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Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques

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ABSTRACT. In central Amazonian white-water floodplains (várzea), different forest types become established in relation to the flood-level gradient. The formations are characterized by typical patterns of species composition, and their architecture results in different light reflectance patterns, which can be detected by Landsat TM image data. Ground checking comprised a detailed forest inventory of 4 ha, with Digital Elevation Models (DEM) being generated for all sites. The results indicate that, at the average flood level of 3 m, species diversity and architecture of the forests changes, thus justifying the classification into the categories of low várzea (várzea baixa) and high várzea (várzea alta). In a first step to scale up, the study sites were observed by aerial photography. Tree heights, crown sizes, the projected crown area coverage and the gap frequencies provide information, which confirms a remotely sensed classification into three different forest types. The structure of low várzea depends on the successional stage, and species diversity increases with increasing age of the formations. In high várzea, only one successional stage was found and species diversity is higher than in all low-várzea formations. The more complex architecture of the high-várzea forest results in a more diffuse behaviour pattern in pixel distribution, when scanned by TM image data.

KEY WORDS: Amazonia, aerial photography, digital elevation model, flooding gradient, Landsat TM, remote sensing, species distribution, succession, várzea

INTRODUCTION

The várzea forests of central Amazonia are seasonally flooded by white-water rivers (Prance 1979), which occur along the River Amazon and its main affluents. They are characterized by periodic floods, reaching an average amplitude of 10 m and lasting up to 230 d each year (Junk 1989). Tree species composition and structure of várzea vary along the flood gradient: typical vegetation units and forest communities become established at different flood levels.

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Junk (1989) described three tree-level communities with characteristic species compositions in the várzea. Each community is determined by the flood-level gradient and duration of flooding. The water column can reach up to 15 m in exposed stands (Kubitzki 1988). Ayres (1993) also correlated different forest types with the annual flood level. He described the 'chavascal' as a community influenced by water height of 5–7 m and flood duration of 6–8 mo every year. The 'restinga baixa' undergoes 2.5–5 m flooding (4–6 mo), and the 'restinga alta' an average of 1–2.5 m (2–4 mo).

In addition to the influence of flooding, the natural development of forests defines tree species composition, species diversity and architecture of várzea forests. Without taking the flood gradient into consideration, Worbes (1997) found five main successional stages, from the first establishment of pioneer species on recent sedimentation bars to the climax stage with trees reaching ages of up to 400 y. Most of the earlier detailed floristic studies concentrated on the 'restinga baixa', and they used small plots. Scaling up of the results was not possible because of methodological limitations.

The present study deals with a large-scale investigation of different várzea forest communities. Data obtained through ground inventories were compared with data obtained from aerial photography. The architecture of the forest types was analysed, to check the possibility of their detection by Landsat TM images. TM data indicate the quantity of light reflected from the upper canopy. Light reflectance in a forest depends on several factors, such as the arrangement, morphology and quantity of leaf cells, on different leaf morphologies and the spatial arrangement of leaves and branches (Hallé *et al.* 1978, Hildebrandt 1976, Hönsch 1993, Sellers 1985). In this study, we analysed the density and structure of high-canopy tree tops, especially projected crown areas, as well as gap sizes and gap frequency of the different forest types. According to Butera (1986) and Peterson *et al.* (1986), these are the most important factors that influence spectral variations in the upper canopy. Finally, the spatial distribution of the different forest types classified within the várzea of the Mamirauá Sustainable Development Reserve (MSDR), as detected by TM image data, is presented.

STUDY AREAS

The main part of the study was carried out within the focal area at the MSDR (2°51′S, 64°55′W), approximately 70 km north-west of the city of Tefé and 50 km upstream from the confluence of the Japurá River into the Solimões, in western central Amazonia, Brazil. The focal area of MSDR amounts to 260 000 ha, and approximately 90% of the area is covered by closed-canopy forests (Sociedade Civil Mamirauá *et al.* 1996). The study area is influenced by annual inundations of the Japurá and Solimões Rivers. A preliminary investigation was conducted at Ilha da Marchantaria in the lower Rio Solimões, an

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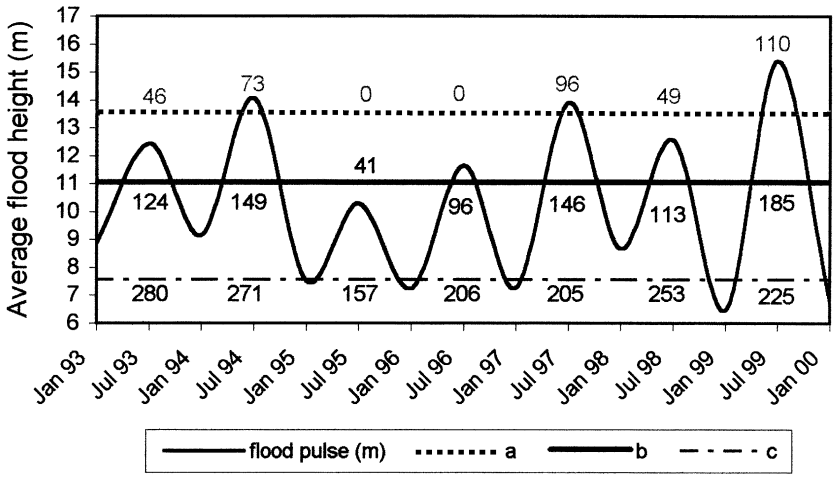


Figure 1. Relative location of the study sites along the average flood gradient (m). With days of submersion per year in (a) high várzea (1 ha), (b) low várzea (3 ha) and (c) closed-forest borderline.

island with an area of approximately 45 km^2 (3°15′S, 59°58′W), located 20 km south-west of the city of Manaus.

