Paraná–PR	1174	30.71	2.67	63	1.00	⩾15
	Riparian forest, Rio Paraná– PR	858.59	42.46	2.51	33	0.49	⩾15
	Riparian forest, Rio Baía-MS	1245	27.85	1.63	18	0.33	⩾15
Assis (1991)	Riparian/semi-deciduous Forest, Rio Ivinhema-MS	959	29.2	3.09	67	1.00	⩾16
Campbell et al. (1992)	Várzea (high), Rio Juruá Amazon	523	25.5	3.6	106	1.00	⩾31
	Várzea (médium), Rio Juruá, Amazon	420	27	3.51	73	1.00	⩾31
	Várzea (low), Rio Juruá, Amazon	777	25.7	1.82	20	1.00	⩾31
Klinge et al. (1996)	Várzea, Rio Solimões, Amazon	1,086	45		47	0.75	⩾16
Ferreira & Prance (1998)	Igapó, Rio Tapajós, Amazon (área 1)	252	0.7	*	21	1.00	⩾16
	Igapó, Rio Tapajós, Amazon (área 2)	271	*	*	30	1.00	⩾16
	Igapó, Rio Tapajós, Amazon (área 3)	489	10.9		24	1.00	⩾16
Damasceno-Junior (unpb).	Semi-deciduous forest (Capão) Pantanal	622	60.85	2.9	43	0.70	⩾15
Ratter et al. (1988)	Semi-dec. Forest (Cordilheira) Pantanal	573	26.1	*	26	*	⩾30
Dubs (1994)	Semi-dec. Forest (Cordilheira) Pantanal	361	18.8	*	24	1.00	⩾31
Dubs (1994)	Semi-dec. Forest (Cordilheira) Pantanal	545	29.4	*	31	0.42	⩾31
Dubs (1994)	Semi-dec. Forest (Cordilheira)Pantanal	532	44.4	*	35	0.40	⩾31
Dubs (1994)	Seasonally flooded forest, Pantanal	495	38.8	*	7	0.20	⩾31

The numbers in brackets correspond to the results using gbh ⩾31 cm.
* Data not provided by survey.

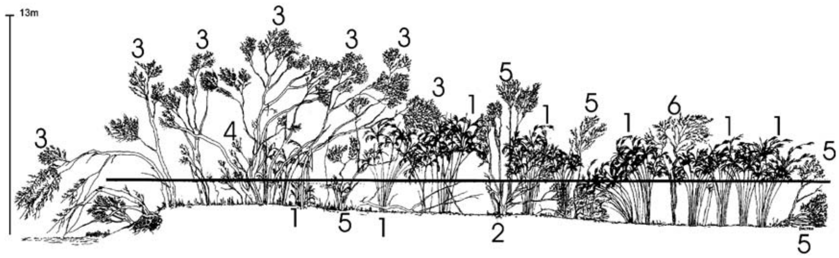

Fig. 5. Profile diagram of 40 × 10 m across the riparian forest of Rio Paraguai in Corumbá, Mato Grosso do Sul State, Brazil. The line indicates the water mark left by 1995 flooding on the tree trunks. (1) Bactris glaucescens; (2) Eugenia cf. polystachya; (3) Inga vera; (4) Pterocarpus micheli; (5) Triplaris gardneriana; (6) Albizia inundata.

Table 3. Phytosociological parameters obtained in a 1.08 ha sample for species (GBH > 15 cm) listed in decreasing order of importance value in the riparian forest of the Rio Paraguai, Corumbá, Mato Grosso do Sul State

