

Tree Species Composition, Structure, and Aboveground Wood Biomass of a Riparian Forest of the Lower Miranda River, Southern Pantanal, Brazil

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Abstract The aboveground wood biomass (AWB) of tropical forests plays an important role in the global carbon cycle, and local AWB estimates provide essential data that enable the extrapolation of biomass stocks to ecosystem or biome-wide carbon cycle modelling. Few AWB estimates exist in Neotropical freshwater floodplains, where tree species distribution and forest structure depend on the height and duration of periodic inundations. We investigated tree species composition, forest structure, wood specific gravity, and AWB of trees ≥ 10 cm dbh in 16 plots totalling an area of 1 ha in a seasonally inundated riparian forest of the lower Miranda River, southern Pantanal, Brazil. The 443 tree individuals belonged to 46 species. Four species (*Inga vera*, *Ocotea suaveolens*, *Tabebuia heptaphylla* and *Cecropia pachystachya*) comprised more than 50% of the Total Importance Values (TIV), and floristic similarities between the plots averaged 38%. Although we detected an overall increase in species diversity correlated with decreasing flood levels, the most important tree species had almost identical distribution patterns

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along the flooding gradient. The stand basal area per plot (\pm s.d.) amounted to $3.0 \pm 1.1 \text{ m}^2$ ($47.8 \pm 18.1 \text{ m}^2/\text{ha}$), and the tree heights averaged $10.9 \pm 1.4 \text{ m}$. Multiplying the individual basal areas by individual tree heights and a form factor of 0.6, we estimated the aboveground wood volume (AWV) for each individual, and for each plot ($24.4 \pm 11.7 \text{ m}^3$, $391.1 \pm 188 \text{ m}^3/\text{ha}$). Wood specific gravity (SG) varied between 0.39 g/cm^3 (*Cecropia pachystachya*) and 0.87 g/cm^3 (*Tabebuia heptaphylla*), with a stand level average of $0.63 \pm 0.12 \text{ g/cm}^3$. Multiplying the individual AWV with species SG, we estimated the plot AWB to be $16.2 \pm 6.4 \text{ Mg}$ ($259.4 \pm 102 \text{ Mg/ha}$). This value is comparable to that reported for late-successional forest stands of Amazonian floodplain forests, and it is close to the worldwide tropical average AWB. Because tree heights in the present forest were comparatively low when compared to other Neotropical forests, we found that resprouting of stems accounted for comparatively high basal areas. We argue that stem resprouting is an adaptation of tree species originating in non-flooded Cerrado to the seasonal inundations of riparian forests.

Keywords Aboveground wood volume · Flooding gradient · Floodplain forest · Pantanal · Resprouting · Species distribution · Wood specific gravity

Introduction

Seasonal inundation of roots and aboveground organs reduces oxygen availability to trees and thus is widely considered as a potential stress factor (Joly 1991). Trees subjected to periodic flooding often compensate anaerobic soil conditions by developing morpho-anatomical adaptations and by reducing metabolism during the waterlogged period, resulting in decreased photosynthetic rates, leaf shedding, and reduced wood growth and/or cambial dormancy (Fernandez et al. 1999; Parolin et al. 2004; Worbes 1997). Inundation is thus a powerful factor selecting the occurrence and distribution of tree species (Jackson and Colmer 2005), which in turn influences structure and biomass of seasonally flooded tree species communities.

In seasonally flooded Neotropical forests, richness and composition of arboreal communities vary along the flooding gradient with its associated geomorphologic and pedologic variables, e.g., in the Orinoco basin (Godoy et al. 1999), in Amazonian floodplain forests (Ferreira 1997; Wittmann et al. 2006a), and in riparian forests of Neotropical savanna (e.g., Cerrado) regions (Oliveira-Filho et al. 1994; Metzger et al. 1997; Veneklaas et al. 2005). Structure and biomass of these forests is linked to the topographic position of forest stands and varies as a function of site colonization, stand age (forest succession) and frequency of natural habitat disturbance (Salo et al. 1986; Terborgh and Petren 1991; Worbes et al. 1992).

The Pantanal is a seasonal wetland that is located in the depression of the upper Paraguay River. It covers approximately $160,000 \text{ km}^2$. Due to the Pantanal's heterogeneous geomorphology formed by spreadings, depressions, relict dunes, inselbergs, and differently-aged alluvial deposits, it is composed of a patchwork of both, seasonally inundated and non-inundated habitats (Sarmiento and Monasterio 1975; Zeilhofer and Schessl 1999). The seasonally inundated vegetation consists of

grasslands and different forest types. Studies on the floristic composition of seasonally inundated forests within the Pantanal were performed, for example, by Prance and Schaller (1982), Pott and Pott (1994), Nunes da Cunha and Junk (2001), and Damasceno et al. (2005). Periodically inundated forests within the Pantanal are often mono-dominant, or composed of a few co-dominant species (Pott and Pott 1994). Riparian forests, which accompany the main rivers and the secondary river-channels, were described as the most species-rich inundation forests within the Pantanal (Pott and Pott 1994; Damasceno et al. 2005).