In both study areas, mean monthly temperatures vary little over the year and range between 25–28 °C. Mean annual rainfall at MSDR is about 3000 mm (1996–2000, Institute for Sustainable Development Research Mamirauá-ISDRM, Tefé), and at Ilha da Marchantaria about 2300 mm (1997–2000, Max-Planck-Institute for Limnology, Plön). Annual water-level fluctuations of the Solimões River were almost similiar in the two regions and ranged between 6.6 and 10.1 m during 1993–2000 (Figure 1).

METHODS

Ground analysis

Between March and September 1999, three rectangular plots of 1 ha (50 × 200 m) were investigated in the MSDR. Additionally, a preliminary survey of a single plot at Ilha da Marchantaria was conducted. The plots were installed next to the river or a river-channel bank, to facilitate their localization by aerial photography. The research plots represent different forest communities and they differ in topography and thus the flood height and duration of flooding. Two plots in the MSDR and the plot on Ilha da Marchantaria are influenced by submersion to about 4.5 m or an average of 122 d y^{-1} (low várzea), while one plot in the MSDR is influenced by submersion to about 2.5 m or 53 d y^{-1} (high várzea) (Figure 1). In the classification of Worbes (1997), the three low-várzea sites represent the successional stages of early secondary, late secondary and the climax stage. The high-várzea site represents a climax stage.

All trees ⩾ 10 cm dbh were identified to species. To determine a possible zonation of species along the flood gradient, each individual tree was entered

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into a three-dimensional coordinate system (position: x, y, elevation: z) using a theodolite (Zeiss Ni2). The vertical position of individual trees was derived comparing 1999 flood marks on trunks with water levels recorded in Tefé and/or Manaus (ISDRM, Tefé/Engenharia dos Portos, Manaus). For each plot, a high resolution Digital Elevation Model (DEM) was generated by Triangulated Irregular Network (TIN), here presented as topographic contour-line maps (Figure 3).

Aerial photography

To scale up from ground analysis to satellite data, perpendicular aerial photography of all study sites was obtained between April and September 1999. In addition to the recognition and processing of all field-sites, at least one additional hectare of the surrounding forest was included in the image analysis.

The aerial photographs were taken at altitudes between 500 and 800 m, using a digital reflex camera (Minolta RD 175, focal distance: 50 mm) and a large-format camera (Linhof Aerotechnica, focal distance: 48 mm) for conventional photos. Scanning was performed on sunny days, between 10h00 and 12h00, to minimize shading and to obtain the maximum contrast of upper-canopy tree tops to the ground surface. In a geometric correction of the digital photographs, line distances and ground control points (GCPs) measured on forest ground were recognized (at least three per image). Photographs were resampled by screening and the function of transformation varied between the images, and sometimes between the screens as well. When intersections did occur, the photographs were turned and cut. Natural geometric displacements, usually established with increasing distance from the nadir-point in each photo, were not considered. All photographs were processed at a scale of approximately 1:1000.

For image enhancements, the RGB (red, green, blue)-scale was processed leading to a better contrast reproduction of single tree crowns. Each recognized crown or crown-fraction was digitized to determine the single-crown area. The area of gaps in proportion to the crown area coverage was examined. Tree heights were determined using overlapping scenes of conventional photos and a stereoscope (Zeiss-Stereochord G3). In stereoscopic vision, the heights were determined by the procedure of paralaxis calculation. For sub-canopy trees, tree heights were estimated in the field.

Satellite imagery

The results of field work and aerial photography were analysed in conjunction with satellite imagery (Landsat Thematic Mapper). For this study, TM images from 1997 and 1998, obtained at the Instituto Nacional de Pesquisas Espaciais (INPE), with the bands 5 (0.63–0.69 μm, red), 4 (0.76–0.90 μm, near IR) and 3 (1.55–1.75 μm, middle IR) were used, representing a common band-combination for the classification of forest vegetation units (Albertz 1991, Butera 1986, Hönsch 1993). The images were geo-referenced using GCPs at

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each plot measured by a Global Positioning System (GPS). Image enhancements were realized by greyscale-stretching by 5%. Texture and pixel distribution of the major forest units were investigated quantitatively and qualitatively by visual image analysis. Using the supervised classification by maximum-likelihood clustering, all areas with the same or similar pixel distributions were classified and assigned to the same or similar forest formation. More distant areas (± 20 km), showing a similar pixel distribution in the colour composite, were visited on site to verify the actual forest type.

