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TREE SPECIES DISTRIBUTION IN *VÁRZEA* FORESTS OF BRAZILIAN AMAZONIA

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Abstract: Amazonian várzea forests are floodplains inundated by nutrient-rich white-water rivers occurring along the Amazon River. They are regularly flooded for up to 210 days per year by water columns of 10–15 m. Topographic variation results in different flooding amplitudes and durations along the flooding gradient, where the different tolerance to flooding of different plant species results in a vegetation zonation. We made a review of literature about the vegetation composition of *várzea* floodplain forests of Brazilian Amazonia along the Amazon River. Twenty-two studies were selected. Basing on the distribution of inventories which are concentrated in three main areas around the three larger cities Belém, Manaus and Tefé, we classified the inventories into three regions: (A) Estuary region with flooding regime influenced by daily inundations linked to the tides; (B) Central Amazonia near Manaus; (C) Western part of Brazilian Amazonia bordering Peru and Colombia, including Tefé and the "Reserva de Desenvolvimento Sustentável Mamirauá". Summarizing the analyzed species lists, 36 tree species were registered in all sampled regions including the estuary. The regions A + C have 63 species in common, region B + C 143, and A + B 50. In the inventories analyzed here, an increase in species numbers from East to West can be confirmed, but it is difficult to state whether this is not an artefact due to local sampling. Vertical zonation patterns are difficult to discuss due to the lack of comparable data. The inventoried areas are small, and there is an urgent need for comparable floristic inventories throughout the basin. Destruction is spreading rapidly and the traditional use of forests and its resources is changing to a destructive exploitation that already has changed much of the physiognomy and diversity of this unique ecosystem.

Keywords: Flood gradient, Inventories, Whitewater floodplain forest, Zonation

Electronic appendix (www.ibot.cas.cz/folia): Tables 2, 3

INTRODUCTION

Várzea floodplain forests of the Amazon are periodically flooded by fertile muddy-white waters. They are the most widespread type of inundated forest in Amazonia, often extending several kilometers back from the riverbank (JUNK 1984). The boundaries of the floodplains are generally distinct (GOULDING 1988, DALY & PRANCE 1989) because of the strong impact of the regular periods of flooding on general structures and functions of the system. However, despite its size and economic importance (PAROLIN 2000b) not much is known about this ecosystem. Basic data like species lists of floodplain sites throughout the basin are still difficult to find, and large areas have never been inventoried. In order to establish a status quo of knowledge about species distribution in Brazilian Amazonia, to know which data exist to detect longitudinal gradients, and if similar forest physiognomies of the high dense forests occurring along the basin present similar floristic compositions (TER STEEGE & HAMMOND 2001, TER STEEGE et al. 2000, 2003) we made a revision of literature of the vegetation composition of tree species in the flooplains of Brazilian Amazonia. We hope, with this, to contribute to create a basis for the establishment of conservation strategies by pointing out the needs for further scientific work.

ECOLOGICAL CONDITIONS OF AMAZONIAN *VÁRZEA* FLOODPLAIN FORESTS

Amazonian tropical lowland forests extend from the Andes to the Atlantic ocean, comprising nine South American countries, but with 69% the largest amount belongs to Brazil. The States of Pará, Amazonas, Maranhao, Goiás, Mato Grosso, Acre, Amapá, Rondônia and Roraima cover an area of 4,871,000 km^2, which to a large extent are – or were originally – covered by tropical lowland forests. Wetlands occupy 8% of Amazonia and have been described by various authors at structural and floristic level (DUCKE & BLACK 1950, RODRIGUES 1961, TAKEUCHI 1962, PRANCE 1979, KEEL & PRANCE 1979, AYRES 1986, 1993, FERREIRA 1991, 1997a,b, 2000, WORBES 1986, WITTMANN 1997, 2002, WITTMANN et al. 2002, WITTMANN & JUNK 2003, SCHÖNGART et al. 2002, SCHÖNGART 2003). PIRES & PRANCE (1985) recognized seven principal types of wetlands based on the type of inundation, water and soil quality, geological origin and species structure and composition. Within these wetland types, the most widespread is the *várzea*, a floodplain forest inundated by white-water rivers.

