Vegetation and environmental heterogeneity relationships in a Neotropical swamp forest in southeastern Brazil (Itirapina, SP)

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ABSTRACT

Patterns in substrate, canopy openness, tree species composition and structure were studied in a swamp forest in southeastern Brazil (Itirapina, SP), using a fine spatial scale ($\sim$0.05 km^2). Sixty quadrats of $10\,m \times 10\,m$ were divided into three sample plots, located in the centre and at both ends of the forest remnant (upstream and downstream), encompassing different environmental conditions. In each quadrat we quantified and identified individuals with CBH (circumference at breast height) ≥ 10 cm, the chemical properties of the soil, the drainage (flooded area) and the percentage of canopy openness. We keep 5124 individuals distributed over 37 species and 25 families. The downstream site presented a lower frequency of flooding, canopy openness, species richness (15 species) and density of individuals. In the central site we found different patterns of drainage and light incidence, the greatest species richness (31 species) and density of individuals, but smaller trees both in height and in diameter. The upstream site was subject to higher frequency of flooding, with intermediate values for density and species richness (27 species). Floristic and structural variation between and within sites reflects the different environmental conditions related to substrate and canopy openness. However, a larger number of species were correlated with drainage pattern (21 species) rather than with canopy openness (14 species), suggesting that the main factor responsible for the spatial organization of the plant community in swamp forests is soil drainage.

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1. Introduction

Many types of vegetation including open fields to closed forests are found in the Cerrado biogeographical province, which covers about 22% or 2 million km^2 of Brazilian territory (Goodland, 1971; Oliverira-Filho et al., 1989). Different physiognomies are associated with water courses, such as gallery and swamp forests, *veredas* (valley-side marshes with *Mauritia flexuosa* palm) and wet fields, according to the level of water in the soil and its seasonal variations (Ratter et al., 1973; Oliveira-Filho et al., 1990; Oliveira-Filho and Ratter, 2002; Tannus and Assis, 2004). Swamp forests occur in depressions, lowlands, headwaters and water course margins, on soil that is almost permanently waterlogged due to the outwelling of the water table. Because these forests are restricted to very small areas of the landscape where permanently waterlogged soils occur, they are naturally split into fragments surrounded by other kinds of vegetation and become isolated because of agriculture. These habitats are threatened by agricultural and urban expansion, palm heart and tree extraction, highway activities, and by the construction of dams (Teixeira et al., 2008).

In swamp forests, small topographical differences associated to variation in the height of the water table may cause local changes in the drainage pattern (Scarano et al., 1997; Toniato et al., 1998). The mosaic of situations created by micro-topography includes well-drained mounds, pits (permanently flooded) and natural drainage channels, with permanent or seasonal water (Souza and Martins, 2005; Teixeira et al., 2008). These local variations are closely linked with different strategies for colonization and survival of plants, which may have developed mechanisms for flood-tolerance or flood-escape (Urquhart, 2004). Thus, depending on the predominance of well or poorly drained soils, different patterns of spatial distribution of species can be found, resulting in structurally diverse communities in different sites of a single remnant of swamp forest (Scarano, 2006; Koponen et al., 2004; Teixeira et al., 2008). Canopy gaps can also result in a mosaic of habitat types, involving the creation of a variety of light levels within and between gaps, to which many forest seeds and seedlings are sensitive (Kellman and Tackaberry, 1993). Canopy dynamics may help explain the coexistence of many tree species in the tropics (Denslow, 1987), and the different levels of light incidence in gaps or forest edges may
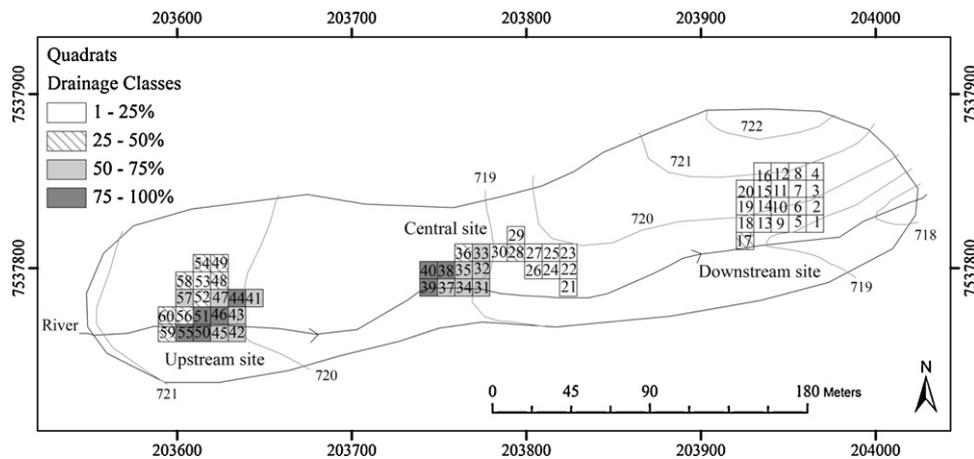
Fig. 1. Distribution of quadrats into three sampled sites in the Itirapina swamp forest.

influence the structure and spatial distribution of tree populations in peat swamp or riparian forests (e.g. MacDougall and Kellman, 1992; Gavin and Peart, 1997).