RESULTS

Ground analysis

Field inventory yielded a total of 2080 individual trees ⩾ 10 cm dbh on the entire research area of 4 ha. They could be assigned to 226 species and 45 families. Tree species distribution, species abundance and thus the structure and architecture of forest communities in the research plots differed considerably.

There is an important floristic and structural differentiation between the low várzea (várzea baixa) and the high várzea (várzea alta), separated by a border-line at the average flood level of 3 m. Ninety-four tree species occurred exclusively in the three low-várzea sites, whereas 103 species were restricted to the single high-várzea site. Only 27 tree species were represented in both habitats, showing the striking floristic difference between the low and the high várzea.

In the low-várzea formations, flood height and flood duration are the limiting factors and determine the closed-forest border between 7.5–8 m or 228 d of submersion y^{-1} on average (Figure 1). Below that, no closed-forest units were found in the study areas. In the early secondary forest (plot 1), the inventory exhibited a comparatively high number of individuals ⩾ 10 cm dbh, belonging to a small number of species (Table 1). The seven most abundant species represented 78% of all species found in the plot. Judging by species composition, the forest is approximately 30 y old. The late secondary forest (plot 2), located on Ilha da Marchantaria, includes the *Crataeva benthamii* and the *Pseudobombax munguba* forest types, with an estimated age between 40 and 100 y. While the small number of individuals in this plot indicates a later stage of succession compared with plot 1 (Table 1), the low species diversity seems to be atypical. Low species diversity in plot 2 could be a result of a natural lower diversity in the region of the lower Solimões River, but could also have been caused by anthropogenic influence, which is more intense at Ilha da Marchantaria due to its proximity to the city of Manaus. The inventory of the climax formation (plot 3) of low várzea had a small number of individuals, but a high number of species. The seven most abundant species represented 33.7% of all species found in the plot (Table 1).

High várzea has not been as thoroughly described in the literature as the

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Table 1. Number of stems ⩾ 10 cm dbh, species abundance and diversity of the four investigated plots.

	Species	Abundance	%	Σ%
Low várzea: early secondary stage				
1	*Cecropia latiloba* Miq.	185	27.9	
2	*Crataeva benthamii* Eichl.	87	13.1	
3	*Laetia corymbulosa* Spruce ex Benth.	78	11.8	
4	*Maclura tinctoria* (L.) Grisebach.	55	8.3	78.2
5	*Nectandra amazonum* Nees	46	6.9	
6	*Pseudobombax munguba* (Mart. & Zucc.) Dugand	34	5.1	
7	*Luehea cymulosa* Spruce ex Bentham	33	5.0	
8 to 45		144		21.8
Σ		662		
Low várzea: late-secondary stage				
1	*Vitex cymosa* Bert. ex Spreung.	132	29.0	
2	*Laetia corymbulosa* Spruce ex Bentham	58	12.7	
3	*Crataeva benthamii* Eichl.	53	11.6	
4	*Crescentia amazonica* Ducke	48	10.5	82.2
5	*Pseudobombax munguba* (Mart. & Zucc.) Dugand	32	7.0	
6	*Pouteria elegans* (A.DC.) Baehni	32	7.0	
7	*Psidium acutangulum* DC.	19	4.2	
8 to 31		81		17.8
Σ		455		
Low várzea: climax stage				
1	*Cecropia latiloba* Miq.	37	8.1	
2	*Oxandra riedeliana* R.E. Fries	24	5.3	
3	*Pouteria polyphleba* Diels (R.E. Fries)	23	5.1	
4	*Tabebuia barbata* (E. Mey.) Sandwith	20	4.4	33.7
5	*Mabea nitida* Spruce ex Benth.	18	4.0	
6	*Hevea spruceana* Muell. Arg.	16	3.5	
7	*Crataeva benthamii* Eichl.	15	3.3	
8 to 100		301		66.3
Σ		454		
High várzea: climax stage				
1	*Pouteria procera* (Mart.) K. Hammer	27	5.8	
2	*Malouetia tamaquariana* A.DC.	15	3.2	
3	*Aspidosperma riedelii* Muell. Arg.	13	2.8	
4	*Guatteriopsis paraensis* R.E. Fries	12	2.6	21.3
5	*Gustavia augusta* DC.	12	2.6	
6	*Pseudoxandra polyphleba* Diels (R.E. Fries)	11	2.3	
7	*Chomelia* sp.	10	2.1	
8 to 177		369		78.7
Σ		469		

low várzea. The area occupied by high-várzea forests in the study area is small and their location is isolated. The high-várzea plot (plot 4) chosen for this study is influenced by flooding for a comparatively small number of days per year and, in years with low flood pulse, the area is not flooded at all (Figure 1). The inventory found 469 trees ⩾ 10 cm dbh, belonging to 177 species (Table 1); 101 tree species were represented by a single individual. Results of the inventory indicate that the observed forest belongs to the late-secondary or even to the climax stage. The number of individuals counted and the high diversity justify a comparison with the climax of the low várzea.

