Chapter 4
Phytogeography, Species Diversity, Community Structure and Dynamics of Central Amazonian Floodplain Forests

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Abstract Amazonian floodplain forests are classified into nutrient-rich white-water floodplains (várzea) and nutrient-poor black-water and clear-water floodplains (igapó). Tree species distribution depends on sediment- and nutrient-loads of river waters, on flood regimes and hydro-geomorphic disturbance. The distribution of the different floodplain forest types is determined by adaptations of tree species to different levels and periods of flooding, and most habitats and species are strongly zoned along the flooding gradient. This leads to characteristic successional stages

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with distinct species composition, diversity, and forest structure. Amazonian floodplains and especially the várzea is covered by the most-species rich floodplain forest worldwide. Low flooded forests are floristically distinct from highly-flooded forests, and characterized by intense species exchange with the surrounding uplands. Highly-flooded forests are characterized by elevated degrees of endemic tree species. This indicates comparatively stable environmental conditions over large part of the Amazon basin since at least the early Palaeocene. It is likely that the Amazonian floodplains represented linear refuges for moist-sensitive tree species from the Amazonian uplands during periods with dryer climatic conditions.

4.1 Introduction

The high level of precipitation, its seasonality and the generally low slope inclinations in the Amazonian lowland lead to seasonally flooded areas along the main Amazonian river systems. Trees establishing in these floodplains make use of several different adaptations to cope with the periodic lack of oxygen in flooded soils and the associated reductions of the vegetation period. The high sedimentation rates next to white-water river channels, the scarcity of nutrients in the black-water and clear-water floodplains, and the anoxic conditions in the rhizosphere of backwater depressions accentuate the complex phyto-ecological interactions to which floodplain trees are exposed. Accordingly, the species richness of trees in Amazonian floodplains is lower than that in the surrounding terra firme (Prance 1979; Balslev et al. 1987). Recent studies, however, have shown that Amazonian floodplain forests are the most species-rich floodplain forests worldwide (Wittmann et al. 2006a). This can be explained by (a) the high diversity of habitats, whose establishment is dependent on water chemistry as well as on geohydrological (suspension load of the rivers) and biogeographical (e.g., forest succession, geographical diversity gradients, connectivity by means of the rivers) factors; and (b) the relatively stable environmental conditions within the Amazon basin over millions of years influenced, of course, by the changing spatial sizes and patterns of distributions of the areas. Even assuming tectonic and climatic changes during the Tertiary and Quaternary, it is likely that Amazonian floodplains existed over a long geological time span (Junk and Piedade 2010).

The first researchers to provide floristic and ecological descriptions of Amazonian floodplain forests were Huber (1910), Ducke and Black (1953), Takeuchi (1962), and Hueck (1966). Based on the hydrochemical differentiation of Amazonian floodplains in white-water, black-water, and clear-water influenced floodplains, as elaborated by Sioli (1954a,b), Prance (1979) emphasized the floristic differentiation of várzea forests (white-water) and igapó forests (black-water and clear-water). Várzea forests occur along the channels that drain the Andes and/or the Andean foothills, such as those of the Ucayali-Solimões-Amazon, Juruá, Japurá, Purús, and Madeira Rivers. These rivers are rich in suspension load, which is deposited along the river margins as well as in the channel bars, levees, lakes, and backwater depressions along the river courses. Due to the constantly annually persistent and partially extreme input of sediment, white-water rivers form highly dynamic systems of constantly migrating river channels, thus creating a variety of floodplain and forest microhabitats (Salo et al. 1986; Kalliola et al. 1991; Campbell et al. 1992). Várzea floodplains are exceptionally rich in nutrients, as reflected by the elevated net primary production (NPP) of their vegetation cover (Junk and Piedade 1993; Worbes 1997; Schöngart 2003; Schöngart and Queiroz 2010). These forests extend over an area of approximately 200,000 km^2 within the Amazon basin (Junk 1989).

Igapó forests occur along rivers that drain the Paleozoic and/or Precambric shields of Guyana (N) and Central Brazil (S), e.g., the Negro, Tapajós, and Xingú Rivers. These rivers carry low loads of suspended matter and solutes, resulting in a paucity of nutrients. Compared to the hydrogeomorphologic dynamic várzea, igapó forests form relatively stable floodplain habitats. Periodically flooded igapó floodplains cover an area of approximately 100,000 km^2 (Junk 1989). Detailed information on the geochemistry of várzea and igapó is given by Irion et al. (2010) and Furch and Junk (2010) and on wetland forest classification by Junk and Piedade (2010).

In contrast to non-flooded Amazonian forests, for which published databases report more than 250,000 trees in an inventoried area totalling more than 700 ha (Ter Steege et al. 2006), the number of inventoried trees in Amazonian floodplain forests is small. In várzea forests, floristic inventories have covered an area of less than 70 ha and approximately 40,000 voucher specimens (resumed in Wittmann et al. 2006a), whereas the databases for igapó forests contain inventories of less than 20 ha and approximately 11,000 trees (data from Rodrigues 1961; Keel and Prance 1979; Revilla 1981; Piedade 1985, Campbell et al. 1986; Ferreira 1991; Ayres 1993; Ferreira and Prance 1998; Haugaasen and Peres 2006; Inuma 2006). The overwhelming majority of studies on Amazonian floodplain forests have concentrated on várzea forests; consequently, much more knowledge is available concerning their botany, taxonomy, phytogeography, ecology, and tree physiology than is the case for igapó forests. This chapter summarizes our knowledge about the forest structure, tree species distribution along vertical and geographical gradients, and tree species diversity of Amazonian floodplain forests in relation to their abiotic environments. A classification of the different forest types is presented, and species oligarchies and endemisms within floodplain forests are discussed.

