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Environmental determinants for natural regeneration of gallery forest at the Cerrado/Amazonia boundaries in Brazil

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ABSTRACT
Natural regeneration and structure and their relationship to environmental variables were studied in three sections of a gallery forest, in Eastern Mato Grosso, Brazil (14º43′S and 52º21′W). The assumption was that natural regeneration is constrained by environmental determinants at all stages of development of the tree community. The objective was to analyse the forest structure and to verify the relationship between species distribution and abundance at different stages of regeneration and environmental variables. In each section, 47 contiguous (10x10m) permanent plots were established to sample trees (gbh≥15cm), following a systematic design. Seedlings (0.01 to 1m height), saplings (1.01 to 2m) and poles (from 2.01m height to gbh<15cm) were sampled in sub-plots of 1x1m, 2x2m and 5x5m, respectively. In each plot**,** soil properties, gaps projection, bamboos, rocky cover, declivity and depth of ground watertable were determined. The relationships between the environmental variables with trees and seedling communities were assessed by canonical correspondence analysis. In spite of the sections being near to each other, they presented large differences in floristics, structure and site conditions. The forest soil presented a low cation exchange capacity and a high level of Al saturation. The occurrence of bamboos and gaps and the depth of ground watertable limited the occurrence of poles and trees. The high degree of structural heterogeneity for each regeneration category was related primarily to a humidity gradient; but soil fertility (Ca+Mg) was also a determinant of seedling and sapling communities.

KEYWORDS: Brazil; diversity; riparian forest; soils; tropics.

Determinantes ambientais para regeneração natural de mata de galeria na transição Cerrado/Amazônia no Brasil

RESUMO
Foi estudada a regeneração natural e a estrutura de três seções de uma floresta de galeria no leste de Mato Grosso, Brasil (14º43′S e 52º21′W). O objetivo foi analisar a estrutura da floresta e verificar a relação entre a distribuição e abundância das espécies nos diferentes estágios de regeneração e entre as variáveis ambientais. Em cada seção de floresta foram estabelecidas, sistematicamente, 47 parcelas (10x10m) contíguas e permanentes para amostrar as árvores (CAP≥15cm). As plântulas jovens (0,01 a 1m de altura), as plântulas maiores (1,01 a 2m) e as arvoretas (de 2,01m de altura a CAP≥15cm) foram amostradas em sub-parcelas de 1x1m, 2x2m e 5x5m, respectivamente. Para cada parcela foram determinadas as propriedades do solo, projeção das clareiras, cobertura de bambus, rochosidade, declividade e profundidade do lençol freático. A relação das variáveis ambientais com as árvores e comunidades de plântulas e arvoretas foi determinada a partir de uma análise de correspondência canônica. Apesar das seções de floresta serem próximas entre si, apresentaram diferenças importantes em relação à composição florística, estrutura e variáveis ambientais. Os solos apresentaram reduzida capacidade de troca catiônica e elevados níveis de saturação de alumínio. A ocorrência de bambus e clareiras e a profundidade do lençol freático limitam a ocorrência de arvoretas e árvores. A elevada heterogeneidade estrutural em cada categoria de regeneração esteve relacionada principalmente a um gradiente de umidade, mas a fertilidade do solo (Ca+Mg) também foi determinante nas diferentes comunidades de plântulas.

PALAVRAS-CHAVE: diversidade; floresta ripária; solos; trópicos

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INTRODUCTION

The typical landscape of Central Brazil consists of cerrado on the well-drained interfluves, with gallery forests following the watercourses (Ratter *et al.*, 1997). Gallery forests, which are narrow strips of evergreen or semideciduous mesophytic forests (Ratter *et al.*, 1973), are theoretically protected by law due to their important function in water and wildlife conservation (Oliveira-Filho *et al.*, 1990; Paula-Lima & Zakia, 2000). Nevertheless, often people clear them for subsistence cultivation or shelter for cattle (Felfili, 1997). These forests protect water quality, perform critical functions in both hydrological and biogeochemical cycles and also are widely recognized for their social and recreational values (Rodewald & Bakermans, 2006).

Gallery forests contain *c.* 30% of the species already listed for the Cerrado biome (Felfili *et al.*, 2000) and represent refugia for species from the Atlantic, Amazon and the Paraná basin river forests plus endemic species (Oliveira-Filho & Ratter, 1995).

At the boundaries between the Cerrado and Amazonia biomes, the gallery forests present several species in common with those forests. The same happens in places farther east where common species are found among the Atlantic forests but in the center of the biome a greater number of common species are found between gallery forests and the southern forests of the Paraná river basin. There is little similarity with the dominant savanna physiognomies of the Cerrado biome (Felfili & Silva-Júnior, 1992). Meave *et al.* (1991) regarded them as present day refugia for moist forest species within the savanna dominium. According to Felfili (1997), gallery forests are vulnerable to the influence of external factors such as recurrent fires coming from the neighbouring cerrado formations.

Several surveys have been conducted (Ratter *et al.*, 1973; Oliveira-Filho & Martins, 1986; Oliveira-Filho *et al.*, 1990; Felfili, 1995, 1997, 2000; Silva-Júnior *et al.*, 1996, 2001; Marimon *et al.*, 2001, 2002) in gallery forests but most on just single occasions. Felfili (1995, 1997, 2000), Sevilha (1999) and Miguel & Marimon (2008) have been monitoring permanent sample plots. Their studies have shown that the abundant species regenerate the most in undisturbed forests. Pioneer species occur at higher densities in burned and disturbed environments, especially in gaps. Distinct dry and wet communities were also distinguished in those studies. The differentiation was so great that two tracts of well-drained soils in different forests were more similar between themselves than a dry and wet tract in the same forest (Sampaio *et al.*, 2000). In this study we expect to distinguish different tree communities related to environmental gradients. The assumption is that these communities are self-regenerative with the abundant species regenerating the most and that environmental conditions are constraints to natural regeneration at later stages.

