Sapling communities in Amazonian white-water forests

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Abstract

Aim Structure and floristic composition of forest regeneration (trees between 1 and 10 cm diameter at breast height (d.b.h), ≥ 1 m growth height) was described in three forest types of Amazonian white-water forests (várzea), in order to analyse whether floristic composition of saplings is related to the successional stage of the forests, whether it differs in comparision with the mature flora, and if there exists a zonation of sapling species along the gradients of flooding and irradiation.

Location Mamirauá Sustainable Development Reserve, Western Brazilian Amazon.

Methods The investigated forests were of the low and the high várzea type, on an annual average flooded around 4 and 1 months, respectively. The two low-várzea forests belonged to the secondary and to the late-successional stage, the high-várzea forest also to the late-successional stage. A total of 24 circular sample plots covering 1885 m^2 were installed. They were nested within three rectangular 1 ha permanent sample plots where individuals ≥ 10 cm d.b.h. were formerly inventoried. Average inundation and radiation [relative photosynthetically active radiation (rPAR)] at the forest floor was recorded in all inventoried plots. The Mean spatial Distribution Center (MDC; Ebdon, 1998) for all sapling species was calculated. Sapling species were grouped into associations with respect to their light-demand and their location along the flood-level gradient.

Results Average flood height and average rPAR at the forest floor was highest in the secondary stage of the low várzea and lowest in the high-várzea forest. Overall average density and basal area of the saplings averaged 2250 individuals and 2.3 m^2 ha^{-1} in the secondary stage, 2330 individuals and 2.6 m^2 ha^{-1} in the late-successional stage of the low várzea and 5000 individuals and 4.8 m^2 ha^{-1} in the high várzea. In all forest types, species richness of saplings was lower than species richness of trees ≥ 10 cm d.b.h., and amounted to 25 species in the secondary stage, to 35 species in the late-successional stage of the low várzea and to 88 species in the high-várzea forest. The amount of 'immigrants' (Bazzaz, 1991) at the sapling level increased with proceeding forest succession and amounted to 24 and 29% in the low várzea and to 31% in the high várzea. Sapling species distribution, species richness and individual density was linked to both, the gradient of flooding and the gradient of irradiation. Species richness and individual density was highest in the high várzea and decreased with increasing influence of flooding. The high várzea was predominated by pronounced shade-tolerant sapling species, whereas in the low várzea occured both, light demanding and shade-tolerant species groups.

Main conclusions Influence of flooding seems to be the main factor triggering species composition and structure of sapling communities in várzea forests. Proceeding forest succession reduces the impact of flooding because of the biogenical induced silting up of the forested sites. However, forest succession also alters forest architecture of the overstory and such the light conditions at the sapling level. Therefore, radiation is an important factor influencing species composition of sapling communities in várzea forests.

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INTRODUCTION

Periodic water-level fluctuations of Amazonian sediment- and nutrient-rich white-water rivers influence the aquatic-terrestrial landscape which is called várzea (Prance, 1979). About 60,000–100,000 km^2 of the várzea is covered by forests (Goulding, 1996; Junk, 1997). In Central Amazonia, the forests become established where the water column averages < 7 m, corresponding to a mean submersion period of trees of up to 230 days year^{-1} (Junk, 1989). Because of the hydrological and geomorphological dynamism of the rivers, várzea forests can be differentiated in several communities, differing in age, physiognomy and species composition. Worbes *et al.* (1992) defined several successional stages, from the first establishment of pioneer species on fresh deposited sand bars until climax stages with trees reaching ages of 100–300 years. With proceeding succession, species diversity increases continuously from monospecific stands to stands with *c.* 100 species ha^{-1}. Tree density declines from a maximum of some 1000 stems ha^{-1} in early-successional stages to *c.* 500 stems ha^{-1} in climax stages. Growth height of upper canopy trees increases from 10 to 15 m in early-successional stages to *c.* 30–35 m in subsequent stages and forests develop from mono-layered to multi-layered and well stratified stands (Wittmann *et al.*, 2002). Besides succession, there exists a zonation of tree communities along the flood-level gradient (Junk, 1989; Ayres, 1993). Wittmann *et al.* (2002) mentioned, that forest succession in várzea forests is linked to the biogenical induced silting up, so that succession proceeds in relation to the increasing topographic level of the forested sites. Low-várzea forests establish where the annual water column averages heights of more than 3 m (inundation period > 50 days year^{-1}), whereas high-várzea forests establish where it averages < 3 m. In the high várzea, species richness with more than 150 species ha^{-1} is almost similar to the non-flooded terra firme. Tree density amounts to 300–400 stems ha^{-1}, and upper canopy trees reach heights of up to 45 m.

Most quantitative botanical inventories in várzea forests focused on trees ≥ 10 or 15 cm diameter at breast height (d.b.h.) (Pires & Koury, 1959; Balslev *et al.*, 1987; Campbell *et al.*, 1992; Ayres, 1993; Worbes, 1997; Wittmann *et al.*, 2002). Floristic inventories rarely include understory trees with small diameters and of low growth heights. Thus, information about species composition and structure of forest regeneration in Amazonian floodplains is scarce and mostly concentrated on experimental studies dealing with the seedling establishment of single tree species (Ziburski, 1991; Oliveira, 1998; Parolin, 2000, 2001; Ferreira, 2002). In contrast to the terra firme, where early-successional regeneration is mainly keyed to the light-demand of seedlings and saplings in gaps (e.g. Budowski, 1965; Ashton, 1978; Bazzaz & Pickett, 1980; Denslow, 1980; Uhl, 1982; Bongers *et al.*, 1988; Whitmore, 1989), the flooding is thought to be the most limiting factor for the seedling establishment within floodplain forests (Junk *et al.*, 1989; Puhakka & Kalliola, 1993; Klinge *et al.*, 1995). However, information about the regeneration of tree species along the gradients of flooding or other environmental site conditions in Amazonian floodplain forests is still missing. Foster *et al.* (1986); Hubbell & Foster (1992) and Nebel *et al.* (2001) emphasized the importance of small trees for the local fauna, because they provide shelter and food for many animals. Furthermore, saplings represent the natural potential for cultivation or even recruitment of already endangered tree species, and the creation of basical information about their species composition and structure is of decisive importance for sustainable forest management plans.