4.2 The Várzea Forest

4.2.1 Environmental Gradients and Successional Dynamics

Floodplain forests cover the transitional zone between aquatic and terrestrial habitats, which complicates interpretation of the environmental factors responsible for tree species composition and distribution (Breen et al. 1988). The average extent of flooding depends on the precipitation and discharge regimes as well as on the topography of the floodplains, and it varies along the river course. Thus, flooding can reach up to 16 m in western Amazonia, 10 m in central Amazonia, and 6 m in eastern Amazonia (Junk 1989; Lamotte 1990). The ‘flood pulse’ (Junk et al. 1989) is monomodal and therefore predictable, resulting in well-defined high-water (aquatic phase) and low-water (terrestrial phase) periods during the year.

Flooding superimposes and partially modifies other abiotic and biotic environmental factors that are of crucial importance for forest development (Junk et al. 1989). The periodic inundation of floodplain forests largely determines the species composition and distribution of their trees, because this process imposes a complex mixture of abiotic factors that interact with natural forest succession. On freshly deposited substrates along the main-river channels, new-site colonization by pioneer trees is an ‘allogenic’ induced succession (*sensu* Tansley 1929; Burrows 1990), in which species composition is triggered by the abiotic environment. During the following successional stages, habitats become more stable, particularly with respect to geomorphology, and abiotic factors may become relatively constant over decades, implying that allogenic succession is replaced by ‘autogenic’ succession (Wittmann et al. 2004).

Abiotic variables, such as flood height and duration, sedimentation rates, distance from the main-river channels, soil texture, and solar radiation on the forest floor, but also biotic variables, including species richness, stand density, stand architecture, mean wood density, and increment and growth rates of trees, are variables that change during forest succession and interact with each other. Thus, identification of one or two of these variables allows for reliable predictions about the others. Wittmann et al. (2002b) noted that forest succession in várzea forests is linked to the biogenically induced process of silting-up, so that it proceeds in relation to the increasing topographic level of the forested sites. This leads to the occurrence of distinctive várzea forest types, which differ in species composition and richness, stand age, and forest structure (see Fig. 4.3).

4.2.1.1 The Role of Flooding

Starting from considerations of the heights and durations of the periodic inundations and their impact on plant distributions in floodplains, Pires and Koury (1959) and Hueck (1966) described a zonation of plant communities along the flooding gradient in eastern and central Amazonian várzea. Junk (1989) investigated the distribution of tree species along the flooding gradient in várzea forests near Manaus. He reported different associations of tree species that establish at topographic levels with inundations lasting 140 (high-level tree community), 230 (low-level tree community), and 270 (low-lying shrub community) days year^{-1}. Ayres (1993) also observed the establishment of different várzea-forest types depending on the mean inundation height and length in várzea forests of the lower Japurá River. Applying the nomenclature used by the local population, he classified the forests as *chavascal* (mean inundation of 5.0–7.0 m), *restinga baixa* (2.5–5.0 m), and *restinga alta* (1.0–2.5 m).

Based on floristic inventories totaling an area of 5 ha in várzea forests at the lower Japurá River, near Tefé, and the lower Solimões River, at the confluence with the Negro River near the city of Manaus, Wittmann (2001) and Wittmann et al. (2002b) inventoried 2,631 várzea tree individuals (≥10 cm dbh) belonging to 306 species. Using high-resolution digital elevation models to the nearest 0.1 m together with data obtained from daily water-level records at the harbor of Manaus since 1903, the authors performed a one-dimensional ordination of all inventoried tree species in order to determine their occurrence along the flooding gradient. The results showed that the várzea tree species can be separated according to two main habitats: (a) *low-várzea forests*, influenced by mean inundations with heights between 3.0 and 7.5 m (corresponding to an mean inundation period of 50–230 days year^{-1}), and (b) *high-várzea forests*, influenced by mean inundations with heights of less than 3.0 m (mean <50 days year^{-1}). The terms *restinga baixa* and *restinga alta*, introduced by Ayres (1993), were used in that study in a modified form, because in Brazil *restinga* frequently refers to vegetation habitats in coastal areas, describing ecosystems with vegetation often adapted to edaphically or climatically induced aridity (Eiten 1970; Rizzini 1997; Wittmann et al. 2002a,b).

Of the tree species recorded by Wittmann (2001) and Wittmann et al. (2002b), only 54 (17.5%) occurred in both low várzea and high várzea, demonstrating the striking difference between the two habitats. The majority of the inventoried tree species (50.2%) were concentrated in the high várzea, with 32.3% restricted to the low várzea. Variations in tree species richness were highest between sites subjected to mean inundations between 3.0 and 2.5 m, thus justifying the habitat differentiation between low várzea and high várzea at these elevations (Fig. 4.1).