The *várzea* dominates the Amazonian lowlands, where sediments started to be deposited in the Pleistocene and Holocene. At some sites these sediments are very recent and are not consolidated and stratified yet (ALFAIA & FALCÃO 1993). The suspended particles that originate in the Andean and Pre-Andean soils consist of clay giving the river waters a loamy brownish colour. These waters are classified as white waters (SIOLI 1984). *Várzea* forests cover an area of about 3% of Brazilian Amazonia, corresponding to an area of 200,000 km^2 (JUNK 1992, 1997). When compared to the other important Central Amazonian floodplain ecosystems, the nutrient-poor black-water seasonal *igapó* (sensu PRANCE 1979), nutrient-rich white-water seasonal *várzeas* show a distinctive forest composition and structure, which is related to their peculiar geomorphological and hydrological conditions (IRMLER 1977, SIOLI 1984, AYRES 1986). *Várzeas* occur on geological formations of the Quaternary, which are recent, sediment rich and have high fluvial dynamics, whereas the *igapós* occur on older Tertiary or Precambric formations with very low nutrient contents and low fluvial dynamics (AYRES 1986, WORBES 1997). Studies comparing both ecosystems showed that floristic similarity was very low between black- and white-water floodplain systems (AYRES 1993, AMARAL et al. 1997, ALMEIDA et al. 2003). Some authors have stated that *várzea* forests are more species rich than *igapó* floodplains (KUBITZKI 1989, WORBES 1997), and they have higher productivity than any other Amazonian ecosystem (MORISON et al. 2000), with values of primary production of up to 33.6 t ha^{-1} per year (WORBES 1997), which is two to three times higher than that of non-flooded *terra firme* forests.

The rivers in Amazonia have a cyclic change of water levels, which in Central Amazonia reach 10–15 m, with periods of flooding of 50 to 210 days per year in the areas colonized by trees. The so-called flood pulse (JUNK et al. 1989) is a predictable inundation that occurs every year between December and July related to the precipitation patterns. The flood pulse –

consisting purely of freshwater – is linked to the sea tide only in the most eastern parts of the basin, where a daily inundation occurs in addition to the annual flooding periodicity.

These regular periods of flooding result in a synchronization of most ecological processes with the water periodicity. Plant reproduction, animal migrations, and also human activities like fishing and agriculture are closely linked to the periodical flooding.

Tree species richness, distribution and vegetation structure in Amazonian floodplains are influenced by many factors (AYRES 1986, JUNK 1989, WORBES et al. 1992, FERREIRA 1997a,b, WITTMANN et al. 2002). Factor one is topographic variation, factor two is a sedimentation dynamic (cyclic sedimentation and downwash). Topographic variation results in different flooding amplitudes and durations along the flooding gradient, where the different tolerance to flooding of different plant species results in a clear vegetation zonation (JUNK 1989, AYRES 1993, ROSALES et al. 1999, 2001, WITTMANN et al. 2002, WITTMANN & JUNK 2003). The second factor, the cycle of sedimentation and erosion, promotes processes of succession where communities in different successional stages may occur simultaneously within a limited area (WITTMAN et al. 2002).

ADAPTATIONS OF *VÁRZEA* TREES

In order to withstand the prolonged periods of flooding and waterlogging in a semi-aquatic ecosystem where oxygen supply to the roots is a limiting factor and seedlings are subjected to a complex set of non-terrestrial environmental conditions, plants have to withstand conditions different from the fully terrestrial ones. Specific physiological and morphological adaptations are needed. Only a few species that grow near the estuary possess osmotic regulation mechanisms that enable the plants to withstand 12 hours of flooding per day (ALMEIDA 1995). Most species grow in the areas that are not influenced by the sea and the tides, but are subjected to the flood pulse (JUNK et al. 1989), which means that they are continuously waterlogged or flooded for up to seven months every year. Because of these extreme growth conditions for trees – a growth form that has originally evolved under purely terrestrial conditions – species numbers in *várzea* are lower than in the adjacent non-flooded *terra firme* forests.