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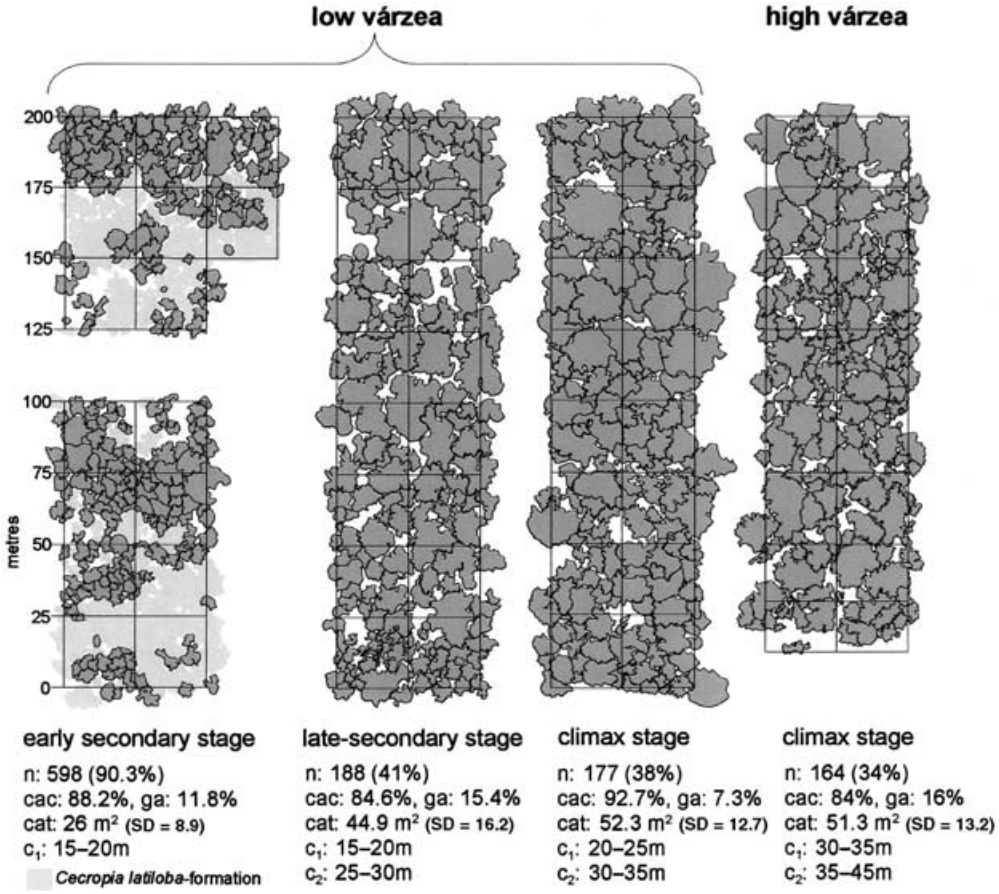


Figure 2. Map of crowns of the four plots, evaluated by aerial photography. With n: number of recognized crowns (correspondent to x % of all trees ⩾ 10 cm dbh in the plot), cac: crown area coverage; ga: gap area; cat: average crown size (SD = standard deviation); and c_x: crown layers from the top (stratification) in m.

Aerial photography

Using aerial photographs, the total projected crown area of 942 individuals was measured within an area of 4 ha. Generally, crown areas differed with forest structure, i.e. with the successional stage. In the early secondary stage (plot 1) of low várzea, 413 crowns or crown-parts could be recognized. This means that a high proportion of trees in the plot (62%) are in the upper canopy (Figure 2). A homogeneous sub-canopy stratum is absent. A high sapling density and a dense herbaceous layer characterize the forest floor. In the upper canopy, the vast majority of trees had a height of about 15–20 m, single individuals reaching up to a maximum height of 25 m. In this young successional stage, no pronounced stratification exists and the canopy forms a generally homogeneous surface. Accordingly, the average gap area ha^{-1} was comparatively small and amounted to 11.5%. The average crown area per tree was 26.0 m^2. *Cecropia*

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latiloba (Cecropiaceae), a fast-growing light-demanding pioneer species, dominated the forest stand with a total coverage of 37%. It forms homogeneous stands, which can be recognized easily in aerial photographs, due to its typical, strikingly light-green, huge leaves. Separation of single *C. latiloba* crowns was difficult because of the high density of its generally small crowns.

In the late-secondary stage (plot 2), 188 tree tops or tree-top parts could be recognized, 41% of all trees in the plot are part of the upper canopy (Figure 2). In contrast to the early successional stages, plot 2 showed an initial stratification. The sub-canopy stratum has an average height of 15–20 m, dominated by *Vitex cymosa* (Verbenaceae), *Crataeva benthamii* (Capparidaceae), *Crescentia amazonica* (Bignoniaceae) and *Psidium acutangulum* (Myrtaceae). In image processing, these species formed a homogeneous 'ground matrix', often shaded by species of the upper-canopy stratum at a height of 25–30 m, which are formed mainly by individuals of *Pseudobombax munguba* (Bombacaceae) and *Laetia corymbulosa* (Flacourtiaceae). Both species are light-demanding pioneers (Pires & Prance 1985, Wittmann 1997), and form good recognizable tree tops, easy to determine using aerial photography. The tree-top size on average amounted to 44.8 m^2 per tree, and was considerably larger than in the early secondary stage. The amount of gaps averaged 15.3%, and the majority of gaps were the result of the recent death of over-aged individuals of *P. munguba*. The high mortality causes a local succession of young light-demanding pioneer species in the gaps, so that a mosaic of heterogeneous tree-top sizes characterizes the whole plot.