Species	NI	NQ	BA (m^2/ha)	R.Dens.	RF	R.Dom	IV
Inga vera ssp. *affinis*	226	77	11.1241	32.52	22.78	61.6	116.9
Triplaris gardneriana	70	25	0.7032	10.07	7.4	3.89	21.36
Ocotea diospyrifolia	56	29	0.6756	8.06	8.58	3.74	20.38
Crataeva tapia	50	24	0.3227	7.19	7.1	1.79	16.08
Vochysia divergens	31	20	0.7557	4.46	5.92	4.18	14.56
Cecropia pachystachya	31	21	0.6457	4.46	6.21	3.58	14.25
Eugenia cf. *polystachya*	21	14	0.0731	3.02	4.14	0.4	7.57
Tabebuia heptaphylla	7	6	0.822	1.01	1.78	4.55	7.33
Myrcia cf. *mollis*	21	12	0.0944	3.02	3.55	0.52	7.09
Albizzia inundata	19	9	0.2474	2.73	2.66	1.37	6.77
Hymenaea courbaril	1	1	0.9026	0.14	0.3	5	5.44
Pterocarpus michelli	10	9	0.0742	1.44	2.66	0.41	4.51
Andira inermis	7	7	0.2317	1.01	2.07	1.28	4.36
Alchornea castaneifolia	12	6	0.1436	1.73	1.78	0.8	4.3
Alchornea discolor	10	6	0.1535	1.44	1.78	0.85	4.06
Neea hermaphrodita	13	6	0.0669	1.87	1.78	0.37	4.02
Coccoloba cf. *alagoensis*	12	6	0.0587	1.73	1.78	0.33	3.83
Casearia aculeata	10	7	0.0315	1.44	2.07	0.17	3.68
Eugenia egensis	8	7	0.0319	1.15	2.07	0.18	3.4
Ruprechtia brachysepala	9	4	0.1372	1.29	1.18	0.76	3.24
Pouteria glomerata	10	5	0.0567	1.44	1.48	0.31	3.23
Couepia uiti	7	6	0.0515	1.01	1.78	0.29	3.07
Vitex cymosa	7	4	0.1425	1.01	1.18	0.79	2.98
Guazuma ulmifolia	7	3	0.1873	1.01	0.89	1.04	2.93
Celtis pubescens	8	4	0.0487	1.15	1.18	0.27	2.6
Acrocomia aculeata	3	2	0.1406	0.43	0.59	0.78	1.8
Bactris glaucescens	6	2	0.0109	0.86	0.59	0.06	1.52
Zygia inaequalis	5	2	0.0221	0.72	0.59	0.12	1.43
Trichilia stellato-tomentosa	4	2	0.0161	0.58	0.59	0.09	1.26
Tocoyena formosa	4	2	0.0104	0.58	0.59	0.06	1.23
Bergeronia sericea	2	2	0.0201	0.29	0.59	0.11	0.99
Sapium obovatum	2	2	0.0054	0.29	0.59	0.03	0.91
Mouriri guianensis	2	2	0.0046	0.29	0.59	0.03	0.9
Salacia elliptica	1	1	0.0327	0.14	0.3	0.18	0.62
Cupania castaneaeifolia	1	1	0.0076	0.14	0.3	0.04	0.48
Genipa americana	1	1	0.005	0.14	0.3	0.03	0.47
Brosimum gaudichaudii	1	1	0.0017	0.14	0.3	0.01	0.45

NI is number of individuals (density); NQ, number of quadrats where the species are present (frequency); BA, total basal area (dominance); R.Dens, relative density; RF, relative frequency; R.Dom, relative dominance and IV, importance value.

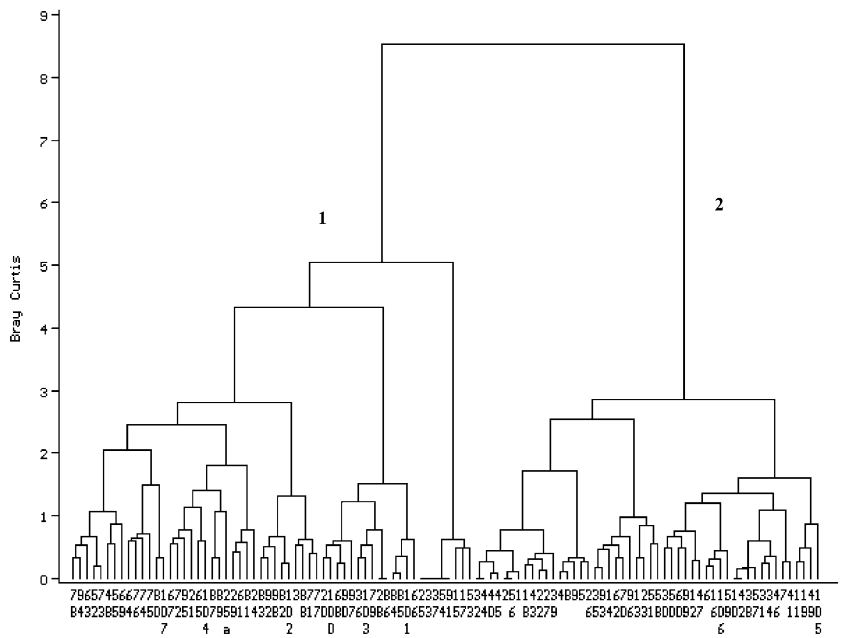

Fig. 6. Dendrogram produced by Ward's method in a Bray Curtis (*Y*-axis) distance matrix on the 108 plots (*X*-axis) of riparian forest of the Rio Paraguai, Corumbá, Mato Grosso do Sul State. Two main groups were distinguished, "1" and "2".

