

# Distribution and population structure of four Central Amazonian high-várzea timber species

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**Abstract** Amazonian white-water (várzea) floodplains harbor many commercially important timber species which in Brazil are harvested following regulations of the Federal Environmental Agency (IBAMA). Although it is well-known that tree physiology, growth, and species distribution of Amazonian floodplain trees is linked to the heights and durations of the periodical inundations, information about timber stocks and population dynamics is lacking for most tree species. We investigated timber stocks and the population structure of four intensely logged tree species in a western Brazilian várzea forest on an area totaling 7.5 ha. Spatial distribution was investigated in all trees as a function of

inundation height and duration and the distance to the river channel, and additionally for saplings (trees <10 cm diameter at breast height—DBH) as a function of the relative photosynthetically active radiation (rPAR). The diameter-class distribution in *Hura crepitans* and *Ocotea cymbarum* indicated that populations are subject to density variations that possibly are traced to small-scale flood variability. In all species, saplings concentrated at higher topographic elevations than the mature tree populations, which suggest that the physical ‘escape’ from a flooded environment is an important acclimation to flooding. While *Ocotea cymbarum* and *Guarea guidonia* were high-density wood species characterized by random dispersion and a pronounced shade-tolerance, *Hura crepitans* and *Sterculia apetala* presented lower wood density, aggregated dispersion, and were more light-demanding. All species presented exploitable stems according to the current harvest regulations, with elevated abundances in comparison to other Amazonian forest types. However, stem densities are below the harvest rates indicating that the harvest regulations are not sustainable. We recommend that the forest management in várzea forests should include specific establishment rates of timber species in dependence of the peculiar site conditions to achieve sustainability.

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## Introduction

Amazonian white-water (várzea) floodplain forests cover an area of approximately 150,000 km<sup>2</sup>. They harbor several tree species that are commercially logged for regional, national, and international timber markets (Schöngart et al. 2007). Timber logging in várzea forests is appealing because round-wood can be transported by the rivers during high-water periods, when the cost of transport is less than that incurred by trucks hauling timber from the uplands (Barros and Uhl 1995; Albernaz and Ayres 1999). According to estimations of the Brazilian Environmental Agency (IBAMA), round-wood production in the Amazonian várzea in the year 1999 amounted to 3 million m<sup>3</sup> year<sup>-1</sup>, which is approximately 10% of the total round-wood production within the Brazilian Amazon. Wood production in the várzea thus contributes US\$ 120 million to the Amazonian gross product and currently directly generates about 30,000 jobs (IBAMA 2000; Bentes-Gama et al. 2002).

Although the Amazonian várzea is covered by the most species-rich floodplain forest worldwide (Wittmann et al. 2006a), commercial timber exploitation is concentrated on comparatively few tree species (Kvist et al. 2001). Approximately 90% of the total timber originating from the Peruvian and western Brazilian várzea involves only nine tree species (Klenke and Ohly 1993). Most of the várzea timber species occur exclusively in high-várzea forests, which are defined by annual inundations <3 m in height, corresponding to a mean flooded period of <50 day's year<sup>-1</sup> (Wittmann et al. 2002). The high várzea concentrates upon channel bars along the banks of river channels, with a width of only few hundreds of meters (Wittmann et al. 2004). These topographic high elevations are covered by the most species-rich forest type within the várzea, sometimes exceeding 150 species ha<sup>-1</sup> ( $\geq 10$  cm DBH) (Nebel et al. 2001; Wittmann et al. 2002). The high várzea is interpreted to be the late-successional stage of the várzea's natural forest succession, and develops in thousands of years from higher inundated low-várzea forest by the continuous silting up of sediments that are deposited by the periodical inundations (Wittmann et al. 2004). Several high-várzea tree species develop diameters of >100 cm, with upper-canopy trees reaching heights of up to 40 m (Ayres 1993). A remote-sensing based classification of the várzea

forest types in western Brazilian Amazonia indicated that the high várzea covers approximately 10–15% of the alluvial landscape (Wittmann et al. 2002).

On the other hand, the high várzea is the area where inhabitants prefer to settle and where the conversion of forest into agricultural areas and pastures occurs. Due to the elevated nutrient content of the alluvial soils, the várzea is the most densely inhabited ecosystem within equatorial Amazonia, enabling fishery, agriculture, crops, and forestry, and offering a variety of natural aquatic and terrestrial resources to the local population (Junk et al. 2000). Deforestation and overexploitation of high-várzea forests previously have led to significant reductions of species populations. Some várzea timber species, such as *Ceiba pentandra* (L.) Gaertn., *Virola surinamensis* (Roll. ex Rottb.) Warb., and *Cedrela odorata* L. disappeared from Amazonian timber markets within a few decades, mainly because of unsustainable logging practices and the lack of information about establishment and growth rates (Schöngart et al. 2005). These timber species were then replaced in the harvest by others such as *Hura crepitans* L., *Couroupita subsessilis* Pilg., *Ocotea cymbarum* Kunth, and *Sterculia apetala* (Jacq.) H. Karst, which actually are the most intensely logged timber trees within Amazonian floodplains (Worbes et al. 2001; Nebel and Meilby 2005; Schöngart et al. 2005).