In the climax stage (plot 3) of low várzea, 177 tree tops or parts of them (39%) were recognized and measured (Figure 2). Here, a higher proportion of all adult individuals are shade-tolerant tree species of the understorey. Trees belong to two significant canopy strata, which were found at 30–40 m (upper canopy) and at 20–25 m (sub-canopy). The forest floor is constantly shaded, almost free of herbaceous species and sparsely populated by young individuals, which form a third stratum at 5–15 m. The area measured for the tree tops averaged 52.3 m^2 per tree, thus representing the highest measured mean value. Also the projected crown area coverage was the highest measured with 92.7%, while the gap area averaged 7.3%.

In the high várzea (plot 4), it was possible to recognize 164 (34.7%) tree crowns, indicating that the majority of all adult trees are part of the sub-canopy stratum (Figure 2). Canopy stratification in the plot is well defined. The upper canopy reached a height of 40–45 m, the highest trees reaching heights of 58 m. A homogeneous sub-canopy stratum occurred at the height of 30 m, followed by a third well-developed stratum at a height of about 15 m. On average, the crown area in the upper canopy amounted to 51.3 m^2, thus it is comparable with the climax stage of the low várzea. The projected crown area coverage amounted to 84.2% while the gap area was 15.8%, respectively.

In addition to the dependence of crown sizes on the successional stage, a

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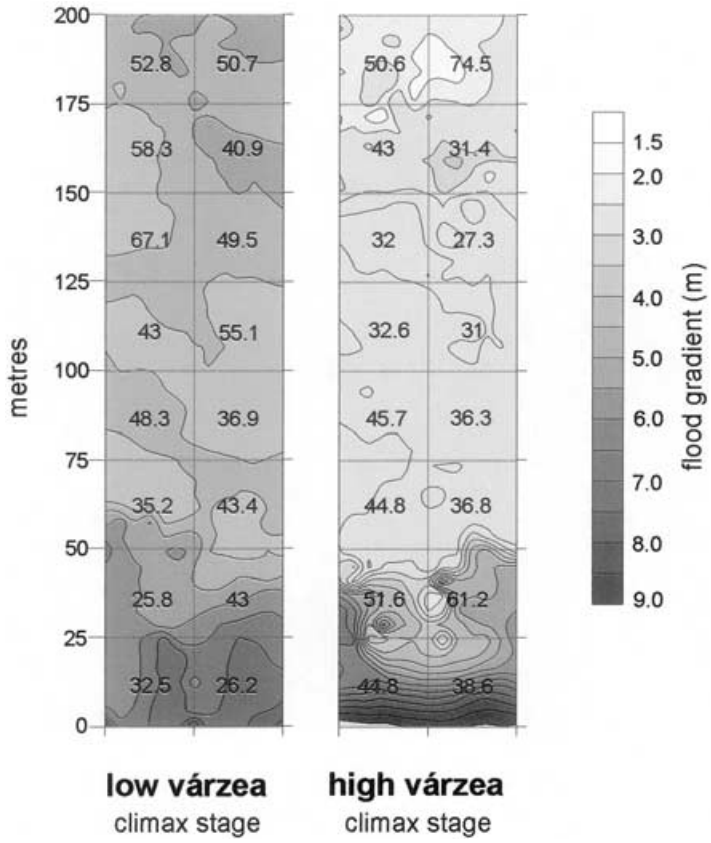


Figure 3. Contour-line map of the climax stages in the low várzea and the high várzea. Average crown area per quadrat = 625 m^2.

correlation exists between crown sizes and topography. Trees with small crowns occur frequently in topographic depressions, whereas trees with extensive crowns dominate the levees. In the low várzea, crown areas increase with elevation, especially in the subsequent successional stages (Figure 3). In the climax stage, the investigation indicated that trees with the smallest crowns (30–40 m^2 on average) were found in the lowest topographic areas with 6 m average flood height each year, whereas the largest crowns (55–70 m^2) are situated on the most elevated areas with 3.5 m average flood height each year. This occurs in the high várzea as well, where the largest tree crowns within an area beyond 67 m^2 were found above the level of 2 m flood height, while the lower elevated areas are covered by trees with average crown areas between 31 and 55 m^2 (Figure 3).