Riparian forests are important landscape units in savanna regions because they consist of both flood-resistant species and immigrants from the adjacent uplands, thereby comprising most of the regional floristic biodiversity (Pither and Kellman 2002). In addition, they offer food and shelter for the terrestrial and aquatic fauna, therefore being recognized as areas with permanent conservation status by the Brazilian environmental legislation. Within the Pantanal, riparian forests are concentrated along the Paraguay River and its major tributaries. Combining the phyto-physiognomic vegetation classification proposed by the IBGE (1992) with remote-sensing data, Silva et al. (2000) calculated the spatial coverage of riparian forests within the Pantanal as approximately 2.4% of the landscape (3,360 km²).

There are comparatively few studies investigating tree species richness and distribution along the flooding gradient in the Pantanal, and investigations focusing on structure and biomass are scarce. However, the biomass of tropical forests plays an important role in the global carbon cycle, both as a reservoir of carbon and as a source of greenhouse gas emissions from deforestation (Fearnside 1997; Mahli et al. 2006). Nunes da Cunha and Junk (2001) investigated the distribution of woody plant communities in the northern part of the Pantanal near the city of Poconé in terms of habitat preference and found approximately 40 flood-resistant tree species, most of them showing a wide distribution range on the topographic gradient, from areas with prolonged flooding to dry habitats that become flooded only during extreme flood events. Damasceno et al. (2005) found 29 flood-resistant tree species ≥ 10.0 cm dbh (diameter at breast height) in seasonally inundated riparian forests of the Paraguay River near Corumbá in an area totalling 1.08 ha. The species associations of these flood-resistant species is clearly linked to the position of trees along the flooding gradient. Haase and Haase (1995) investigated the aboveground biomass of four invasive shrub and tree species in the Pantanal, to test for different allometric equations, but not with reference to abiotic variables. To the best of our knowledge no further studies investigating the impact of flood length and duration on tree species composition, structure, and biomass in the Pantanal have been done.

The present study investigates floristic composition, forest structure, and AWB of a seasonally inundated riparian forest of the Miranda River, southern Pantanal, Mato Grosso do Sul, Brazil. This study aims to analyze whether species composition and diversity depends on the topographic position of individual tree species, and if differences in forest structure and AWB along the flooding gradient can be observed. Additionally, this study provides the first AWB estimate of a seasonally inundated forest stand within the Pantanal, and therefore represents an important contribution to regional or ecosystem-wide carbon cycle models.

Methods

Study Site

The present study was performed on the lower Miranda river (19°34' S, 57°01' W), near the field station of the Universidade Federal de Mato Grosso do Sul (UFMS), southeastern Pantanal, Brazil (Fig. 1). The climate in the southern Pantanal is characterized by a pronounced dry season from May to September and a rainy season from October to April. Annual precipitation near Corumbá amounts to approximately 1,090 mm (Hamilton et al. 1996); mean annual temperatures range between 21°C in December and 27°C in July.

Inventories

Sixteen 25×25 m (625 m²) plots in riparian forests of the Miranda river were established in April 2007, totalling an inventoried area of 1 ha (Fig. 1). Seven plots were placed on the left and nine plots on the right side of the river. All plots were established close to the river bank, with a minimum distance of 50 m between them. Plot location was restricted to areas where forest patches extended more than 25 m inland of the river channel.

All trees ≥10 cm dbh were labelled, numbered, and measured in diameter (dbh). The heights of all trees were determined using a clinometer (Suunto, Vaanta, Finland). Species were identified in the field, and when this was not possible,