The monomodal flood pulse of the rivers causes drastic changes in the availability of nutrients, oxygen levels, and concentrations of phytotoxins (DE SIMONE et al. 2002, HAASE et al. 2003, PAROLIN et al. 2004). As everywhere in the tropics, the plants are subjected to temperature and light conditions that are optimal for plant growth and development all year round. The aquatic phase occurs under conditions favouring growth and trees do not only persist in a dormant state, but grow vigorously – thus needing adaptations that allow them to do so also with flooding (PAROLIN 2000a). The regularity of flooding may have enhanced the evolution of adaptations and specific traits, which partially are well-known from floodplain trees in other tropical and in temperate regions. Different kinds of adaptations are found at the level of structural, physiological, and phenological traits. Among the most important structural adaptations we may cite hypertrophy of lenticels, formation of adventitious roots, plank-buttressing and stilt rooting, development of aerenchyma, and the deposition of cell wall biopolymers such as suberin and lignin in the root peripheral cell layers (SCHLÜTER & FURCH 1992, SCHLÜTER et al. 1993, NASCIMENTO et al. 1998, PIMENTA et al. 1998, WALDHOFF et al. 1998, PAROLIN 2001, DE SIMONE et al. 2002, HAASE et al. 2003). Different types of aboveground roots are closely related to flooding duration and habitat dynamics (WITTMANN & PAROLIN, in press).

Physiological adaptations comprise a progressive and pronounced reduction in leaf physiological activities like photosynthetic assimilation, transpiration, and stomatal conductance (SCHLÜTER et al. 1993, PAROLIN 2000b, WALDHOFF 2003). KREUZWIESER et al. (1999, 2000) demonstrated that roots affected by anoxia produce high amounts of ethanol, which is transported into the leaves where it can be re-metabolized by oxidation, thereby generating acetaldehyde and acetic acid as an intermediate.

Also phenological adaptations are frequently met. Waterlogging causes reduced water conductance and consequently a water deficit in the crown, resulting in leaf senescence and/or shedding and in a period of cambial dormancy (WORBES 1989, FERREIRA 1991, WITTMANN & PAROLIN 1999, PAROLIN et al. 2002, SCHÖNGART et al. 2002). Therefore, in adult trees, periodical growth reductions are reflected by the formation of increment rings and by periodic shoot elongation (WORBES 1986, 1989, 1997, WORBES & JUNK 1989). When plants are submerged, the leaves may shed within days, e.g. in *Crudia amazonica* (*Fabaceae*) or *Senna reticulata* (*Caesalpiniaceae*), to weeks, or they may be kept below water for several months without apparent damage, e.g. in *Gustavia augusta* (*Lecythidaceae*), *Pouteria glomerata* (*Sapotaceae*), *Rheedia brasiliensis* (*Clusiaceae*), *Symmeria paniculata* (*Polygonaceae*), and *Tabernaemontana juruana* (*Apocynaceae*) (WALDHOFF & FURCH 2002).

For several tree species it has been shown that seed production coincides with the flood pulse to be dispersed by water flow and fish (GOTTSBERGER 1978, GOULDING 1980, REVILLA 1981, WORBES 1986, 1997, JUNK 1989, AYRES 1993, FERREIRA & STOHLGREN 1999, FERREIRA 2000, MOEGENBURG 2002, MANNHEIMER et al. 2003). The diaspores show morphological adaptations that enhance flotation, like spongy tissues or large air-filled spaces (KUBITZKI & ZIBURSKI 1994, WILLIAMSON & COSTA 2000). Combinations of adaptations regarding seed germination, seedling development, and traits of roots, shoots and leaves result in a variety of growth strategies among trees (PAROLIN et al. 2004).