TM-classification

Using supervised classification, it was possible to differentiate between the low and the high várzea (Figure 6); although it was difficult to determine the

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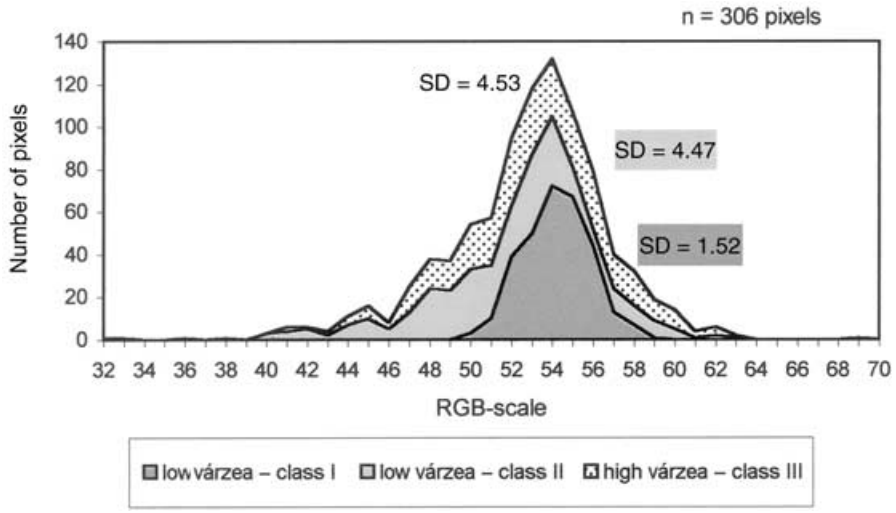


Figure 4. Average pixel distribution (histogram) of the three classified forest communities, each investigated in 10 sites with n = 306 pixel. With class I: early secondary and chavascal forest, class II: late-secondary and climax forest, class III: high-várzea forest.

borders of the different low-várzea formations. Since early successional stages often occur next to the rivers or river-channels on small sand bars, an unequivocal classification was prevented by the comparatively low image resolution of 30 m per pixel. In addition, transparent cloud-borders appeared with the same object-identity (Figure 6), even when the number of unclassified pixels was increased.

The early secondary forest appeared with a constantly low pixel diversity as shown in the histogram (Figure 4). However, the chavascal formations in MSDR showed a similar pixel distribution as the young low-várzea formations. Species diversity in the chavascal is comparable to the early successional formations, but with a higher abundance of palms (*Bactris maraja*) and *Buchenavia* sp. (Combretaceae), trees with a maximum height of 15 m. The early successional stages together with the chavascal formations occur with a frequency of 28.9% within the focal area of MSDR (Figure 5).

Within the low várzea, the late-secondary stages could not be clearly separated from the climax stages. Pixel distribution of both formations was very similar, with almost the same standard deviations presented in the histogram (Figure 4). Moreover, the shadows caused by cloud cover showed the same object identity as class II and had to be cut to result in acceptable area calculations. However, demarcation of these two formations was clearly defined by the early successional stages in the low várzea as well as the formation of the high várzea (Figure 6). In the focal area of MSDR, the late-successional/climax stages of the low várzea dominate the forested area with a cover of 29.6% (Figure 6).

High-várzea formations are characterized by a more complex pattern of pixel distribution than the low-várzea formations, as shown by the relatively high

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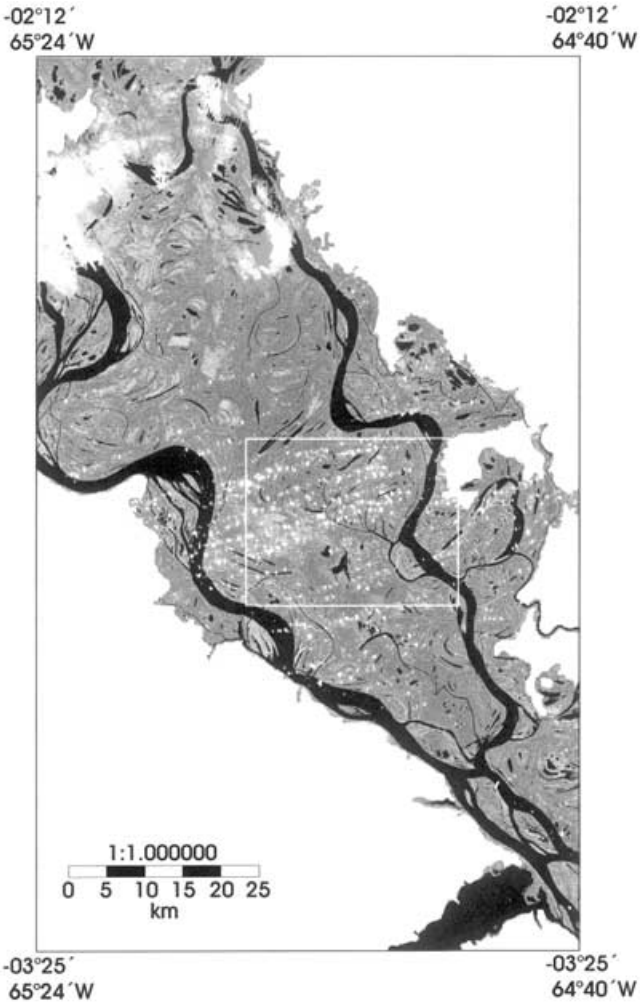


Figure 5. TM-composite (5,4,3-greyscale) of the focal area of the MSDR, localized between the Japurá (north-east) and the Solimões rivers (south-west). The scene shows only várzea formations, used for calculation of the coverage of classified forest types. The rectangle represents the study area chosen for ground analysis and aerial photography.

standard deviations in the histogram (Figure 4). Moreover, a good recognition mark was given by image texture, because high-várzea forests often occur along river channels, reflecting the more elevated channel-bars (Irion 1984), which frequently accompany the channels with a width of some few hundred metres (Figure 6). The area with occurrence of high várzea in the focal area of MSDR amounts to 7.8%.