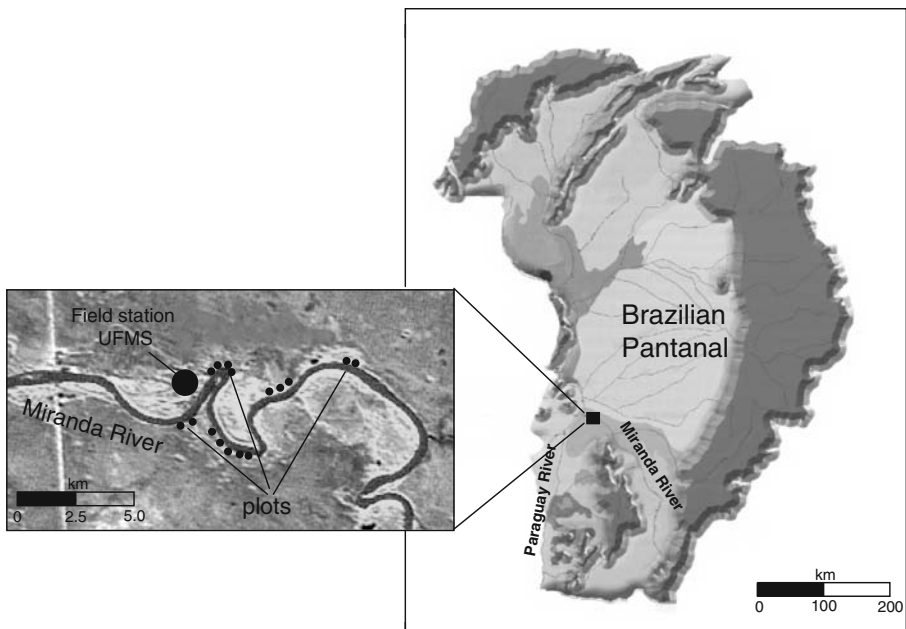


Fig. 1 Location of the study plots within the Brazilian Pantanal. Large map modified from WWF-Brazil (<http://www.wwf.org.br>), small map from CBERS-2 (05/09/2006, 166/122, Instituto Nacional de Pesquisas Espaciais – INPE, Brazil)

identified provisionally as morpho-species with voucher specimens collected for later identification. The position (x- and y-coordinates) of single trees within the plots was measured using the distance along the river bank as the x-axis, and that running inland as the y-axis. The position of trees above water levels was estimated using maximum flood marks of the last inundation (March 2006) on trunks relative to the water level of the Ladário gauge at the Paraguay River, which is located approximately 100 km from the study site. For the relationship of flooding and the species composition, we estimated the mean flooded period of all trees at our study site (days/year) for 1988–2006. Unfortunately, there are no water-level records at the Miranda River. As a tributary of the Paraguay River, the Miranda River is possibly characterized by an individual flooding regime. Maximum water levels at the Ladário gauge normally occur between May–June, those of the upper Miranda River earlier between February and March (Adámoli 1986). We presume, however, that even with different periods of highest water levels, positive relationships exist between the flooding regimes of both river basins because rainfall variability between the catchment areas amounts to less than 200 mm (Junk et al. 2006).

Wood samples of three individuals of each of the 15 most abundant tree species were made at breast height with an increment borer with a sharpened point (inner diameter 5 mm, Haglöf Inc., Sweden). Samples of 1 cm length were taken from different sections of the wood cores using a caliper rule with 0.1 mm accuracy. The samples' fresh volume was estimated multiplying their length by diameter. Mean wood specific gravity (SG) of each species was calculated after 72 h of oven drying the samples at a temperature of 105°C as the ratio between dry weight and volume of the green wood (Fearnside 1997; Nogueira et al. 2005; Wittmann et al. 2006b). Intra-individual and intraspecific wood density variations were not considered in this study. All values are given with standard deviation (s.d.).

Data Analysis

Phyto-sociological studies include the determination of tree species richness per plot, the Total Importance Value (TIV, Curtis and McIntosh 1951, Table 1), the determination of species diversity (Shannon and Weaver 1949, $D = -\sum p_i \ln p_i$; where $p_i = n_i/N$; n_i =number of individuals within a species, N =total number of individuals), and the determination of floristic similarity (Sørensen 1948, $IS = 2a(2a + b + c)^{-1}$; where a =number of species common to both plots, b and c =number of species unique to plot 1 and 2). To investigate the relationships between species occurrence and inundation height, each individual was entered into a three-dimensional coordinate system (position: x, y; height: z), based on Triangulated Irregular Network – TIN (Digital Elevation Model, SURFER Version 5.00, Golden Software). Furthermore, the variation of the species composition was examined as a function of distance to the river bank (forest border effect). For each species, the Mean spatial Distribution Center (MDC; Ebdon 1998) was determined, as a result of the mean inundation and the mean distance to the forest border of all individuals present.

The AWB for species and plots was estimated as a function of the individual aboveground wood volume ($AWV = B * H * F$) multiplied by SG; where B =basal area, H =tree height, and F =form factor of 0.6, taking into account biomass losses of the aboveground wood due to ramifications in the canopy (Cannell 1984; Brown