Although the relationship of environmental variation with plant structure and species distribution is well documented for several vegetation types, no other work confronted data of canopy openness and drainage patterns with the distribution of species in swamp forests. In addition to peculiarities in the drainage pattern, characterized by the key role of freatic water (Teixeira et al., 2008), these forests have a tree height and canopy openness similar to that of young, secondary forests and tree fall gaps in old-growth forests (Souza and Martins, 2005), making them very different from other lowland forests types. In the present study we characterized three sites of a Neotropical swamp forest in southeastern Brazil. We evaluate the relationship between variations in substrate, light intensity, tree species composition and structure of the community at a fine spatial scale (~0.05 km²). We especially addressed the following question: is canopy openness more important than drainage pattern, similar to other lowland forests?

2. Materials and methods

2.1. Study site

The swamp forest (22°15′54″S, 47°40′51″W, ca 720 m a.s.l.) is located in an ecological reserve with an area of approximately 2300 ha (Itirapina Ecological Station – IES) that includes part of Itirapina and Brotas municipalities, in the State of São Paulo, Brazil. Total annual rainfall averages 1523 mm, with a dry season from April to August (265 mm) and a wet season from September to March (1258 mm). The average monthly temperature ranges from 17 °C (minimum) to 23 °C (maximum; Tannus and Assis, 2004).

The relief is made up of smooth, wavy hills with an altitude of 700–760 m and small local amplitudes, and slopes of less than 6% declivity. The main vegetation on the well-drained soils of the interfluves is the Cerrado *sensu lato* (Brazilian savannas) and, on waterlogged soils, hygrophilous vegetation (forests and fields) predominates. The grassland and savanna physiognomies represent over 90% of the area, the remainder being occupied by cerradão (closed woodland), gallery forests and swamp forests (J.L.S. Tannus, L.S. Pinheiro, A.P. Teixeira, unpublished data).

The swamp forest studied has an area of approximately 4.5 hectares, with no evidence of human interference, and is entirely surrounded by wet fields. The forest presents a narrow and elongated shape. The major variations in the drainage system can be observed along the main water course, which runs throughout the

remnant. The herbaceous layer is not very conspicuous; vines and epiphytes are uncommon and forest gaps are rather small in size, caused by falling branches and the toppling of intact trees, since the root system is quite superficial because of the instability of the soil. In the forest, Haplic Organosoils (Histosols) were found, that is hydromorphic organic soils with few minerals (organic matter content exceeding 65%). These soils, with an organic matter layer greater than 1 m in depth, are dark brown to black in color, resulting from the recent accumulation of plant remainders deposited in water-saturated soil.

2.2. Field procedures

Field work was carried out between May 2005 and August 2007. Data were collected in 60 quadrats (10 m × 10 m), divided into three sample plots with 20 contiguous quadrats each (Fig. 1). The distance between each plot was about 90 m. In each quadrat, individual shrubs and trees with CBH (circumference at breast height) ≥ 10 cm were tagged, measured and identified. The individuals with multiple stems were included in the sample when the sum of the basal area of the stems corresponded to the basal area of an individual with CBH ≥ 10 cm. The species were classified into families according to the Angiosperm Phylogeny Group II system (APG II, 2003).

One sample plot was located at one of the extremities of the forest (upstream from the drainage system), characterized by more severely waterlogged soil, the drainage of which formed a diffuse network, with water coming from outside the remnant and from the outwelling of the local water table. In most of this site, the soil is submerged throughout the year. Another plot was placed at the other end of the remnant (downstream), where the topography is very uniform. The stream has a defined bed with a width of about 1.5 m, the water table remains at the soil surface even in the dry season, and flooded areas are smaller than in other sections of the forest in the wet season. The third plot was placed in the central part of the forest remnant, where the diffuse network of drainage coming from upstream converges to a single water course from this section, defining it as a transition environment between the two forest extremes. Micro-topographic variations result in a mosaic of drainage conditions that are regularly repeated: mounds of up to 2 m in diameter and 0.4 m in height are surrounded by many natural drainage channels and flooded pits.