DISCUSSION

The tree species distribution and community structure of várzea forest communities depend primarily on two factors: first, as described by Junk (1989) and

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Ayres (1993), on different topography resulting in different flood heights and duration of flooding, and second, on the natural forest succession, as described by Worbes (1997). Investigating the tree species distribution, it is necessary to consider both factors to describe the main forest vegetation units.

The results of this study indicate that the várzea forests contain two significantly different habitats with respect to forest structure and species composition, reflecting the topography of the environment. Both the low várzea and the high várzea are characterized by the dominance of typical tree species, probably defined by their adaptations to the annual flood stress. Below a flood level of 3 m, natural forest succession results in different forest types, in which species diversity and architectural complexity increases with increasing age. Above a flood level of 3 m, only one successional stage was found and species diversity, population dynamics and architecture of high várzea are more complex than in all low-várzea formations.

We support the classifications of closed várzea forests of Junk (1989) and Ayres (1993). However, the terminology of Ayres (1993) will be used in a modified form, because the term 'restinga' is frequently used in Brazil for vegetation habitats in coastal areas, describing ecosystems with vegetation often adapted to edaphically or climatically induced aridity (Eiten 1970, Rizzini 1997). For this reason, we suggest the terminology 'chavascal' according to Ayres (1993), and, instead of 'restinga', the term 'várzea baixa' and 'várzea alta' according to Bahri (1992). We suggest that the chavascal represents a special vegetation unit occurring within the low várzea, influenced by flood stress during the whole year in topographical depressions that do not drain.

The impact of the prolonged flooding on the trees growing in the low várzea is evident through phenological changes (Wittmann & Parolin 1999, Ziburski 1991) and reductions of wood growth during the aquatic phase (Worbes 1986, 1997). Also, many physiological, morphological and anatomical adaptations were found on low várzea trees during flooding (Fernandes-Corrêa & Furch 1992, Schlüter *et al.* 1993, Worbes 1985). Until now, few inventories in high-várzea forests have been made. In non-flooded terra firme forests of central Amazonia, the diversity of tree species $\geqslant$ 10 cm dbh is approximately 300 species ha^{-1} (Ribeiro *et al.* 1999). With more than 170 species ha^{-1}, the high várzea forms the main transitional vegetation unit between flooded and non-flooded forest areas.

The highly dynamic geomorphology of Amazonian white-water rivers influences the development and the natural succession of low várzea. On new sand bars, after herbaceous plants and grasses, the first pioneer tree species, such as *Salix martiana* (Salicaceae) or *Alchornea castaneiifolia* (Euphorbiaceae) become established (Junk 1989, Worbes 1986). Both species are pioneers with respect to light demand and/or the high sedimentation rates (Wittmann 1997). When sedimentation bars grow in height, water-flow velocity decreases, and homogeneous *Cecropia latiloba* formations form the first closed-forest units. In subsequent successional stages the increasing density of large-stemmed trees leads

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to higher sedimentation rates, and species diversity of the low-várzea forest increases as well as the topography of the site. Finally, a low-várzea forest can develop into a high-várzea forest, a fact that might explain why no young successional stages of high várzea were found in this study. On the other hand, a high-várzea forest could also be a regressive forest type, formed from previous forests of more elevated Pleistocene terraces, as a consequence of the constantly changing river beds of white-water rivers (G. Irion, *pers. comm.*). Forty-six species found in the high várzea also occur in the terra firme (Ribeiro *et al.* 1999). Such regression could possibly explain the small size and isolated character of patches of high-várzea forest.

Even though many attempts have been made to quantify the different floodplain habitats of the Amazonian várzea using remote-sensing techniques (De Costa *et al.* 1996, 1998; Hess *et al.* 1990, 1995; Hönsch 1993, Mertes *et al.* 1995, Novo *et al.* 1997*a*, *b*; Radambrasil 1976, Saatchi *et al.* 2000), sometimes even with higher resolution SAR- or SLAR-image data, no satisfactory and comprehensive classification of the different forest types has been presented up to now. Multi-spectral TM-images are still a convenient and economical remote-sensing resource for differentiating and classifying tropical forest communities. However, the utilization of multi-temporal optic-based images of the Amazon Basin is strongly affected by cloud cover (De Costa *et al.* 1998), and cloudless scenes are scarce. In addition, the relatively low resolution of 30 m per pixel often does not allow a clear definition of community borders, especially when forest communities are small.

A reliable classification by satellite imagery depends on the quantity and the quality of ground checks. Therefore, aerial photography is an important method to scale between ground and Landsat data. The determinant factors in the upper canopy are difficult to obtain by field work alone. In this study, it was possible to differentiate between three main várzea-forest communities using satellite-image data. Aerial photographs can quantify the architecture of forest types. Each community is determined by typical features of growth heights and crown extensions, which increase with the age of the forest types and/or the increasing topography of their stands. In early successional stages, low species diversity, homogeneous tree heights and small crown extents result in a smooth canopy surface. Therefore, the limited range of light reflection allows a good detection of these forests by TM image data. More diverse late-secondary and climax stages of low várzea show initial stratification. Gaps caused by the mortality of big trees, and the local establishment of pioneer species, result in a more complex architecture to the forests. Finally, high-várzea formations are characterized by the most complex architecture, resulting in the most intense light scattering and the most diffuse patterns in pixel distribution, when scanned by TM images.