Table 1 Number of trees (*n*), total basal area (BA), mean tree height (H), total aboveground wood volume (AWV), mean wood specific gravity (SG), and total aboveground wood biomass (AWB) of the species in the study plots

| Species | <i>n</i> | BA (m ² /ha) | Mean H (m) | AWV (m ³ /ha) | SG (g/cm ³) | Reference | AWB (Mg/ha) |
|---|----------|-------------------------|------------|--------------------------|-------------------------|-----------|-------------|
| 1 <i>Inga vera</i> Willd. | 87 | 17.31 | 11.63 | 139.97 | 0.65 | own study | 90.98 |
| 2 <i>Tabebuia heptaphylla</i> (Vell.) Toledo | 53 | 5.72 | 14.66 | 58.62 | 0.87 | own study | 51.00 |
| 3 <i>Ocotea suaveolens</i> (Meisn.) Benth. & Hook f. | 51 | 5.65 | 11.93 | 46.94 | 0.66 | own study | 30.98 |
| 4 <i>Helicteres lhotzkiana</i> (Schott & Endl.) K. Schum. | 4 | 2.97 | 11.36 | 24.97 | 0.70 | own study | 17.48 |
| 5 <i>Vitex cymosa</i> Bertero ex Spreng. | 16 | 2.27 | 13.11 | 20.96 | 0.66 | own study | 13.83 |
| 6 <i>Cecropia pachystachya</i> Trécul | 73 | 2.80 | 10.89 | 20.56 | 0.39 | own study | 8.02 |
| 7 <i>Pouteria ramiflora</i> (Mart.) Radlk. | 5 | 1.11 | 9.36 | 8.94 | 0.77 | own study | 6.88 |
| 8 <i>Erythrina fusca</i> Lour. | 1 | 1.11 | 26.48 | 17.59 | 0.32 | 5 | 5.63 |
| 9 <i>Attalea phalerata</i> Mart. ex Spreng. | 7 | 1.63 | 9.21 | 8.37 | 0.63 | * | 5.27 |
| 10 <i>Casearia aculeata</i> Jacq. | 2 | 0.61 | 12.25 | 6.70 | 0.56 | 5 | 3.75 |
| 11 <i>Erythroxylum anguifugum</i> Mart. | 23 | 0.95 | 7.82 | 5.11 | 0.67 | own study | 3.42 |
| 12 <i>Cassia grandis</i> L.f. | 2 | 0.28 | 18.77 | 3.75 | 0.84 | 6 | 3.15 |
| 13 <i>Albizia niopoides</i> (Spruce ex Benth.) Burkart | 4 | 0.52 | 11.69 | 5.12 | 0.59 | own study | 3.02 |
| 14 <i>Alibertia edulis</i> (Rich.) A. Rich. ex DC. | 15 | 0.64 | 8.12 | 4.14 | 0.55 | own study | 2.28 |
| 15 <i>Pouteria glomerata</i> (Miq.) Radlk. | 14 | 0.62 | 6.44 | 2.42 | 0.67 | own study | 1.62 |
| 16 <i>Yochysta divergens</i> Pohl | 2 | 0.29 | 18.20 | 3.24 | 0.43 | 2 | 1.39 |
| 17 <i>Genipa americana</i> L. | 6 | 0.26 | 8.51 | 1.62 | 0.77 | own study | 1.25 |
| 18 <i>Copernicia alba</i> Morong ex Morong & Britton | 6 | 0.20 | 14.57 | 1.80 | 0.63 | * | 1.13 |
| 19 <i>Trichilia stellularis</i> Kuntze | 4 | 0.26 | 8.58 | 1.50 | 0.70 | 6 | 1.05 |
| 20 <i>Celtis pubescens</i> Spreng. | 2 | 0.38 | 9.59 | 1.79 | 0.56 | 6 | 1.00 |
| 21 <i>Triplaris americana</i> L. | 9 | 0.30 | 9.94 | 1.74 | 0.56 | 6 | 0.98 |
| 22 <i>Andira inermis</i> (W. Wright) Kunth. ex DC. | 1 | 0.19 | 11.71 | 1.35 | 0.64 | 4 | 0.87 |

