PATTERNS OF STRUCTURE AND SEEDLING DIVERSITY ALONG A FLOODING AND SUCCESSIONAL GRADIENT IN AMAZONIAN FLOODPLAIN FORESTS

Astrid de Oliveira Wittmann[1]
Maria T. F. Piedade[1]
Florian Wittmann[2]
Jochen Schöngart[2]
Pia Parolin[2]

Abstract

Structure and species diversity of tree seedlings (1 - 100 cm plant height) was described in three white-water (várzea) floodplain forests in the western Brazilian Amazon. The forests are of different successional stages and they are subjected to different heights of flooding. A total of 24 square sample plots with the sizes of 1 m^2 were installed, nested within three rectangular 1-ha permanent sample plots where adult trees (? 10 cm dbh) and saplings (1 - 10 cm dbh and ? 1 m growth height) were formerly inventoried. Mean inundation and relative photosynthetic active radiation (rPAR) on the forest floor was recorded. Average density of seedlings was reduced with proceeding forest succession associated with decreasing impact of flooding. Simultaneously, within-habitat and between-habitat seedling species similarity declined, and species diversity increased. The biomass of tree seedlings amounted to at least 3.28 Mg ha^{-1} in the early successional stage, corresponding to about 13 % of the total aboveground wood biomass of adult trees, whereas in the later successional forests, these values are lower. Stand structure, species richness and beta-diversity of tree seedlings in várzea forests are strongly linked to the height and duration of the annual inundations. Flooding superimposes the influence of other abiotic and biotic factors, which normally are of crucial importance for tree establishment in non-flooded Neotropical forests. On the other hand, proceeding forest succession implies architectural changes in the overstory, which reduce solar radiation intensity at the forest floor. This increases the amount of possible niches in late successional várzea forests, contributing to elevated seedling diversity.

***Key words**: Seedlings, Biomass, Floodplain forest.*

---

[1] Instituto Nacional de Pesquisas da Amazonia, Av. André Araújo 2936, 69083-000 Manaus/AM-Brazil
[2] Max-Planck-Institute for Limnology, August Thienemann-Str. 2, P.O. Box 165, 24302 Plön-Germany

PESQUISAS, BOTÂNICA N° 58: 119-138 São Leopoldo : Instituto Anchietano de Pesquisas, 2007.

Introduction

Amazonian várzea forests establish within the periodical flooded landscape that occur along the system of white-water rivers originating from the Andes. The forests cover an area of 60.000 – 100.000 km^2 and establish where the water column reaches heights less than 7 m and where submersion of trees averages less than 230 d every year (Junk, 1989; Wittmann *et al.*, 2002). Flooding represents a limiting factor influencing ecophysiology of trees (Junk *et al.*, 1989; Parolin *et al.,* 2002; Schöngart *et al.*, 2002). Thus, tree species composition and richness in várzea forests is linked to the location of forest types along the flood-level gradient, and ranges from monospecific stands at the highest flood-levels to up to 150 species ha^{-1} in low flooded sites (Junk, 1989; Worbes *et al.*, 1992; Nebel *et al.*, 2001; Wittmann *et al.*, 2002).

Floristic inventories in várzea forests mainly dealt with overstory trees, mostly defined as trees ? 10 or 15 cm diameter at breast height - dbh (e.g., Pires & Koury, 1959; Balslev *et al.,* 1987; Campbell *et al.,* 1992; Worbes *et al.,* 1992; Cattanio *et al.,* 2002; Wittmann *et al.,* 2002). Only a few inventories also considered saplings, defined as trees of low growth heights and < 10 cm dbh (Worbes, 1986; Colonnello, 1990; Nebel *et al,.* 2001; Wittmann & Junk, 2003). At the seedling level (normally defined as trees < 1 m growth height), some information was obtained by experimental studies, which focused on the establishment of single tree species (Ziburski, 1991; Parolin, 2001; Oliveira, 1998; Ferreira, 2002). However, there is no information about stand structure, species composition and richness of tree seedlings in Amazonian floodplain forests. Regeneration behavior in most várzea trees is still unknown, and no information exists about the content of tree seedlings within total forest biomass and net primary production (NPP).

Based on data collected by Adis *et al.* (1979) and Worbes *et al.* (1992), Worbes (1997) estimated the total biomass (trees ? 10 cm dbh) in várzea forests to 279 Mg ha^{-1}. Schöngart (2003) instead demonstrated that the aboveground wood biomass of trees ? 10 cm dbh depends strongly on the stand age of várzea forests, and increases from 19 Mg ha^{-1} in a 7-yr old early successional stages to 206 Mg ha^{-1} in late secondary stages with stand ages of 240 yrs. In subsequent successional stages, biomass decreases to 186 - 194 Mg ha^{-1}. NPP in central Amazonian várzea forests was estimated to range between 23.8 Mg ha^{-1} year^{-1} in early successional stages (stand age: ± 40 years) and to 33.6 ha^{-1} year^{-1} in secondary forests (± 80 years, Worbes, 1997). No NPP data are available for late successional várzea forests. Additionally, biomass and NPP ratios lack data about small understory trees, saplings, and seedlings.

Information about the regeneration behaviour 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, seedlings 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 to understand and protect this ecosystem, i.e, by the development of sustainable forest management plans. In the present study we therefore present a floristic inventory of tree seedlings (1-100 cm in height) in three different forest types of the Western Brazilian várzea. Average inundation and radiation measurements were recorded in order to test whether seedling structure and species diversity is linked to these environmental gradients. The biomass of the most abundant seedling species was determined and total seedling biomass in the different forest types estimated to calculate its content within total forest biomass. In seedlings identified to the species level, we compared the population structure between seedlings, saplings and mature trees and discuss different regeneration behaviors among tree species and successional stages.