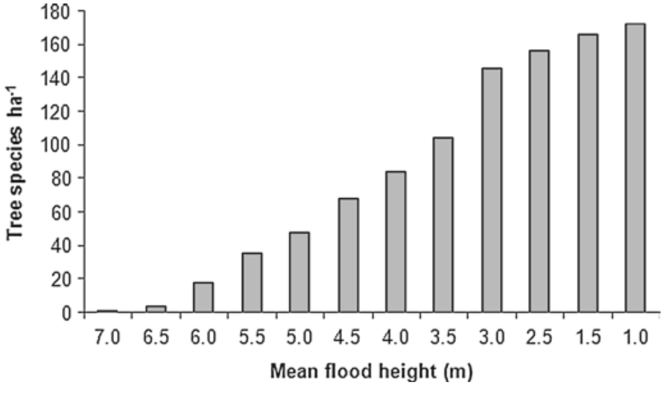

Fig. 4.1 Tree species richness ≥10 cm dbh along the flooding gradient. Highest variations in species richness occur between forest plots with mean flood heights of 3.5–3.0 m. Data are from forest inventories of the Mamirauá Sustainable Development Reserve, near Tefé, and at the lower Solimões River, near Manaus (Wittmann 2001), where 83 plots of 625 m^2 were nested along the mean inundation height (daily water-level records in the harbor of Manaus from 1903 to 2003) of 2,631 individual trees

The continuous increase in species richness with decreasing inundation height and length, and the pronounced species zonation of trees in várzea forests along the flooding gradient were later investigated on a continental-wide scale. Wittmann et al. (2006a) made use of data from 44 floristic inventories totaling an inventoried area of 62.34 ha scattered over ten regions along the Amazonian várzea river system, including sites in Brazil, Peru, Bolivia, Colombia, and Ecuador. These authors found that mean species richness in low-várzea forests averaged 56.9 species ha^{-1}, with 100.8 species ha^{-1} in high-várzea forests (≥10 cm dbh).

The pronounced zonation of várzea tree species along the food-level gradient leads to characteristic species associations and forest types. Only a few tree species occur along the entire flooding gradient; instead, most of them are restricted to very small topographic amplitudes (Wittmann 2001; Parolin et al. 2002c; Wittmann et al. 2002b). Section 2.1.3 provides an overview of várzea-forest types and cites the most characteristic tree species.

4.2.1.2 Geomorphologic Site Dynamics and Habitat Stability

Besides flooding, the processes of sedimentation and erosion and the physical features of the substrate are determining environmental factors in the development of different várzea-forest types (Salo et al. 1986; Terborgh and Petren 1991). Species composition in floodplains varies widely, depending on the frequency of river disturbances (Oliveira-Filho et al. 1994). The periodic deposition and removal of litter and thus of seed banks affect seed and seedling recruitment, and therefore the selection of species able to survive in these areas (Metzger et al. 1997). Next to the main-river channels, sedimentation on slip-off slopes can reach 0.3–1 m $year^{-1}$ (Junk 1989; Campbell et al. 1992) (Fig. 4.17b). On undercut slopes, erosion can wash out several hectares of forests during a single high-water period (Wittmann 2001, Fig. 4.17c). The unstable habitat conditions caused by sedimentation and erosion result in a highly diverse patchwork of microhabitats (Kalliola et al. 1991; Campbell et al. 1992), which is reflected by the floristic and physiognomic structure of the forest cover (Fig. 4.17a).

In general, sedimentation and soil texture are linked to both the distance of the sites from the main-river channels and the period of inundation to which the sites are subjected (Mertes et al. 1995; Wittmann et al. 2004). Moreover, there exist strong linear correlations between these variables (Fig. 4.2). Water current is highest next to the main-river channels, where sedimentation rates are high and relative coarse fractions, such as sand, are deposited at the banks of islands and river margins. With increasing distance from the rivers, current energy is reduced by the water resistance posed by levees and the vegetation cover, resulting in low sedimentation rates. Consequently, mostly fine grained matter, such as silt and clay, is deposited, especially when the floodwaters are non-turbulent and persist for several weeks or months in oxbows, lakes, and backwater depressions. Due to reduced flood duration and current energy, the substrate of high-várzea forests in general has a finer texture than that of low-várzea forests near the main-river channels.