Succession, species richness and structure of the mature tree population in várzea forests are related to inundation. Thus, we expect that the 'flood pulse' (Junk *et al.*, 1989) reflects the distribution of sapling species to a similar way. The present study provides a quantitative description of the floristic composition and structure of saplings (1–10 cm d.b.h., ≥ 1 m growth height) in three successional stages of Amazonian várzea forests. Comparisons between saplings and mature tree communities (≥ 10 cm d.b.h.) were performed on the same sites. Average inundation and radiation measurements were recorded in order to determine whether there is a sapling species zonation along the environmental gradients.

METHODS

Study area

The study was completed in the focal area of the Mamirauá Sustainable Development Reserve (MSDR) (2°51'S, 64°55'W), *c.* 70 km NW of the city of Tefé, in the Western Brazilian Amazon. The focal area of the MSDR covers a area of *c.* 3900 km^2 and is located between the confluence of the Solimões and the Japurá Rivers (Fig. 1). Mean monthly temperatures in the MSDR vary little over the year and range between 25 and 28 °C. Between 1996 and 2000, mean annual rainfall was *c.* 3000 mm [Institute for Sustainable Development Research Mamirauá (ISDRM), Tefé].

Annual water-level fluctuations of the Solimões and Japurá Rivers ranged between 6.6 and 10.1 m during 1993–2000 (ISDRM, Tefé). The alluvial landscape is a small-scale mosaic of levees, depressions, lakes and river channels, periodically interconnected with each other and the main river system. The vegetation cover near the highly inundated river banks and lakes is dominated by aquatic and semi-aquatic macrophytes. About 90% of the focal area of
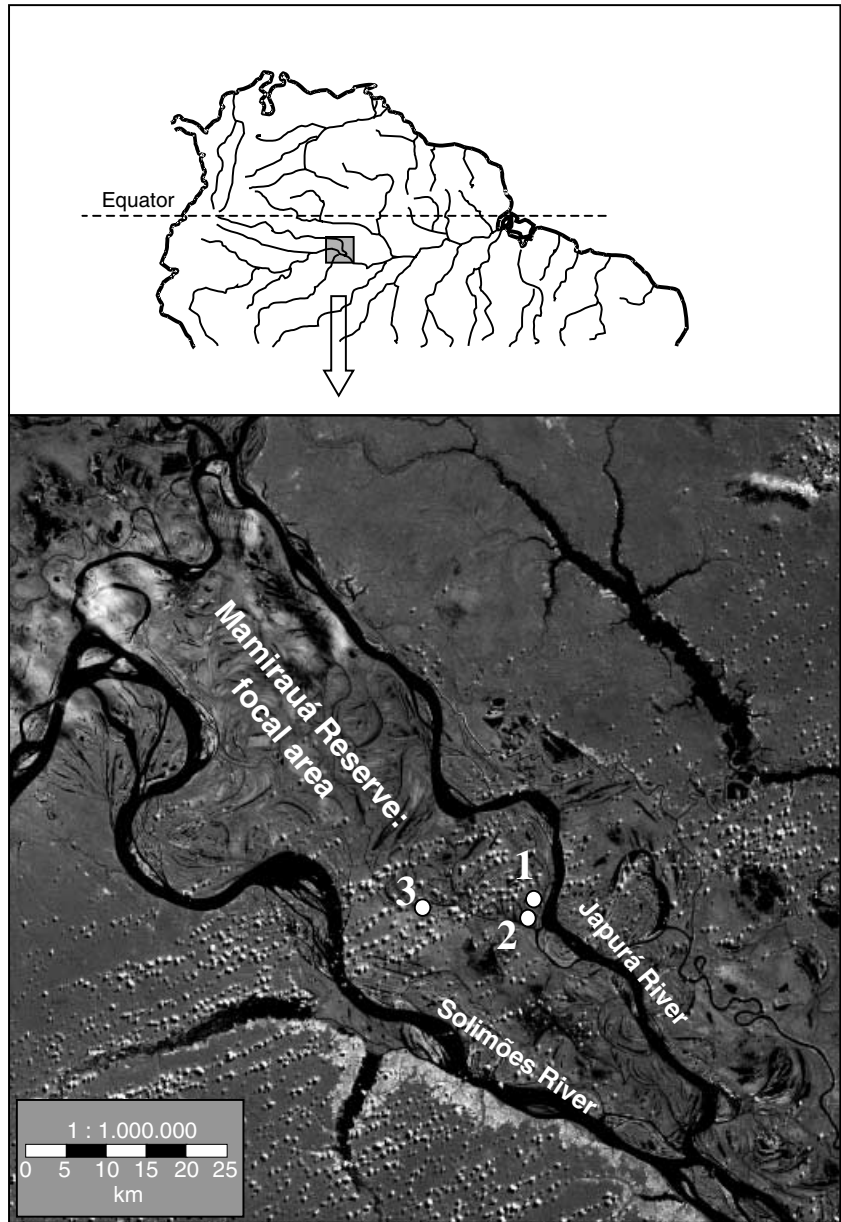
Figure 1 Studied sites within the focal area of the Mamirauá Sustainable Development Reserve, located between the Japurá- and the Solimões Rivers. Site 1: secondary stage, site 2: late-successional stage, both low várzea; site 3: late-successional stage of the high várzea.