| | | | | | | | | |
|----|--|---|-------|-------|--------|------|-----------|--------|
| 23 | <i>Combretum laxum</i> Jacq. | 8 | 0.26 | 5.96 | 0.99 | 0.45 | own study | 0.45 |
| 24 | <i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook f. | 1 | 0.08 | 10.88 | 0.50 | 0.81 | 2 | 0.41 |
| 25 | <i>Banara arguta</i> Briq. | 8 | 0.14 | 7.06 | 0.61 | 0.66 | own study | 0.40 |
| 26 | <i>Cupania castaneifolia</i> Mart. | 6 | 0.16 | 6.82 | 0.64 | 0.62 | 6 | 0.40 |
| 27 | <i>Campomanesia eugenioides</i> (Cambess.) D.Legr. | 1 | 0.13 | 7.97 | 0.60 | 0.63 | * | 0.38 |
| 28 | <i>Zygia inaequalis</i> (Humb. & Bonpl. ex Willd.) Pittier | 1 | 0.07 | 15.50 | 0.61 | 0.47 | 4 | 0.29 |
| 29 | <i>Chomelia</i> sp. | 1 | 0.10 | 5.57 | 0.34 | 0.72 | 1 | 0.24 |
| 30 | <i>Casearia decandra</i> Jacq. | 3 | 0.20 | 6.23 | 0.43 | 0.55 | own study | 0.23 |
| 31 | <i>Hymenaea courbaril</i> L. | 1 | 0.05 | 8.90 | 0.27 | 0.74 | 2 | 0.20 |
| 32 | <i>Eugenia florida</i> DC. | 5 | 0.11 | 6.43 | 0.40 | 0.46 | own study | 0.18 |
| 33 | <i>Guazuma ulmifolia</i> Lam. | 3 | 0.08 | 7.89 | 0.34 | 0.54 | 6 | 0.18 |
| 34 | <i>Ruprechtia</i> sp. | 1 | 0.08 | 6.20 | 0.29 | 0.63 | * | 0.18 |
| 35 | <i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum. | 2 | 0.06 | 7.10 | 0.27 | 0.63 | * | 0.17 |
| 36 | <i>Duguetia</i> sp. | 2 | 0.03 | 9.12 | 0.17 | 0.84 | 3 | 0.15 |
| 37 | <i>Maclura tinctoria</i> (L.) D Don ex Steud. | 3 | 0.07 | 4.91 | 0.20 | 0.71 | 5 | 0.14 |
| 38 | <i>Salacia elliptica</i> (Mart. ex Schult.) G.Don | 2 | 0.03 | 9.18 | 0.19 | 0.71 | 3 | 0.14 |
| 39 | <i>Neea hermaphrodita</i> S. Moore | 1 | 0.03 | 7.20 | 0.15 | 0.52 | 5 | 0.08 |
| 40 | <i>Cordia glabrata</i> (Mart.) A. DC. | 1 | 0.02 | 6.80 | 0.09 | 0.55 | 2 | 0.05 |
| 41 | <i>Inga uruguensis</i> Hook. & Arn. | 1 | 0.01 | 9.80 | 0.07 | 0.67 | 2 | 0.04 |
| 42 | <i>Fagaria hassleriana</i> Chodat | 1 | 0.01 | 7.91 | 0.05 | 0.79 | 6 | 0.04 |
| 43 | <i>Rollinia</i> sp. | 1 | 0.02 | 6.66 | 0.08 | 0.55 | 2 | 0.04 |
| 44 | <i>Coccoloba ochroleata</i> Wedd. | 1 | 0.01 | 6.10 | 0.03 | 0.58 | 4 | 0.03 |
| 45 | <i>Mouriri guianensis</i> Aubl. | 1 | 0.01 | 6.18 | 0.03 | 0.79 | 5 | 0.02 |
| 46 | <i>Capparis speciosa</i> Griseb. | 1 | 0.01 | 4.95 | 0.04 | 0.63 | * | 0.02 |
| | Mean | | 47.84 | 10.86 | 391.14 | 0.63 | | 259.45 |

References used for mean SG values: 1 – Enquist et al. (1999); 2 – Feamside (1997); 3 – Nogueira et al. (2005), 4 – Wittmann et al. (2006b); 5 – Wittmann et al. (in press); 6 – Wood density database (<http://worldagroforestrycentre.org/sea/Products/AFDbases/WD/>); * – Stand-level average SG (no SG data available in literature)

1997; Chave et al. 2005). SG of the other species was obtained from literature, or estimated using SG values from species of the same genus (Table 1). However, no SG could be obtained for the palm species *Attalea phalerata* and *Copernicia alba*, and for the dicot species *Campomanesia eugenoides*, *Ruprechtia* sp., *Tocoyena formosa*, and *Capparis spinosa*. When SG of single species is not available, Baker et al. (2004) suggests the application of the stand-level average SG on the individuals of these species. Accordingly, we used the stand-level average SG of our study plots (0.63 g/cm^3) for these species.

Results

Inundation

Mean amplitude between lowest and highest water levels of the Ladário gauge, Paraguay River during the last 19 years amounted to 311.4 ± 89.9 cm. Assuming a linear dependence between the water levels of the Ladário gauge and the period of inundation at our study sites, the topographic lowest point in our plots was inundated for 74.1 ± 58.5 days/year (14 inundations during the last 19 years, mean inundation height 65.2 cm), whereas the topographic highest point was inundated for only 21.0 ± 38.2 days/year (six inundations during the last 19 years, mean inundation height 18.5 cm). The mean inundation length in our study plots thus amounts to 39.4 ± 46.2 days/year, corresponding to a mean inundation height of 30.44 ± 15.63 cm (Fig. 2).

Floristic Composition and Species Diversity

A total of 443 individuals, belonging to 26 families, 42 genera, and 46 species, were inventoried. The most important family was the Fabaceae (approximately 26% of all individuals), followed by the Bignoniaceae, Urticaceae, and Lauraceae (each with approximately 10% of all individuals). The four most important species accounted for 52.8% of the TIV (*Inga vera*, *Cecropia pachystachya*, *Ocotea suaveolens*, and *Tabebuia heptaphylla*), whereas 16 tree species were represented by only a single individual (Table 1).