2.3. Data collection on soil, drainage and light availability

We collected soil samples of at least six random points per quadrat at a depth of 0–20 cm. The soil samples from each quadrat were mixed to obtain a composite sample of about 0.4 L and sent to

Table 1
Number of individuals (NI) and importance value (IV, in percentage) of tree and shrub species (CBH ≥ 10 cm) found in the Itirapina swamp forest. Values in bold represent the 10 most important species of each site.

Species/families	Downstream		Centre		Upstream		Total	
	NI	IV	NI	IV	NI	IV	NI	IV
Calophyllum brasiliense Cambess. (Clusiaceae)	141	**13.5**	616	**27.2**	767	**36**	1524	26.1
Protium spruceanum (Benth.) Engl. (Burseraceae)	210	**19.2**	259	**9.6**	112	**5.9**	581	11.1
Euterpe edulis Mart. (Arecaceae)	774	**33.5**	14	1.1	15	1.3	803	10.0
Xylopia emarginata Mart. (Annonaceae)	57	**8.2**	216	**8.5**	217	**9.7**	490	8.8
Tapirira guianensis Aubl. (Anacardiaceae)	17	**4.1**	111	**8.3**	102	**9.2**	230	7.4
Styrax pohlii A. DC. (Styracaceae)	17	**3.1**	131	**5.8**	78	**5.2**	226	4.8
Geonoma brevispatha Barb. Rodr. (Arecaceae)	30	**3.1**	106	**4.2**	101	**4.3**	237	3.9
Magnolia ovata (A. St.-Hil.) Spreng. (Magnoliaceae)	25	**4.3**	24	2.2	69	**4.7**	118	3.6
Guarea macrophylla Vahl.(Meliaceae)	21	**2.7**	122	**4.7**	23	2.0	166	3.2
Podocarpus sellowii Klotzch ex Endl. (Podocarpaceae)	3	0.9	144	**5.3**	17	1.4	164	2.7
Hyeronima alchorneoides Allemao (Phyllantaceae)	11	**2.4**	12	1.4	61	**4.3**	84	2.6
Tabebuia umbellata (Sond.) Sandwith (Bignoniaceae)	–	–	51	**3.1**	36	**3**	87	2.3
Dendropanax cuneatus Decne & Planch. (Araliaceae)	12	2.1	27	2.3	27	**2.4**	66	2.2
Rapanea gardneriana (A. DC.) Mez (Myrsinaceae)	–	–	78	**3.2**	15	1.9	93	1.9
Posoqueria latifolia (Rudge) Roem. & Schult. (Rubiaceae)	–	–	23	2.0	19	2.1	42	1.5
Byrsonima cf. *ligustrifolia* A. St.-Hil. (Malphigiaceae)	–	–	37	2.4	4	0.6	41	1.1
Myrcia laruottena Cambess. (Myrtaceae)	–	–	34	1.7	4	1	38	1.1
Myrcia hartwegiana (O. Berg) Kiaersk. (Myrtaceae)	–	–	22	1.9	8	0.5	30	0.9
Cecropia pachystachya Trécul (Urticaceae)	–	–	–	–	14	0.8	14	0.8
Pera obovata (Klotzch) Baill.(Euphorbiaceae)	–	–	14	1.2	3	0.5	17	0.6
Miconia elegans Cogn. (Melastomataceae)	1	0.2	2	0.3	9	0.8	12	0.5
Ouratea castaneifolia (DC.) Engl. (Ochnaceae)	–	–	11	1.0	1	0.2	12	0.5
Ocotea lancifolia (Schott) Mez (Lauraceae)	–	–	6	0.6	4	0.7	10	0.5
Ocotea aciphylla (Nees) Mez (Lauraceae)	8	1.7	–	–	–	–	8	0.4
Ocotea tristis (Nees & Mart.) Mez (Lauraceae)	–	–	7	0.6	–	–	7	0.3
Pseudolmedia laevigata Trécul (Moraceae)	7	0.3	–	–	–	–	7	0.3
Daphnopsis racemosa Griseb. (Thymelaeaceae)	–	–	3	0.4	–	–	3	0.2
Clusia criuva Cambess. (Clusiaceae)	–	–	2	0.3	–	–	2	0.1
Gaylussacia brasiliensis (Spreng.) Meisn. (Ericaceae)	–	–	2	0.1	–	–	2	0.1
Ocotea diospyrifolia (Meisn.) Mez (Lauraceae)	–	–	–	–	2	0.3	2	0.1
Ocotea velloziana (Meins.) Mez (Lauraceae)	–	–	1	0.1	1	0.2	2	0.1
Erythroxylum cuneifolium (Mart.) O.E. Schulz (Erythroxylaceae)	–	–	1	0.1	–	–	1	0.1
Pera glabrata (Schott) Baill. (Euphorbiaceae)	–	–	–	–	1	0.1	1	0.1
Persea punctata Meisn. (Lauraceae)	–	–	1	0.1	–	–	1	0.1
Persea venosa Nees (Lauraceae)	–	–	1	0.1	–	–	1	0.1
Miconia chamissois Naudin (Melastomataceae)	–	–	1	0.1	–	–	1	0.1
Miconia pseudonervosa Cogn. (Melastomataceae)	–	–	–	–	1	0.1	1	0.1