Methods

Study area and plot descriptions

This study was conducted in three permanent 1 ha-sample plots (Wittmann *et al.* 2002) within the Mamirauá Sustainable Development Reserve (MSDR) (2°51´ S, 64°55´ W), approximately 70 km NW of the city of Tefé, in the western Brazilian Amazon (Fig. 1). The MSDR is influenced by annual inundations of the Solimões and the Japurá Rivers. Mean monthly temperature ranged between 25 - 28°C, and mean annual rainfall was about 3000 mm during 1996-2000 (Institute of Sustainable Development Mamirauá - IDSM, Tefé). Annual water-level fluctuations of the Solimões and Japurá Rivers amounted to 11.3 m during 1993 - 2000 (IDSM, Tefé).

Two of the forest plots chosen for this study were of the low-várzea type (plot I and II), where mean annual inundation height amounts up to 3 m (submersion period > 50 d year^{-1}), and one plot (plot III) of the high-várzea type (inundation height < 3 m, submersion period < 50 d year^{-1}; Wittmann *et al.,* 2002). In the classification of Worbes *et al.* (1992), the forest of plot I represents an early successional stage, whereas the forests of plot II and III represent late successional stages. Structure and species composition of trees ? 10 cm dbh was known for all trees within the 1-ha plots (Wittmann *et al,.* 2002), whereas structure and species composition of saplings (1-10 cm dbh, > 1m growth height) was known for each 625 m^2 per 1-ha plot (Wittmann & Junk, 2003). The plot characteristics are summarized in Table 1.

Seedling inventories

In each of the three 1 ha-plots, eight randomly distributed sites of 1 m^2 in size were installed for the seedling inventories during the end of the terrestrial phase, October/November 2000. All seedlings were numbered and identified to morphospecies, when they developed cotyledons and at least one primary leaf, and when they had growth heights of 1 - 100 cm. According to Harper (1977), the exact taxonomic determination of seedlings is not necessary for richness and diversity calculations. However, for the classification of different seedling species, we used morphological patterns of stalks and leaves in the field, i.e., form and arrangement of leaves, presence of hair and glands, etc. In several morphospecies, identification to the species, genus or family level was possible by later identification in the Herbarium of the National Institute for Amazonian Research (INPA), Manaus.

Average inundation of the seedling sites was derived comparing 1999 flood marks on the next localized tree stem with water levels recorded in the Lago Tefé (IDSM, Tefé). We calculated the length of the terrestrial phase for the study site from the daily water-level records (1903-2000) at the port of Manaus, because data of water-level fluctuations of the study area are only available since 1993. Despite the long distance of ~550 km, the available data sets (1993-2000) of water-level fluctuations of the Japurá River in the MSDR and the lower Solimões River at Manaus show a strong correlation ($R^2 = 0.80$, $p < 0.001$), with a difference of only 9 cm in the mean amplitude (Schöngart *et al.,* 2005).

The relative photosynthetically active radiation (rPAR) was recorded on forest ground within all inventoried seedling sites, using an integrating quantum photometer (Li-cor, Li 188b) at fixed horizontal positions in the centre of the sites (90° to light incidence). The measurements were recorded at the time of the highest sun position, between 11h 00 and 13h 00, in a total of eighteen 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 $\mu mol\ s^{-1}\ m^{-2}$.

Determinations of the floristical similarity (Sørensen, 1948) and the beta-diversity (`beta-turnover´, Shmida & Wilson, 1985) were performed, and the stand density of seedlings compared to that of saplings and adult trees. One-dimensional ordinations were performed to check for the zonation of seedling species along the gradients of flooding and solar radiation intensity at the forest floor. T-statistics of multiple regression analysis were calculated between the floristic similarity of the species composition of tree seedlings as dependent variable, and the mean water level at the study site and the corresponding rPAR as independent variables (STATISTICA).

Biomass of the 16 most frequent seedling species was determined collecting 30 specimens with different growth heights of every tree species. From each collected individual, the aboveground growth height was measured on the stalk, from the main root until the vegetation cone. After oven drying at 110 °C during a period of 72 h, the dry weight of all individuals was determined.

Seedling biomass was correlated (Pearson) with individual plant heights in the field.

Results

Environmental conditions

Mean water column averaged 4.8 m (corresponding to a submersion period of 131 d year^{-1}) in the early successional forest (plot I) and 3.7 m (101 d year^{-1}) in the late successional forest (plot II) of the low várzea during 1993 - 2000. In the late successional stage of the high várzea (plot III), mean water column averaged 2.2 m (41 d year^{-1}).

Among the forest types, the amount of relative photosynthetically active radiation (rPAR) reaching the forest floor depended on the forest architecture of the overstory. In plot I, the overstory trees formed a non-stratified canopy. The amount of rPAR measured on forest ground averaged 17.3 % (min. 7.8 %, max. 29.3 %). The overstory of the plots II and III was well stratified, and the amount of rPAR reaching the seedling sites averaged 7.9 % (min. 3.9 %, max. 44 %) in plot II and 3.1 % in plot III (min. 1 %, max. 6.2 %).

Structure and species composition of seedlings

Field inventory yielded a total of 2,882 tree seedling individuals on the entire research area of 24 m^2, belonging to 83 morphospecies. The stand densities summarizing the eight seedling sites in each forest were 2,627 individuals in plot I, corresponding to a density of 328 ± 112 individuals m^{-2} (3,280,000 individuals ha^{-1}), 167 individuals in plot II, corresponding to 21 ± 7 individuals m^{-2} (210,000 individuals ha^{-1}), and 88 individuals in plot III, corresponding to 11 ± 4 individuals m^{-2} (110,000 individuals ha^{-1}).