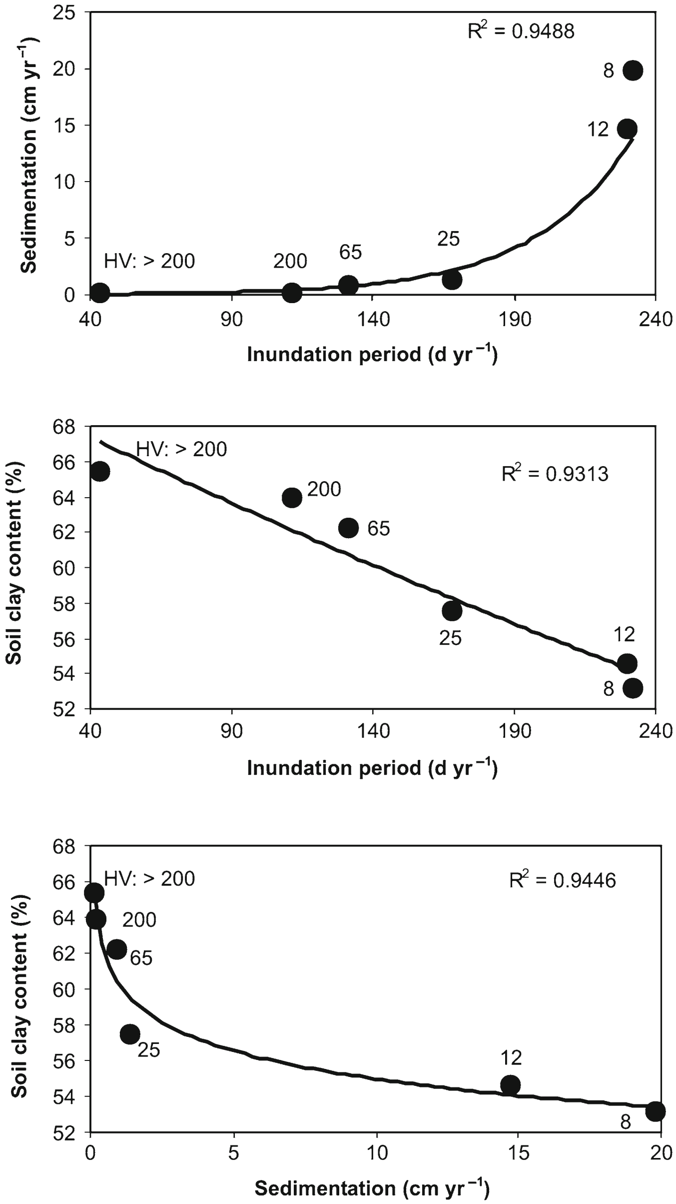

Fig. 4.2 Mean inundation period plotted against annual sedimentation rates (**a**) and the soil clay content (**b**) in forest plots (each 1 ha) with mean stand ages of 8, 12, 25, 65, 200, and >200 years (HV = high várzea); annual sedimentation rate plotted against soil clay content (**c**). Data originate from Wittmann (2001), Schöngart (2003), and Wittmann et al. (2004)

The small-scale changes of sedimentation rates and substrate texture directly influence the distribution of tree species (Wittmann et al. 2004). On the one hand, drainage in coarse-grained soils is better than in fine-grained soils, where oxygen is rapidly consumed due to the decomposition of accumulated organic matter by microorganisms (Larcher 1994). On the other hand, sites with coarse-grained substrates undergo high sedimentation rates, which impede seed germination and seedling establishment, and which cover surface roots and thus affect aeration for mature individuals. Only a few tree species, including *Salix martiana* Leyb. and *Alchornea castaneifolia* (Humb. & Bonpl. ex Willd.) A. Juss. in central Amazonian and *Tessaria integrifolia* Ruiz & Pav. in western Amazonian várzea, are sufficiently adapted to establish at these sites (Lamotte 1990; Worbes et al. 1992). These species avoid anoxia at the root level by forming new-root layers above the annual deposits (Wittmann and Parolin 2005). They also develop deep reaching primary roots, which improve stability against water turbulence during high-water periods and also may facilitate water uptake from river and ground waters during terrestrial phases.

Off the main-river channels, topographic depressions in the form of oxbows and lakes are characterized by slow-current floods. As a consequence of the typically concentric shapes of depressions and levees, floodwaters reach these sites from downstream, against the vector of river currents (Irion 1984b). Sediments deposited in these depressions thus lack coarse grains and drain poorly. Due to the long-term inundation, organic material accumulates. Anoxia at the root level may persist throughout the year. The type of forest that becomes established in these depressions is known as *chavascal* (in Brazil, Ayres 1993) and *bajeal* (in Peru, Lamotte 1990). In addition, a specific form of swamp forest can develop on floating islands of organic material and is locally called *matupá* (Junk 1983; Junk and Piedade 1997).

4.2.1.3 Forest Succession and the Várzea Forest Types

Worbes et al. (1992) defined the várzea-forest types of the lower Solimões River near Manaus by the abundance and dominance of characteristic tree species, and the age structure of forest stands as determined through dendrochronological methods. After the establishment of grasses on freshly deposited alluvial sediments, the first-colonizing pioneer trees form monospecific stands, but these are swiftly replaced by tree species of early-secondary stages. Late-secondary species are, in turn, replaced by intrusion of late-successional or ‘climax’ species. The successional sequence (sere *sensu* Ricklefs 1990) results in a continuous increase in species diversity but a decrease in stand densities. The sere is, moreover, characterized by a reduction of the mean diameter increments and an increase in mean wood-density, as a consequence of the higher abundance of slow-growing, long-living shade-tolerant species in late-successional forests (Lamprecht 1986; Worbes 1997; Schöngart et al. 2003).

The classification of várzea forests by Worbes et al. (1992) along the successional sequence is valid for most low-várzea forests of central Amazonia. Forest succession proceeds in a well-established sere and in interaction with changing environmental conditions. However, the successional model does not take into account three other várzea-forest types, which are scarce in the region near Manaus but very frequent in the western Amazonian várzea: (1) high-várzea forests, (2) primary successions along lakes, and (3) chavascal. These forest types are present when the strength of habitat dynamics is reduced.

Based on the floristic inventories of Wittmann (2001) and Schöngart (2003), who accumulated data from 10 ha in the Mamirauá Sustainable Development Reserve (confluence between the Solimões and the Japurá Rivers) and near the city of Manaus (lower Solimões River), different types of várzea forests can be distinguished. These are characterized by typical patterns of tree species occurrence, dominance, diversity, and by forest structure. In the following, the most important types of várzea forest are presented. The nomenclature used is that of Worbes et al. (1992) and Ayres (1993), but in the modified and completed form suggested by Wittmann et al. (2002a,b, 2004) and Schöngart (2003) and discussed in Junk and Piedade (2010).