The objective was to compare the structure of the forest regarding natural regeneration (seedlings, saplings and poles) and adult trees; analyze whether the species are regenerating; and whether there is any relationship between species abundance at different stages of development and environmental variables in a gallery forest at the transition zone between the Cerrado and Amazonian biomes.

METHODS

STUDY SITE

This study was carried out in three sections (upper, middle and lower) of the gallery forest alongside the Bacaba stream in the Biological Reserve "Bacaba Park" (14º43′ S and 52º21′ W), in Nova Xavantina, Mato Grosso, Brazil (Figure 1). The Reserve covers approximately 500ha; the average altitude is 346m; and the climate is Aw by Köppen, with annual precipitation from 1300 to 1500mm and a mean monthly temperature of 25ºC according to the climatological station of Nova Xavantina.

The main physiognomy in the Reserve is the cerrado *sensu stricto* (savanna woodland) (Marimon *et al.*, 1998) but there are areas covered with *Campo* (grasslands), *Cerradão* (dense savanna woodland) (Marimon-Júnior & Haridasan, 2005; Abad & Marimon, 2008) and a gallery forest, alongside the Bacaba stream (Marimon *et al.*, 2001, 2002). At the sections of this gallery forest with higher altitude and declivity Litosols predominates with the presence of rocky outcrops whereas alluvial soils occur where the relief is less steep.

Three forest sections were selected within an extension of 1 km alongside the Bacaba stream covering the topographic gradient (Figure 1). The **upper section** is characterized by the presence of quartzite rocks, litosols, and a waterfall (10m high) in the rainy season; during strong rains, the streambed overflows, but the drainage is, in general, rapid. The **middle section** is also rocky and the soils are litosols, but the declivity is smaller. In this section, in the steeper sites, the conditions are similar to the upper, but on shallower sloping sites and, during the rainy season, the watertable flows over the surface. Rocks are absent in the **lower section**; the soils are alluvium and the relief is flat; the soil drainage is poor and the watertable either flows or remains close to the surface most of the year (Marimon *et al.*, 2001, 2002).

VEGETATION INVENTORY AND ENVIRONMENTAL VARIABLES

In each section of the gallery forest, 47 contiguous permanent plots 100m^2 (10m x 10m) were established, following a systematic design (Philip, 1994), giving a total sampling area of 1.41ha. These plots were allocated perpendicularly to the stream, going from the streambanks to the forest edges according to the methodology proposed by Felfili (1995). All trees and lianas with girth at breast height

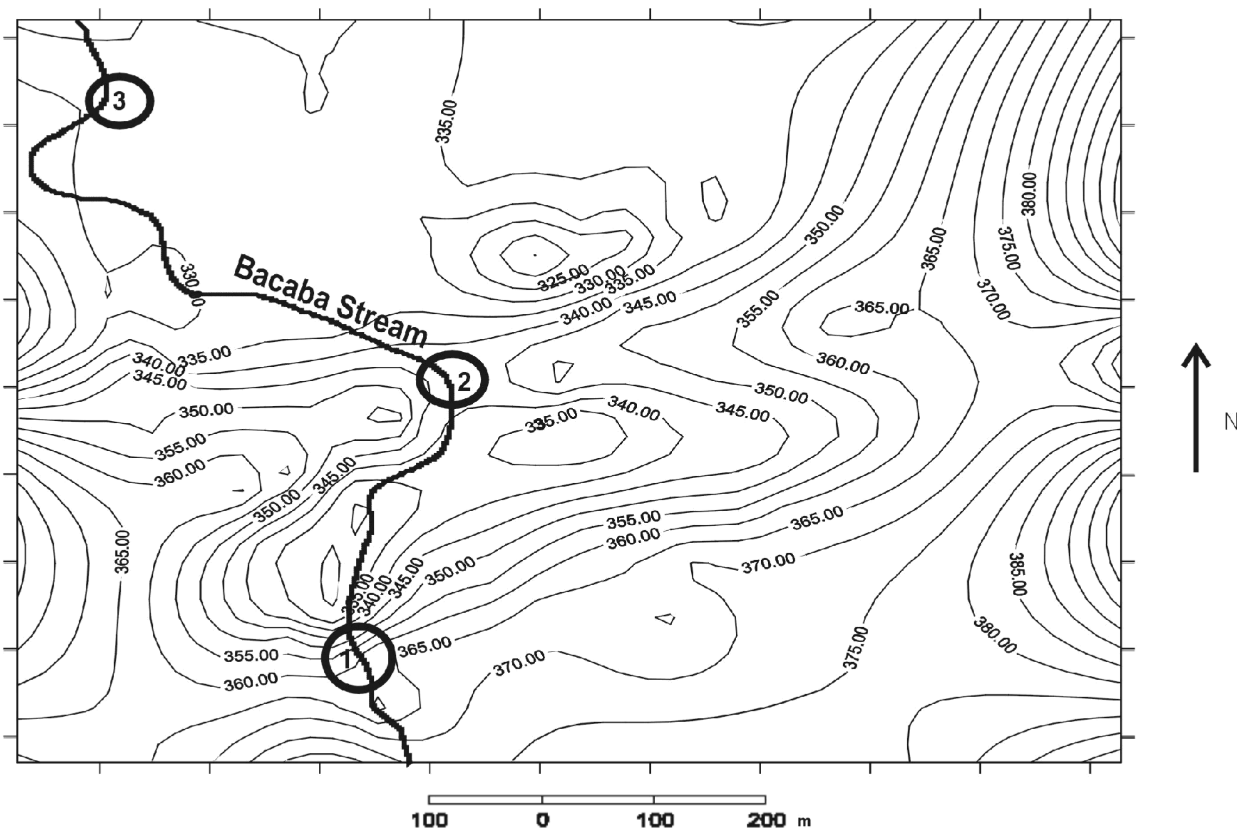

Figure 1 - Location of the study site at the Bacaba gallery forest, Nova Xavantina, Mato Grosso, Brazil. Upper (1), middle (2) and lower (3) sections.