the Universidade Federal de São Carlos, in the Araras municipality, where the concentration of phosphorus (P), organic matter (OM), pH, potassium (K), calcium (Ca), magnesium (Mg), potential acidity (H + Al), aluminum (Al), aluminum saturation (m), sum of bases (SB), cation exchange capacity (CEC), base saturation (V), sulfur (S), boron (B), copper (Cu), iron (Fe), manganeses (Mn) and zinc (Zn) were calculated. The procedures for the chemical analysis followed Van Raij (1983). A granulometric analysis of the samples was not performed because the organic matter content of the soils was over 50% and this analysis is performed only for mineral soils.

We classified the quadrats into four drainage classes, according to the flooded area above the soil surface. We assigned values to the following variables: (1) flooded area between 75 and 100%, (2) between 50 and 75%, (3) between 25 and 50%, and (4) from 1 to 25%. To reduce the estimation error of the flooded area, each quadrat was divided into four sub-quadrats of 5 m × 5 m. These records were taken at the end of the dry season (the month of August, 2007), since in the rainy season the distribution of water on the soil surface is more homogeneous.

The incidence of light in the community was represented in each quadrat by the percent of canopy openness, which was measured by the average of four photographs per quadrat, taken with a Nikon camera, film and fish eye lens, 16 mm 1:2.8 D. The photographs were taken from the centre of the 5 m × 5 m sub-quadrats, using a tripod at 1.25 m high. The photographs were digitized and the percentage of canopy openness was estimated in the GLA (Gap Light Analyzer) program, version 2 (Frazer et al., 1999), considering only the central part of the photograph, equivalent to about 1/9.

2.4. Data analysis

For each site, we calculated the diversity index of Shannon and Weaner (*H′*), based on the natural log, Fisher's α and Pielou's equitability (*J′*). For species, the importance value index was calculated, which is the sum of relative density, frequency and dominance values (Matteucci and Colma, 1982). The individual rarefaction method was used to compare the species richness between sites. For this analysis we used the Past program, version 1.84 (Hammer et al., 2001). Histograms with height and diameter classes were used to evaluate the vegetation structure in each site. The height
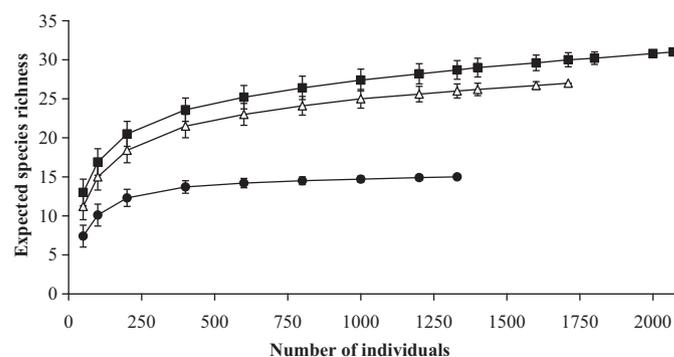

Fig. 2. Species rarefaction curves of three sampled sites in the Itirapina swamp forest. (●) downstream site; (■) central site; (△) upstream site.

Table 2
Floristic and structural descriptors of the trees and shrubs sampled (CBH ≥ 10 cm) in the Itirapina swamp forest.

Descriptors	Downstream	Centre	Upstream	Total
Number of species	15	31	27	37
Shannon's diversity index (H')	1.47	2.45	2.08	2.39
Fischer's α diversity	2.37	5.17	4.55	5.40
Pielou's equitability (J')	0.54	0.71	0.63	0.66
Number of families	14	23	21	25
Number of individuals	1334	2079	1711	5124

and diameter class distributions were tested for independence between sites using chi-square tests (χ^2) for contingency tables. We assessed micro-scale variations among quadrats nested in sites regarding tree height and diameter, as well canopy openness by means of a nested ANOVA. When the nested ANOVA indicated significant differences among sites, pairwise differences were checked using Tukey post hoc tests.

Edaphic variables were compared between sites through Tukey post hoc tests when ANOVA indicated significant differences. To confront data of drainage patterns and canopy openness with the distribution of the 26 most abundant species (with seven or more individuals) we used Spearman rank correlation coefficients.