MSDR is covered by closed-canopy forests (Sociedade Civil Mamirauá *et al.*, 1996). As a result of the small-scale irregular topography of the landscape, they form a patchwork of different forest types. About 92% of the closed-canopy forests in the focal area of MSDR are diferent successional stages of the low-várzea type, whereas *c.* 8% of the forests are of the high-várzea type (Wittmann *et al.*, 2002).

Within the focal area of the MSDR, Wittmann *et al.* (2002) investigated species composition and stand structure of trees ≥ 10 cm d.b.h. in three successional stages, installing rectangular plots each with the size of 1 ha (50 m × 200 m), and each subdivided in 16 square plots of 625 m². Topography and average inundation of the studied plots was recorded using a theodolite (Zeiss Ni2, Carl Zeiss, Jena, Germany) and high resoluted Digital Elevation Models (DEM) were generated (Fig. 2). The vertical position of individual trees relatively to the water-level was derived comparing flood marks on trunks with water levels recorded in Tefé (ISDRM). Two plots were localized in the low várzea and one plot in the high várzea (Table 1). Relative abundance, relative dominance, relative frequency and the [Total Importance Value Index (TIV); Curtis & McIntosh, 1951] of the 10 most frequent tree species ≥ 10 cm d.b.h. in each forest type is presented in Table 2.

Inventories

In each of three formerly investigated 1 ha-plots, each eight circular plots were installed for the sapling inventory. The circular plots with the size of 78.5 m² (*r* = 5 m) were nested in the centre of eight square plots (Fig. 2). Total inventoried
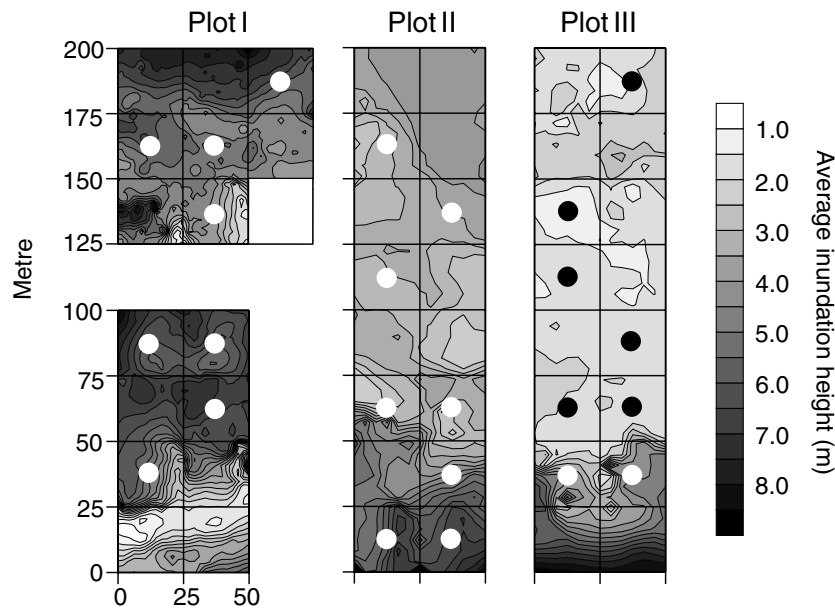
Figure 2 Digital elevation models of the three 1 ha plots, installed for the inventory of trees ≥10 cm d.b.h. (Wittmann *et al.*, 2002). Plot I: secondary stage, Plot II: late-successional stage, both low várzea; plot III: late-successional stage of the high várzea. Circles represent the plots installed for the inventory of saplings (< 10 cm d.b.h.; ≥1 m in height).

Table 1 Plot characteristics (trees ≥ 10 cm d.b.h.)

Plot	I	II	III
Average water column (m)	4.8	4.1	2.2
Submersion (days year^{-1})	131	111	36
rPAR on forest floor (%)	17	12	3
Individuals (ha^{-1})	641	434	469
Species (ha^{-1})	45	91	172
Growth height of upper canopy trees (m)	10–15	30–35	35–45
Amount of canopy layer	1	3	3
Basal area (m^2 per ha^{-1})	31	40	33
Successional stage*	Secondary	Late-successional	Late-successional
Estimated age (years)*	10–80	100–300	/
Other designations	Cecropia latiloba-/ Crataeva benthamii – forest type*	Piranhea trifoliata – forest type*	Restinga alta[†] high várzea[‡]

*Worbes *et al.* (1992); [†]Ayres (1993); [‡]Wittmann *et al.* (2002).

area amounted to 628.3 m^2 per forest type and 1 ha plot (1885 m^2 in total).

All individual trees between 1 and 10 cm d.b.h. and above 1 m in height presented in the circular plots were numbered and their diameters measured. The diameters in individuals with heights below 130 cm (breast height) were recorded 10 cm above the ground surface. All individuals were identified to the genera and, when possible, to the species level.

The relative photosynthetically active radiation (rPAR) was recorded on forest ground within all inventoried sapling plots, using a integrating quantum photometer (Li 188b, Li-cor, Lincoln, Nebraska, USA) at fixed horizontal positions in the centre of the plots (90° to light incidence). The measurements were recorded at the time of the highest sun position, between 11.00 and 13.00 hours, in a total of fourteen times during the terrestrial period 2000.