(gbh)≥ 15cm were labeled with permanent aluminum tags, identified and measured (total height and gbh).

Each $100m^2$ plot contained sub-plots for sampling the natural regeneration that was classified according to the stage of development of the individuals according to Felfili (1997): seedlings (0.01 to 1m height), saplings (1.01 to 2m) and poles (2.01m height to gbh< 15cm). They were sampled in sub-plots of 1x1m, 2x2m and 5x5m, respectively. The total height of seedlings, saplings and poles were measured.

In each sampled plot (10x10m), gap projections (Brokaw, 1982) on the soil were measured and registered. Bamboo and grass, typical of degraded sites in gallery forests (Oliveira-Filho *et al.*, 1994b; Felfili, 1997) and rocky cover were recorded and the declivity was measured in each plot with a clinometer. The level of ground watertable was measured at weekly intervals with 5cm diameter perforated PVC tubes, which had been inserted into 1m deep auger holes. Averages of the level of ground watertable in the rainy (November to March) and dry (May to September) seasons were obtained for each two adjacent plots.

A single 0.5 l soil sample was collected from 0-10cm depths, at the center of each plot. Granulometric and chemical analyses of the samples were made at the Soil Laboratory of the Agronomy Faculty at the Federal University of Mato Grosso. Laboratory procedures followed that of EMBRAPA (1997). Phosphorus and potassium were extracted with Mehlich solution (HCl 0.05N + H_2SO_4 0.025N), P was measured with a colorimeter and K with a photometer. Calcium plus magnesium and aluminium were extracted with a 1N KCl solution. Aluminium was titrated with NaOH 0.025N solution**,** while Ca+Mg were titrated with EDTA 0.025N. Soil pH was measured with a potentiometer in a 1:2.5 soil/water suspension. Organic matter was determined by the Walkley-Black method (Tan, 1996). Texture was obtained by the densimetric Bouyoucos method.

DATA ANALYSIS

Species densities (Mueller-Dombois & Ellenberg, 1974) were calculated and compared. The average number of individuals, number of gaps, the cover of bamboos and rocks, declivity, depth of ground watertable per plot and soil properties were compared between the sections. These analyses were carried out using the Program SAS v. 8.1 (SAS, 1999-2000), using Kruskal-Wallis test.

Canonical correlation was used to investigate the relationships between the number of individuals in each regeneration categories (seedlings, saplings, poles and trees) and environmental variables in the plots. The matrix of environmental variables per plot initially included the number of gaps, bamboos and rocky covers, declivity, level of ground watertable in the rainy and dry seasons and all the chemical and physical soil properties described in Table 1. The relationships between variables were examined to ensure approximate normality, linearity and to find outliers (Tabachnick & Fidell, 2001). After a preliminary analysis (SAS, 1999-2000), seven environmental variables were eliminated due to either high redundancy or poor correlation.

Trees and seedlings were used to analyse the relationship between them and environment, because they represent two extreme groups regarding plant development. Trees represent established plants, and seedlings represent the most immediate group after reproduction. For each category (trees and seedlings) two input matrixes were used. The species matrix contained the density per plot for those with more than eight individuals in the total sample. For trees, the matrix had 50 species per 140 plots and for seedlings, 22 species per 104 plots. The environmental matrix contained the values of 16 environmental variables. After preliminary analyses, we eliminated all variables with low correlation with the first two ordination axes (< 0.4), and the final analysis was performed with five environmental variables. The program CANOCO 4 (Ter Braak & Smilauer, 1998) was used to perform CCA and the graphs were drawn using CANODRAW 3.0 (Smilauer, 1992).

RESULTS

ENVIRONMENTAL GRADIENTS AND FLORISTIC COMPOSITION

Soil pH in water, P, K, Ca+Mg and Al showed significant differences between forest sections (Table 1). The pH in water ranged from strongly acidic (4.1), in the lower section, to mean acidic (5.3), in the upper. The soil of most plots (61%) was very acidic (< 5) with a high Al content. Phosphorus was very low in the upper and lower section. The content of macronutrients was always higher in the middle section, which had moderate Al toxic levels for cultivated plants and also higher P contents compared to the other two sections. Organic matter and soil texture showed no significant difference. Texture was sandy in the three sections of the forest with clay contents under 15 percent. Soil features were highly variable (Table 1).

The number of gaps were similar at the tree sections, they ranged from 15m^2 to 20m^2 being typically small gaps. Watertable level were much closer to the surface at the lower section than the others, both during the rainy and dry season. At the lower section bamboo cover and declivity were very low and rocks were absent. At the upper sections, bamboo cover was twice as high as the middle sections, while rock cover was the opposite. Therefore, humidity and the physical barriers to regeneration imposed by declivity, rock and bamboo cover constituted the main physical gradients (Table 2).