The discussion about the impact of deforestation and the drivers of climate change that arose especially during the last decade caused an increasing consciousness about the establishment of sustainable management practices. In Brazilian Amazonia, several Sustainable Development Reserves (SDR's) established during this period, some of them also in várzea floodplains. These SDR's include specific programs for the sustainable harvest of timber trees. The management of natural timber resources in the Brazilian Amazon is based on harvest regulations established by the IBAMA, requiring a polycyclic system with a cutting cycle between 25 and 35 years, minimum logging diameters (MLD) of 50 cm, and a maximum yield of five stems ha<sup>-1</sup> (Worbes et al. 2001; Schöngart et al. 2005). A persistent problem in the development and implementation of sustainable forest management systems in tropical forests is, however, the lack of ecological information that can be applied to determine the impacts of selection

logging on populations of extracted species and the sustainable level of harvest (Nebel and Meilby 2005). Particularly, a more profound knowledge regarding the distribution and population ecology of commercial tree species is needed to support a well-adapted management of their populations (Hubbell 1995; Whitmore 1995; Nebel and Meilby 2005).

Despite the huge importance of várzea tree species for timber supply within the Amazon, little knowledge about the distribution, ecology, and population dynamics of the tree species is available. Nebel and Meilby (2005) investigated the population structure of eight tree species in sample plots covering 18.6 ha in a Peruvian várzea forest and found a significant relationship of seedling mortality and the duration of the flooding period. That seed germination, seedling establishment and mortality of many Amazonian várzea tree species is related to the height and durations of the annual inundations was previously confirmed by several authors (i.e., Gottsberger 1978; Goulding 1983; Kubitzki and Ziburski 1994; Parolin 2002). Floristic inventories in Amazonian várzea indicated that most tree species are characterized by a restricted spatial distribution along the flooding gradient (Junk et al. 1989; Ayres 1993; Wittmann et al. 2002, 2004), which can be explained by the degree of adaptations that were developed to tolerate the seasonal anaerobic site conditions caused by the monomodal, predictable ‘flood-pulse’ (Junk et al. 1989). Those adaptations were mainly studied in tree species occurring in Amazonian low várzea (mean inundation height  $>3$  m, corresponding to a mean inundation period  $>50$  day’s year<sup>-1</sup>; Wittmann et al. 2002), and can be morpho-anatomical (i.e., aerenchyma, adventitious roots, hypertrophic lenticels), physiological (i.e., leaf shedding during waterlogging, reduced metabolism and growth), and/or biochemical (i.e., induction of activity of fermentative enzymes) (i.e., Worbes 1997; De Simone et al. 2002; Schöngart et al. 2002; Wittmann and Parolin 2005; Parolin 2009).

Although never explicitly studied, it is thought that high-várzea tree species are poorly-flood adapted and thus react very sensitive to small-scale flood variations (Wittmann et al. 2002; Wittmann and Junk 2003; Schöngart et al. 2004). Investigating the floristic composition of understory trees ( $<10$  cm DBH) in relation to that of the overstory ( $\geq 10$  cm DBH) Wittmann and Junk (2003) and Wittmann et al.

(2006b) stated that most high-várzea tree species are late-successional species, and thus characterized by pronounced shade-tolerance, generally slow growth rates, elevated wood densities, and highly specialized regeneration strategies. However, if and to what extent flooding and/or other environmental factors affect species distribution and shape the population structure of high-várzea timber species is unknown. In addition, there is no information on the basic structural parameters of timber species in undisturbed forest, such as stem densities, tree diameter and height distributions, and the aboveground wood volumes. Therefore, it is highly speculative if the current harvest regulations in Amazonian várzea forests are sustainable.

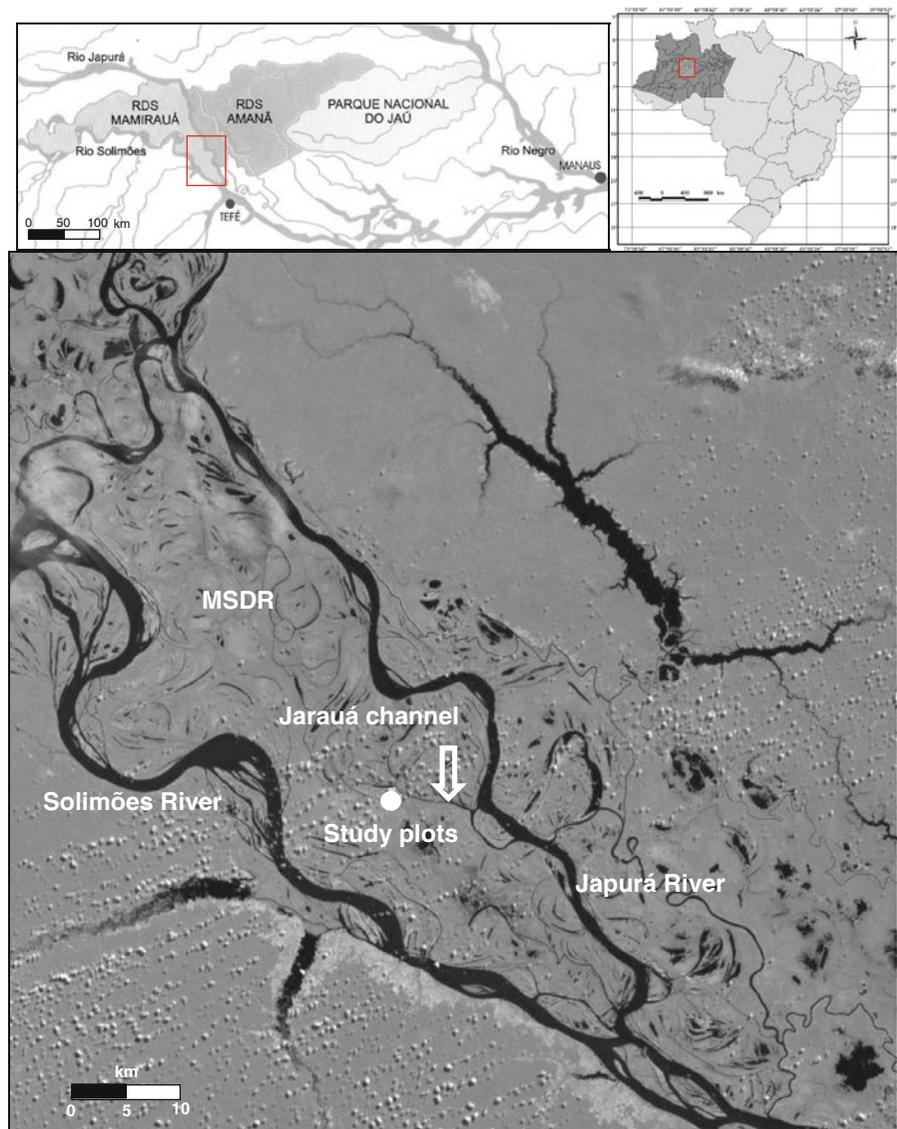
The present study provides a quantitative inventory of the timber stocks of four intensely logged tree species in an undisturbed western Brazilian high-várzea forest. Aim of this study is to test whether the distribution and population structure differs between species, and if it is linked to flooding and/or incoming solar radiation at the forest floor. In addition, we provide information on the population structure of the investigated timber species that allow for an evaluation of the current harvest regulations. Specifically, we want to examine if the harvest regulations are sustainable when applied to still undisturbed várzea timber stocks.