Simultaneously, control measurements of the absolute irradiation were performed on a fixed point outside the forests. The measured unit was μmol s^{-1} m^{-2}.

Data analysis

Calculations of the TIV, determinations of floristical equitability ('eveness', Shannon & Weaver, 1949) and floristical similarity (Sørensen, 1948) were performed to compare floristic composition among the sapling plots and between saplings and trees ≥ 10 cm d.b.h.. For each sapling species, the Mean spatial Distribution Center (MDC; Ebdon, 1998) was determined, as a result of the mean inundation and irradiation values on all present individuals. Sapling species with similar environmental requirements were grouped into associations.

Table 2 Relative abundance (ra), relative dominance (rd), relative frequency (rf) and TIV of the 10 most important tree species ≥ 10 cm d.b.h. in the three investigated forest types

	Species	ra	rd	rf	TIV	∑TIV (1–10)
Plot I (secondary stage)						
1	*Cecropia latiloba* Miq. S.	27.3	24.06	6.67	58.03	230.03 (76.7%)
2	*Nectandra amazonum* Nees	7.18	15.72	6.67	29.56	
3	*Crataeva benthamii* Eichl.	13.57	7.53	8.33	29.44	
4	*Laetia corymbulosa* Spruce	12.01	6.51	7.78	26.3	
5	*Luehea cymulosa* Spruce	5.3	11.86	6.11	23.27	
6	*Maclura tinctoria* (L.) Grisebach	8.42	4.66	7.22	20.3	
7	*Pseudobombax munguba* Dugand	5.15	8.07	6.11	19.33	
8	*Simaba multiflora* A. Juss.	1.87	2.24	5	9.11	
9	*Tabebuia barbata* Sandwith	1.87	2.19	4.44	8.5	
10	*Cecropia* sp.	2.18	1.78	2.22	6.18	
11–45		15.13	15.4	39.44	69.97	
∑		100	100	100	300	
Plot II (late-successional stage)						
1	*Couepia* sp.	0.92	9.49	4.84	15.25	104.52 (34.8%)
2	*Cecropia latiloba* Miq. S.	8.53	1.97	3.63	14.12	
3	*Symmeria* sp.	3.23	3.68	4.03	10.94	
4	*Tabebuia barbata* Sandwith	4.61	3.39	2.82	10.82	
5	*Vitex cymosa* Bert. ex Spreng	2.07	3.11	4.44	9.62	
6	*Coccoloba* sp.	1.15	3.92	4.44	9.51	
7	*Pouteria elegans* (A.DC.) Baehni	4.84	2.17	2.42	9.43	
8	*Hevea spruceana* Muell. Arg.	3.69	4.34	0.4	8.43	
9	*Piranhea trifoliata* Baill.	3.23	2.7	2.42	8.35	
10	*Crataeva benthamii* Eichl.	3.46	1.78	2.82	8.06	
11–100		64.29	63.45	67.74	195.48	
∑		100	100	100	300	
Plot III (late-secondary stage, high várzea)						
1	*Pouteria procera* (Mart.) K. Hammer	6.45	1.65	3.76	11.86	78.91 (26.3%)
2	*Eschweilera* sp.	0.23	10.02	0.31	10.57	
3	*Eugenia* sp.	0.23	8.05	1.88	10.17	
4	*Homalium guianense* (Aubl.) Oken	0.69	6.98	0.94	8.61	
5	*Xylopia calophylla* R.E. Fries	1.15	6.63	0.63	8.41	
6	*Aspidosperma riedelii* Muell. Arg.	3	0.51	2.82	6.33	
7	*Malouetia tamaquarina* A.DC.	3.46	0.04	2.82	6.32	
8	*Piranhea trifoliata* Baill.	0.46	5.07	0.63	6.16	
9	*Pseudobombax munguba* Dugand	2.07	2.97	0.31	5.35	
10	*Tapura juruana* (Ule) Rizzini	2.07	2.12	0.94	5.13	
11–177		80.19	55.96	84.96	221.09	
∑		100	100	100	300	

RESULTS

Flooding and irradiation

The average flood height in the sapling plots was 4.8 m (±0.1) in plot I, 4.1 m (±0.4) in plot II and 1.9 m (±0.4) in plot III. Average rPAR reaching the forest floor amounted to 17.3% (±4.2) in plot I, to 12.3% (±5.3) in plot II and to 3.1% (±1) in plot III (Table 1).

Species composition and stand structure of saplings

Field inventory yielded a total of 611 individual trees between 1 and 10 cm d.b.h. and ≥ 1 m in height on the entire research area of 1885 m² , belonging to 134 species and 49 families. Species belonging to the Euphorbiaceae dominated with a total of 18.9% of individuals, followed by Rubiaceae (11.3%), Moraceae (6.2%) and Annonaceae (5.7 %) (Fig. 3).

The stand densities were 141 individuals in plot I, 146 individuals in plot II and 316 individuals in plot III. Tree-species richness amounted to 25, 35 and 88 species, respectively.

The distribution of saplings by diameter class showed a decreasing number of individuals with increasing diameters (Fig. 4). Total sapling basal area per forest type and per 628.3 m² amounted to 0.15 m² in plot I, to 0.16 m² in plot II and to 0.3 m² in plot III (corresponding to 2.33, 2.56 and 4.67 m² ha^{-1}, respectively). In all forest types, the average growth heights of the saplings were related to the individual diameters (Fig. 4).