TREE SPECIES DISTRIBUTION AND DIVERSITY

The flooding gradient creates different habitats that are inhabited by species with habitat-specific adaptations (JUNK 1989, FERREIRA & STOHLGREN 1999, ROSALES et al. 1999, 2001, WITTMANN et al. 2002, WITTMANN & JUNK 2003), thus enhancing species diversity. Still, Amazonian floodplains are less diverse and species rich than the adjacent non-flooded *terra firme* forests (CAMPBELL et al. 1986, BALSLEV et al. 1987). In a 1000 km^2 forest of *terra firme* near Manaus 1300 tree species were found (LAURANCE 2001). The world record of tree species was found by GENTRY (1992) in the Peruvian lowlands, with 300 species on one hectare of *terra firme* forest. For Amazonian floodplains, to date no precise overview of species numbers and distribution is available.

We made a revision of literature concerning the vegetation composition of *várzea* floodplain forests of Brazilian Amazonia along the Amazon River. Twenty-two studies that present floristic inventories with species lists were available to us. Using the distribution of the inventories that are concentrated in three main areas around the three larger cities Belém,

Table 1. Characteristics of the regions A, B and C according to the cited inventories.

Region	A	B	C
Location	Eastern Amazonia, estuary region near Belém	Central Amazonia near Manaus	Western part of Brazilian Amazonia near Tefé
Flooding periodicity	Annual flood pulse + daily inundations linked to the tides	Annual flood pulse	Annual flood pulse
No. of studies included	6	10	6
Total no. of species cited	133	371	480
Total no. of genera	93	197	238
Sites and references	Ilha do Marajó, Rio Guamá: PIRES & KOURY 1959, ANDERSON 1991, SILVA et al. 1992, ALMEIDA 1995, BARROS & UHL 1999, ALMEIDA et al. 2003	Ilha de Marchantaria, Costa do Catalão: WORBES 1983, 1986, 1989, 1997, REVILLA 1991, PAROLIN 1998, WITTMANN et al. 2002; Ilha do Careiro: RANKIN DE MERONA 1988; Lago do Janauari: AMARAL et al. 1997	Reserva de Desenvolvimento Sustentável Mamirauá: AYRES 1986, 1993, QUEIROZ 1995, ALBERNAZ & AYRES 1999, WORBES et al. 2001, WITTMANN & JUNK 2003

Manaus and Tefé, we divided the inventories according to three regions (Table 1, Fig. 2): one in the estuary region near Belém, where flooding regime is influenced by daily inundations linked to the tides (Region A), one in Central Amazonia near Manaus (Region B), and one in the western part of Brazilian Amazonia bordering Peru and Colombia but still part of Central Amazonia when regarding the whole basin, near Tefé, and the "Reserva de Desenvolvimento Sustentável Mamirauá" between the River Solimoes and Japurá, which – with ten hectares – represents the largest inventoried area of *várzea* available (Region C). In the cited floristic inventories different sampling methods were used and only a few of the cited studies (e.g. WORBES 1983, 1986) mention the age of the inventoried sites. Therefore we did not perform floristic analyses, but we used numbers of species and genera for our discussions. Nomenclature of the plant names is based on TROPICOS database (www.mobot.org – Missouri Botanical Garden).

The focus of all available inventories around the three main cities (Belém, Manaus, Tefé) and their adjacent floodplains emphasizes the lack of information about the *várzeas*. No floristic studies were published to date about the vast regions between these cities.

There appears to be an East-West gradient of increasing species numbers in the *várzea* (Table 1, Fig. 3). In the studies located in the western part of Brazilian Amazonia (Region C) there were 3.6 times more species and 2.6 times more genera than in the same number of studies (6) in the eastern parts of Brazilian Amazonia near the estuary (Region A).