From the 83 morphospecies recorded, 24 were identified to the species level (9 in plot I, 10 in plot II and 6 in plot III), 14 to the generic and 17 to the family level, whereas 28 morphospecies remained without taxonomical identification. Total species richness amounted to 29 morphospecies in plot I, to 43 morphospecies in plot II and to 32 morphospecies in plot III.

The distribution of seedlings by height class showed, with exception of plot I, an increasing number of individuals until reaching growth heights of 10 - 20 cm (Fig. 2). In plot I, the occurrence of 2,086 individuals of *Cecropia latiloba* Miq. with heights of 1 - 2 cm distorted the height-class distribution of the plot. However, in all forest types, the number of seedlings decreased continuously above heights of 20 cm (Fig. 2).

Floristic patterns along the environmental gradients

Within-habitat floristic similarity (between seedling sites of the same forest plot) amounted to 37.3 ± 15.9 % in plot I, to 17.7 ± 9.5 % in plot II and to 10.4 ± 7 % in plot III. Between-habitat similarity amounted to 24.9 % between the plots I and II and decreased to 9.4 % and 5.9 %, respectively, when species composition of these plots was compared with those of plot III.

The multiple regression analysis indicated significant correlation (R^2 = 0.53, Inundation: T (81) = 2.81, P = 0.006; rPAR: T (81) = 3.32, P = 0.001) between species similarity and the location of seedling sites along the inundation and radiation gradients (Fig. 3), indicating that similarity increases with increasing impact of flooding and with increasing solar radiation intensity at the forest floor.

Constructing a hypothetical beta-diversity profile (SWI, Shmida & Wilson 1985), the studied sites were compared in spatial order along the flood-level and along the radiation gradients with those of other, neighbouring sites. The SWI averaged 0.45 ± 0.16 in plot I, and 0.84 ± 0.11 in plot II. The highest SWI was in plot III (0.87 ± 0.13) (Fig. 4).

Population structure

From the nine identified seedling species in plot I, six also showed the presence of individuals at the sapling and/or adult tree level (Wittmann *et al.* 2002, Wittmann & Junk 2003). In these species, a reverse J-shaped population structure prevailed (Fig. 5). *Cecropia latiloba* Miq., *Albizia subdimidiata* (Splitg.) Barneby & Grimes and *Ficus anthelmintica* Rich. ex DC. were presented with seedlings and adult trees, but were less abundant or even absent at the sapling level (U-shaped population structure).

From the 10 identified seedling species in plot II, eight were recorded at the sapling and/or adult tree community level. *Cecropia latiloba*, *Crataeva benthamii* Eichl. and *Pseudobombax munguba* Dugand showed a reverse J-shaped population structure, whereas it was U-shaped in the other species (Fig. 5). The U-shaped population structure prevailed also in the species of plot III (six identified species with the presence of individuals at the sapling and/or adult tree community, Fig. 5). In this plot, only *Licania mollis* Benth. showed a reverse J-shaped population structure.

Biomass

There was a strong correlation between the individual plant heights of the 16 investigated seedling species and the individual dry weights (Fig. 6). This justifies the estimation of seedling biomass by stand densities and growth height measurements. Seedling biomass decreased with increasing successional stage and increasing elevation of the sites and amounted to 246.7 g m^{-2} in plot I, to 108.9 g m^{-2} in plot II and to 97.1 g m^{-2} in plot III (corresponding to 2.47, 1.09 and 0.97 Mg ha^{-1} respectively).

Discussion

Structure and species zonation of seedlings along environmental gradients

The zonation of várzea tree species along the flood-level gradient was described by several authors (Junk, 1989; Ayres, 1993; Cattanio *et al.,* 2002; Wittmann *et al.,* 2002, 2004). According to Kubitzki (1989), many várzea trees can be considered as ecotypes from the surrounding terra firme, which immigrated to the nutrient-rich várzea. Once established, the species gradually developed adaptations to the periodical inundations, such as the development of adventitious roots, hypertrophic lenticels, a reduced metabolism during waterlogging and hydrochoric and ichtyochoric seed dispersal (e.g., Goulding, 1983; Kozlowski, 1984; Kubitzki & Ziburski, 1994; Waldhoff *et al.,* 1998; Piedade *et al.,* 2000; Parolin, 2001; Schöngart *et al.,* 2002). With increasing height of the water column and increasing length of the inundation period, natural selection resulted in only a few pioneer species able to survive at the highest flood-levels. This evolutionary induced trend of tree species zonation along the flood-level gradient is also reflected by the behavior of tree regeneration. In contrast to the terra firme, where early-successional regeneration is mainly keyed to the light-demand of seedlings in gaps (e.g., Budowski, 1965; Ashton, 1978; Bazzaz & Pickett, 1980; Denslow, 1980; Bongers *et al.,* 1988; Whitmore, 1989), the flooding is thought to be the most limiting factor for the establishment within floodplain forests (Junk *et al.,* 1989; Klinge *et al.,* 1995; Wittmann & Junk, 2003). The results of the present study confirm this statement. The few pioneer species that are able to survive at the highest flood-levels, such as *Cecropia latiloba*, are characterized by fast growth and the production of a vast number of small seeds which are overall dispersed by wind, water or fish (Goulding, 1983; Parolin *et al.,* 2002). Accordingly, species richness and beta-diversity in the present study was lowest in the highly flooded early successional stage, whereas seedling densities were comparatively high.