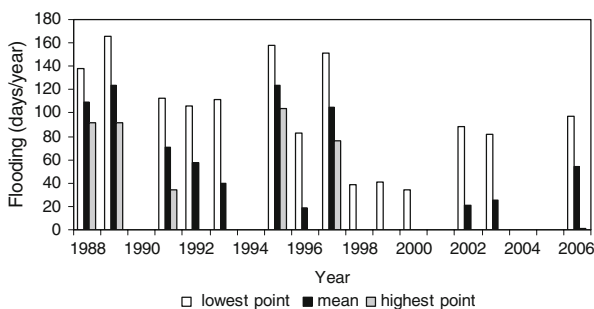


Fig. 2 Mean flooding period of trees in our study plots during 1988–2006, estimated from daily flood-level data of the Ladário gauge, Paraguay River (DNAEE – Departamento Nacional de Águas e Energia Elétrica, Brazil)

Within the 16 plots of our study, tree species richness varied between six and 13 species per plot (625 m²), and the species diversity between 0.75 and 2.17 (mean: 1.43 ± 0.39). Floristic similarity between the plots averaged 38.25% (min: 8.33; max: 77.77).

Floristic Patterns Along the Flooding Gradient

We detected a significant correlation of increasing species diversity with decreasing period of flooding (Fig. 3). The MDC of the species, based on the variables flood height/period of waterlogging, and distance of individuals to the river bank indicated similar ecological requirements especially of the common species (Fig. 4). The mean period of waterlogging in these species ranged from 26.0 ± 17.7 days/year (*Vitex cymosa*) to 42.7 ± 10.8 days/year (*Pouteria glomerata*), and the mean distance to the river bank from 6.6 ± 4.6 m (*Erythroxylum anguifugum*) to 12.3 ± 8.2 m (*Alibertia edulis*); the MDC of the most important species *Inga vera*, *Cecropia pachystachya*, *Ocotea suaveolens*, and *Tabebuia heptaphylla* was almost identical (Fig. 4). Differences in species distribution patterns thus were mainly restricted to the MDC of the rare species (Fig. 4).

Forest Structure, Wood Specific Gravity, and Aboveground Wood Biomass

The tree distribution by dbh-class showed a reverse j-shaped curve, indicating that most individuals had diameters of 10–15 cm. The basal area per plot (BA) averaged 2.99 ± 1.13 m², corresponding to a total BA of 47.84 ± 18.1 m²/ha. Average tree height amounted to 10.86 ± 1.37 m, with most trees being characterized by heights below 10 m (Table 1). There was a strong exponential relationship between tree dbh and height of the common tree species (Fig. 5), but the significance was reduced when rare tree species were included in the analysis ($R^2=0.69$, $P=0.001$).

The plot AWV averaged 24.45 ± 11.75 m³, showing a strong correlation to the plot's basal areas ($R^2=0.88$, $P=0.001$), whereas no significant relation was detected between AWV and tree heights ($R^2=0.188$, $P=0.52$). Total AWV amounted to 391.14 ± 188.05 m³/ha. Although single species showed trends of increasing AWV with decreasing height/period of flooding (e.g., *Tabebuia heptaphylla*, $R^2=0.234$, $P=0.01$), there was no significant relationship between these variables and flooding when more or even all species were included in the analysis.

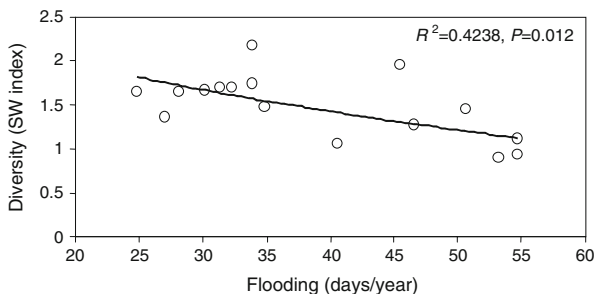


Fig. 3 Species diversity (Shannon and Weaver 1949) in the 16 study plots plotted against the mean flooded period

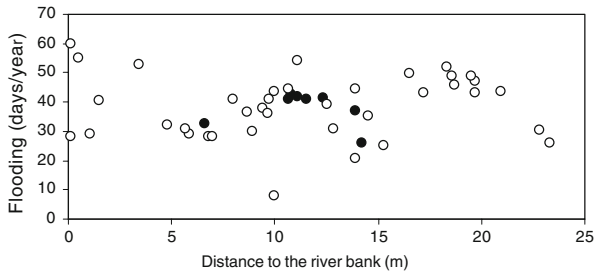


Fig. 4 Mean spatial distribution center (MDC, Ebdon 1998) of the tree species in the study plots based on the mean inundation period during the last 19 years and the distance of individuals to the river bank. *Black circles* – common tree species (8 species with ≥ 10 individuals, $n=334$), *white circles* – rare species (38 species with <10 individuals, $n=111$)