The TIV of the 10 most important species showed coherences to the stage of succession. Within the low várzea,
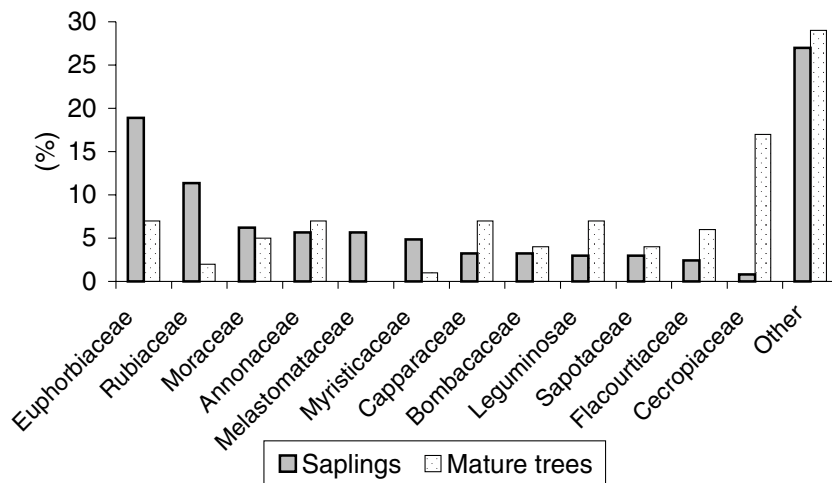
Figure 3 Tree family distribution at the sapling- and the overstory level.
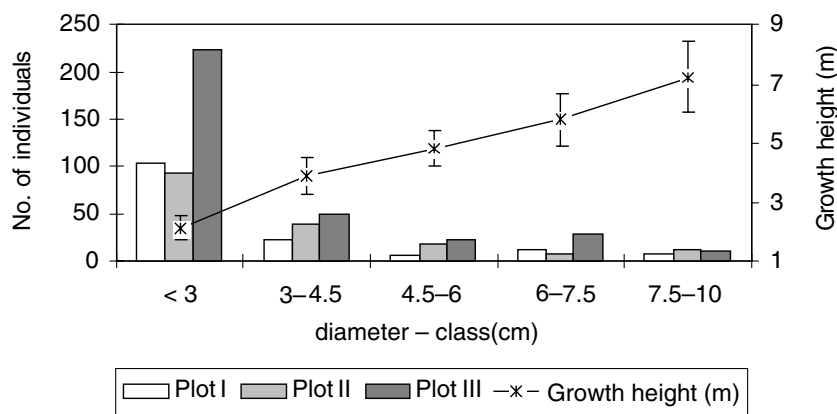

Figure 4 Distribution of saplings by d.b.h.-class (cm) and average growth heights (m).

the 10 most important species account for 86.5% of the TIV in plot I and for 65% in plot II. In the high várzea, the 10 most important species account for 37.9% of the TIV (Table 3).

Species equitability was most uniform among the inventoried circles of plot I, indicating the relative even distribution of species in the secondary stage. Most heterogeneous species distribution was among the sites of the high-várzea plot (Fig. 5).

Comparison of saplings with trees ≥ 10 cm d.b.h.

The total basal area of the inventoried saplings projected to the area of 1 ha in size corresponded to 7.5% of the basal area of trees ≥ 10 cm d.b.h. in plot I, to 6.3% in plot II and to 14.3% in plot III.

In all plots, sapling species richness was lower than those of mature trees. The inventoried area installed for regeneration amounted to only 6.3% of the inventoried area installed for the adult flora. However, species richness of the saplings reached to 55.5% of those of the adult forest in plot I, to 38.5% in plot II and to 51.2% in plot III.

The comparison between the species composition of saplings and the overstory indicated already differences at the family level (Fig. 3). At the species level, floristical similarity between saplings and mature trees amounted to 54.3% (±9.4) in plot I, to 39.7% (±7.7) in plot II and to 30.6% (±3.5) in plot III.

About 24% of the sapling species recorded within plot I were absent in the adult flora (n = six species). In the late-successional stages, the amount of 'immigrants' (Bazzaz, 1991) at the sapling level increased with increasing species diversity. In plot II, 28.6% (n = 10) of the sapling species were absent in the adult flora, in plot III 30.6% (n = 50).

Relationship between saplings and environmental site conditions

The relative species richness and the relative individual density showed decreasing numbers of species and individuals with increasing inundation (Fig. 6). The ordination of sapling species along the gradients of flooding and irradiation showed a exponential J-shaped curve, indicating different species distribution patterns between the low and the

Table 3 Relative abundance (ra), relative dominance (rd), relative frequency (rf) and TIV of the 10 most important sapling tree species (< 10 cm d.b.h.; ≥ 1 m in height) in the three investigated forest types