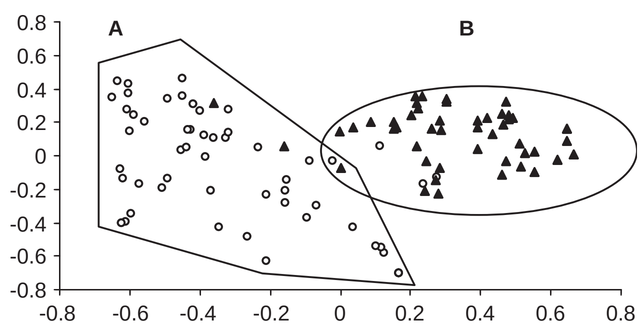

Fig. 7. Scatter plot showing the ordination produced by Principal coordinate analysis (PCO) in the Bray Curtis distance matrix for the 108 plots in the riparian forest of Rio Paraguai, Corumbá, Mato Grosso do Sul State. Two main groups were distinguished: "A" and "B". The groups obtained by Wards dendrogram are represented by triangles and circles.

cymosa, *Pterocarpus micheli* and *Andira inermis*). The fourth block (D), with nine species, consists of those that are typical of the lowest and medium topographic position. *Albizia inundata*, *Ruprechtia brachysepala* and *Tabebuia heptaphylla* occurred in the lowest locations. The two most abundant species in this group were *Triplaris gardneriana* and *Crataeva tapia*. These species seem to be well-adapted to regular flooding (all years) and resistant to staying under water most of the year.

The topographic positions were also grouped into four bands by TWINSPAN analysis (Table 4). These bands ranged from 3.2 to 4.0 m; from 4.2 to 5.2 m; from 5.4 to 5.8 m and from 6 to 6.6 m. All of them have been subjected to a different flooding regime (Fig. 10). The only topographic position that was not sequentially classified by this method was 6.4 m, probably because only one species occurred there with a few individuals.

The first topographic band split by the method was at the highest topographic position and was subjected only to sporadic and unpredictable flooding, mainly during extreme events. The mean time of inundation, when it occurs, ranges from 11 to 42 days per year. Ten species occurred here with a low number of individuals. This environment is dominated by species from block A, like *Celtis pubescens* and *Tocoyena formosa*, and indifferent species such as *Inga vera* (Fig. 10 and Table 4). The second band at the other extreme was at the lowest position with regular flooding during almost all of the 23 years analyzed, lasting for a mean flooding duration of 150 to 220 days per year. Twelve species were present in this group, often with few individuals. *Triplaris gardneriana*, *Albizia inundata*, *Ruprechtia brachysepala* and *Crataeva tapia* dominate this environment. The third and fourth bands were at intermediary positions. The flooding regime on the third band was also predictable. Inundation occurred in at least 20 of the years under analysis, and flooding remained for an average of 100–135 days per year. Twenty-one species occurred in this group, with a relatively high number of individuals. Species that dominated here tend to be those that are indifferent to levels of flooding, such as *Inga vera*, *Ocotea diospyrifolia* and *Cecropia pachystachya*. Besides these, *Triplaris gardneriana* and *Crataeva tapia* are also

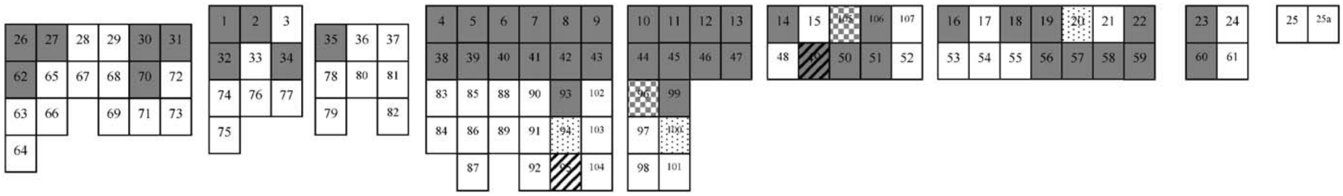

Fig. 8. Spatial representation for the 108 plots surveyed showing the groups separated by cluster analysis (Wards dendrogram) in the riparian forest of the Rio Paraguai, Corumbá, Mato Grosso do Sul State. The white plots are group 1, and the gray plots are group 2. Comparing with the PCO analysis, the cross-hatched plots were in intermediate position between the two groups; the checkered plots are from Wards Gray group and were spatially in group A; and dotted plots were from Wards white group but were spatially at the other.