A total of 137 species of 110 genera in 50 families were sampled in the three sections of the forest. *Tetragastris altissima* (Aubl.) Swart., *Bauhinia outimouta* Aubl. (liana) and *Pouteria gardneri* (Mart. & Miq.) Baehni were the only species common to the three sites and were found in all regeneration categories. Only 25 percent of the 129 species found as trees did not have juveniles in any category of regeneration. Species richness increased from saplings, to seedlings, poles and trees (Table 3).

STRUCTURE

A total of 58 of the 129 species found as trees did not have any seedlings. However, 62 species had saplings and 84 had poles in at least one section of the forest. The Pearson´s correlation between the density of trees and

Table 1 - Chemical and physical properties of the soil at the upper, middle and lower sections of the Bacaba gallery forest, Nova Xavantina-MT, Brazil. Mean (and Standard Deviation) of 47 samples in each forest section and probabilities of the Chi-square between the sections (Kruskal-Wallis test).

Properties	Upper	Middle	Lower	Chi-square	P
		Chemical:			
pH in water	4.7 (0.78)	5.3 (0.31)	4.1 (0.15)	75.103	< 0.0001
pH in $CaCl_2$	3.4 (0.28)	3.6 (0.70)	3.3 (0.16)	4.688	0.0959
P (mg/dm^3)	0.87 (1.54)	6.98 (11.73)	1.71 (2.88)	13.370	0.0012
K (mg/dm^3)	52.85 (46.51)	76.74 (33.76)	43.87 (27.05)	29.378	< 0.0001
Ca+Mg (cmol$_c$/dm^3)	1.54 (0.78)	2.85 (2.92)	1.27 (0.32)	15.830	0.0004
Al (cmol$_c$/dm^3)	1.34 (0.46)	0.94 (0.60)	1.46 (0.35)	21.184	< 0.0001
Organic Material (g/dm^3)	5.39 (3.56)	5.91 (2.69)	5.56 (2.91)	4.186	0.1233
		Physical: Texture (g/Kg)			
Sand	782.3 (104.18)	835.3 (58.52)	802.3 (85.62)	5.847	0.0537
Silt	68.1 (24.81)	61.1 (20.97)	70.4 (15.60)	5.437	0.0660
Clay	149.6 (91.34)	103.6 (52.06)	127.3 (80.77)	5.930	0.0515

Table 2 - Average number of gaps, cover of bamboos (%), rocks (%), declivity (%), and depth of ground watertable (cm) in the rainy and dry seasons per plots of the Bacaba gallery forest, Nova Xavantina-MT, Brazil. Mean (and Standard Deviation) of 47 samples in each forest section and probabilities of the Chi-square between the sections (Kruskal-Wallis test).

	Upper	Middle	Lower	Chi-square	P
		Nr. or depth (cm) per plot			
Gaps	0.82 (0.70)	0.89 (0.66)	1.00 (0.75)	1.233	0.5397
Water table (rain)	91.98 (37.47)	81.06 (38.11)	39.96 (24.42)	43.127	< 0.0001
Water table (dry)	> 100	> 100	82.36 (29.11)	55.566	< 0.0001
		Percentage per plot			
Bamboos	14.64 (17.27)	7.10 (8.22)	1.61 (4.27)	29.981	< 0.0001
Rocks	7.42 (8.77)	13.70 (11.69)	0.00	91.994	< 0.0001
Declivity	41.11 (18.46)	31.62 (18.83)	4.85 (5.51)	78.318	< 0.0001

Table 3 - Total of individuals (individuals/ha) of seedlings (Se), saplings (Sa), poles (P) and trees (or lianas) (T) at the upper, middle and lower sections of the Bacaba gallery forest, Nova Xavantina-MT, Brazil. Pearson's correlation between each regeneration category and trees.

Parameters	Upper				Middle				Lower			
	Se	Sa	P	T	Se	Sa	P	T	Se	Sa	P	T
Total of individuals	38781	3719	1593	965	47661	7131	2877	938	40211	3396	2501	1257
Total of species	43	36	55	74	38	29	59	86	41	25	57	77
Pearson´s correlation	0.73	0.68	0.56		0.45	0.65	0.58		0.13	0.28	0.59	

poles varied from 0.56 to 0.59 at the three forest sections, suggesting that the future forest composition and structure will be maintained with some fluctuations and that there is a positive correlation between density of trees and density of juveniles (poles) (Table 3). Most species occurred at low densities. *Tetragastris altissima*, with 11,064 seedlings and 1,542 saplings/ha at the middle section was the most abundant species. *Ephedranthus parviflorus* S. Moore, with 374 ind./ha in the middle section, had the most poles, while *Cecropia pachystachya* Tréc., a pioneer species (Felfili, 1995), presented the highest number of trees (126 ind./ha) in the lower section. Some species, which were abundant as trees, had little or no regeneration, such as *C. pachystachya*; and some species abundant as seedlings or saplings (*Erythroxylum daphnites* Mart., *Copaifera langsdorffii* Desf. and *Myrcia tomentosa* (Aubl.) DC.) had few trees.

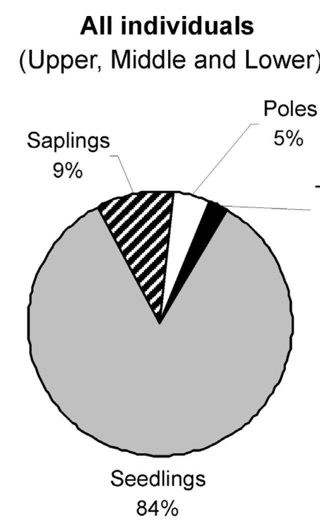

Figure 2 - Community structure of the Bacaba gallery forest in Nova Xavantina-MT, Brazil.