|	Species	ra	rd	rf	TIV	∑TIV (1–10)
Plot I (secondary stage)						
1	*Adelia ricinella* L.	31.91	24.52	13.79	70.23	259.66 (86.5%)
2	*Crataeva benthamii* Eichl.	7.8	20.06	9.34	37.21	
3	*Conceveiba* sp.	8.51	17.64	8.62	34.77	
4	*Tococa* sp.	12.77	9.7	5.17	27.64	
5	*Maclura tinctoria* (L.) Grisebach	8.51	5.82	8.62	22.95	
6	*Pseudobombax munguba* Dugand	4.96	5.35	8.62	18.93	
7	*Laetia corymbulosa* Spruce	4.96	4.96	6.26	16.18	
8	*Simaba multiflora* A. Juss.	2.84	3.35	5.17	11.35	
9	Boraginaceae sp.	1.42	7.07	1.72	10.21	
10	Malpighiaceae sp.	3.55	1.47	5.17	10.19	
11–25		12.77	0.06	27.52	40.3	
∑		100	100	100	300	
Plot II (late-successional stage)						
1	*Symmeria paniculata* Benth.	16.13	11.51	6.89	34.53	195.05 (65%)
2	*Pouteria elegans* Baehni	15.49	13.43	5.17	34.09	
3	*Pseudobombax munguba* Dugand	10.97	7.89	5.17	24.03	
4	*Pouteria glomerata* Radlk.	7.1	11.94	1.72	20.76	
5	*Tovomita rostrata* Poepp. & Planch.	5.16	9.94	5.17	20.27	
6	*Cecropia latiloba* Miq. S.	10.32	4.18	3.44	17.94	
7	*Ilex* sp.	3.87	3.78	5.17	12.82	
8	*Margaritaria* sp.	2.58	4.55	3.44	10.57	
9	*Oxandra riedeliana* R. E. Fries	1.94	4.63	3.44	10.01	
10	Apocynaceae sp.	3.23	3.2	3.44	9.87	
11–35		23.23	24.94	56.78	104.95	
∑		100	100	100	300	
Plot III (late-successional stage, high várzea)						
1	Rubiaceae sp. *(1)*	7.59	5.26	3.76	16.61	113.62 (37.9%)
2	*Virola calophylla* Warb.	7.91	4.21	3.76	15.88	
3	*Rudgea cornifolia* Standley	7.29	3.64	3.76	14.68	
4	*Sorocea duckei* Burgcr.	5.7	5.12	3.14	13.95	
5	Myristicaceae sp.	3.22	5.98	3.14	12.33	
6	*Guatteria innundata* Mart.	1.58	6.93	1.88	10.4	
7	*Duguetia quitarensis* Benth.	1.58	6.22	0.25	8.06	
8	Rubiaceae sp. *(2)*	3.16	2.25	2.51	7.92	
9	*Virola elongata* Warb.	2.85	2.06	2.51	7.42	
10	*Diospyros subrostrata* Hiern	1.27	3.14	1.88	6.28	
11–88		58.23	54.75	73.4	186.38	
∑		100	100	100	300	
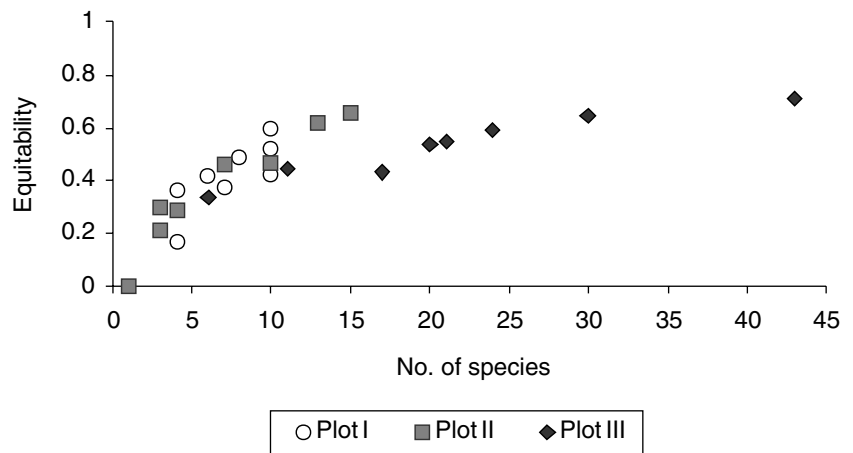
Figure 5 Shannon & Weavers equitability index of all inventoried plots. $(J) = H \ln(S)^{-1}$ where H = Shannons diversity index $(H = -\sum P_1 \ln P_1$, where P_1 = number of individuals of species A/total number of individuals of all species), S = total number of species.
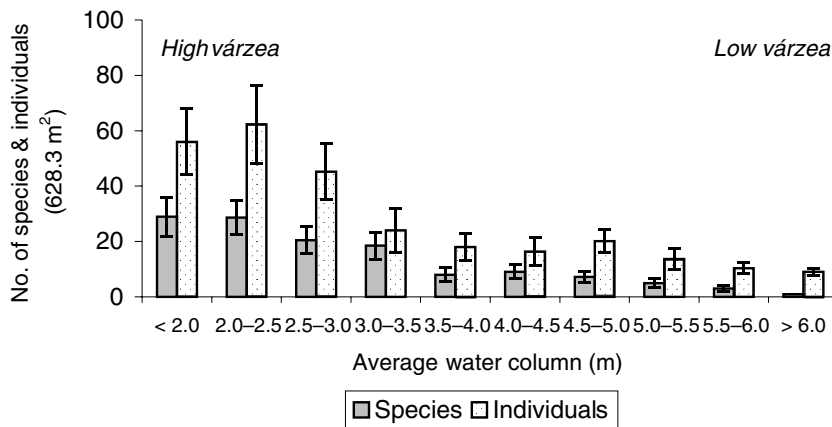
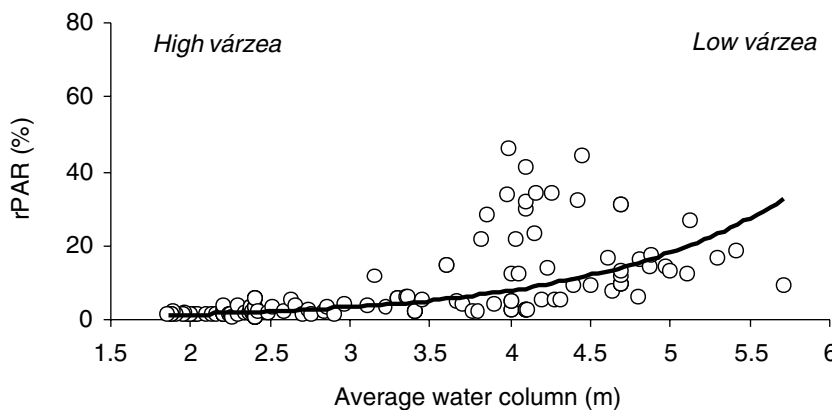**Figure 6** Relative number of species and individuals along the flood-level gradient.