In undisturbed equatorial terra firme forests the regeneration cycle commonly starts in small to medium (<1 ha) sized gaps caused by mortality of single trees, or collapse of groups of trees in the top canopy. In contrast the regeneration cylce in the várzea is driven by the forces of erosion and deposition, which continuously create large areas for new-site colonization (Fig. 4.18f, g). Basically, two types of primary successions in várzea forests can be distinguished. These depend on the hydrogeomorphologic site conditions and the period of plant community development (Fig. 4.3). Both types eventually result in late-secondary forests.

Primary Succession Type One: Pioneer Forests Along Rivers and River Channels On freshly deposited sediments, the first colonizing tree species of the pioneer forest at flood-levels below 7.5 m (corresponding to mean flooding periods of 230 days year^{-1}) are *Alchornea castaneifolia* and *Salix martiana*. These species possess adaptations against high and prolonged inundations and against high sedimentation rates, but they only establish at sites where relative photosynthetic active radiation (rPAR) amounts to 70–100% (Wittmann and Junk 2003). As light-demanding pioneer species, they are characterized by fast growth, relatively short life cycles, and a high potential for vegetative and sexual reproduction (Puhakka and Kalliola 1993; Worbes 1997). The buoyant seeds of *S. martiana* germinate while the seeds float on the water surface, thus enhancing plant establishment as soon the seedlings land on a substrate, which marks the beginning of the terrestrial phase (Oliveira Wittmann et al. 2007a). Pioneer forests generally form stands with uniform and single-storied and open canopies (Wittmann et al. 2004). Mean maximum tree ages are only 10 years (Worbes et al. 1992). At the central Amazon várzea, *A. castaneifolia* is generally more abundant in pioneer forests than *S. martiana*. The latter seems to undergo cyclic reproduction and establishment periods, disappearing locally from stands for periods of several years (Oliveira 1998).

The establishment of the pioneer forest promotes sedimentation because the stems and roots of the trees reduce water current energy, thus leading to a continuous up-lifting of the topographic levels of the stands (Wittmann et al. 2002a,b, 2004).

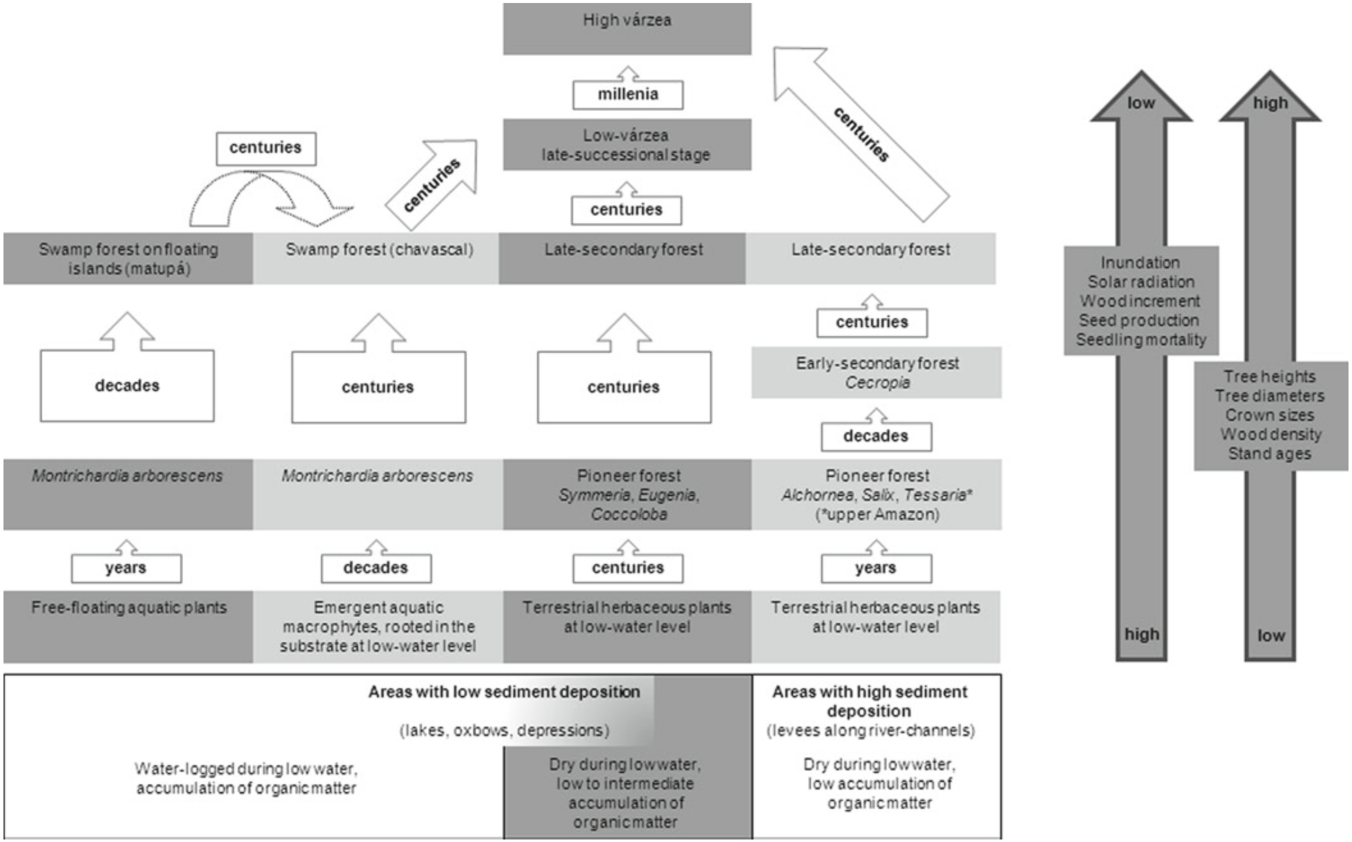

Fig. 4.3 Schematic types of forest succession in várzea floodplains. Note that the term "secondary forest" not refers to antropogenic disturbance, but to natural stages of forest succession according to Budowski (1965) and Worbes et al. (1992)