Similar results were found when regarding single studies along the Amazon basin. Fifty-three species ha^{-1} were described in a study performed in Eastern Amazonia (Guamá River, Pará; PIRES & KOURY 1959), 109 in Central Amazonia (near Manaus and Tefé; AYRES

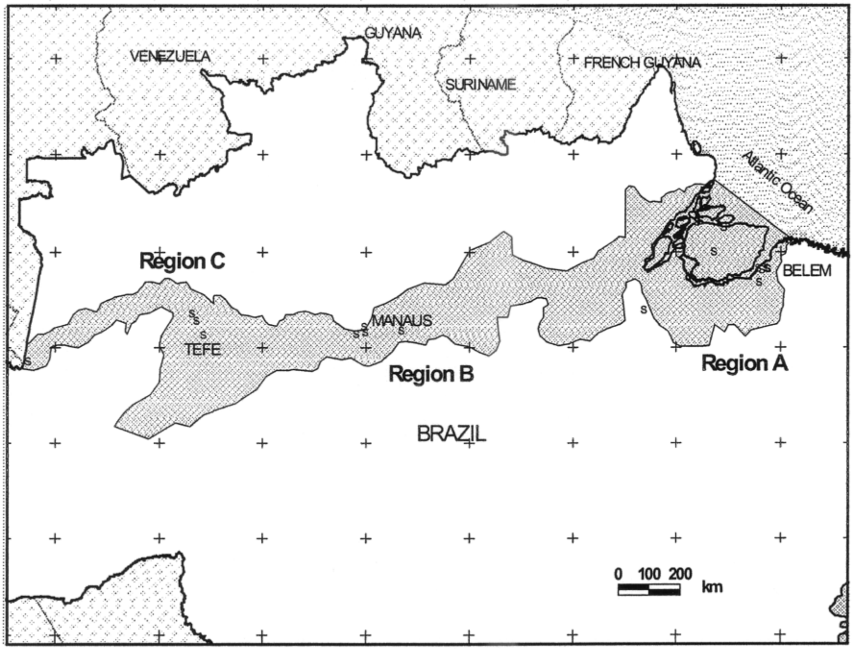

Fig. 1. Division of *várzea* forests in the Amazon / Rio Solimoes basin in Brazilian Amazonia into Region A (near Belém, estuary region, Eastern Amazonia), Region B (near Manaus, Central Amazonia) and Region C (near Tefé / Mamirauá, Central Amazonia – Western Brazil), with locations of cited studies (S; several studies are at close locations, therefore less dots than studies appear). The dotted area delimits the floodplain forests.

1993), and 149 in Western Amazonia (Napo River region, Ecuador; BALSLEV et al. 1987). A similar trend was also found in *terra firme* forests. This perhaps may be explained by the edaphic and climatic conditions (PITMAN et al. 2001), in floodplains mainly by the increasing fluvial dynamics of the rivers closer to the Andes and thus higher habitat heterogeneity. Obviously it is difficult to state whether these results are not an artefact due to local sampling only and different inventory techniques and densities. Only detailed inventories with identical sampling methods covering representative areas can give evidence if the East-West gradient really exists.

In the available lists (Table 2), 36 species were registered in regions A+B+C, i.e., in all sampled regions (Table 3). The region A (estuary) and C (Mamirauá) have 63 species in common indicating that potentially they occur along the whole Brazilian Amazon river system. The region B (mainly Careiro and Marchantaria Island) and C (Mamirauá) have 143 species in common. The higher number as compared to the 63 species in common in region A and C may be related to the shorter distance between region B and C, and also to the influence of the daily inundations in the estuarine region. A and B have 50 species in common.