The structure of the forest community as a whole is shown in the Figure 2, and the population structure of the most important species (Marimon *et al.*, 2002) in each forest section is shown in Figure 3. *Mauritia flexuosa* L., a palm tree indicator of swampy sites, had a high density at all stages in the lower section, while *Diospyros obovata* Jacq. was abundant only as seedlings in the upper, and *Hymenaea courbaril* L. var. *stilbocarpa* (Hayne) Lee & Langenheim had a large number of large trees (i.e. gbh= 215cm) at the middle.

SPECIES X ENVIRONMENTAL GRADIENTS

Seedlings, saplings and poles were more abundant in the middle, and the number of trees was higher in the lower (Table 3).

The first canonical correlation (regeneration categories *vs.* environmental variables) was 0.689 (*c.* 47% overlapping variance, F= 4.25 and P< 0.0001), the second was 0.511 (*c.* 26% overlapping variance, F= 2.37 and P= 0.0004) and the eigenvalue explained *c.* 90% of the variance. Data on the first two pairs of canonical variates are in Table 4.

Considering a 0.3 *cutoff correlation* (Tabachnick & Fidell, 2001), the first pair of canonical variates had high loadings for poles and trees regarding the regeneration categories and for pH in water, declivity, clay, bamboos, gaps and depth of ground watertable in the dry season regarding the

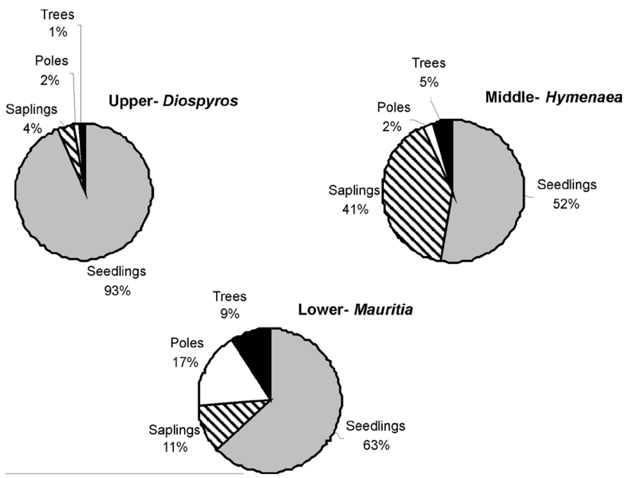

Figure 3 - Population structure of *Diospyros obovata* (main species of the forest upper section), *Hymenaea courbaril* (middle) and *Mauritia flexuosa* (lower) at the Bacaba gallery forest, Nova Xavantina-MT, Brazil.

Table 4 - Correlations and percents of variance between regeneration categories and environmental variables and their corresponding canonical variates in the sections of the Bacaba gallery forest, Nova Xavantina-MT, Brazil.

	First Canonical Variable	Second Canonical Variable	
	Correlation	Correlation	
	Regeneration Categories		
Seedlings	-0.0204	0.3809	
Saplings	0.0714	0.7360	
Poles	-0.4689	0.7951	
Trees	-0.9584	-0.1386	
Variance	28.60%	33.45%	Total= 62.05%
Redundancy	13.59%	8.76%	Total= 22.35%
	Environmental Variables		
pHwater	0.3650	-01083	
Al	-0.2022	-0.6840	
Ca+Mg	0.2978	0.5320	
Bamboos	0.7186	0.0359	
Gaps	0.6244	-0.4231	
Watertable (dry season)	0.5509	-0.0514	
Clay	0.4329	-0.1029	
Declivity	0.3012	0.2028	
Organic matter	0.0534	-01833	
Variance	20.22%	11.45%	Total= 31.67%
Redundancy	9.61%	3.00%	Total= 12.61%
Canonical correlation	0.6893	0.5116	

environmental variables (Table 4). Thus, low densities of poles and trees were related to high pH in water, declivity, clay levels, bamboo cover, gaps number and high depth of ground watertable in the dry season.

The second pair of canonical variates had high loadings for seedlings, saplings and poles of the regeneration categories and Al, Ca+Mg and gaps for the environmental side (Table 4). A high density of seedlings, saplings and poles were related to a small number of gaps, low Al and high Ca+Mg levels.

The first canonical variate extracted 28.60% of variance from the regeneration categories and 20.22% of variance from the environmental variables. The second canonical variate pair extracted 33.45% of variance from the regeneration categories and 11.45% of variance from the environmental variables.

Together, two environmental variable variates "explained" 22.35% of the variance in the regeneration categories. The first regeneration category variate accounted for 9.6% and the second for 3% of the variance in the environmental set of variables (Table 4).

The environmental variables were, apparently, enough to explain most of the species abundance distribution as shown by the CCA results (comparing density of the species for trees and seedlings with six environmental variables) (Figure 4a) with eigenvalues of the first and second axis, of 0.545 and 0.444. The species-environment correlations yielded by these axes were 0.823 and 0.720, and their cumulative percentage variances were 32.5 and 58.9%. This was reinforced by the Monte Carlo test (F= 3.55, P< 0.01) that indicated a significant correlation between environmental variables and the species abundance distribution. For correlations among environmental variables and trees (Figure 4b), the eigenvalues of the first and second axis, were 0.479 and 0.340. The species-environment correlations yielded by these axes were 0.850 and 0.799 and their cumulative percentage variances were 43.8 and 75%. These values and the result of the Monte Carlo test (F= 4.02, P< 0.01) also indicated a highly significant correlation between environmental variables and species abundance distribution.