3. Results

3.1. Plant community

We recorded a total amount of 5124 individual plants distributed over 37 species and 25 families (Table 1). The species rarefaction curves of the three sites showed significant differences in the expected number of species, with a lower species richness predictable for the downstream site (Fig. 2). Moreover, the downstream site was characterized by a lower species diversity, equitability and density of individuals (Table 2). In the central site we found the greatest number and diversity of species and individuals, whereas the upstream site was intermediate.

Significant differences were found in height ($\chi^2 = 550.76$; Df = 12; $P < 0.001$) and diameter ($\chi^2 = 156.19$; Df = 10; $P < 0.001$) class distributions among the three sites. The distribution of individuals in classes of height and diameter was similar in downstream and upstream sites, whereas smaller individuals, both in height (canopy between 6 and 8 m; Fig. 3A) and in diameter (only 2.5% of individuals with CBH > 15 cm; Fig. 3B) were
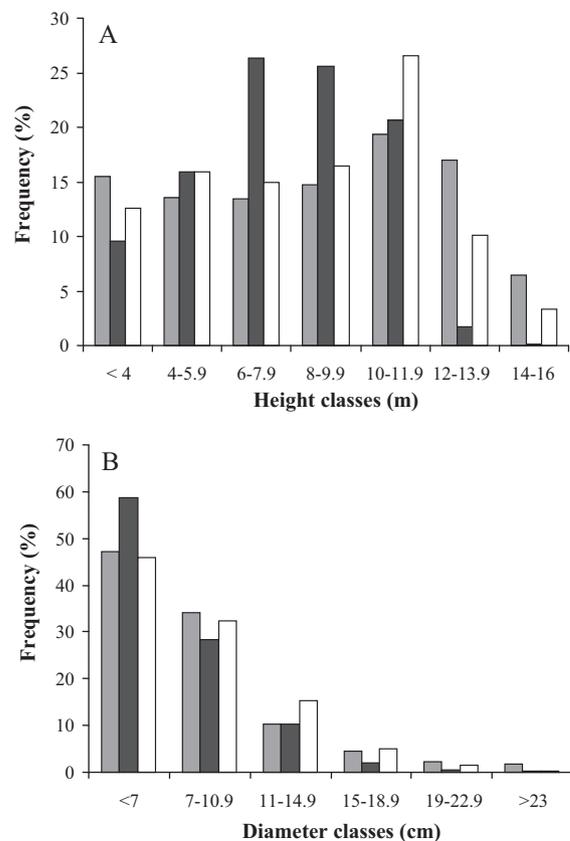

Fig. 3. Distribution of individual shrubs and trees in classes of height (A) and diameter (B), in three sampled sites in the Itirapina swamp forest. (▨) downstream site; (■) central site; (□) upstream site.

recorded in central site. Regarding tree height, nested ANOVA confirmed the differences among sites ($F_{(2, 5064)} = 153.10$; $P < 0.001$) and showed micro-scale variations among quadrats nested in sites ($F_{(57, 5064)} = 8.53$; $P < 0.001$, Fig. 4A). The analysis also confirmed differences in mean diameter among sites ($F_{(2, 5064)} = 55.76$; $P < 0.001$), as it showed micro-scale variations among quadrats nested in sites ($F_{(57, 5064)} = 3.27$; $P < 0.001$, Fig. 4B). Whilst variations in height were greater in the central site, we observed large variations in diameter within each site.

Table 3
Edaphic variables and canopy openness of the sampled sites in the Itirapina swamp forest. Figures are means for quadrats within sites, followed by standard errors. Values followed by different letters indicate significant differences in Tukey tests ($P \leq 0.05$) and ns means non-significant; $N = 20$ quadrats for each site.