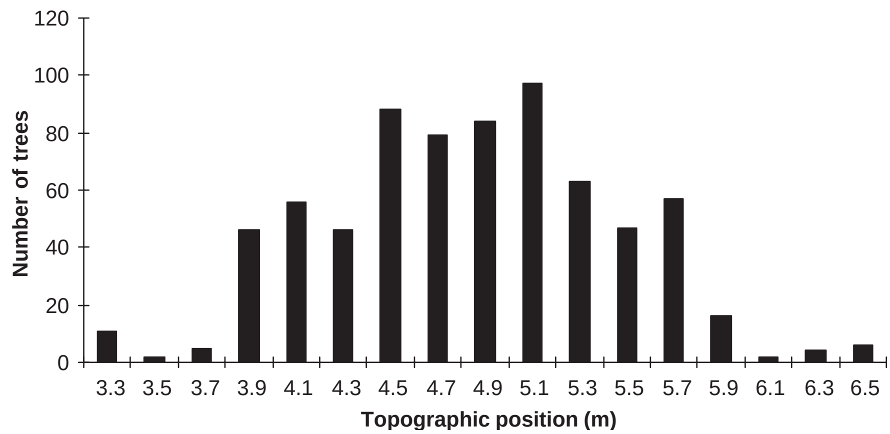

Fig. 9. Frequency of sampled trees and shrubs on different topographic levels in the riparian forest of the Rio Paraguai in Corumbá, in reference to the zero of the Ladário gauge. The height-class interval is 0.2 m and the central values of each class are indicated on the *X*-axis.

common. In the fourth group inundation is very unpredictable. Inundation occurred less than half of the years under study, and, at some points, the number of maximum consecutive years without inundation was greater than those that were inundated. When flooding occurred, it lasted a mean of 61–90 days per year. Twenty-five species occurred in these areas, with the highest incidence of individuals registered in this study. The main species in this group are the same as the "indifferent" species from the previous band, with the addition of *Vochysia divergens* and *Myrcia* cf. *mollis*.

Inga vera, *Ocotea diospyrifolia* and *Alchornea discolour* occurred in all four topographic bands classified by TWINSPAN analysis, with a higher incidence of individuals at medium and medium-high topographic positions.

Discussion

Structure, species richness and diversity

The Shannon index and the number of species obtained were in the same range as some riparian forests of Rio Paraná as well as some non-flooded vegetation in the Pantanal such as the 'cordilheiras' and 'capões'. Some lower 'várzeas' and 'igapós' of the Amazon, as well as one riparian forest and an island of the Rio Paraná were less rich than the study area (Table 2). This is probably associated with the heterogeneity of the inundation regime on this small piece of land. On the other hand, some high 'várzeas' and areas in transition to semi-deciduous forest showed higher diversity and number of species (Table 2).

The flooding here seems to prevent encroachment on riparian forests by the neighboring deciduous and semi-deciduous forest vegetation, with species characteristics of dry environments (see Juracy et al., 1999; Ratter et al., 1988). The levels and duration of flooding here tend to determine the degree of exchange of species between dry and flooded environments, and contribute to the impoverishment of the riparian forests. Here, the intermediary richness and diversity in relation to the other riparian sites (Table 2) are a result of the existence of micro-environments. These are subjected to inundation events that range from seasonal to rare. In addition, riparian forests of the Rio Paraguai function as a group of narrow and fragmented islands, where the non-flooded areas for species occupation are restricted, and

Table 4. Two-way indicator species analysis (TWINSPAN) performed in species that occurred with 4 or more individuals in the sampling of the Rio Paraguai riparian forest, Corumbá, Mato Grosso do Sul State, Brazil