Wood specific gravity in the 15 investigated species ranged from $0.39 \pm 0.03 \text{ g/cm}^3$ (*Cecropia pachystachya*) to $0.87 \pm 0.02 \text{ g/cm}^3$ (*Tabebuia heptaphylla*), and averaged $0.63 \pm 0.12 \text{ g/cm}^3$ (Table 1). AWB in our plots was highly variable, and averaged $16.22 \pm 6.38 \text{ Mg}$, totalling $259.45 \pm 102.02 \text{ Mg/ha}$. Plot AWB correlated with AWV ($R^2=0.93$, $P=0.001$), which basically could be traced back to the significant correlations between AWB and BA ($R^2=0.85$, $P=0.001$), whereas no significant correlations existed between plot AWB and mean SG, plot AWB and tree heights, and plot AWB and the number of individuals present. Although we detected a slight increase of the plot AWB with decreasing impact of flooding, this trend was non-significant ($R^2=0.014$, $P=0.7$).

Discussion

The Pantanal is one of the Neotropical floodplains subjected to a monomodal flood-pulse (Junk et al. 1989). The flood pulse is a major driving force for species distribution and diversity, because it determines ecological processes and thus triggers the level of adaptation and species selection. The small-scale mosaic of alluvial and basin topography within the Pantanal creates sites from almost permanently waterlogged to rarely inundated, which is reflected by the vegetation cover (Silva et al. 2000; Nunes da Cunha and Junk 2001). The periodic inundations

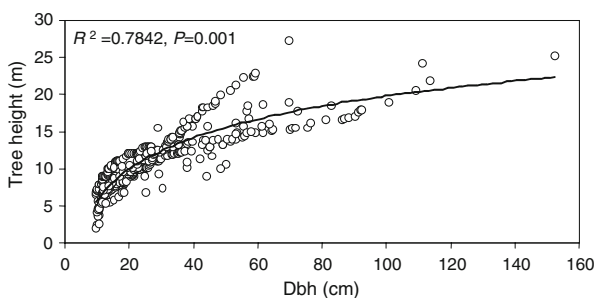


Fig. 5 Tree heights of common tree species (8 species with ≥ 10 individuals, $n=334$) plotted against dbh

and the related potential stressful conditions often lead to mono-dominant forests (Pott and Pott 1994), which are defined as forests where one species shows dominance of $\geq 50\%$ (Connell and Lowman 1989).

The riparian forest investigated in our study is not mono-dominant *sensu* Connell and Lowman (1989), but is characterized by four almost evenly weighted species (*Inga vera*, *Cecropia pachystachya*, *Ocotea suaveolens*, and *Tabebuia heptaphylla*) that comprise more than 50% of the total importance. While *I. vera*, *O. suaveolens*, and *T. heptaphylla* were almost evenly distributed across the inventoried forest, *C. pachystachya* showed a strongly clumped distribution pattern with more than the half of its total of individuals being restricted to only one plot. It is well known that the genus *Cecropia* comprises pioneer species that often initiate secondary forest succession (Franco-Rosselli and Berg 1997). The high importance of *C. pachystachya* in our forest is thus probably the result of natural or anthropogenic disturbance (fire, deforestation) in the past in one of our plots, followed by secondary colonization by this species.

The other co-dominant species have almost similar ecological requirements. With regard to the topographical position occupied, the species undergo mean annual flooded periods of 40.9 (*I. vera*), 41.0 (*O. suaveolens*) and 41.6 (*T. heptaphylla*) days/year, thus occupying a very restricted spatial distribution along the flooding gradient. Flooding at these levels, however, varies extremely and can be between 0 (i.e., 1990, 1994, 1998–2001) and 123 days/year (1995).

Characteristic morpho-anatomical and/or physiological adaptations of tree species to flooding, such as they occur in many species of Amazonian floodplain forests (e.g., pneumatophores, adventitious roots, lenticels, and pronounced leaf shedding during periods of highest water levels) are unknown within tree species of the Pantanal. Junk et al. (2006) stated that there are no endemic tree species within the Pantanal, most species being immigrants from the adjacent Cerrado biome with a wide tolerance of periodic dry and wet conditions. The restricted distribution along the flooding gradient combined with highly variable inundation periods affects tree species at the population level, and probably defines tree establishment and distribution. There is some evidence that many tree species of flooded forests in both temperate zones (poly-modal flooding) and Amazonia (mono-modal flooding) depend on establishment in consecutive periods with exceptionally low inundations (Wittmann and Junk 2003; Schnitzler et al. 2005). We thus argue that the high flood variability in riparian forests of the Pantanal favours the dominance of a few tree species that regenerate during consecutive years with low water levels, and that are highly competitive especially during the early stages of life. The high variability of the inundation level of the Miranda River thus would explain the co-dominance of a few tree species in our riparian forest.