There is no evidence that gap frequency is linked to crown area coverage or tree-top density. On the other hand, gap frequency tends to increase with

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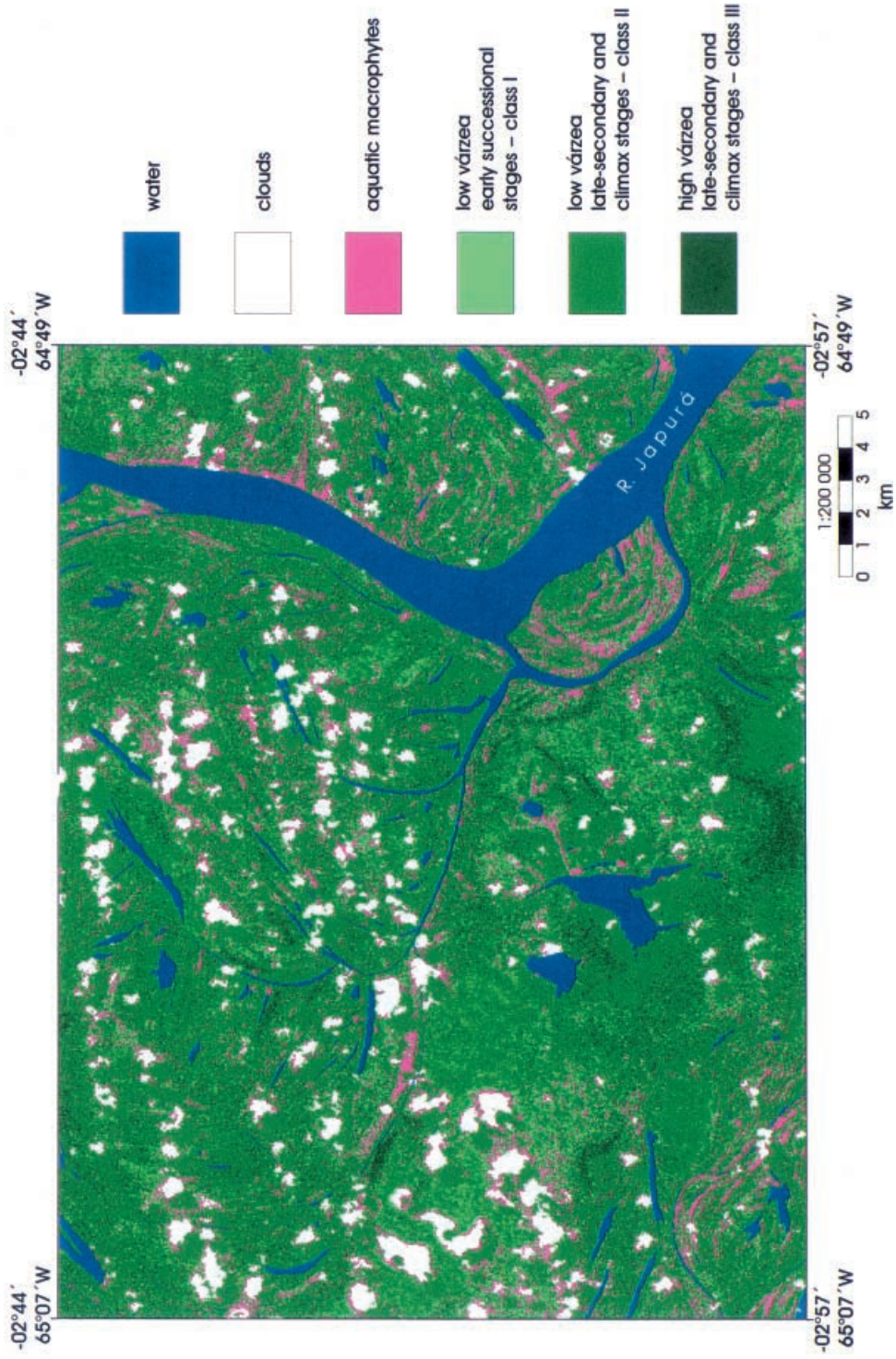


Figure 6. Study area in the MSDR, with classified forest formations.

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increasing age of the forests. Local gaps with significant sizes are absent in early successional stages, and the whole forest changes overall in species, leading continuously to subsequent successional stages. From the late-secondary stages, the importance of gaps and local succession to light reflectance increases, because the mortality of big trees causes local succession. However, increasing tree-crown size in subsequent successional stages compensates the trend of increasing gap frequency. Therefore, the importance of tree-crown density influencing light reflection cannot be confirmed within the closed-canopy forests of the várzea. Rather, we suppose that all the factors quantified by aerial photography in this study result in the different light-reflection patterns of the classified forest formations.

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