		2				3				4						1								
	Topographic position (m) Species	38	32	34	36	40	42	44	46	48	50	52	54	64	56	58	60	62	66					
4	*Albizzia inundata*	2	—	2	—	3	2	2	1	1	—	—	—	—	1	1	—	—	—	0	0	0	0	0
	Ruprechtia brachysepala	—	—	2	—	3	2	—	—	—	—	—	—	—	—	—	—	—	—	0	0	0	0	0
	Triplaris gardneriana	—	1	1	—	4	4	2	5	3	2	2	2	—	—	1	—	—	—	0	0	0	0	0
	Pouteria glomerata	1	—	—	—	2	—	—	—	—	2	2	—	—	—	—	—	—	—	0	0	0	0	1
	Tabebuia heptaphylla	—	1	—	1	1	1	—	—	—	1	—	1	—	1	—	—	—	—	0	0	0	0	1
	Alchornea castaneifolia	1	—	—	—	—	3	2	—	1	—	—	—	—	—	—	—	—	—	0	0	0	1	
	Crataeva tapia	1	—	—	—	3	2	4	4	3	2	2	1	—	1	—	—	—	—	0	0	0	1	
	Eugenia cf. *polystachya*	—	—	—	—	2	2	—	3	2	2	—	2	—	—	2	—	—	—	0	0	0	1	
	Eugenia egensis	—	—	—	—	1	—	—	—	1	2	1	—	—	1	2	—	—	—	0	0	0	1	
3	*Coccoloba* cf. *alagoensis*	—	—	—	—	—	2	1	2	2	2	—	1	—	—	—	—	—	—	0	0	1	0	0
	Pterocarpus michelli	—	—	—	—	—	1	2	1	2	2	—	1	—	—	1	—	—	—	0	0	1	0	0
	Vitex cymosa	—	—	—	—	—	—	—	1	1	—	—	1	—	—	2	—	—	—	0	0	1	0	0
	Zygia inaequalis	—	—	—	—	—	2	—	—	—	1	—	—	—	—	—	—	—	—	0	0	1	0	0
	Andira inermis	—	—	—	—	—	—	—	—	1	—	1	1	—	—	2	—	—	—	0	0	1	0	1
	Couepia uiti	—	—	—	—	—	—	—	—	—	—	2	2	—	—	1	—	—	—	0	0	1	0	1
	Myrcia cf. *mollis*	—	—	—	—	—	1	1	—	1	—	1	3	—	4	2	—	—	—	0	0	1	0	1
	Neea hermaphrodita	—	—	—	—	—	—	—	1	2	2	—	—	—	2	2	—	—	—	0	0	1	0	1
	Vochysia divergens	—	—	—	—	—	—	2	—	1	2	4	3	—	2	2	1	—	—	0	0	1	1	
2	*Casearia aculeata*	—	—	—	—	—	1	1	—	2	2	—	1	—	1	1	1	—	—	0	1	0		
	Cecropia pachystachya	—	—	—	—	—	—	2	3	2	1	2	3	—	2	3	2	—	—	0	1	0		
	Inga vera	—	—	1	1	1	4	3	5	6	6	7	5	2	4	4	2	1	—	0	1	0		
	Ocotea diospyrifolia	—	2	—	—	2	2	4	3	3	2	3	2	—	3	2	1	—	—	0	1	0		
	Alchornea discolor	—	—	—	—	1	2	—	2	—	—	—	—	—	—	1	—	—	1	0	1	1		
1	*Celtis pubescens*	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	2	—	2	1				
	Guazuma ulmifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—	—	1	1				
	Tocoyena formosa	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	2	1				
	Trichilia stelato-tomentosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	1				
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1					
		0	0	0	0	0	1	1	1	1	1	1	1	1	1	1								
		0	1	1	1	1	0	0	0	0	1	1	1	1	1	1								
											0	0	0	0	1	1								

The numbers correspond to the topographic bands and blocks of species.

the neighboring forest vegetation is distant and, in most cases, separated by flooded grasslands. Other studies in the Amazon (Campbell et al., 1992) and the Pantanal (Dubs, 1994) also found these patterns.

In addition to the effects of inundation, low values in stand density and basal area are probably associated with the following features: (1) the tree canopies are very low and the understorey is poorly developed, probably limiting the number of smaller understorey trees that can grow; (2) limitations on the establishment of large individuals are perhaps the result of dense clusters of palms like *Bactris glaucescens*, which occur mainly in the lower parts of the sampled area (Fig. 5).

If *Inga vera* were to be removed from the list, the difference in the IV among the next five species would be minimal. This suggests that, besides *Inga vera*, there is no other species present that is so well-adapted to the conditions of the survey area (Table 3). Even if other edaphic features were disregarded, *Inga vera* still seems to be important in forests of central-western and southeastern Brazil that experience regular events of inundation, like the Rio Mogi Guaçu, (Gibbs and Leitão-Filho, 1978; Gibbs et al., 1980) and the Rio Cuiabá (Guarin-Neto et al., 1996), in the seasonally flooded cambarazal in the northern part of the Pantanal (Nascimento and Nunes Da Cunha, 1989), and in the flooded forest of the Rio Grande in the state of Minas Gerais (Oliveira-Filho et al., 1994a). When this species occurs in places with V-shaped riverbeds with very narrow belts that are subjected to sporadic and fast