Tree species richness and diversity is linked to the flooding gradient, and is thus similar to other seasonal flooded Neotropical forests (Oliveira-Filho et al. 1994; Metzger et al. 1997; Wittmann et al. 2006a). The zonation of tree species along the flooding gradient is, however, less pronounced than in Amazonian floodplains, where it can occupy a vertical height of up to 9 m (Ferreira 1997). In the riparian forest of the present study, increasing diversity with decreasing impact of flooding is strongly linked to the presence of rare species that are represented by a single or few individuals. These species are tolerant of seasonal inundations, but not restricted to

highly inundated habitats. This probably reflects the short period of floristic evolution and climatic instability within the Pantanal in the past in comparison to other Neotropical floodplains like the Amazon. The main period of subsidence resulting in the Pantanal wetland depression is related to the last compressional pulse of the Andes during the upper Plio- lower Pleistocene about 2.5 million years ago (Junk et al. 2006). In addition, climatic changes during the Quaternary led to intermittent periods of large-scale flooding and severe droughts (Ab'Saber 1988; Assine and Soares 2004). In comparison, it is thought that floodplain forests in the Amazon basin have persisted at least since the early Paleocene (Kubitzki 1989). Quaternary climatic changes affected these extensive floodplains to a comparatively low extent, whereas they interrupted evolutionary processes in floodplains of the Pantanal. This would explain the absence of specifically flood-adapted tree species associations within the Pantanal.

The AWV and AWB in the riparian forest of the present study are comparable to those reported in late-successional inundation forests of the Amazon basin (between 206 and 382 Mg/ha, Nebel et al. 2001; Schöngart 2003), and close to the worldwide tropical average AWB given by Clark et al. (2001) (278 Mg/ha). This is somewhat surprising when the structure of these forest types is compared. Depending on the topographic position along the flooding gradient, late-successional inundation forests in the Amazon basin are highly stratified, the upper canopy establishing at heights between 20–35 m (Worbes et al. 1992; Wittmann et al. 2002). Upper-canopy trees represent 58%–65% of the total aboveground wood biomass in these forests (Schöngart 2003). Mean tree height in the riparian forest of the Miranda River is only about one-half to one-third of that of Amazonian floodplain forests. High AWV and AWB in our forest is thus the result of comparatively high stand-level basal area. The high basal area in many of the tree species recorded was due to a high number of ramifications below breast height (i.e., in *Alibertia edulis*, *Casearia decandra*, *Erythroxylon anguifugum*, *Eugenia florida* and *Triplaris americana*). High resprouting tendencies in these species may be a response to the irregular flooding conditions. In Amazonian floodplain forests, Wittmann and Parolin (2005) reported the intense resprouting of highly inundated tree species of the genus *Symmeria*, *Alchornea*, *Salix*, and *Buchenavia*. Resprouting increases root and stem surfaces in these species and thus facilitates aeration during flooding (Lüttge 1997). In addition, it allows for the persistence of many shrubs and trees after catastrophic events such as fire (Matlack et al. 1993; Olson and Platt 1995; Cirne and Scarano 2001). It is thus possible that species originating from the adjacent Cerrado, and with high resprouting ability, have an important pre-adaptation that makes them competitive when establishing in seasonal flooded areas of the Pantanal.

AWB estimates of forest communities undergo different uncertainties, which include errors in height and dbh measurements especially in irregular-shaped trunks, intraindividual and intraspecific SG variations, and imprecisions of allometric models used for tree volume estimation (Chave et al. 2005). Because dbh generally is related to tree height, AWV, and AWB, many biomass estimates in tropical forests are based on dbh measurements as single variable, and use stand-level SG estimates (Brown 1997; Clark et al. 2001; Baker et al. 2004; Mahli et al. 2006). Although the present study was not designed to investigate the possible error propagation of the different variables used in biomass estimates, we attempt to minimize uncertainties

in our AWB approximate by the inclusion of exact tree height measurements, and SG determinations of the most important species. However, the comparatively high variations in forest structure and AWB between our plots demonstrate the difficulties in the assessment of confident stand-level AWB estimates. The riparian forest of the Miranda River is highly variable in both floristic composition and forest structure. Local hydraulic changes of the meandering river and the highly variable flood regime might be important factors contributing to the development of different riparian forest types, and to the small-scale AWB variations.

Acknowledgements This study was performed with Post-graduate students from the Ecology and Conservation course of the Federal University of Mato Grosso do Sul (UFMS), Campo Grande, Brazil. Field work was made possible by financial support from the UFMS. We wish to thank Wolfgang J. Junk and three unknown referees for valuable comments on the manuscript.

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Received: 3 September 2007 / Revised: 29 April 2008 / Accepted: 29 April 2008 /

Published online: 2 December 2008