For seedlings (Figure 4a), the first axis was mainly correlated to topographic features [declivity (-)] and levels of Al (+). The second axis was best correlated to Ca+Mg levels (+) and a humidity gradient (distance from the stream and watertable depth). The most distinct group was formed by the plots of the lower section (lowest declivity, lowest watertable depth and highest Al saturation). Species distribution was wider along the second axis compared to the first and, apparently, their distribution was mainly related to humidity and macronutrients (Ca+Mg) gradients. *Astronium fraxinifolium* Schott. seedlings were related to soils with more Ca+Mg at the middle section of the forest while *Mauritia flexuosa* seedlings occurred in the lower section where the relief is flat, the watertable remains close to the surface most of the year, soil is acidic and nutrient poor.

For trees (Figure 4b), the first axis was best correlated to a humidity gradient [distance from the stream (+) and watertable depth (+)] and the second axis was mainly correlated to declivity (-). The plots of the lower section

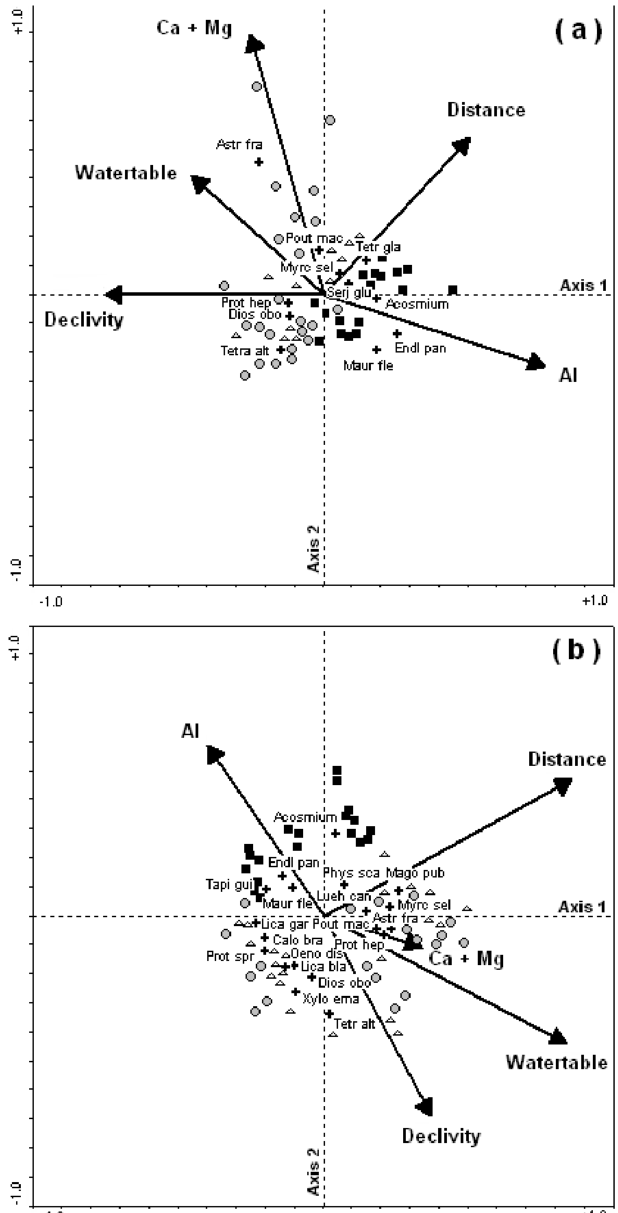

Figure 4 - Ordination diagrams produced by Canonical Correspondence Analyses (CCA) of the 141 plots based on the number of individuals per plot of the species of trees and seedlings (≥ 8 individuals) and 16 environmental variables. The diagrams show the CCA for seedlings (a) and trees (b) species and environmental variables. The forest sections are identified by: triangle (upper), circle (middle) and square (lower). Species are identified by their abbreviated names (*Astronium fraxinifolium* Schott., *Calophyllum brasiliense* Cambess, *Diospyros obovata* Jacq., *Endlicheria paniculata* (Spreng.) Macbr., *Licania blackii* Prance, *Licania gardneri* (Hook. f.) Fritsch, *Luehea candicans* Mart., *Magonia pubescens* St. Hil., *Mauritia flexuosa* L., *Myrcia sellowiana* Berg, *Oenocarpus distichus* Mart., *Ormosia excelsa* Benth. (Acosmium in the figure), *Physocalymma scaberrimum* Pohl, *Pouteria gardneri* (Mart. & Miq.) Baehni (Pout mac in the Figure), *Protium heptaphyllum* (Aubl.) March., *Protium spruceanum* (Benth.) Engl., *Serjania glutinosa* Radlk., *Tapirira guianensis* Aubl., *Tetragastris altissima* (Aubl.) Swart., *Tetrapterys glabra* (Spreng.) Griseb., *Xylopia emarginata* Mart.) The diagrams use the same scale.

were clearly separated from those from the high and middle sections. They were mainly related to topographic variables. Species distribution was wider along the second axis compared to the first, reflecting a topographic gradient. *Ormosia excelsa* Benth., *Endlicheria paniculata* (Spreng.) Macbr. and *Mauritia flexuosa* trees were related to the lower section and *Xylopia emarginata* Mart., *Diospyros obovata* Jacq. and *Licania blackii* Prance to the upper and middle sections.