Subsequent successional stages establish at topographical higher elevations, because dunes and large stem building trees slow down water energy, favor the deposition of sediment and therefore lead to a biogenical induced silting up of the forested sites (Wittmann *et al.,* 2004). Less adapted tree species to flooding establish, resulting in increasing seedling diversity in these forests. On the other hand, increasing seedling diversity with proceeding Forest succession also depends on structural changes in the overstory, therefore reflecting the forest architecture of the actual successional stage. Várzea pioneers are light-demanding species, which allows them to colonize the fresh deposited sand bars next to the riverbanks (Parolin *et al.,* 2002; Wittmann *et al.,* 2004). Due to the relative high solar radiation intensity at the forest floor, they still dominate the seedling layer in early successional stages, whereas their successful establishment is reduced to small-scaled gaps and to forest borders in the well-stratified late-successional forests. Once established in mature forests, seedlings of pioneer species might also be quickly eliminated by pathogens and/or predation (Lieberman *et al.,* 1985), because herbivory is thought to be more effective in lower inundated than in higher inundated forests (Wittmann & Junk, 2003).

The complex forest architecture in late-successional forests implies a high number of ecological niches at the seedling level. The presence of both, a closed canopy and local gaps cause a variety of microhabitats, therefore favoring high seedling species diversity. Nevertheless, the comparatively low species richness in the high-várzea forest recorded in this study contrasted the high species richness found at the sapling and the overstory level. An explanation could be that our inventory was performed during a couple of weeks, thus representing a comparatively short period compared to the period of the terrestrial phase in this forest, which is about 300 d year^{-1}. Thus, seeds of further species might have a relative long period for their successful establishment available. Furthermore, the inventoried area might be too small especially in late successional forests, where many tree species occur with natural low abundances.

Tree regeneration and population structure

Many várzea tree species are characterized by hydrochory and ichthyochory, which favour long-distance dispersal (Kubitzki, 1989; Ziburski & Kubitzki, 1994; Wittmann & Junk, 2003). Thus, it is likely that seedlings in our plots originate from immigrated seeds, and, the other way, that mature trees in our plots disperse to other sites. It is therefore impossible to give values about survival and mortality rates of tree species *in situ*. Nevertheless, assuming that seed import and export in our plots is within the same range, we can estimate species mortality and compare it between the different forest types.

The comparison between the number of seedlings and the number of saplings and adult trees indicate different regeneration behaviors of tree species in the different stages of succession. Trees of early successional stages normally are characterized by short life cycles and high reproduction rates, leading to an advantage during the establishment under extreme environmental conditions (Budowski, 1965; Pianka, 1970; Swaine & Whitmore, 1988). In the present study, the majority of tree species in the early successional stage presented individuals at the seedling, sapling and mature tree level. This indicates that regeneration in these species occurs frequently, despite the comparatively high impact of flooding. However, mortality in these species is high: the ratio mature trees – saplings – seedlings in this early stage of succession was 100 – 0.07 – 0.02. Thus, seedling mortality in this forest amounts to at least 99.98 %. Furthermore, several pioneer species are characterized by continuous reproduction during the whole year (Oliveira, 1998; Parolin *et al.,* 2002), indicating that seedling mortality might be much higher.

Proceeding forest succession and decreasing impact of flooding leads to an increasing number of tree species able to get ages of up to 400 years (Worbes, 1997) and with lower, but more efficient reproduction. Consequently, the seedling densities in late successional stages are low, and mortality rates decrease: The ratio mature trees – saplings – seedlings amounted to 100 – 1.1 – 0.2 in the late successional forest of the low várzea and to 100 – 4.6 – 0.4 in the high-várzea forest. On the other hand, our study revealed that the major part of tree species in late successional forests were characterized by an U-shaped population structure, indicating comparatively low abundances or even the absence of individuals at the sapling level. Despite the low impact of flooding in these forests, we therefore assume that flooding remains a limiting factor influencing the establishment of late successional species. In high-várzea forests, many tree species from the surrounding terra firme establish. Successful regeneration in these species might be inhibited by the periodical inundations. Thus, it might be linked to years with consecutive low inundations (Wittmann & Junk, 2003), which i.e. occur during El-Niño events (Schöngart *et al.,* 2004).

Biomass

The results of our study indicate that seedlings in early successional stages contribute to a significant part to the total biomass of várzea forests. With about 2.5 Mg ha^{-1}, seedling biomass amounts to about 13 % of the total aboveground wood biomass of trees ? 10 cm dbh (data from Schöngart, 2003). However, the importance of tree seedlings for biomass estimations decreases in subsequent successional stages: in both, low várzea and high várzea late-successional stages, the seedling biomass corresponds to only 0.5 - 0.6 % of the total aboveground wood biomass. The highly significant correlation between plant heights and dry weights allows for rapid biomass estimations of tree seedlings by density determinations. However, we expect high population dynamics at the seedling level, especially in highly flooded low-várzea forests. The high mortality in early successional forests suggests that tree seedlings contribute significantly to the total NPP, indicating that described values might strongly underestimated. Therefore, repeated seedling density determinations should be performed to allow for reliable biomass values of tree seedlings in várzea forests and their percentage of total NPP.

Acknowledgements: We wish to thank the Institute for Sustainable Development Research Mamirauá (ISDRM) and the Instituto Nacional de Pesquisas da Amazônia (INPA) for assistance, and Paulo Apostolo (Department of Botany, INPA) for the species determinations. The fieldwork was made possible by financial support from the INPA/Max-Planck Project.