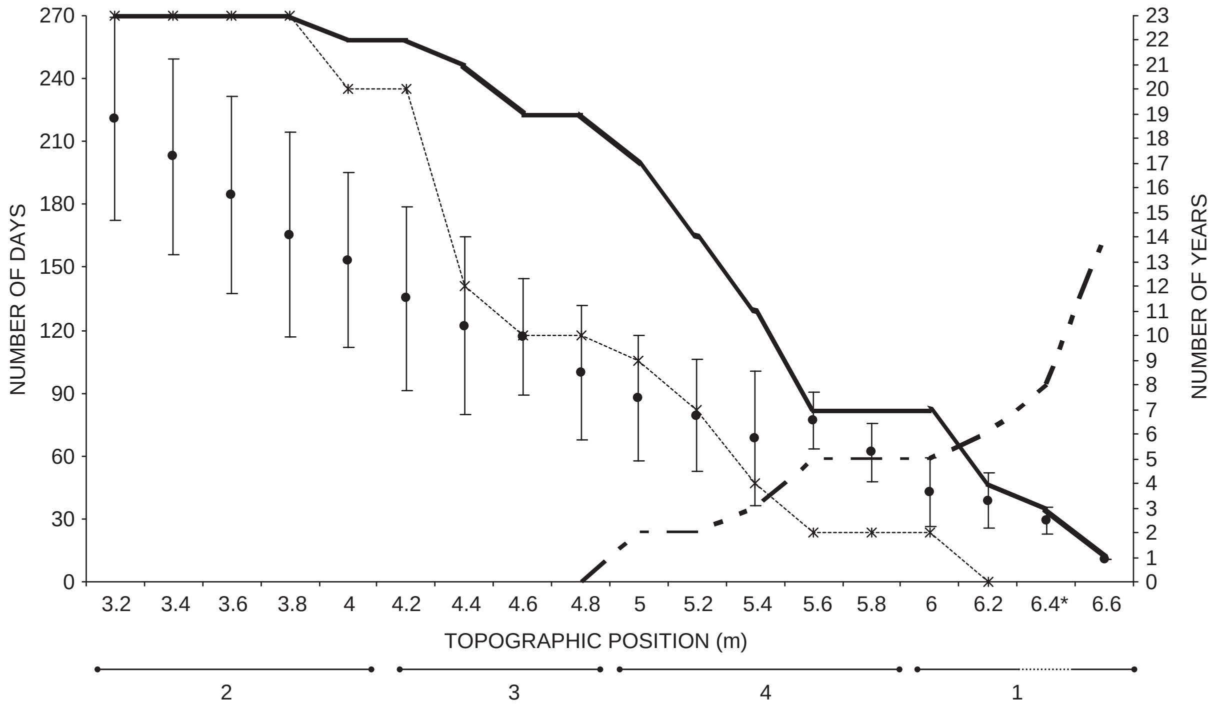

Fig. 10. Topographic positions in the riparian forest of Rio Paraguai, Corumbá – Mato Grosso do Sul State between 1974 and 1996 showing: ▬, total number of years inundated; -----, number maximum of consecutive years inundated; ●, mean and standard deviaton of days/yr flooded (only for flooded years); ▬ ▪, maximum number of consecutive years without flooding. The position of the four topographic bands split by TWINSPAN analysis are also indicated below (* belongs to the fourth group).

inundations, it seems to be less important (pers. obs., cf. Bertani et al., 2001; Metzger et al., 1997).

The fruits of *Inga vera* can be found almost throughout the year, but mainly during the flooding season (pers. obs.), and they are consumed by howler monkeys (Melo et al., 1999), birds (Oliveira-Filho et al., 1994b) and fishes (Pott and Pott, 1994). According to Oliveira-Filho et al. (1994b), when this fruit falls into the water it invariably floats, and when fish remove its mucilage, the seeds sink. Seeds have been found germinating, with part of their cotyledons consumed, inside the gut of *Piaractus mesopotamicus,* a Pantanal fish (Proença and Damasceno-Junior, unpub. data). *Inga vera* can also germinate and grow under water (Lieberg and Joly, 1993). These features may help to explain the successful occupation of space in almost every topographic position in this riparian forest.

Distribution of species

The classification and ordination methods employed resulted in two groups: one with more plots near the river margin and another one with more plots near the border. Species that were exclusive to the border group nearly match the low-lying block from the TWINSPAN analysis. Although the species of higher plots were not so clearly split by classification and ordination, the species from the higher locations tend to occur mainly in plots near the river margins, where the riverbank is high. Conversely, species from lower locations are, in general, border species, and are typically found in transition areas to the flooded grasslands. The distribution pattern of species like *Tabebuia heptaphylla* can be best described by a comparison between all of the classification and ordination methods. This species was found in the low/medium category as determined by TWINSPAN, and in a ''margin'' group as determined by Ward's Dendrogram and PCO. This species often occurred at the lowest locations on the river's shore, where the water reaches its minimum level. Nunes Da Cunha and Junk (2001) also found these *Tabebuia heptaphylla* patterns in the northern Pantanal.