| Edaphic data	Downstream	Centre	Upstream
P (mg dm^{-3})	81.0 ± 4.5 a	51.7 ± 2.4 b	60.3 ± 2.9 b
Organic matter – OM (g dm^{-3})	115.5 ± 5.8	104.0 ± 5.0	105.0 ± 3.6 ns
pH (in CaCl$_2$)	3.3 ± 0.02	3.3 ± 0.03	3.3 ± 0.04 ns
K (mmol$_c$ dm^{-3})	3.2 ± 0.2 a	4.9 ± 0.4 b	6.2 ± 0.4 b
Ca (mmol$_c$ dm^{-3})	6.6 ± 0.7 a	9.0 ± 0.6 ab	11.7 ± 0.8 b
Mg (mmol$_c$ dm^{-3})	4.8 ± 0.4 a	5.1 ± 0.3 a	7.9 ± 0.5 b
H + Al (mmol$_c$ dm^{-3})	290.5 ± 11.2	293.0 ± 10.3	311.9 ± 13.4 ns
Al (mmol$_c$ dm^{-3})	50.2 ± 2.4 a	66.7 ± 4.6 b	63.5 ± 3.0 b
Aluminum saturation – m (%)	77.7 ± 1.4 a	77.1 ± 1.4 a	71.0 ± 1.3 b
Sum of bases (mmol$_c$ dm^{-3})	14.7 ± 1.2 a	18.9 ± 1.0 a	25.8 ± 1.3 b
Cation exchange capacity (mmol$_c$ dm^{-3})	305.1 ± 11.3	311.9 ± 10.8	337.7 ± 14.4 ns
Base saturation – V (%)	4.9 ± 0.4 a	6.1 ± 0.3 b	7.7. ± 0.3 c
S (mg dm^{-3})	66.1 ± 5.1	78.5 ± 6.7	70.3 ± 6.7 ns
B (mg dm^{-3})	7.2 ± 0.5 a	9.7 ± 0.8 b	9.4 ± 0.7 b
Cu (mg dm^{-3})	0.1 ± 0.03 a	0.2 ± 0.04 b	0.2 ± 0.03 b
Fe (mg dm^{-3})	406.0 ± 9.3 a	344.2 ± 14.0 b	289.9 ± 16.2 c
Mn (mg dm^{-3})	22.3 ± 1.9	22.0 ± 2.1	21.0 ± 2.0 ns
Zn (mg dm^{-3})	1.0 ± 0.1 a	1.4 ± 0.2 ab	1.7 ± 0.2 b
Canopy openness (%)	10.3 ± 0.6 a	17.9 ± 1.3 b	12.8 ± 0.5 c
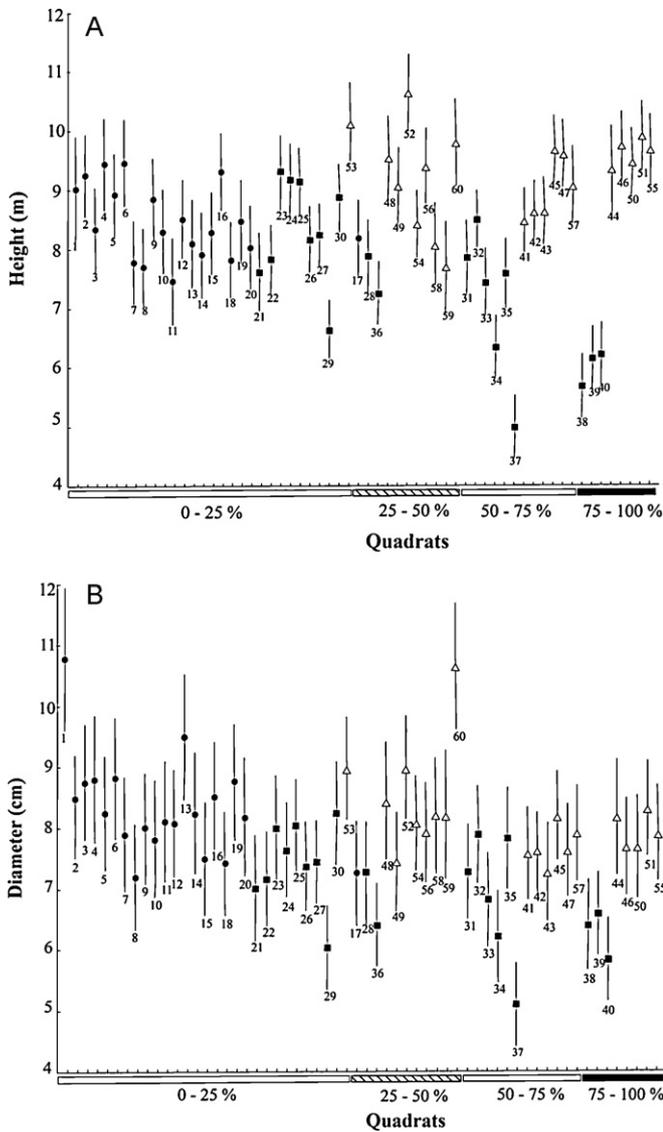
Fig. 4. Mean and standard error values for trees height (A) and diameter (B) for quadrats within sampled sites in the Itirapina swamp forest. Quadrats (identified by numbers below s.e. bars) were ordinated by their percentage of flooded area (drainage classes). (●) downstream site; (■) central site; (△) upstream site.
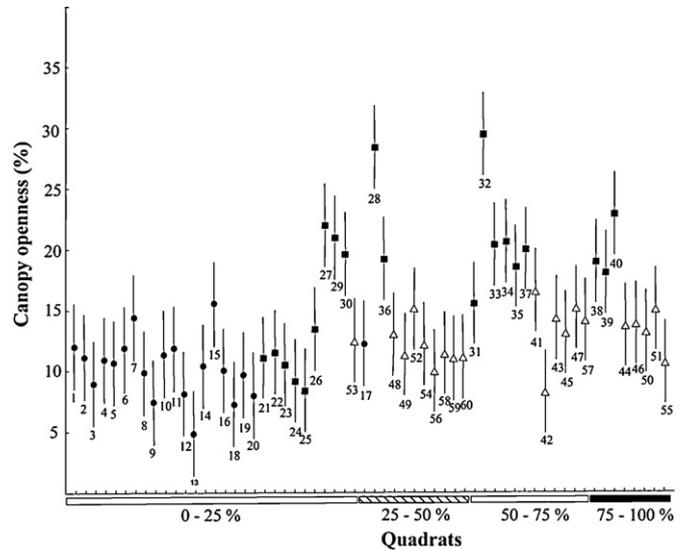