Figure 7 Mean spatial Distribution Center (MDC) (Ebdon, 1998) of sapling species along the gradients of flooding and irradiation.

high várzea (Fig. 7). The MDC of the high várzea species ($n = 63$) averaged a flood height of 2.35 m (± 0.23) and a mean rPAR of 2.3 % (± 1.45). For the low várzea species ($n = 70$), the MDC averaged a flood height of 4.15 m (± 0.6) and a mean rPAR of 13.58% (± 11.53). Besides the strongly developed zonation along the flood-level gradient, light demanding and shade-tolerant species were detected.

Along their position at the flood-level gradient, three species associations were distinguished (Table 4). However, the associations also showed coherences to the amount of incoming irradiation. A total of 206 individuals (33.7%), belonging to 54 sapling species (40.6%) concentrated on the high várzea, where rPAR was lower than 5%. Only six species (e.g. *Sorocea duckei* Burgcr.) also established were rPAR ranged between 5 and 25%.

A total of 284 individuals (46.5%) belonging to 46 species (34.6%) were restricted to the low várzea (Table 4). Most of the low-várzea species concentrated on flood heights between 4 and 6 m. *Symmeria paniculata* Benth., *Pseudobombax munguba* Dugand, *Crataeva benthamii* Eichl. and *Buchenavia sp.* were the only species where flooding exceeded 6 m in height. 81% of the low-várzea species concentrated where the rPAR exceeded 5%. Light demanding pioneer species, such as *Adelia ricinella* L., *P. munguba* Dugand and *Cecropia latiloba* Miq. S. where restricted to

the forest border or to small scaled gaps, where rPAR exceeded 25%.

The intermediate association was composed of 17 species (12.8%) and 121 individuals (19.8%) which were distributed over the whole flood-level gradient (Table 4). Eleven species were restricted to rPAR values below 5% (e.g. *Virola calophylla* Warb., *Tovomita rostrata* Poepp. & Planch. and *V. elongata* Warb.), whereas six species concentrated on higher rPAR values. However, no species was restricted to rPAR values above 25%.

DISCUSSION

The mature tree population (≥ 10 or 15 cm d.b.h.) in Amazonian várzea forests is characterized by a well-defined species zonation along the flood-level gradient (Junk, 1989; Ayres, 1993; Wittmann *et al.*, 2002). This zonation is evident through the form and amount of adaptation strategies of trees to the prolonged inundations. For low-várzea trees, many physiological, morphological and anatomical adaptations to flooding were described, such as phenological responses (Wittmann & Parolin, 1999; Parolin *et al.*, 2002b; Schöngart *et al.*, 2002), reductions of the photosynthetic activity during the aquatic phase (Parolin, 1998, 2001), anaerobic metabolism (Fernandes-Corrêa & Furch, 1992;

Table 4 Species groups along the gradients of flooding and irradiation

	Light requirement (% rPAR)			Average water column (m)*							
	<5	5–25	>25	<2	2–3	3–4	4–5	5–6	>6	Σ	
1 *Virola calophylla*	x			7	13	5				25	Intermediate
2 *Tococa* sp.		x	x	1	3	3	18			25	association
3 *Tovomita rostrata*	x			1	1	4	4	1		11	
4 *Virola elongata*	x				6	1	1	1		9	
Σ5–17	x	x	x	6	20	6	18	1		51	
18 Rubiaceae sp. *2*	x			3	20	1				24	High-várzea
19 *Rudgea cornifolia*	x			3	19	1				23	association
20 *Sorocea duckei*	x	x		4	13					17	
21 Rubiaceae sp. *1*	x			7	4					11	
22 Rubiaceae sp. *3*	x			1	7	2				10	
23 Hippocrateaceae sp.	x			2	5	1				8	
Σ24–77	x	x		23	88	2				113	
78 *Adelia ricinella*			x			1	39	7		47	Low-várzea
79 *Symmeria paniculata*		x	x				1	17	8	26	association
80 *Pouteria elegans*		x	x			1	6	18		25	
81 *Pseudobombax munguba*			x			13	4	3	4	24	
82 *Cecropia latiloba*			x			2	15			17	
83 *Crataeva benthamii*		x	x			2	8	2	1	13	
84 *Maclura tinctoria*			x				4	9		13	
85 *Conceveiba* sp.		x					5	7		12	
86 *Pouteria glomerata*		x					11			11	
87 *Simaba multiflora*			x			3	4	1		8	
Σ88–134	x	x	x			26	53	8	1	88	
				58	199	74	191	75	14	611	

*Values represent absolute abundances per 1885 m^2.

Schlüter *et al.*, 1993), the formation of adventitious roots (Worbes, 1986) and reductions of wood growth during the aquatic phase (Worbes *et al.*, 1992; Worbes, 1997). For high-várzea trees, no information about adaptations of trees to flooding is available.