References

ADIS, J.; FURCH, K. & IRMLER, U. 1979. Litter production of a central amazonian inundation forest. *J. Trop. Ecol*. 20: 236-245.

ASHTON, P.S. 1978. Crown characteristics of tropical trees. In: TOMLINSON, P.B. & ZIMMERMANN, M.H. (eds.) *Tropical trees as living systems*. London: Cambridge University Press, pp. 591-615.

AYRES, J.M. 1993. As matas de várzea do Mamirauá. In: SOCIEDADE CIVIL MAMIRAUÁ (ed.), *Estudos de Mamirauá*, Vol. 1, pp. 1-123.

BALSLEV, H.; LUTTEYN, J.; YLLGAARD, B. & HOLM-NIELSEN, L. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Op. Bot.* 92: 37-57.

BAZZAZ, F.A. & PICKETT, S.T.A. 1980. Physiological ecology of tropical succession: a comparative review. *Ann. Rev. Ecol. Syst.* 11: 287-310.

BONGERS, F.; POPMA, J.; DEL CASTILLO, J.M. & CARAIBAS, J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55-80.

BUDOWSKI, G. 1965. Distribution of tropical American rain forest species in the light of successional processes. *Turrialba* 15: 40-42.

CAMPBELL, D.G.; STONE, J.L. & ROSAS, A. 1992. A comparison of the phytosociology and dynamics of three floodplain (várzea) forests of known ages, Rio Juruá, western Brazilian Amazon. *Bot. J. Linn. Soc*. 108: 213-237.

CATTANIO, J.H.; ANDERSON, A.B. & CARVALHO, M.S. 2002. Floristic composition and topographic variation in a tidal floodplain forest in the Amazon Estuary. *Rev. Bras. Bot.* 25(4): 419-430.

COLONNELLO, G. 1990. A Venezuelan floodplain study on the Orinoco River. *For. Ecol. Managem*. 33/34: 103-124.

DENSLOW, J.S. 1980. Gap partitioning among tropical rain forest trees. *Biotropica* 12: 47-55.

FERREIRA, C.S. 2002. *Germinação e adaptações metabólicas e morfo-anatômicas em plântulas de* Himatanthus succuuba *(Spruce) Wood., de ambientes de várzea e terra firme na Amazônia Central.* MSc-Diss. Manaus: Universidade do Amazonas-UA, Instituto Nacional de Pesquisas da Amazônia-INPA.

FOSTER, R.B., ARCE, J.B. & WACHTER, T.S. 1986. Dispersial and the sequential plant communities in Amazonian Peru floodplain. In: ESTRADA, A. & FLEMING, T.H. (eds.). *Frugivores and seed dispersial*. Dordrecht: Dr. W. Junk Publishers, pp. 357-370.

GOULDING, M. 1983. The role of fishes in seed dispersal and plant distribution in Amazonian floodplain ecosystems. In: KUBITZKI K. (ed.). Dispersal and distribution. *Sonderarbeiten des naturwissenschaftlichen Vereins Hamburg* (7), pp. 271-283.

HARPER, J.L. 1977. *Population biology of plants*. London: Academic Press.

HUBBELL, S.P. & FOSTER, R.B. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* 63: 48-61.

JUNK, W.J. 1989. Flood tolerance and tree distribution in central Amazonian floodplains. In: HOLM-NIELSEN, L.B.; NIELSEN, I.C. & BALSLEV, H. (eds.). *Tropical Forests: botanical dynamics, speciation and diversity*. New York, pp. 47-64.

JUNK, W.J., BAYLEY, P.B. & SPARKS, R.E. 1989. The Flood pulse concept in river-floodplain systems. In: DODGE, D. (ed.), Proceedings of the International Large River Symposium, Ottawa. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 110-127.

KLINGE, H., ADIS, J. & WORBES, M. 1995. The vegetation of a seasonal várzea forest in the lower Solimões river, Brazilian Amazon. *Acta Amazonica* 25(3/4): 201-220.

KOZLOWSKI, T.T. 1984. Plant responses to flooding of soil. *Bio. Sci.* 34(3): 162-166.

KUBITZKI, K. 1989. Die Flora der amazonischen Überschwemmungswälder und ihre ökologischen Beziehungen. In: HARTMANN, G. (ed.). *Amazonien im Umbruch, Symposium über aktuelle Probleme und deutsche Forschungen im größten Regenwaldgebiet der Erde*, pp. 215-226.

KUBITZKI, K. & ZIBURSKI, A. 1994. Seed dispersal in floodplain forest of Amazonia. *Biotropica* 26(1): 30–43.

LIEBERMAN, D.; LIEBERMAN, M.; HARTSHORN, G. & PERALTA R. 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *J. Trop. Ecol.* 1: 97-109.

NEBEL, G.; DRAGSTED, J. & VANCLAY, J.K. 2001. Structure and floristic composition of flood plain forests in the Peruvian Amazon II. The understorey of restinga forests. *For. Ecol. and Managem*. 150: 59-77.

OLIVEIRA, A.C. 1998. *Aspectos da dinâmica populacional de* Salix martiana *LEYB. (Salicaceae), em áreas de várzea da Amazônia central*. (MSc-Diss.) Manaus: Instituto Nacional de Pesquisas da Amazônia, pp. 65.

PAROLIN, P. 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia* 128: 326-335.

PAROLIN, P.; OLIVEIRA,A.C.; PIEDADE, M.T.F.; WITTMANN, F. & JUNK, W.J. 2002. Pioneer trees in amazonian floodplains: three key species form monospecific stands in different habitats. *Folia Geobot.* 37: 225-238.

PIANKA, E. R. 1970. On r- and K-selection. *Nature* 104: 592-597.