## Methods

### Study area and species selection

The study was carried out in the Mamirauá Sustainable Development Reserve (MSDR, 20°51’S, 64°55’W), which is located between the confluence of the Solimões and Japurá Rivers, located approximately 70 km NW of the city of Tefé, in the western Brazilian Amazon (Fig. 1). The MSDR was founded in 1990 and comprises an area of 11.240 km<sup>2</sup> of várzea floodplain. Since 1992, a variety of community-based management systems commenced within the Reserve, including fishery, agriculture, ecotourism, and forestry. While the management of natural resources takes place in several sectors of the MSDR, its central part is permanently protected from resource extraction (‘permanent conservation zone’ *sensu* Ayres et al. 1998).

**Fig. 1** Study area along the Jarauá channel within the focal area of the Mamirauá Sustainable Development Reserve (MSDR), located between the Japurá and Solimões Rivers, western Brazilian Amazon. Small maps from originate from the Institute for Sustainable Development Research Mamirauá, Tefé, large map derived from Landsat TM (001-062, 25.11.2000, Instituto Nacional de Pesquisas Espaciais—INPE)



The alluvial landscape of the MSDR is a small-scale mosaic of levees, depressions, lakes, and river channels, periodically interconnected with each other and the main river system (Wittmann and Junk 2003). The climate is characterized by a mean daily temperature of 26.9°C and an annual precipitation of approximately 3,000 mm. Annual water-level fluctuations of the Solimões and Japurá Rivers within the MSDR amounted to 10.9 m between 1993 and 2005 (Institute of Sustainable Development Mamirauá, Tefé). Approximately 90% of the MSDR is covered by closed-canopy forest from which 12% is high-várzea forest (Wittmann et al. 2002).

We selected four high-várzea timber species to study their timber stocks, distribution, and population structure: *Hura crepitans* L. (Euphorbiaceae), *Ocotea cymbarum* Kunth (Lauraceae), *Sterculia apetala* (Jacq.) H. Karst (Malvaceae), and *Guarea guidonia* (L.) Sleumer (Meliaceae). All species are widely distributed across the Neotropics, and not restricted to flooded habitats. Within the Amazon basin, however, species abundance is highest in the várzea, whereas it is generally low in nutrient-poor black- and clear-water floodplains (igapó *sensu* Prance 1979) and non-flooded uplands (Wittmann et al. in press). Although of wide geographic distribution, the population

structure and dynamics of the investigated species were poorly studied, with most information originating from Amazonian floodplains. *H. crepitans* is the most important commercial timber tree in both the Brazilian and the Peruvian várzea (Nebel and Meilby 2005; Schöngart et al. 2005), summarizing up to 90% of all logged trees within the MSDR in the year 2003 (Forest Management Program Mamirauá). Specific wood gravity (SG) ranges between 0.36 and 0.42 g cm<sup>-3</sup> (Table 1). Its round-wood is used for home and houseboat construction, the timber for carpentry, furniture, flooring, paneling, and as plywood. SG in *O. cymbarum*, *S. apetala*, and *G. guidonia* range between 0.58 and 0.62, 0.33–0.36, and 0.51–0.57 g cm<sup>-3</sup>, respectively (Table 1). Main use of *O. cymbarum* and *S. apetala* is timber for home construction and carpentry, whereas timber from *G. guidonia* is preferentially used for furniture.

### Species sampling

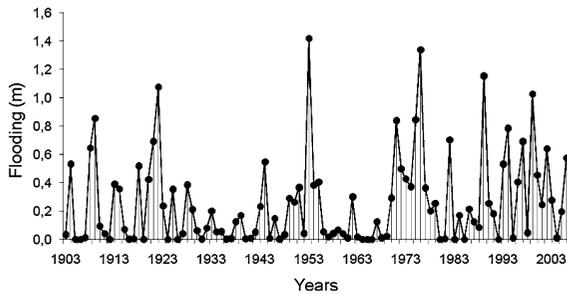
We established 30 plots in high-várzea forests of the permanent conservation zone of the MSDR (Fig. 1), each with the size of 50 × 50 m (2,500 m<sup>2</sup>), totaling an inventoried area of 7.5 ha, during September 2006 and April 2007. All individuals ≥1 m height of the selected species were labeled, numbered, and measured in DBH. The diameters in individuals with height <130 cm (breast height) were recorded 10 cm above the ground surface. Tree heights were measured with the aid of a clinometer (Blume Leiss BL6, Zeiss, Jena).