The duration, amplitude and predictability of the inundated period have a strong influence on species distribution (JUNK 1989). Some authors stated an increase of species numbers with decreasing flood duration in the *várzea* (AYRES 1986, 1993, RANKIN DE MERONA 1988,

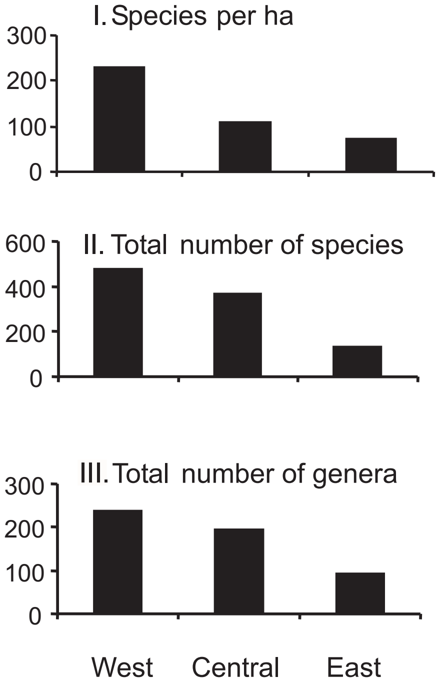

Fig. 2. East-West gradient of increasing tree species numbers in Brazilian Amazonian *várzea*. Species per ha (I), basing on data from PIRES & KOURY 1959, GENTRY 1982, 1986, 1988, BALSLEV et al. 1987, AYRES 1993, WORBES 1997, WITTMANN et al. 2002. Total number of species (II) and genera (III) of the 22 studies included in the present paper and calculations.

KUBITZKI & ZIBURSKI 1994, WITTMANN & JUNK 2003) and also in *igapó* (KEEL & PRANCE 1979, REVILLA 1981, FERREIRA 1991, 1997a,b, 2000, AYRES 1993) suggesting that differences in flooding duration result in a gradient of vegetation communities. Still, the responses to the variation of the flooding cycles vary greatly between species, depending on their genetical constitution, age, water sediment load, etc. (JUNK et al. 1989, WORBES et al. 1992).

As a consequence of the different tolerance to flooding, there is a sequential appearance of species along the topographic gradient, which has also been related to different successional stages (HUBER 1906, PIEDADE 1985, AYRES 1986, JUNK 1989, FERREIRA 1991, 2000, WORBES et al. 1992, KING 2003). On the lower levels, communities with lower species numbers occur, changing from mainly semi-aquatic macrophytes to secondary woody vegetation. With decreasing flood duration species numbers increase, and on the highest levels, bordering with the non-flooded *terra firme*, mature forest stands dominate (JUNK 1989, AYRES 1993, ALMEIDA 1995). In the intermediate topographic positions communities of different successional stages may be found (WITTMANN et al. 2002).

The identification of the successional stage is related to the dominating species in a community (WITTMANN et al. 2002). For Central Amazonian *várzeas*, JUNK (1989) described three communities determined by the flooding gradient, the low-level shrub community, the mid-level and the high-level tree community. A division into three basic types was also suggested for the middle Solimões: the “chavascal” subjected to high flooding amplitudes (5–7 m) with periods of flooding of 6–8 months per year; “restingas baixas” for locations flooded by a water column of 2.5–5 m, and “restingas altas” with flooding heights of 1–2.5 m and flooded for 2–4 months a year (AYRES 1993). The latest and most complete classification of *várzea* floodplain gradients, aided by remote-sensing techniques, was performed by WITTMANN et al. (2002) in Mamirauá and in the region of Manaus. Similarly to AYRES (1993), they divided the gradient into non-forested chavascal, low *várzea* forest and high *várzea* forest. The ordination of trees ≥10 cm dbh showed a well defined species zonation along the flood-level gradient. About 27% of the species in their inventories were restricted to average flood heights between 7–3 m ("low-*várzea* association"), 30% to flood heights between 6–1 m ("low to intermediate association") and 40% to average flood heights between 3–1 m ("high-*várzea* association"). The high *várzea* forests were climax stages that established above the average flood gradient of 3 m (inundation less than 50 days per year). Species richness ranged between 80–170 species ha^{-1}, and individual density amounted to about 400 individuals ha^{-1}. Only 3% of all species recorded showed a wide spatial distribution along the whole inventoried area.