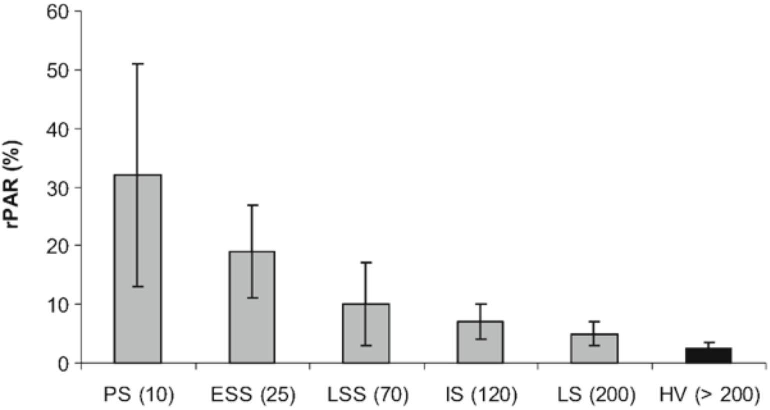

Fig. 4.4 Mean rPAR (relative photosynthetic active radiation) at the forest floor in six different successional stages (with mean stand age in years). Data are from repeated measurements taken from at least seven aleatoric points within 1-ha forest plots (Wittmann 2001; Schöngart 2003; Wittmann and Junk 2003). PS, pioneer stage; ESS, early-secondary stage; LSS, late-secondary stage; IS, intermediate stage; LS, late successional stage of the low várzea; HV, late successional stage of the high várzea

Moreover, the species comprising these forests shade their environment, reducing the establishment of grasses and promoting the growth of other, moderately light-demanding tree species (‘inhibition’ and ‘facilitation’ *sensu* Connell and Slatyer 1977). After the establishment of early-secondary tree species, pioneer species no longer regenerate because the light conditions necessary for successful establishment are no longer present. The rPAR below the canopy of early-secondary species decreases already to about 32% ± 19% (Wittmann 2001; Fig. 4.4). The initial establishment of *Salix* and *Alchornea* is severely hindered by the perennial, highly productive C_4 grasses *Paspalum fasciculatum* Willd. ex Flügge and *Echinochloa polystachya* (Kunth) Hitchc., which compete with these trees for light (Piedade et al. 1991, Fig. 4.18i).

Primary Succession Type Two: Pioneer Forests in Floodplain Lakes Sediment input in floodplain lakes is low and the grain size of the sediments is fine. The substrate of the bottom of the lakes is composed of poorly aerated clays. Lake margins that are exposed to annual inundations of less than about 270 days year^{-1} are colonized by highly flood-resistant shrubs (*Symmeria paniculata* Benth., *Eugenia* spp., *Cocoloba* spp.); either isolated or forming dense stands (Fig. 4.18j). In contrast to the chavascal, which establishes in topographic depressions, organic material near the lake margins is removed by wind-induced currents. In the inner part of dense stands of *Symmeria paniculata*, a litter layer may accumulate, because the stands fall regularly dry. *Salix* and *Alchornea* do not occur, probably because of the poor aeration of the clay soils. *S. paniculata* stands may be stable for many decades because of the low sediment input (Fig. 4.3). These shrubby species often rejuvenate and propagate vegetatively, and seedling establishment occurs only in multi-annual periods of extremely low water levels (Junk 1989). Allogenic succession with species of late-secondary forests proceeds only when the length of the flood period decreases as a result of the build-up of the rise of the lake bottom.

Early-Secondary Stage Along Rivers and River Channels These stages are dense and often monospecific non-stratified, mono-layered stands of *Cecropia latiloba* Miq. (Worbes et al. 1992) (Fig. 4.18i), with up to 1,000 individuals ha^{-1} (≥10 cm dbh; Schöngart 2003). Mean maximum tree ages are 15–20 years (Worbes et al. 1992; Schöngart 2003). These forests often can be found near main-river channels. Their canopy height is related to the age of the deposited sediment and the sequence of establishment. In central Amazonia, early-secondary stages occur on sites where the mean inundation height ranges from 6.0 to 4.5 m. With their dense stands, these forests also favour the biogenic silting-up of their sites, by reducing the impact of flooding and stabilizing the substrate. Combined with the reduced solar radiation below their canopies (Fig. 4.4), early-secondary forests facilitate the establishment of late-secondary tree species.

Late-Secondary Stages Late-secondary stages near river shores are composed of about 500–600 individuals, belonging to 20–50 tree species ha^{-1} (Wittmann et al. 2004) (Fig. 4.17d). This stage is characterized by a beginning stratification. Characteristic species in the upper canopy are *Pseudobombax munguba* (Mart. & Zucc.) Dugand, *Laetia corymbulosa* Spruce ex Benth., and *Luehea cymulosa* Spruce ex Benth., while those in the lower canopy are *Maclura tinctoria* (L.) D.Don ex Steud., *Nectandra amazonum* Nees, and *Crateva benthamii* Eichler. The inundation height is generally between 5.0 and 4.0 m, with the inundation period lasting 210–160 days year^{-1}. Mean maximum stand ages are 60–80 years (Worbes et al. 1992). The rPAR reaching the forest floor averages 10% ± 7% (Fig. 4.4). In lake basins, tree densities and species richness are often lower because of long flood periods.