Fig. 5. Canopy openness mean and standard error values for quadrats within sampled sites in the Itirapina swamp forest. Quadrats (identified by numbers below s.e. bars) were ordinated by their percentage of flooded area (drainage classes). (●) downstream site; (■) central site; (△) upstream site.
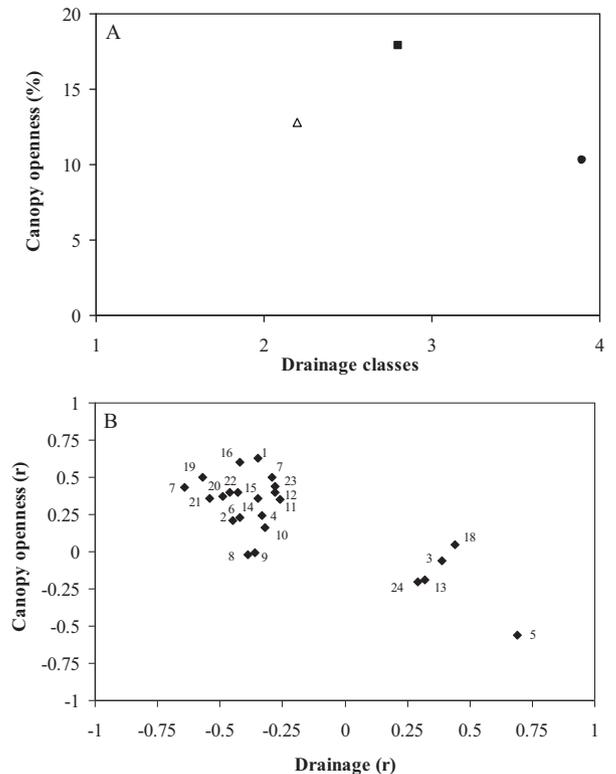

Fig. 6. Sampled sites ordination (A) and Spearman's rank correlation coefficients between tree species density and drainage and canopy openness (B) in the Itirapina swamp forest. (●) downstream site; (■) central site; (△) upstream site. Species are identified by numbers: 1 – *Byrsonima* cf. *ligustrifolia*, 2 – *Calophyllum brasiliense*, 3 – *Cecropia pachystachya*, 4 – *Dendropanax cuneatus*, 5 – *Euterpe edulis*, 6 – *Geonoma brevispatha*, 7 – *Guarea macrophylla*, 8 – *Hyeronima alchorneoides*, 9 – *Magnolia ovata*, 10 – *Miconia elegans*, 11 – *Myrcia hartwegiana*, 12 – *Myrcia laruottena*, 13 – *Ocotea aciphylla*, 14 – *Ocotea tristis*, 15 – *Pera obovata*, 16 – *Podocarpus sellowii*, 17 – *Posoqueria latifolia*, 18 – *Protium spruceanum*, 19 – *Rapanea gardneriana*, 20 – *Styrax pohlii*, 21 – *Tabebuia umbellata*, 22 – *Tapirira guianensis*, 23 – *Xylopia emarginata*, 24 – *Pseudolmedia laevigata*.

3.2. Environmental conditions

The downstream site was characterized by relatively better drained soils (95% of the quadrats fall into class 4 drainage, i.e. flooding between 1 and 25%), the highest level of phosphorous and Fe. The upstream site was characterized by poor drainage (55% of the quadrats flooded in more than 50% of the area) and higher concentration of exchangeable bases. At the central site there was a greater variation in waterlogged soil (45% of the quadrats belonged to category 4, 10% to 3, 30% to 2 and 15% to 1) and the chemical properties of the soil had intermediate values, which were at times more similar to the upstream values and at others to the downstream ones (Table 3).

Nested ANOVA showed significant differences in canopy openness among sites ($F_{(2, 180)} = 99.93$; $P < 0.001$) and among quadrats nested in sites ($F_{(57, 180)} = 4.76$; $P < 0.001$), being that the central site had a greater canopy openness and a larger local variation in the incidence of light (Figs. 5 and 6A).