Some species showed a similar pattern at both stages, seedlings and trees, such as *Diospyros obovata* found in both stages mostly at the upper and middle sections, on the steepest sites nearer to the streambank; *Mauritia flexuosa* and *Ormosia excelsa* had most seedlings and trees individuals at the lower, flatter, swampy sites with high Al content. Seedlings of *Tetragastris altissima* occurred mostly in sites near to the streambank but the trees were on the steepest sites.

DISCUSSION

ENVIRONMENTAL GRADIENTS AND FLORISTIC COMPOSITION

The acidic pH in water showed values within the range found by Haridasan & Araújo (1988), Felfili (1995), Silva-Júnior *et al.* (1996) and Delitti & Burger (2000), for gallery forests. The wet community soils (lower section, see level of ground watertable in Table 2) showed lower pH's (Table 1) when compared with the upper and middle sections while Al levels had the opposite trends. Silva-Júnior *et al.* (1996) also observed that the wet community soils showed a lower pH in gallery forests of Central Brazil. The increasing acidity towards the lower section is probably related to a corresponding increase in soil moisture. Las Salas (1987) observed that high soil moisture favours organic matter decomposition and the release of CO_2, which acidifies the soil by reacting with water.

The middle section is richer in mineral nutrients (P, K, Ca+Mg) than the upper and lower sections. Hornung (1990) also observed that upper topographic areas, in general, are poorer in most mineral nutrient than lower areas because of differential erosion. Nutrients are probably lost from the upper to the middle section, where the drainage is rapid. The lower section was the poorest in P, K and Ca+Mg probably due to swampy conditions that favour a low pH. Mineral elements are immobilized by free Al found under low pH (Furley & Ratter, 1988; Brady & Weil, 1996). P levels were very low (CFSEMG, 1978), but within the levels found for other gallery forests (Felfili, 1995; Silva-Júnior *et al.*, 1996).

Some indicator species of richer soils according to Askew *et al.* (1971) such as *Sterculia striata* St. Hil. & Naud., *Vitex polygama* Cham., *Dilodendron bipinnatum* Radlk., among others, were found in the middle section with higher content of Ca+Mg. Patches of fertile soils can be found within Central

Brazil where dystrophic soils predominate (Furley & Ratter, 1988; Prado & Gibbs, 1993) supporting dry seasonal forests in which those species predominate.

The aluminium contents in the study area are high, reaching levels considered toxic for cultivated plants (Araújo & Haridasan, 1988). Even though, gallery forest species seem to have mechanisms to cope with acidic and aluminium toxic soils as well as the species from the savanna physiognomies of the biome pointed by Furley & Ratter (1988). The lowest figures for aluminium were found at the more fertile middle section where soil-rich indicator species were found.

Different soil types were found in the studied sections of this forest**,** supporting some studies in Central Brazil (Felfili, 1995; Silva-Júnior *et al.*, 1996) showing the occurrence of gallery forests on a variety of soils other than the hydromorphic which are usually shown by regional soil mappings.

The absence of seedlings, saplings and poles of 25% of the species may be a reflection of an episodic pattern of regeneration as suggested by Clark & Clark (1987) for some tropical species or to traits of their life history as shown by Felfili (1997) for gallery forest species. This author suggested that the *Cecropia pachystachya*, a pioneer species, do not form a seedling bank, as its seedlings either pass quickly from sapling to pole phase or die in a short time. However, seedlings and saplings of a more tolerant species, such as *Copaifera langsdorffii*, may remain for a long period under arrested development in the understorey, forming a seedling bank which is just developing into trees when the environmental conditions change by the formation of gaps. Hubbell & Foster (1987) also found tropical species forming a seedling bank of species with arrested development under shade.

In this forest, some species were abundant as trees such as *Cecropia pachystachya* but had none or little natural regeneration, while others were rare as trees, such as *Ouratea castaneaefolia* (DC.) Engl., and were abundant as seedlings or saplings. The former, a pioneer, is probably loosing its importance in the forest, while the second, a shade tolerant (Felfili *et al.*, 2000), is increasing.

The patterns found in the forests are determined by several environmental and genetic factors and their interaction. Hubbell (1979), Clark & Clark (1987), Swaine & Whitmore (1988) and Swaine (1989) suggested that differences in patterns of seed dispersion, reproductive systems, intensity and quality of light, root competition and predation probably play an important role on the maintenance of tree diversity in tropical forests. According to Felfili (1997) these variations play a substantial role in the maintenance of the structure and floristic composition of gallery forest communities, favouring different species at different times within the distinct microsites determined by forest dynamics and canopy layers (Medina, 1995). According to Kellman *et al.* (1994), the maintenance of local biotic diversity in gallery forests requires a diversity of alternative opportunities and coexisting assemblages of species and must be "niche-specialized" in some way. It is clear that some species such as *Mauritia flexuosa* are specialized on swampy sites in gallery forests and others such as *Copaifera langsdorffii* on more drained patches. These species may occur very near to each other but under completely different conditions regarding humidity and light. Gallery forests consist of a very complex environment containing a complex mosaic in a narrow area along the watercourse.

A large number of generalist species in this gallery forest (*Xylopia aromatica* (Lam.) Mart., *Protium heptaphyllum* (Aubl.) March., *Tapirira guianensis* Aubl., *Siparuna guianensis* Aubl., *Tabebuia serratifolia* (Vahl) Nichols, and others) at the transition Cerrado/Amazonia where there is contact among the main hydrographical basins of South America reinforce the role of these forests as ecological corridors, joining different physiographic units (Silva *et al.*, 2006). These linkings through riparian corridors allowed past and current floristic contact as suggested by some studies (Pires & Prance, 1977; Pinto & Oliveira-Filho, 1999; Ivanauskas *et al.*, 2003; Miguel & Marimon, 2008) and continues to allow the gene flow through the Amazonian and Cerrado biomes.