Late-Successional Stage Low-Várzea Forests Late-successional stage forests of the low várzea contain 70–90 species ha^{-1}. The inundation height is between 4.5 and 3.0 m, corresponding to an inundation period of 50–120 days year^{-1}. These forests are well-stratified, but the sub-canopy stratum is characteristically poor in individuals (Fig. 4.17e). About 40% of all trees (≥10 cm dbh) belong to the upper canopy at a height of 30–35 m. Characteristic species in the upper canopy are *Piranhea trifoliata* Baill., *Tabebuia barbata* (E. Mey) Sandwith, and *Hevea* spp., in the lower canopy *Pouteria* spp., *Oxandra* spp., and *Duroia duckei* Huber. The rPAR at the forest floor in low-várzea late-successional stages averages 3–5% (Fig. 4.4). Maximum stand ages of approximately 400 years were recorded in *Piranhea trifoliata* (Worbes et al. 1992). According to Worbes' model of forest succession, the elevated ages of the trees suggest that late-successional forests of the low várzea are the mature 'climax' stage of the successional sere. This is certainly true in areas distant from river channels, where sedimentation rates are very low (<1 mm year^{-1}). The floristic inventories of Cattanio et al. (2002) in eastern Amazonia, Wittmann et al. (2002b) in central Amazonia, and Balslev et al. (1987), Dallmeier et al. (1996), and Nebel et al. (2001d) in western Amazonia, however, suggest that low-várzea late-successional forests are vulnerable to the changing environmental site conditions, and are eventually replaced by forests of the high várzea. Depending on the sedimentation rates in late-successional low-várzea forests, this development may require several centuries to millennia and thus allows for the establishment of several intermediate late-succession forest types.

High-Várzea Forest These are the most species-rich of the various types of várzea forests. In the central and western parts of Amazonia, tree species richness may be as high as 120–160 species ha^{-1} (Balslev et al. 1987; Dallmeier et al. 1996; Nebel et al. 2001; Wittmann et al. 2002b). High-várzea forests establish above a mean flood level of 3.0 m. Depending on the position along the flood-level gradient, the mean inundation period in high-várzea forests barely reaches more than 50 days year^{-1} and may fail completely during exceptionally dry years (e.g., during El Niño events; Schöngart et al. 2004). Many tree species occur with low abundances, often being represented by only one individual ha^{-1}. These forests show a distinctive stratification, with an upper canopy height at 30–35 m and emergent trees reaching heights of up to 45 m. Due to the relatively long terrestrial phases, trees regenerate during most of the year, thus leading to a characteristically dense under-storey (Fig. 4.18l). In central Amazonia, abundant genera in the upper canopy include *Terminalia, Aspidosperma*, and *Guarea*; in the mid-canopy, *Pouteria*, *Brosimum*, and *Eschweilera*; and in the low canopy, *Inga*, *Duguetia*, and *Annona*.

High-várzea forests can be classified as the climax of the várzea's successional sequence (Wittmann et al. 2002a,b). They often establish along the elevations along the banks of rivers and secondary-river channels (Fig. 4.18k). Due to the relatively long period of their geomorphologic development, which increases the probability of habitat fragmentation through the constantly moving beds of rivers and river channels, high-várzea forests occur on approximately 10–15% of the várzea's forested landscape (Wittmann et al. 2002a,b). The overwhelming fraction of its substrate is clayish (Fig. 4.2). The rPAR at the forest floor averages only 1–3%, which is similar to the light conditions found in undisturbed terra firme forests (Wittmann and Junk 2003; Fig. 4.4).

Chavascal The term *chavascal* (Ayres 1993) was first used during the nineteenth century in the *Flora Brasiliensis* (Martius 1840–1906) to describe species-poor and dense gallery forests in the Caatinga of southern Mato Grosso. In the central Amazonian várzea, the chavascal is a dense and species-poor forest that establishes in depressions and oxbows. The trees often develop stilt roots and aerial roots as outgrowths on their stems to improve aeration by increased root superficies (Wittmann and Parolin 2005). The chavascal cannot be included in the successional sequence that occurs next to the main-river channels, because succession follows a non-cyclic sere (*sensu* Schroeder 1998) in which changes in environmental conditions occur more slowly than near the highly dynamic river banks (Fig. 4.3). As an alluvial relict developing in old river oxbows or lakes, the chavascal is characterized by the slow silting-up of clayish deposits and organic matter in still waters (Wittmann et al. 2004). The input of fine-grained deposits during aquatic phases leads to an impermeable substrate, known as *tabatinga* to the Brazilian floodplain inhabitants. The poor drainage induces waterlogging of the vegetation cover even during low-water periods. Sedimentation rates measured in a chavascal at the lower Japurá River were 0.1–0.2 cm year^{-1}, and the soil clay content exceeded 80% (Wittmann et al. 2004).