The position (x- and y-coordinates) of the trees within the plots was measured using the distance along the river bank as x-axis, and that running inland as the y-axis. The position of trees above water-levels (z-coordinates) was determined using maximum flood marks of the last inundation (June 2006) on trunks relative to the water-level of the Manaus gauge at the Solimões/Negro Rivers, which reports daily water levels since 1903. Despite the distance of 550 km to the study area, Manaus shows strong correlation with the water levels in the MSDR, with a difference of only 9 cm in the mean amplitude (Schöngart et al. 2005). For the relationship of flooding and the species distribution, we estimated the mean flooded period of all trees at our study site (day's year<sup>-1</sup>) for the period 1903–2006 (Fig. 2).

**Table 1** Mean stem densities, basal areas (BA), tree heights (H), aboveground wood volumes (AWV), wood specific gravity (SG), and distribution of the investigated species populations in relation to the mean distance to the river channel (all individuals), mean rPAR (individuals <10 cm DBH), and mean inundation height and duration at the study site

	N (ha <sup>-1</sup> )	BA (m <sup>2</sup> ha <sup>-1</sup> )	H (m)	AWV (m <sup>3</sup> ha <sup>-1</sup> )	SG (g cm <sup>-3</sup> )	Mean distance to river channel (m)	Mean rPAR (%)	Mean flood height (cm)	Mean flood period (day's year <sup>-1</sup> )	Years with waterlogging (out of 100) <sup>a</sup>
<i>Hura crepitans</i>	12.13 ± 5.95	2.35 ± 0.4	11.4 ± 10.5	39.07 ± 7.1	0.36–0.42	26.0 ± 16.1	3.2 ± 1.8	23.9 ± 40.7	24.1 ± 32.6	42.7
<i>Ocotea cymbarum</i>	17.07 ± 7.09	1.03 ± 0.07	16.4 ± 6.9	13.8 ± 1.15	0.58–0.62	26.5 ± 16.8	1.9 ± 0.7	29.5 ± 42.9	28.1 ± 34.2	48.5
<i>Guarea guidonia</i>	11.07 ± 4.44	0.44 ± 0.06	11.9 ± 5.1	4.48 ± 0.71	0.51–0.57	15.0 ± 17.6	1.5 ± 0.6	8.1 ± 28.8	9.7 ± 21.9	18.4
<i>Sterculia apetala</i>	5.6 ± 3.99	0.38 ± 0.18	10.9 ± 8.9	6.45 ± 3.81	0.33–0.36	17.3 ± 17.6	2.5 ± 1.4	11.1 ± 32.7	12.6 ± 25.2	23.3
Total	45.87 ± 4.48	4.2 ± 0.21	–	63.82 ± 4.09	–	–	–	–	–	–

<sup>a</sup> Years with waterlogging were derived from daily water-level records at the harbor of Manaus from 1903 to 2006, and standardized to 100 years. SG values were obtained from Wittmann et al. (2006b). All values with SD



**Fig. 2** Mean height of the water column in the studied plots during 1903–2006. Data were derived from 344 measurements that were related with the daily water-level records of the Manaus gauge (Engenharia dos Portos, Manaus)

To test whether the amount of incoming solar radiation at the forest floor influences species distribution of tree regeneration, we recorded the relative photosynthetically active radiation (rPAR) on the forest ground on all individuals <10 cm DBH (saplings), using an integrating quantum photometer (Li 188b, Li-cor, Lincoln, Nebraska) at fixed horizontal positions (90° of light incidence). The measurements were performed at time of highest sun position, between 11.00 and 13.00 h, in a total of 10 times in each individual during the terrestrial period 2006/2007. Simultaneously, control measurements of the absolute irradiation were performed on a fixed point outside the forest. The measured unit was  $\mu\text{mol s}^{-1} \text{m}^{-2}$ , expressed as percentage of incoming radiation at the individuals.

#### Data analysis

The population structures were investigated by creating classes of basal areas (BA), tree heights (H), and aboveground wood volumes (AWV). The AWV was estimated multiplying the individual BA with individual H and a form factor of 0.6, taking into account volume losses of the aboveground wood due to ramifications in the canopy (Brown 1997; Chave et al. 2005). We plotted individual BA against individual H, and both variables against individual AWV to test for significances between these structural variables. Future inventories thus may restrict measurements of structural variables in the field to those that best explain the others.