The six species with the highest IVs showed a zonation at different topographic positions in the riparian forest: *Inga vera* ssp. *affinis*, *Vochysia divergens* and *Cecropia pachystachya* dominated the higher locations**,** while *Triplaris gardneriana*, *Ocotea diospyrifolia* and *Crataeva tapia* dominated the lower ones (Table 4). Keel and Prance (1979) and Campbell et al. (1992) also observed tree species zonation in inundated forests in the Amazon. Despite the possible regional differences and the limitations of the present survey, some species found here show similar distribution patterns in other sub-regions of the Pantanal (Damasceno-Junior et al., 1999; Dubs, 1994; Nunes Da Cunha and Junk, 1999, 2001; Pott and Adámoli, 1999).

The individuals are concentrated in areas that were not inundated every year, but most years. These locations were flooded for a mean duration of 3–5 months per year during the 7–22 years between 1974 and 1996. This suggests that the community has an optimum flooding tolerance at those levels. Topographic sites located between elevations of 3.2–3.8 m had a low number of individuals, probably because the inundation occurred every year, with a mean of 6–8 months per year. This matches the findings of Ferreira and Stohlgren (1999) and Ferreira (2000) in the Amazon, where basal area and density varied with topographic increases. On the other hand, sites from 6.0 to 6.6 m hight presented a low number of individuals due to a limited number of locations on the riverbank at these topographic levels.

Length of the hydroperiod and frequency of inundation seem to be the two main features associated with the zonation of species found here. The topographic bands observed revealed two extremes: first, where the inundations were very rare, short and unpredictable; and, at the second extreme, where they occurred every year with great duration. The other bands were related to variations in the flood regime. These features act to segregate plant communities mainly at the stages of seed germination and seedling establishment (Casanova and Brock, 2000; Scarano et al., 1997). The oxygen deprivation induced by flooding can act selecting different kinds of metabolism in woody species according to its distance from the river channel, contributing to the zonation of species (Joly, 1994).

Additionally, these plants are adapted to amphibious environments, needing both dry and inundated periods (Crawford, 1996), and any change in a flooding regime can modify this assemblage of species, even after a community has been established. For example, the riparian forest of the Rio Negrinho (a secondary channel of the Rio Paraguai near the study site) had been totally inundated between 1996 and 2000 as a consequence of an intense siltation in its bed. Then, all trees died, except *Pterocarpus michelli* (pers. obs.), which is not the species that occupies the lowest topographic position in the studied community. This species seems to be shade tolerant, with its occurrence restricted to established communities (Table 5). Certainly, other features such as chemical composition, texture of soils, light, and ecology of seed dispersal may interact to determine topographic position. Some diaspores in inundated places are dispersed at different flooding times, determining the topographic location of the seeds, seedlings and trees (Kubitzki and Ziburski, 1994; Lobo and Joly, 2000; Lopez, 2001).

Topographic distribution and the analysis of the total time in which each species remains flooded provide an excellent management tool in the Pantanal. The first

Table 5. Classification of some species found in the riparian forest of the Rio Paraguai, Corumbá, Mato Grosso do Sul State, according to its topographic position, successional stage, stratification and light requirements based on field observations

Species	Top. position	Succ. stage	Stratification	Light requirements.
Inga vera ssp. *affinis*	Indifferent	Pi	Canopy	LD
Ocotea diospyrifolia	Indifferent	LS	Canopy	ST
Cecropia pachystachya	Indifferent	Pi	Gap	LD
Albizzia inundata	Low/medium	Pi	Canopy	LD
Triplaris gardneriana	Low/medium	Pi	Canopy	ST/LD
Ruprechtia brachysepala	Low/medium	Pi	Canopy	LD
Tabebuia heptaphylla	Low/medium	LS	Canopy	LD
Alchornea castaneifolia	Low/medium	Pi	Canopy	LD
Eugenia egensis	Low/medium	LS	Understorey	ST
Vochysia divergens	Medium/high	Pi	Canopy	LD
Coccoloba cf. *alagoensis*	Medium/high	LS	Understorey	ST
Neea hermaphrodita	Medium/high	LS	Understorey	ST
Pterocarpus michelli	Medium/high	LS	Canopy	ST
Vitex cymosa	Medium/high	LS	Canopy	ST/LD
Zygia inaequalis	Medium/high	LS	Understorey	ST
Celtis pubescens	High	Pi	Gap	LD
Guazuma ulmifolia	High	Pi	Canopy	LD
Tocoyena formosa	High	LS	Understorey	ST
Trichilia stelato-tomentosa	High	LS	Understorey	ST

Pi, pioneer; LS, late successional; LD, light demanding; ST, shade tolerant.

question individuals often ask when planning the use of land in the Pantanal is, ‘‘How long is the annual inundated period?’’ If a given group of species reported in this survey is present, then it would be possible to use it to predict the length of the inundation period.