The differences in the patterns of species richness (higher richness of trees than seedlings and saplings) found among the regeneration categories are probably related to the presence of many rare species as trees. Some may be disappearing from the forest while others may be entering it (Felfili, 1995, 1997) and their regeneration may be scarce or episodic. The dynamics of forest communities is very complex in time and space (Oliveira-Filho *et al.*, 1994c) and fluctuation in diversity and structure over time have been registered (Felfili, 1995, 1997).

STRUCTURE

A much larger proportion of juveniles to trees (84% seedlings, 9% saplings, 5% poles and 2% trees) was found in this study as shown in Figure 2. These figures suggest that only one of 42 seedlings becomes a mature tree at the Bacaba gallery forest. This concentration of density in juveniles is a trait of tropical forests (Whitmore, 1990) and a similar proportion (1:50) to those found here have also been registered for undisturbed gallery forests of Central Brazil (Felfili, 1997, 2000).

Some non-pioneer light demanding species, abundant as trees, such as *Tetragastris altissima* and *Diospyros obovata* were scarce as poles probably due to unfavorable light conditions for establishment. In gallery forests, the gaps are few and small under close canopy, a condition where less than 2% of solar radiation reach the understorey, that favours the regeneration of shade tolerants reducing then, the density of pioneers and species that demands light (Felfili, 1997; Felfili & Abreu, 1999).

Mabea pohliana (Benth.) Muell. Arg. and *Siparuna guianensis* are small dimension understorey species (Felfili, 1997) that may reach maturity showing a smaller size than most species.

The population structure of the most abundant species varies with *Diospyros obovata* (upper) abundant as seedlings and trees, but scarce as saplings and poles (Figure 3). The seedlings form a dense grouping under the mother-tree with only a few saplings scattered around seeming to be survivors of a strong competition among the clustered seedlings as suggested by Brown & Whitmore (1992) and Lieberman (1996) for some tropical plants. *Hymenaea courbaril* (the most important in the middle) had an abundance of saplings (Figure 3). *Mauritia flexuosa* (lower), a palm tree, was abundant at all regeneration stages with seedlings representing 60 percent of the total density in contrast to the current 10 percent of trees (Figure 3). Nascimento & Hay (1990) and Felfili (1997) suggested that species presenting this pattern have stable, self-regenerating populations and will remain as important in the forest canopy.

Pearson´s correlations indicated that the floristic composition and structure of the forest would be fairly similar in the future depending on the current pole population. For the upper and the middle, even the seedlings and saplings populations are fairly well correlated to the trees. The low correlation between seedlings, saplings and trees in the lower is probably due to the death of juveniles after germination during the early stages of establishment in those swampy sites.

REGENERATION CATEGORIES AND ENVIRONMENTAL GRADIENTS

The lower, wetter site had the highest density of trees per plot. In this site, the soil coverage by bamboos and rocks was smaller than in the others, the declivity was less accentuated and the ground watertable was closer to the surface. This result confirms that a high number of individuals is a trait of swampy gallery forests (Sampaio *et al.*, 2000). Seedlings, saplings and poles were more abundant at the middle, where rocky cover was high but bamboos and slope were at an intermediary level. The high declivity of the upper probably cause seed loss by run off in the rainy season. The topographic gradient and the ground watertable level have a direct influence on the pattern of establishment and immigration of the species at each section of this forest. According to Kellman *et al.* (1994), these factors contribute to the maintenance of diversity in gallery forests once they favour high immigration rates.

High cover of bamboos, gaps and deep watertable in the dry season were inversely correlated to density of poles and trees, according to the first canonical variable. A higher competition and less water available at the surface are limiting to plant development. The second canonical variable showed that the presence of seedlings, saplings and poles was inversely correlated to gaps and Al but directly to higher Ca+Mg levels. According to Whitmore (1984) and Oliveira-Filho *et al.* (1994b), bamboos, once established, can interfere with the tree community for long periods. Oliveira-Filho *et al.* (1998) observed that species distribution and abundance were correlated with both the relative area of canopy gaps and the soil-topography gradient, and suggested that the critical factors involved in these gradients are light and ground water regimes.

These correlations suggested that the physical structure (bamboos, gaps and ground watertable) is probably an important component in determining tree communities, while soil fertility (Ca+Mg) is an important component in determining seedling, sapling and pole communities.

The tree and seedling communities showed a continuous distribution of species, even though there were differences amongst the forest sections. The lower section turned out to be the most differentiated community (Marimon *et al.*, 2001, 2002), leading to a particular set of species (trees and seedlings) with peculiar establishment strategies linked especially to a humidity gradient. These findings agree with those of Oliveira & Felfili (2005) studies of natural regeneration of a gallery forest in Central Brazil.

In the Bacaba forest the seedlings and mature tree distribution were coincident for several species such as *Mauritia flexuosa,* an exclusive species of humid sites, indicating that some species are strongly associated to certain environmental conditions during all their life cycle.

Among the environmental variables that presented variations among the forest sections the most important were declivity, watertable depth and distance from the stream. Oliveira-Filho *et al.* (1994a) and Felfili (1995) found strong correlations between species distribution, soil variation and distance from the watercourse, suggesting that a humidity gradient is related to those physical features that determine species distribution.

The presence of indicator species of nutrient-rich sites such as *Sterculia striata* was determined by higher levels of P, K and Ca+Mg at the middle section of the forest.

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