Each individual was entered into a three-dimensional coordinate system (position: x, y; height: z) based on Triangulated Irregular Network—TIN

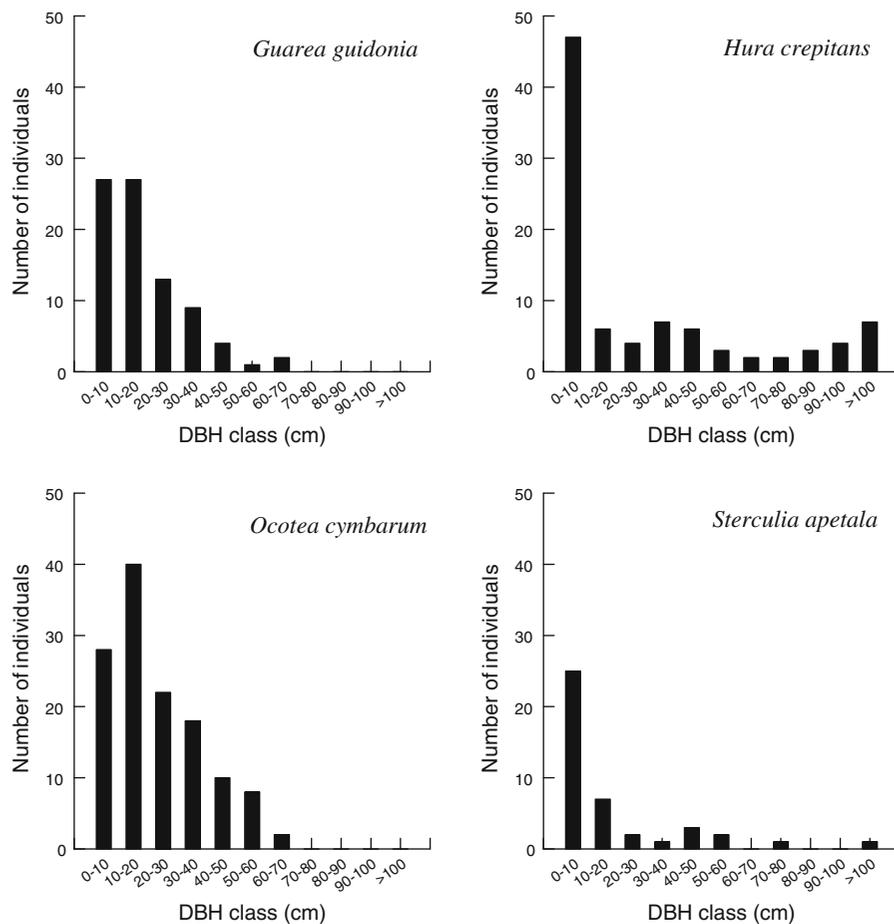
(Digital Elevation Model, Surfer Version 5.00, Golden Software). For each species, the Mean Spatial Distribution Center (MDC, Ebdon 1998, Wittmann and Junk 2003) was determined, as a result of the mean flood duration (all individuals), and the mean rPAR (saplings). Species distribution was further examined as a function of individual distance to the river bank (forest border effect). This variable was included in the analysis because it may substantially influences species distribution by increasing the chance of hydrochoric seed dispersal and/or increased solar radiation (Wittmann et al. 2008). Where appropriate, we separated the individuals in mature and sapling trees to investigate differing distribution patterns. We performed multivariate F-tests to test for dependencies between the spatial distribution of saplings and mature trees and the environmental parameters.

To test if species are dispersed randomly or aggregated, we applied the Morisita's index of dispersion (Morisita 1959):  $Id = n [(\sum x^2 - N)/N(N - 1)]$ , where  $n$  is the number of plots,  $N$  is the total number of individuals counted in all plots, and  $x$  is the numbers of individuals per plot, summed over all plots. According to Brower and Zar (1984) an  $Id > 1.0$  describes an aggregated dispersion, an  $Id < 1.0$  a regular dispersion, and an  $Id = 1.0$  a perfect random dispersion.

## Results

### Population structure

Field inventory yielded a total of 344 individuals on the research area of 7.5 ha (Table 1). Out of all recorded individuals, 137 (39.8%) had diameters <10 cm (saplings). Among species, the ratio saplings—adult trees was highest in *S. apetala* (59.5%), followed by *H. crepitans* (51.6%), *G. guidonia* (44.6%), and *O. cymbarum* (21.9%). With a total of 21 individuals  $\geq 50$  cm DBH (MLD according to the harvest regulation), *H. crepitans* presented the highest numbers of exploitable stems (2.8 stems  $\text{ha}^{-1}$ ), followed by *O. cymbarum* (10 individuals, 1.3 stems  $\text{ha}^{-1}$ ), *S. apetala* (4 individuals, 0.5 stems  $\text{ha}^{-1}$ ), and *G. guidonia* (3 individuals, 0.4 stems  $\text{ha}^{-1}$ ). The distribution of trees by DBH-class indicated higher numbers of individuals in larger classes than in smaller



**Fig. 3** DBH—class distribution in the four investigated timber species

ones in *O. cymbarum* and *H. crepitans* (Fig. 3). Total BA in the four investigated species amounted to  $4.2 \pm 0.2 \text{ m}^2$  (Table 1), from which *H. crepitans* represented 56%, which basically was due to the occurrence of several individuals with diameters  $>100 \text{ cm}$  (Fig. 3). *O. cymbarum* represented 24.5% of the total recorded BA, whereas *G. guidonia* and *S. apetala* both represented 10%.