3.3. Species distribution

Spearman's rank correlation coefficient indicated significant correlations ($-0.29 \leq r \geq 0.29$) between 24 of the 26 species and drainage or canopy openness (Fig. 6B), 21 species were associated with drainage and 14 species to canopy openness. According to habitat preference, the species can be classified into five groups: indifferent species (*Ocotea lancifolia* and *Ouratea castaneifolia*); species that prevailed on relatively better drained soils (*Euterpe edulis*, *Pseudolmedia laevigata*, *Ocotea aciphylla* and *Protium spruceanum*); those associated with highest light incidence (*Myrcia hartwegiana* and *Myrcia laruotteana*); those that prevailed on sites of highest light availability and poorly drained soils, such as *Byrsonima* cf. *ligustrifolia*, *Ocotea tristis*, *Pera obovata*, *Podocarpus sellowii*, *Posoqueria latifolia*, *Rapanea gardneriana* and *Tabebuia umbellata*; and those that prevailed on poorly drained soils, such as *Calophyllum brasiliense*, *Geonoma brevispatha*, *Hyeronima alchorneoides* and *Magnolia ovata*.

4. Discussion

Our results showed that the tree species composition and structure of the swamp forest varied on a spatial scale of a few hundred meters, as well as within each section of the forest. The mosaic of the swamp forest vegetation is probably related to spatial heterogeneity in environmental conditions. In riverside forests associated with springs and headwaters of small water courses, such as the swamp forest investigated, the outwelling of the freatic water is unpredictable and occurs in any season of the year, due to the local rainfall and flat topography. The frequent flooding and poorly consolidated substrate determine a great instability to the soil and a wide spatial and temporal variation in the tree-falls. The disturbances caused by recurrent floods and tree-falls may increase the environmental heterogeneity and determine patches of plant assemblages with reduced sizes and distinct species composition in the studied forest.

The greater diversity of species found in sites with larger local variations in the drainage pattern and canopy openness (in the central and upstream sites) reinforce that the heterogeneity is an important factor for species coexistence. Pollock et al. (1998) observed that diversity of species will tend to increase in a community if the micro-topography serves as a source of spatial variation for the flooding. Similarly, the wider opening of the canopy allows species with greater demands for light to coexist with less tolerant species (Budke et al., 2008). Moreover, niche differentiation may be further reduced by uniform conditions imposed by the superficial water layer (Duivenvoorden, 1996) or by the homogeneity in canopy openness.

The pattern described above is supported by the relationship between the species distribution and the environmental conditions, since most of the species were associated with drainage or canopy openness. The coexistence of species in heterogeneous environments may be a consequence of specializations for microhabitat, since many tropical species cannot be distributed randomly over different soil conditions (Clark et al., 1998). In forests subject to flooding, many species present reproductive and eco-physiological adaptations, as well as morphological responses to flooding, such as adventitious and tabular roots, stem buttressing, hypertrophy of lenticels, and development of aerenchyma in the roots and stems (Naiman and Décamps, 1997; Parolin et al., 2004; Gomes et al., 2006; Ferreira et al., 2009).

Although natural disturbances may increase the species diversity because of the creation of different habitats (Kellman and Tackaberry, 1993), the species richness in the studied forest was low when compared with other studies on Neotropical swamp forests that used the same criteria for inclusion of individuals and similar sample areas (e.g. Guarino and Walter, 2005; Scarano, 2006; Teixeira and Assis, 2009). The lower species richness found in Itirapina can be attributed to the anoxic environment and to the spatial isolation of the remnant. As the surrounding vegetation has a grassland physiognomy, spatial isolation could be a limiting factor for the sharing of species between the swamp forest and the adjacent forest formations. In Brazil, amongst species found in swamp forests, elements of semi-deciduous forests (Toniato et al., 1998; Rocha et al., 2005; Teixeira and Assis, 2005), cerrados (Marques et al., 2003; Teixeira and Assis, 2009) or Atlantic forest *sensu stricto* (Scarano, 2002), have been found, amongst others, confirming that the presence of surrounding forests work as agents responsible for increasing local diversity.

The high correlation of species distribution with drainage shows that the drainage pattern is the main factor associated with species composition in the studied forest. While tree-falls are not unique to riparian forests, flooding regimes may create a higher than normal frequency of these events in this forest type (Kellman and Tackaberry, 1993). Thus, we conclude that, unlike other forests types in which dynamic gaps have a fundamental role in their structure, floristic composition and species distribution, the main factor responsible for spatial organization of the plant community in swamp forests is the drainage, although the canopy openness also affects the partitioning of species.

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