PIEDADE, M.T.F.; JUNK, W.J. & PAROLIN, P. 2000. The flood pulse and photosynthetic response of trees in a white water floodplain (várzea) of the Central Amazon, Brazil*. Int. Vereinigung Theor. Limnol. Verh*. 27: 1-6.

PIRES, J.M. & KOURY, H.M. 1959. Estudo de um trecho de mata de várzea próximo a Belém. *Boletim Goeldi* 36: 3-44.

SCHÖNGART, J.; PIEDADE, M.T.F.; LUDWIGSHAUSEN, S.; HORNA, V. & WORBES, M. 2002. Phenology and stem growth periodicity of tree species in Amazonian floodplain forests*. J. Trop. Ecol*. 18: 581-597.

SCHÖNGART, J. 2003. Dendrochronologische Untersuchungen in Überschwemmungswäldern der várzea Zentralamazoniens. In: BÖHNEL, H.; TIESSEN, H. & WEIDELT, H.J. (eds.). *Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen*, Vol. 149, Göttingen, pp. 1-257.

SCHÖNGART, J.; JUNK, W.J.; PIEDADE, M.T.F.; AYRES, J. M.; HÜTTERMANN, A. & WORBES, M. 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Nino-Southern Oscillation effect*. Global Change Biology* 10: 1-10.

SCHÖNGART, J.; PIEDADE, M.T.F.; WITTMANN, F.; JUNK, W.J. & WORBES, M. 2005. Wood growth patterns of Macrolobium acaciifolium (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests*. Oecologia* 145: 454-461.

SHMIDA, A. & WILSON, M.V. 1985. Biological determinants of species diversity. *J. Biogeo.* 12: 1-20.

SØRENSEN, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Det Kongelige Danske Videnskabers Selskab Biologiske Skrifter* 5: 1-34.

SWAINE, M.D. & WHITMORE, T.C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.

WALDHOFF, D.; JUNK, W.J. & FURCH, B. 1998. Responses of three Central Amazonian tree species to drought and flooding under controlled conditions. *Int. J. Ecol. Environ Sci.* 24: 237-252.

WHITMORE, T.C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70: 536-537.

WITTMANN, F.; ANHUF, D. & JUNK, W.J. 2002. Tree species distribution and community structure of Central Amazonian várzea forests by remote sensing techniques*. J. Trop. Ecol.* 18(6): 805-820.

WITTMANN, F. & JUNK, W.J. 2003. Sapling communities in Amazonian white-water forests. *J. Biogeo*. 30(10): 1533-1544.

WITTMANN, F.; JUNK, W.J. & PIEDADE, M.T.F. 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. *For. Ecol. Managem*. 196:199-212.

WORBES, M.; KLINGE, H.; REVILLA, J.D. & MARTIUS, C. 1992. On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia*.* *J. Veg. Sci*. 3: 553-564.

WORBES, M. 1997. The forest ecosystem of the floodplains. In: JUNK, W. (ed.). *The central Amazon floodplain: Ecology of a pulsating system. Ecological Studies*, Vol. 126, Berlin, pp. 223-265.

ZIBURSKI, A. 1991. Dissemination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens*. Akademie der Wissenschaften und der Literatur, Mathematisch-Naturwissenschaftliche Klasse: Tropische und Subtropische Pflanzenwelt* 77, Mainz.

Table 1: Plot characteristics. *Trees ? 10 cm dbh; **Trees 1-10 cm dbh, > 1m height, *** Trees 1 - 100 cm height, with developed cotyledons and at least one primary leaf.

Inundation				**Overstory* (ha^{-1})**		**Saplings** (ha^{-1})**		**Seedlings*** (ha^{-1})**	
Plot	Height (m)	Length (d year^{-1})	rPAR (%)	Ind.	Species	Ind.	Species	Ind.	Species
I	4.8	131	17.3	641	45	2,256	25	3,280,000	29
II	3.7	92	7.9	434	91	2,336	35	210,000	43
III	1.9	31	3.1	469	172	5,056	88	110,000	32