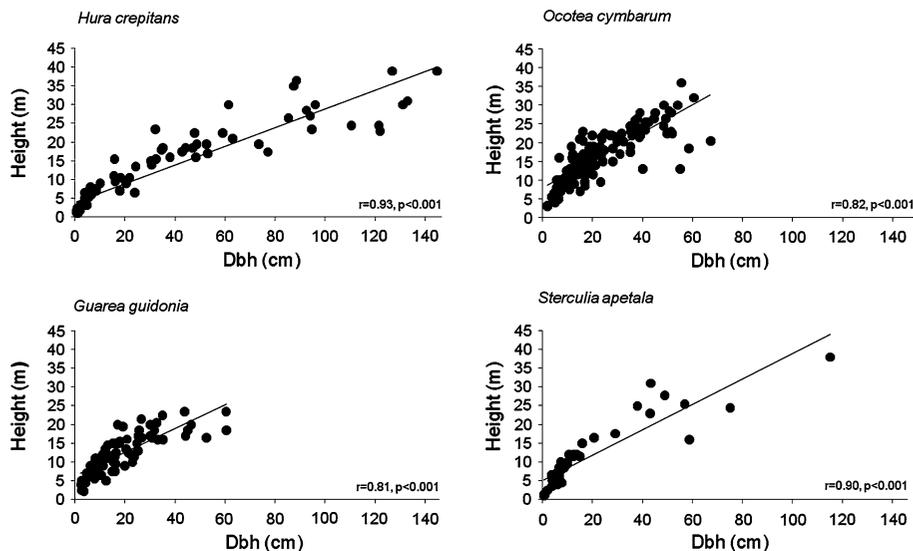
Mean tree height of the populations ranged between 10.9 (*S. apetala*) and 16.4 m (*O. cymbarum*) (Table 1), the highest trees reaching 23 m (*G. guidonia*), 36 m (*O. cymbarum*), 38 m (*S. apetala*), and 39 m (*H. crepitans*). Individual tree heights were significantly correlated with individual BA among both, all recorded individuals ( $r = 0.82$ ,  $P < 0.0001$ ), and species populations (Fig. 4).

Total AWW and exploitable AWW (MLD 50 cm) were highest in *H. crepitans*, and lowest in *G. guidonia* (Table 1). In all species, AWW was

strongly correlated to BA (all with  $r > 0.96$ ,  $P < 0.0001$ ), whereas individual tree heights explained 68% (*S. apetala*) 69% (*G. guidonia*), 77% (*O. cymbarum*), and 78% (*H. crepitans*) of the AWW (Pearson). In *S. apetala*, one single individual represented more than 60% of the total exploitable AWW. In contrast, the tallest individuals in the other species, *G. guidonia*, *H. crepitans* and *O. cymbarum* represented approximately 34, 14, and 12% of the total exploitable AWW, respectively.

#### Species distribution

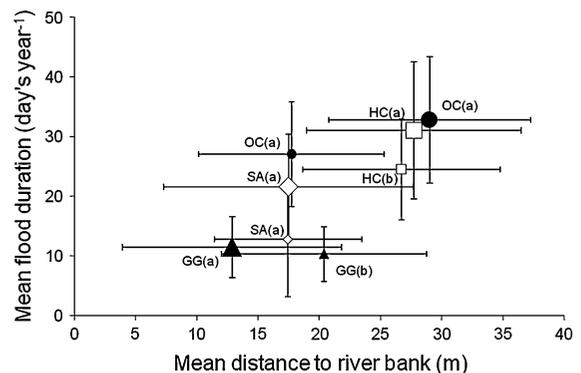
Mean inundation height and duration of the populations ranged between 8 cm (10 day's year<sup>-1</sup>) in *G. guidonia* to 30 cm (28 day's year<sup>-1</sup>) in *O. cymbarum* (Table 1). These small-scale topographic differences, however, significantly affect the mean inundation period especially in years with



**Fig. 4** Diameters of all recorded individuals plotted against tree heights

exceptional low or high inundations. Using the historical water-level records from the harbor of Manaus over a 103-years period, we detected that variability in inundation height at our trees ranged between 0 (e.g., 1934–1938, 1956–1961, 1963–1969, 1995, 1998, 2004) and 168 cm (1953), corresponding to flooded periods between 0 and 118 days year<sup>-1</sup>. During the past 100 years, inundations of the Solimões River surpassed the mean maximum flood-level (MMFL) in a total of 49 years. Out of these flood events, inundations exceeded 50 cm > MMFL in 23 and 100 cm > MMFL in nine years. On the other hand, the species populations were prevented from floods in a total of 51.5 (*O. cymbarum*), 57.3 (*H. crepitans*), 76.7 (*S. apetala*), and 81.6 years (*G. guidonia*) (standardized values to 100 years, Table 1).

In all species, the major part of individuals (*O. cymbarum*: 53.9%; *H. crepitans*: 57.1%; *G. guidonia*: 77.1%; *S. apetala*: 69%) established at higher topographic positions than the mean flood-level derived for the whole populations. Saplings (<10 cm DBH) distributed to mean inundation heights of 19 cm, whereas the mature individuals distributed to mean inundation heights of 29 cm ( $F_{[1.342]} = 10.48$ ;  $P < 0.001$ ). This was especially pronounced in *H. crepitans* ( $F_{[1.89]} = 4.02$ ;  $P = 0.048$ ) and *G. guidonia* ( $F_{[1.81]} = 5.7$ ;  $P = 0.019$ ) (Fig. 5).