AYRES (1993) inventoried *várzea* forests in the Rio Japurá / Mamirauá Reserve in habitats with great topographic variation subjected to high differences of flooding. In the same region, WITTMANN et al. (2002) found 94 tree species that are exclusive for low *várzea*, and 103 restricted to high *várzea*, whereas only 27 species were common to both low and high *várzea*. Also in the Mamirauá Reserve, ALBERNAZ (1996) found the highest species numbers at intermediate flooding levels. In her study, 40% of the variation was explained by topographic variation indicating that there must be other factors affecting species distribution. The highest levels were dominated by *Astrocaryum murumuru* and *Theobroma cacao*, suggesting that there might be an effect of human impact on the higher sites (ALBERNAZ 1996).

For most inventories, the available information is not sufficient to compare zonation patterns. Also in geographical comparisons like the east-west gradient it has to be borne in mind that non-analyzed topographical variation is included. For further studies it is therefore important to include inventory replicates on different levels in the gradient.

RIVER DYNAMICS AND SUCCESSION

With the high deposition of sediments, the formation of new sand banks that are rapidly colonized by pioneer trees are typical processes in the highly dynamic Amazonian *várzeas*. Although they have been documented intensively only for the western Amazon (KALLIOLA et al. 1991a,b), they occur along the whole river and its affluents.

The high river dynamics influence the succession of plant species. The first forms of vegetation that colonize a newly deposited sand bank are *Poaceae* and *Cyperaceae*, which cover the soil and fix the sediment. Woody species, shrubs, vines, trees and rhizomatous arborescent herbs increase the soil vegetation cover. In the Peruvian *várzea*, the first vegetation cover is formed by *Gynerium sagittatum* (*Poaceae*) and *Tessaria integrifolia* (*Asteraceae*) (SALO et al. 1986, KALLIOLA et al. 1991a,b).

After the herbs, the first establishing woody pioneers are *Salix martiana* (*Salicaceae*) and *Alchornea castaneifolia* (*Euphorbiaceae*) (WORBES 1986, 1997, JUNK 1989, PAROLIN et al. 2002). These species are highly tolerant towards high sedimentation and erosion (WITTMANN et al. 2002). *Salix martiana* may produce new stratified roots when it is covered by a new sediment layer after the flooded period. *Alchornea castaneifolia* produces a high quantity of adventitious roots to increase the efficiency of gas exchange (W.J. JUNK, pers. comm.). Once the first woody species are established, sedimentation and water current processes are influenced in a way that favours the establishment of further woody species and the formation of a first closed canopy. *Cecropia latiloba* (*Cecropiaceae*) then may dominate (PAROLIN 2002, PAROLIN et al. 2002). In the following successional sequence several early successional trees appear, like *Crataeva benthamii* (*Capparidaceae*), *Pseudobombax munguba* (*Bombacaceae*), *Psidium acutangulum* (*Myrtaceae*), *Vitex cymosa* (*Verbenaceae*), and *Crescentia amazonica* (*Bignoniaceae*). Finally, on the higher terraces, and especially on those of Pleistocene origin, the "várzeas altas" occur. They are subjected to short periods of flooding and are characterized by dense forests with high species richness and diversity. These sites are colonized mainly by *Pseudoxandra polyphleba* (*Annonaceae*), *Gustavia augusta* (*Lecythidaceae*), *Malouetia tamaquarina* (*Apocynaceae*), and many others.

CONCLUSIONS

Looking at the total area of *várzea* floodplains in Amazonia, the inventoried areas are very small and probably not necessarily representative. There is an urgent need for a large amount of comparable floristic inventories throughout the ecosystem. Especially remote places far from larger cities have hardly been analyzed, and even more seldom the collected data sets have been published and are thus available to the scientific and also to the local community.

Since the *várzea* is among the most densely populated ecosystems in the Amazon basin, and human pressure is increasing especially in the nutrient-rich productive and accessible sites along the main white-water rivers, destruction is spreading rapidly and the traditional use of the forests and their resources is changing to a destructive exploitation that has already changed much of the physiognomy and diversity of this unique ecosystem.

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