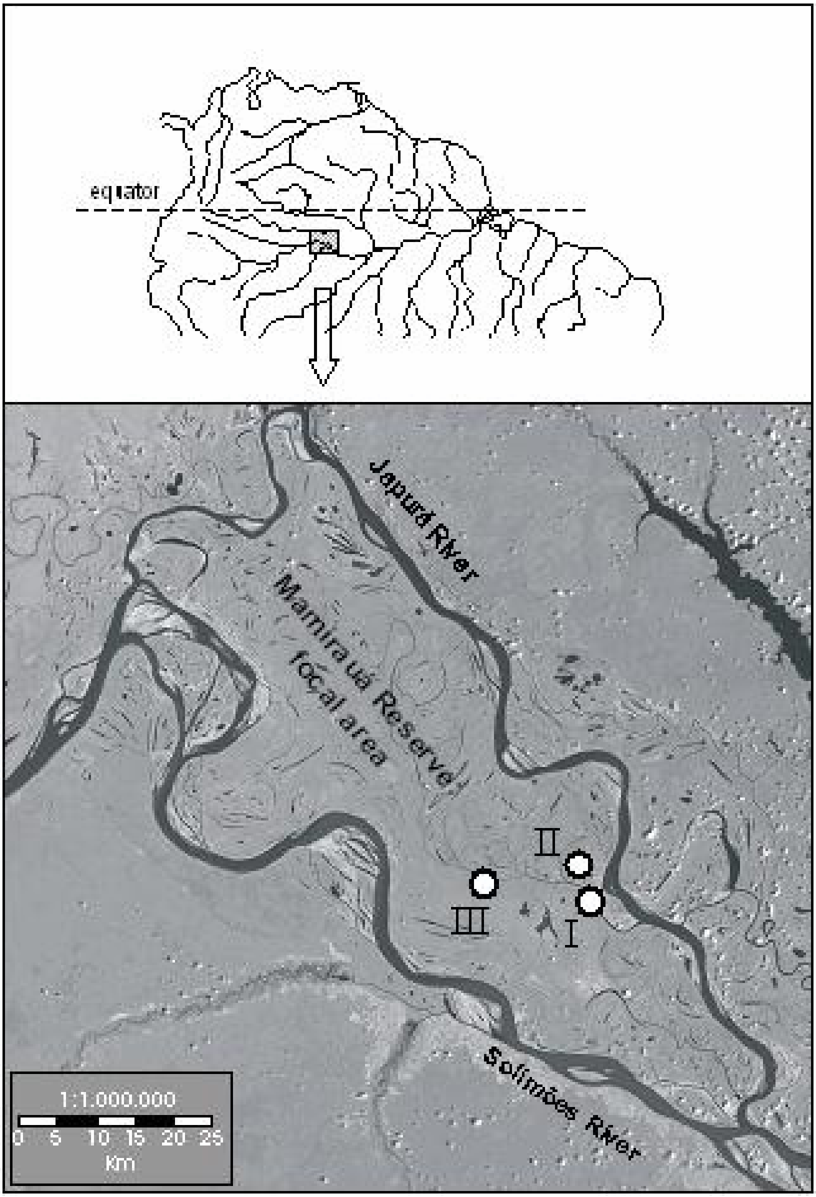


Figure 1: Studied sites within the focal area of the Mamirauá Sustainable Development Reserve, located between the Japurá- and the Solimões Rivers.

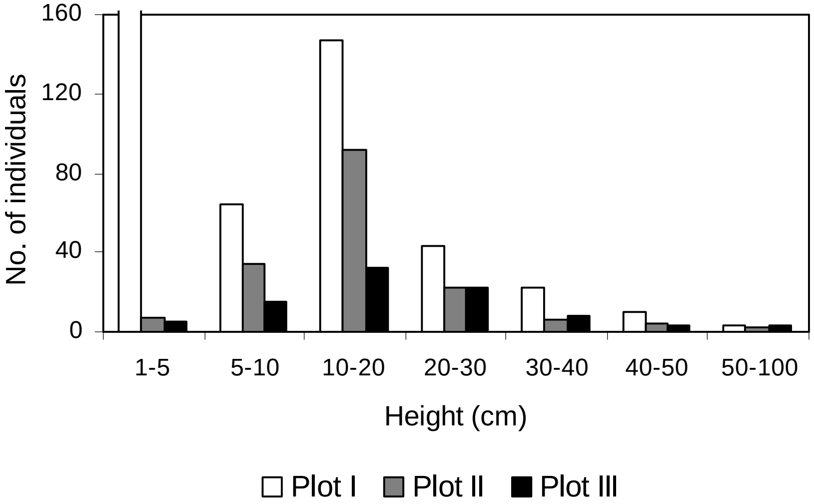
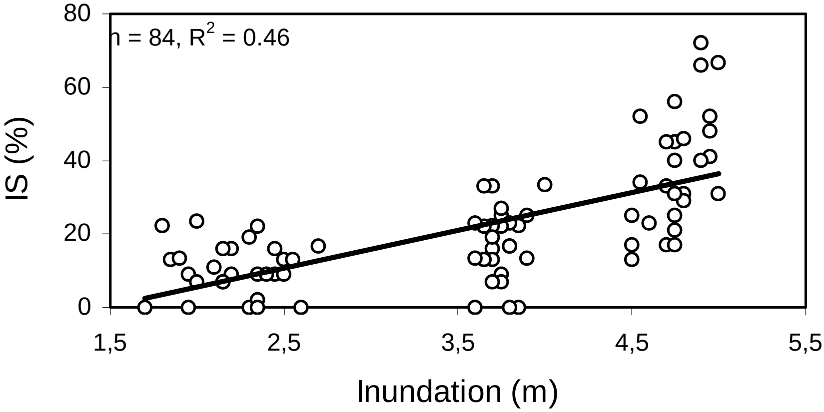


Figure 2: Distribution of seedlings by height class. For covering forest types see Figure 1.



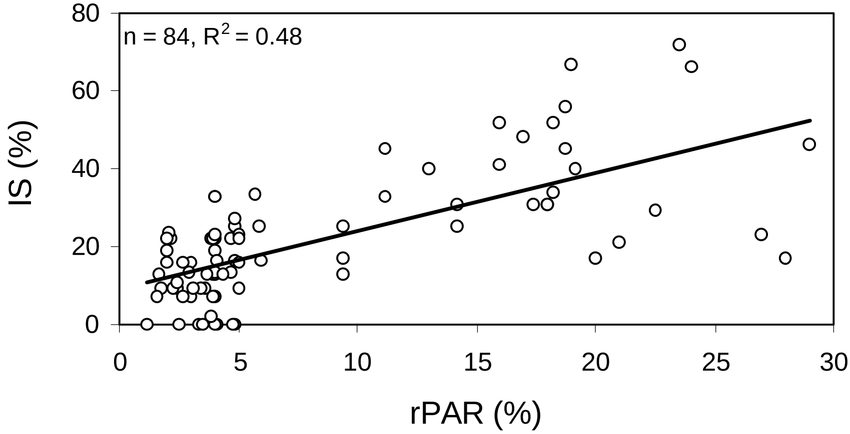


Figure 3: Within-habitat similarity in the three investigated forests plotted against the gradients of flooding and solar radiation intensity (Pearson). Sørensen's index of similarity $IS = 2a(2a + b + c)^{-1}$, where a = No. of species common to sites 1 and 2, b and c = No. of species unique to site 1 and 2. For covering forest types see Figure 1.