**Fig. 5** Mean distribution center (MDC, Ebdon 1998) of adult ( $\geq 10$  cm DBH, large symbols) and sapling populations ( $< 10$  cm DBH, small symbols) of *Ocotea cymbarum* (OC), *Hura crepitans* (HC), *Guarea guidonia* (GG) and *Sterculia apetala* (SA) as a function of the mean distance of individuals to the river channel and mean flood duration year<sup>-1</sup>. Error bars = SD. Differing letters between adult and sapling populations in brackets indicate significant differences in mean flood duration ( $\alpha < 0.05$ )

The distribution of saplings in *O. cymbarum* and *S. apetala* differed significantly from that of the mature trees, with *O. cymbarum* preferentially regenerating closer to the river channel (=forest border) and *G. guidonia* regenerating further inland as the mature populations (Fig. 5). Applying the Morisita's index of species dispersion, *O. cymbarum* and *G. guidonia* best approximated random dispersion ( $I_d = 1.04$ ,  $I_d = 1.05$ ). *H. crepitans* showed

intermediate random dispersion ( $Id = 1.08$ ), and *S. apetala* most aggregated dispersion ( $Id = 1.96$ ). Except *O. cymbarum*, all species showed more pronounced spatial aggregation at the sapling than at the mature tree populations ( $Id = 2.63–0.98$  in *H. crepitans*,  $2.05–1.07$  in *G. guidonia*, and  $2.3–1.76$  in *S. apetala*). In *O. cymbarum*, the sapling population was less aggregated than the mature tree population ( $Id = 0.95–1.04$ ) indicating a distinct dispersal and establishment strategy in this species.

The rPAR was measured in a total of 125 saplings (26, 26, 28, and 45 in *G. guidonia*, *S. apetala*, *O. cymbarum*, and *H. crepitans*, respectively). The rPAR recorded among all individuals was low, and ranged between 0.4 and 16.1%. The correlations between specific sapling densities and rPAR were not significant. However, the saplings of *H. crepitans* and *S. apetala* showed tendency to distribute to sites with higher light incidence than the saplings of *G. guidonia* and *O. cymbarum* (Table 1).

## Discussion

### Timber species distribution and population structure

Several authors stated that the seasonal inundations are the most powerful factor influencing the establishment, population dynamics, distribution, and the growth of Amazonian várzea trees (i.e., Kubitzki 1989; Schöngart et al. 2002; Wittmann et al. 2006a; Oliveira Wittmann et al. 2007; Parolin 2009, Parolin et al. 2010). Flooding affects trees especially in the earliest stages of life, where seedlings undergo submergence for several weeks or months and where the period of establishment is restricted to the non-flooded period (Parolin et al. 2004). The exceptional high and prolonged floods led to the development of specific adaptations of trees to the unfavorable periods of waterlogging and/or submersion. These adaptations are especially common in highly flooded low-várzea tree species that grow at elevations where flooding is unavoidable.

Contrary to the low várzea, flooding in high-várzea forests is highly variable in both magnitude and duration, and less predictable than at higher flooded sites. It may fail completely during consecutive years, as demonstrated in Table 1. Specific adaptations of

trees to flooding in high-várzea tree species are unknown. Kubitzki (1989) stated that the origin of many várzea trees is the surrounding terra firme. When they immigrated to the floodplains, they gradually developed adaptations to the periodical inundations. High-várzea species thus are rarely endemic to flooded habitats and generally characterized by wide geographic distribution across Amazonia and even the Neotropics (Terborgh and Andresen 1998; Wittmann et al. 2006a). For this reason, many high-várzea species probably developed less adaptations to flooding than low-várzea species (Wittmann et al. 2002; Wittmann and Junk 2003), and thus may react very sensitive even to small flood-pulse variations.

The results of the present study indicate that population dynamics in at least two investigated timber species (*O. cymbarum*, *H. crepitans*) is shaped by flooding. In tropical forests, the distribution of trees by DBH-classes in late-successional tree species is typically a negative exponential curve ('reverse J-shaped curve'), as a result of lower numbers of individuals of larger diameters than that of smaller diameters (i.e., Lieberman and Lieberman 1987; Whitmore 1989; Wittmann et al. 2004; Zent and Zent 2004). Exceptions occur when populations are subject to disturbance leading to elevated mortality at the seedling level. As there are no indications of wind- and/or human-induced disturbance (i.e., gaps) in the investigated high-várzea forest, exceptional floods how they i.e. occurred in 1999, 1989, and 1976 are the most probable events promoting disturbance for establishment and causing the irregular shaped diameter distributions in *O. cymbarum* and *H. crepitans*.

While the interpretation on the impact of flood variability on species population dynamics is speculative, our results about the spatial distribution of adult and sapling trees provide stronger evidence for flood stress: Tree regeneration in all species occurred preferentially at sites subjected to lower and shorter floods in comparison to the mature tree populations (Fig. 5). This physical 'escape' from a submerged environment is a common acclimation in poorly flood-adapted species (Voisenek et al. 2003). Besides establishment at topographically higher sites, it is often related to accelerated growth, which enables seedlings to maintain parts of aboveground organs above water levels in order to facilitate the entrance

of oxygen and the outward ventilation of gases (Voesenek and Blom 1999; Voesenek et al. 2003). For várzea tree species, it was previously observed in an experimental study on establishment rates performed by Parolin (2002). In that study, the author proposed that várzea tree species occurring on less flooded areas (high várzea species) try to escape from complete submergence by fast growth to keep at least a part of the crown out of the water.

Conversely, the elevated abundances recorded in the investigated species hardly can be found in other Neotropical old-growth forests. Tree species of most Amazonian upland forests have natural low abundances (i.e., Clark et al. 1998; Harms et al. 2001; Pitman et al. 2002), except when they are low-diverse young-successional stages that recover disturbed sites after natural or man-made catastrophic events (Phillips et al. 2003; Pitman et al. 2005); or when forests develop at sites with climatically or edaphically induced growth limitations (Sombroek 2000; Pélissier et al. 2002). Despite flood-induced disturbance, the species thus not only tolerate, but perform very well under irregular flood conditions. The investigated species account for only 2.3% of the total species richness described in a 1-ha high-várzea forest plot nearby our study site, but for approximately 10% of its total stem density, and 13% of its basal area (Wittmann et al. 2002). Successful establishment during consecutive years with low flood levels (i.e., during El Niño events, Schöngart et al. 2004) in combination with the physical ‘escape’ from a submerged environment (Voesenek et al. 2003), particularly during the earliest stages of life, seem to be the most important acclimations to the irregular floods in the investigated species. As such, these species dominate central Amazonian high-várzea forests with elevated abundances, and thus are particularly interesting as timber resource.