Human influences

There are three blocks of current human impacts that could influence the structure of the riparian vegetation in the Rio Paraguai on a broad scale. The first one, of low magnitude and widespread in many points along this river in the Pantanal, is caused by the households in the environment. They perform logging of some species to build houses, fences and canoes. According to the local people, until the middle of the twentieth century, crews from steam ships bought wood from farmers and the riverine inhabitants. The main riparian species sold, according to local people, was *Inga vera*, which is the main species in IV found here. Due to the pioneer nature of this species, this activity, probably, didn't have a strong influence on the structure of the riparian forests. Some species were probably introduced in these environments by these households. An example is *Acrocomia aculeata*, which occurred in the studied area and has its distribution associated with South American Indians (Pott and Pott, 1994). The second impact is caused by the navigation. The main consequence of this activity is the effect of the waves on the riverbank. These waves, produced by small boats used in tourism and big boats used in commercial transportation, cause some destruction in the riverbanks and consequently the fall of the trees. The third are the activities that can change the levels and time of flooding in the riparian forests (Hamilton, 2002). These, by the reasons previously discussed, can produce modification in the floristic composition of the riparian forests. One of such activities, the construction of raised roads and dikes, occurs in the floodplain. In high parts of the watershed, two other activities can promote these changes: the building of dams, which can decrease the water volume reaching the floodplain, and the deforestation which promotes an increase in the sedimentation of the riverbed as has been occurring in the rivers Piquiri, Taquari and São Lourenço, which are affluents of the Rio Paraguai (Hamilton, 2002).

Successional aspects

Nearly all the species with high IV values are pioneers and indifferent to the inundation level, although they appear to have preferences in this regard. Of these species, only *Triplaris gardneriana* was restricted to one environment. Except for *Tabebuia heptaphylla* and *Ocotea diospyrifolia*, the other species that occurred in places which remained flooded more than 50% of the time exhibit pioneer behaviour. They can colonize flooded grasslands and/or recently built-up riverbanks that remain inundated more than 60% of the time every year (pers. obs.).

The predominant species are pioneers and are growing on a recently deposited riverbank. This community is clearly in the early primary successional stage. The colonization sequence seems to start with the occupation of the new riverbank by the indifferent, light-demanding pioneer species. They are followed by pioneer low/medium light-demanding species, which provide shade necessary for understorey species like *Eugenia egensis* in low places and *Neea hermaphrodita* in medium/high locations, and canopy species like *Pterocarpus michelli*. Using field observation and the data from this study, a classification of some species encountered here is presented in Table 5.

Probably due to levels of inundation in the surveyed region, this is the most developed successional stage reached by this community. Junk (1989) discusses the importance of these and other factors in maintaining the conditions for species distribution in inundated locations in the Amazon. The perturbation offered by regular flooding and dry conditions plays an important role in maintaining this community at this stage. In addition, exceptionally high floods and movements of the river channel build and destroy the riverbank periodically over the long term. In the long run, when the river deposits more sediment in the basin, these riverbanks will probably support another type of vegetation.

The main example of this in the Pantanal is found in the Nhecolandia sub-region, where there are many long patches of slightly elevated grounds (1–2 m above the level of the flooded grasslands). These formations, locally named as ‘‘cordilheiras’’, almost never inundate and, as suggested by Dubs (1994), can be ancient riverbanks that resulted from the changing in the Rio Taquari beds and its secondary channels. One kind of vegetation that occupies these formations is the dry forests (as defined by Prado, 2000). Species like *Enterolobium contortisiliqum*, *Astronium fraxinifolium*, *Aspidosperma australe*, *Sapindus saponaria* and *Albizzia niopoides* can be found in the dry forests that occur in the ‘‘cordilheiras’’ and also in the dry forests occurring in the hills adjacent to the riparian forests of the Rio Paraguai (Damasceno-Junior pers. obs – see also Ratter et al., 1988). Probably these species do not reach the riparian forests studied because of their levels and time of flooding. In other riparian forests of the Pantanal like in the Rio Miranda, where the flooding does not reach the proportions of the Rio Paraguai, some of these elements can also be easily found (Damasceno-Junior pers. obs). Probably, in the long run, when the riparian forests of the Rio Paraguai are less subjected to flooding, elements like these examples, of the dry forests, which nowadays grow in the adjacent hills, will occupy these environments as a late phase of the successional process. The time for this occurrence is on a geological scale, once the floodplain of the Rio Paraguai is very flat and still has hundreds of kilometers to receive sediments.

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