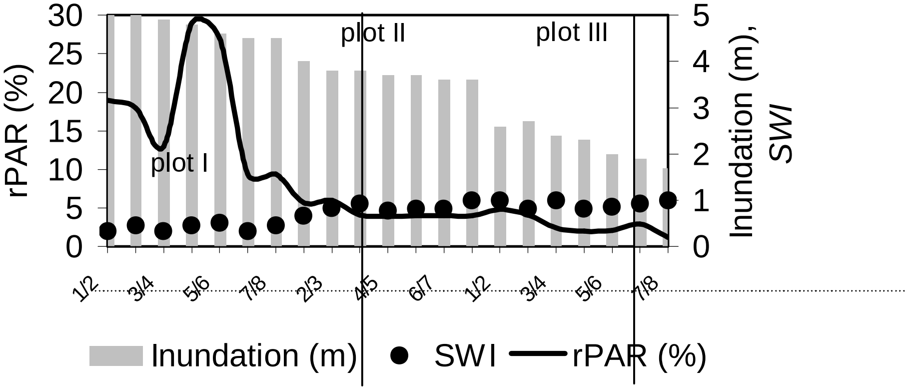


Figure 4: Hypothetical beta-diversity profile between seedling sites along the gradients of flooding and solar radiation intensity. Shmida & Wilson's index *SWI* = (*g* + *l*)/(*a* + *b*), where *g* and *l* = gained and lost species from site 1 to site 2; *a* and *b* = No. of species in site 1 and 2. For covering forest types see Figure 1.

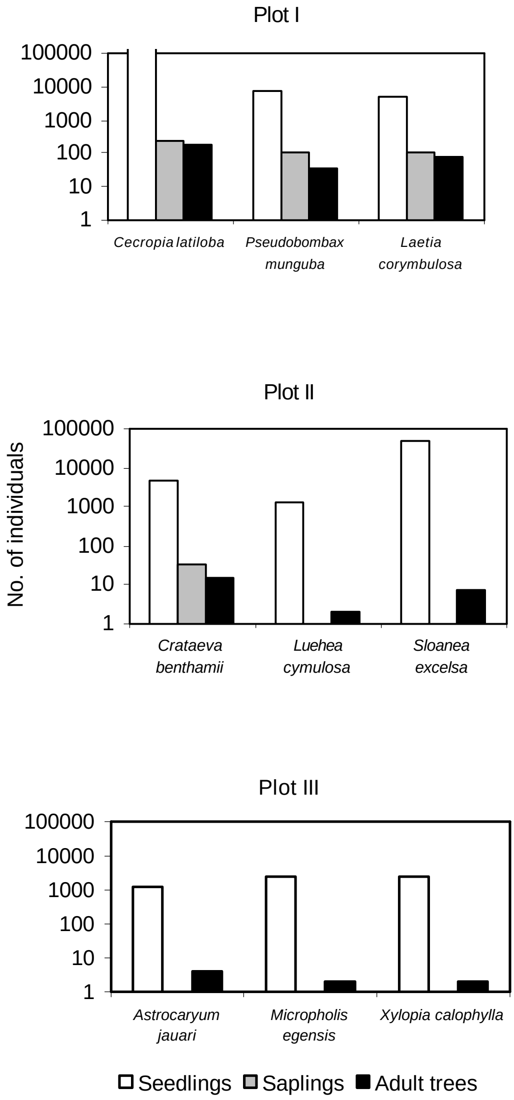


Figure 5: Population structure of species identified seedlings with individuals at the seedling (1 - 100 cm plant height, with developed cotyledons and at least one primary leaf), the sapling (1-10 cm dbh, > 1m height) and the mature tree (? 10 cm dbh) level.

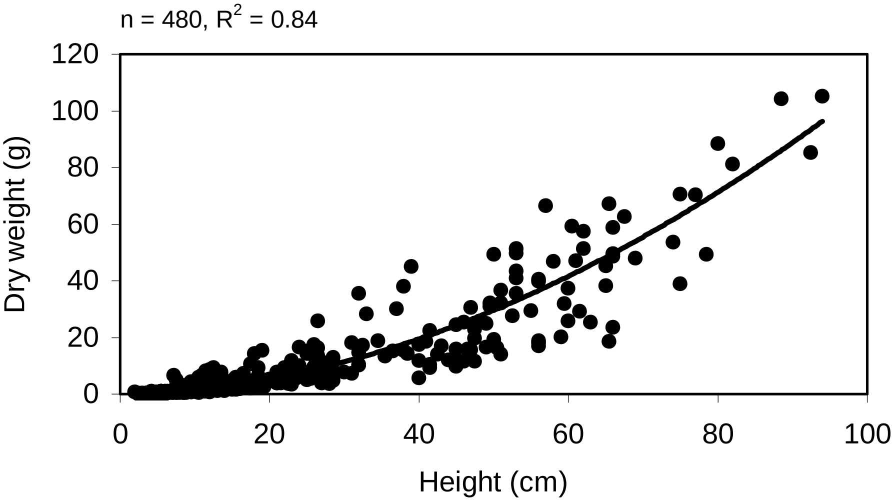


Figure 6: Dry weight of each 30 individuals of the 16 most abundant seedling species plotted against plant height (Pearson).