Besides stress-induced implications for plant distribution and growth, flooding also affects seed dispersal and germination rates and thus contributes to explain differing distribution patterns between the investigated várzea timber species. Many várzea tree species synchronize fruit production with periods of high water-levels to benefit from hydrochory (i.e., Pires and Prance 1985; Kubitzki 1989; Parolin 2002). Although there is little information about the reproductive phenology of high-várzea tree species,

Conserva (2006) has shown that germination rates in *O. cymbarum* increased when seeds were subjected to waterlogging, whereas seeds not germinated in waterlogged seeds from *H. crepitans* and *S. apetala*. In the present study, we found that *O. cymbarum* best approximated random dispersion, and that saplings concentrated near the river channel. This indicates that seed dispersal in *O. cymbarum* is mainly by floodwaters. *H. crepitans* is known for its explosive dispersal, with fruits scattering the seeds to distances of up to 45 m (Swaine and Beer 1976). Accordingly, we found tendencies of spatial clumping in this species, whereas it remains unclear if the seeds are predated and subject to zoochoric dispersal. *S. apetala* is known for its bird-dispersed seeds in the Brazilian Pantanal, however, no data are available for Amazonian individuals. No information about the dispersal strategy of *G. guidonia* is available.

The results from our PAR measurements suggested no significant differences between sapling densities and light-incidence at the sapling level, how it was described in many opportunist species in old-growth upland forest (i.e., Lieberman and Lieberman 1987; Bazzaz 1991; Whitmore 1989). Instead, all investigated species appeared to be typical ‘shadow-bearers’ (*sensu* Whitmore 1989). This is especially true in timber species where wood quality is reflected by comparatively slow growth rates and high wood densities. However, *H. crepitans* and *S. apetala* tended to concentrate on sites with slightly higher light incidence than the other species. Both species also are characterized by considerably lower SG (Table 1). SG is generally a robust indicator of the stage of ecological succession, with less dense species being more light-demanding than high-density species (Wiemann and Williamson 1989; Muller-Landau 2004; Nogueira et al. 2005). Wittmann and Junk (2003) stated that most high-várzea tree species are characterized by pronounced shade-tolerance. However, the authors also reported on small-scale differences in the architecture of the upper canopy of high-várzea forests which indicate a large number of micro-sized gaps. That *H. crepitans* and *S. apetala* preferentially establish in these micro-sized gaps is also reflected by its spatial aggregation. Besides flooding, small-scale differences in light incidence thus are important for explaining the distribution of high-várzea timber species.

## Implications for the sustainable forest management

Besides low costs of logging and transport, our study demonstrates that timber logging in the várzea is profitable because of comparatively high stem densities of commercial tree species in comparison to most Amazonian upland forests. However, our results also suggest that logging of the investigated species is not sustainable when managed by the current harvest regulations: Even the most abundant species *O. cymbarum* and *H. crepitans* maximally account for two or three exploitable stems  $\text{ha}^{-1}$ . Therefore, especially the less abundant species *G. guidonia* and *S. apetala* are in risk of overexploitation. Moreover, *H. crepitans* and *S. apetala* are species that tend to spatial aggregation, thus the extraction of few mature individuals may substantially reduce regeneration pools at local and regional scales.

Investigating the growth of *O. cymbarum*, *H. crepitans*, and *S. apetala* through dendrochronological methods in the MSDR, a recent study from Rosa (2008) has shown that the average radial increment of stems in these species is  $1.01 \text{ cm year}^{-1}$ ,  $1.29 \text{ cm year}^{-1}$ , and  $1.26 \text{ cm year}^{-1}$ , respectively (no data are available for *G. guidonia*). The species have average ages of 59, 41, and 47 years when reaching the MLD of 50 cm. Radial increments of 10 cm (one DBH class) thus are achieved during 10–12 years (Rosa 2008). Applying these increment rates to our populations, and presuming that all individuals will survive, the number of stems surpassing the MLD during the next 25 years ranges between 0.5 stems  $\text{ha}^{-1}$  in *G. guidonia* to 3.6 stems  $\text{ha}^{-1}$  in *O. cymbarum*. These numbers drastically illustrate that the current practiced cutting cycles substantially reduce timber species populations.

Based on specific growth-age determinations, Rosa (2008) suggested that the harvest of high-várzea species only is sustainable by the simultaneous increase of the individual MLD's. The results of the present study reinforce this statement: Establishment seems to be triggered by small-scaled flooding and radiation gradients. Establishment variations, however, are not predictable without site- and species-specific investigations on population dynamics. Given the facts of comparatively low sapling abundance in *O. cymbarum*, the physical 'escape' from flooding in saplings of all species, tendencies of

spatial aggregation in *H. crepitans* and *S. apetala*, and the irregular shaped diameter-class curves in *H. crepitans* and *O. cymbarum*, all species are subject to the risk of overexploitation when managed by the current harvest regulations. Besides large-scale floristic inventories and reliable growth-age determinations as performed by Rosa (2008), our study demonstrates that the investigation on specific population structures and particularly the regeneration patterns of potentially harvested timber species is essential to guarantee sustainability of timber management in várzea forests.

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