The present study demonstrates, that structure, distribution and species richness of sapling communities in várzea forests is strongly linked to the flood-level gradient. Flooding seems to be the most limiting factor influencing sapling species distribution. However, species composition also depends on forest structure of the overstory and on the amount of radiation during the time of plant establishment. Therefore, it reflects the actual successional stage of the overstory. In competition with terrestrial and semi-aquatic macrophytes [e.g. *Paspalum fasciculatum* Willd. ex. Fluegge and *Echinochloa polystachia* (H.B.K.) Hitchcock, Junk & Piedade, 1993], trees of early-successional stages establish on fresh deposited sand bars of the highly dynamic river banks, where incoming radiation is high. They are composed by a few light-demanding pioneer species, such as *Salix martiana* Leyb., *Alchornea castaneifolia* A. Juss. and *C. latiloba* Miq. S., which tolerate the high and prolonged inundations, the mostly associated high sedimentation rates and the anaerobic conditions at the root level or the whole plant (Parolin *et al.*, 2002a). As typical 'r-strategists' (Pianka, 1970) they are characterized by a high potential of sexual and vegetative reproduction (Puhakka

& Kalliola, 1993; Worbes, 1997). Germination occurs during the short terrestrial phase and succeeds in monospecific stands, where seedling density can reach up to 1000 individuals m^{-2} (e.g. *C. latiloba.*, pers. obs). However, seedling and sapling mortality is high when compared with individuals of later successional stages (Liebermann *et al.*, 1985). In low situated sites along the flood gradient, only a few individuals survive the first flooding, which persits during the most part of the year. For this reason, sapling density of these species in general is low, and their successful establishment may be linked to consecutive years with exceptional low inundations.

With proceeding succession, influence of flooding and geomorphological dynamic decreases, because large stemmed and buttresses building trees establish, slowing down water energy and favouring the deposition of fine grained sediments. The biogenical induced silting up results in sites which grow in topographic height (Wittmann *et al.*, 2002). Species richness of mature trees increases and forest physiognomy changes because of the establishment of large trees and the development of multi-layered stands. Together with decreasing impact of flooding, the more complex forest architecture in late-successional stages implies a high number of ecological niches at the seedling and sapling level. Species richness and density of saplings increase, resulting in shade-tolerant species groups which establish under closed forest canopies, and in light tolerant

species groups which establish near the forest borders and in gaps.

In the high várzea, height and duration of flooding is reduced to that way that regeneration properties in the most part of the year are terrestrial, and thus similar to non-flooded habitats. However, the flood pulse in high-várzea forests probably remains a limiting factor influencing species composition at the sapling level. Kubitzki (1989) stated that the origin of many várzea trees is the surrounding Terra Firme. When they immigrated to the floodplains, they gradually developed adaptations to the periodical inundations. For this reason, many high-várzea species probably developed less adaptations to flooding than low-várzea species (Wittmann et al., 2002), and may react very sensitive even to small flood pulse variations.

In comparison with the different light environments found within the forest types of the low várzea, the present study revealed a relative small radiation gradient in the high-várzea forest. The low incoming irradiation at the forest floor favours the establishment of pronounced 'shadow-bearers' (Whitmore, 1989) which germinate and establish below a closed canopy and often persist several decades with growth rates reduced to a minimum (Lamprecht, 1986). As there was no recent gap in our plot, information about composition of high-várzea gap regeneration is still missing. However, observations in fresh eroded high-várzea forests next to the banks of the Solimões and Japurá Rivers indicated that pronounced light-demanding species in high-várzea forests are scarce. Rather we expect that the occurrence of gaps in the high várzea favour the growth of already installed shadow bearers. As such, the majority of high-várzea species can be defined as typical 'opportunists' (Whitmore, 1989).

Many studies in tropical lowland forests revealed that species composition of forest regeneration differs significantly to that of the adult forest (e.g. Budowski, 1965; Brokaw, 1985; Lamprecht, 1986; Liebermann & Liebermann, 1987; Bazzaz, 1991; Nebel et al., 2001). Within the three inventoried plots in the present study, the amount of immigrants increased with proceeding successional stage and increasing topography, reaching the highest pecentage in the high várzea. In general, a high amount of immigrants in floodplain forests becomes evident with regard to the strategies of seed dispersal. Many várzea trees are known to fruit during the aquatic phase (Ziburski, 1991; Wittmann & Parolin, 1999; Parolin et al., 2002b). Dispersal in many species is hydrochoric and ichtyochoric and seeds may disperse to long distances (Goulding, 1983; Ziburski, 1991). In the high várzea, long-distance dispersal may contributes to the relative high species richness. In several tropical lowland forests, mortality has been shown to be density dependent, and therefore is greatest near the parent tree, presumably because of effects of herbivores or pathogens (Janzen, 1970; Connell, 1971). As such, the few seeds that disperse to a greater distance are most likely to grow into seedlings that survive (Whitmore, 1989). Besides, the availability of both, the aquatic and the terrestrial pool of species enables many immigrants to establish.

CONCLUSIONS

The seedling establishment and the floristic composition of regeneration species in várzea forests is strongly related to the height and the duration of the annual inundations and to natural forest succession. This leads to a characteristic zonation of species groups along the flood-level gradient. This knowledge is fundamental to enable a sustainable forest management and must considered even when focus to single species to be managed. However, for a better understanding of forest dynamics, more inventories considering richness and distribution of understory trees and their abiotic and biotic interactions in várzea forests are desirable. Long-termed plots may allow researches about possibilities of a sustainable management and can provide data for modelling the várzea forests.

Because of their high species richness, the high várzea is of an exceptional ecological importance. As high-várzea forests cover the transitional zone between flooded and non-flooded habitats, they cover the area designated for intensive agronomical use. Present forests may be only relicts of former coverages, and they still are endangered through the consecutive pressure caused by human impact. For this, high-várzea forests need preservation and particular attention in sustainable management plans.

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BIOSKETCHES

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