The longstanding stable geomorphologic conditions combined with the anoxia at the root level during most of the year leads to a successional sequence in which primary stages reach ages of several decades. Characteristic species of primary successional stages within the chavascal are, especially, Polygonaceae of the genus *Symmeria*, and Myrtaceae of the genus *Calyptranthes* and *Eugenia*. These mostly arbustive trees form monospecific and highly dense stands (Wittmann and Parolin 2005). They establish at the banks of depressions, tolerating inundation heights of 7.0–7.5 m (up to 230 days year^{-1}). Year-ring counting on stem-discs obtained within the Mamirauá Reserve from *Calyptranhtes multiflora* Poepp. ex O. Berg and *Eugenia ochrophloea* Diels indicate maximum tree ages of 40–60 years (J. Schöngart and F. Wittmann, 2005, unpublished data).

The pioneer stages of the chavascal migrate towards the center of depressions, as silting-up proceeds and new sites become available for tree colonization. When inundation is reduced to <7.5 m high (<230 days year^{-1}), pioneer species of the chavascal are replaced by palms (mainly *Bactris* spp.) and a few dicots, such as *Buchenavia oxyxarpa* and *Pseudobombax munguba*. The mineral soil-surface of the chavascal is often undulated because tree fall leads to the formation of small elevations and depressions that become filled with water, also during the low-water period, and accumulate organic debris. In a floristic inventory of 625 m^2 within the Mamirauá Reserve, Wittmann et al. (2004) recorded eight tree species (≥10 cm dbh) in a chavascal inundated by a mean water column of 6.8 m. Stand density in this forest exceeded 600 individuals ha^{-1}; the non-stratified canopy was recorded at heights between 12 and 18 m.

Matupá A specific type of swamp forest develops on floating islands of organic material, locally called *matupá* (Fig. 4.3). These islands can develop in small lakes that do not fall dry. Floating aquatic plants build an organic layer that becomes colonized by moisture-tolerant sedges, ferns, and other herbaceous plants. When the tree-like *Montrichardia arborescens* (L.) Schott (Araceae) invades this layer, it stabilizes the organic material with its strong stolons and allows colonization by trees such as *Cecropia latiloba*, *Vismia* spp., and *Pseudobombax munguba*. The floating layer follows the water-level fluctuations of the lake. Permanent waterlogging reduces decomposition of the organic material, whereas extreme floods and droughts can destroy these islands (Junk 1983; Junk and Piedade 1997).

4.2.1.4 Forest Structure

In várzea forests, the successional sere is characterized by a typical distribution of tree densities, tree heights, tree diameters, crown sizes, and crown area coverage (Klinge et al. 1996; Worbes 1997; Wittmann et al. 2002b; Schöngart 2003).

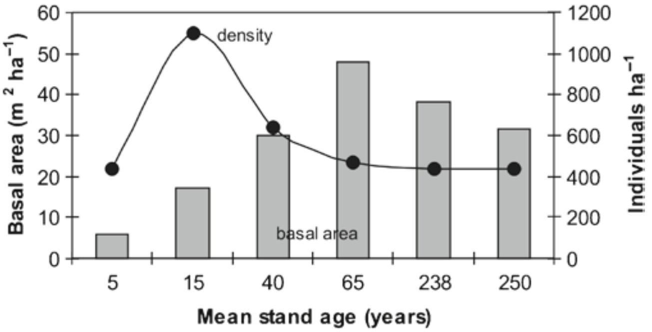

Fig. 4.5 Stand density and basal area of forest stands (trees ≥10 cm dbh) plotted against mean stand age (Data from Wittmann 2001; Schöngart 2003)

In pioneer stages along rivers and channels, tree densities ≥10 cm dbh average 400–500 individuals ha^{-1}, with the highest values occurring in early-secondary stages (800–1,000 individuals ha^{-1}). In subsequent successional stages, tree densities decline continuously to the average level (Fig. 4.5). The basal area of trees ≥10 cm dbh increases from the pioneer stages until the forests reach stand ages of 60–100 years. In later successional stages, the basal area declines (Fig. 4.5). The basal area of tree regeneration, however, shows an opposite trend: it tends to increase continuously from pioneer stages to old-growth forests (Wittmann and Junk 2003).

Mean and maximum tree heights, sizes of individual tree crowns, and the crown area coverage of várzea forests show a strong logarithmic relationship to the mean stand age of forests along the successional sere (Fig. 4.6, Wittmann et al. 2002b; Schöngart 2003). Pioneer stages and early-secondary stages are characterized by a non-stratified canopy establishing at heights of 8–12 m and 15–20 m, respectively. Late-secondary forests show a beginning stratification, with an upper canopy at heights of 20–25 m and a lower canopy at 10–15 m. Low-várzea late-successional forests are well-stratified: the upper canopy is established at 30–35 m, the mid-canopy stratum at 15–20 m, and the low-canopy at 5–10 m (Wittmann et al. 2002b). This stratification pattern is also valid in high-várzea forests, but here emergent trees of up to 45 m are found. By contrast, the chavascal is characterized by a single-layered canopy at heights of 12–18 m (Wittmann et al. 2004).

The different forest-structure patterns in the várzea allow for a reliable classification of várzea-forest types by remote-sensing techniques (Wittmann et al. 2002a,b). The non-stratified, homogeneous, upper-canopy surfaces of young successional stages and the chavascal are due to dense stands, generally small tree crowns, and high crown area coverage, which in turn result in homogeneous light reflectance patterns, as seen in aerial photographs and optically based satellite image data, such as SPOT HRV and Landsat TM (Fig. 4.7). In contrast, the more complex architecture of late-successional stages and, in particular, high-várzea forests can be

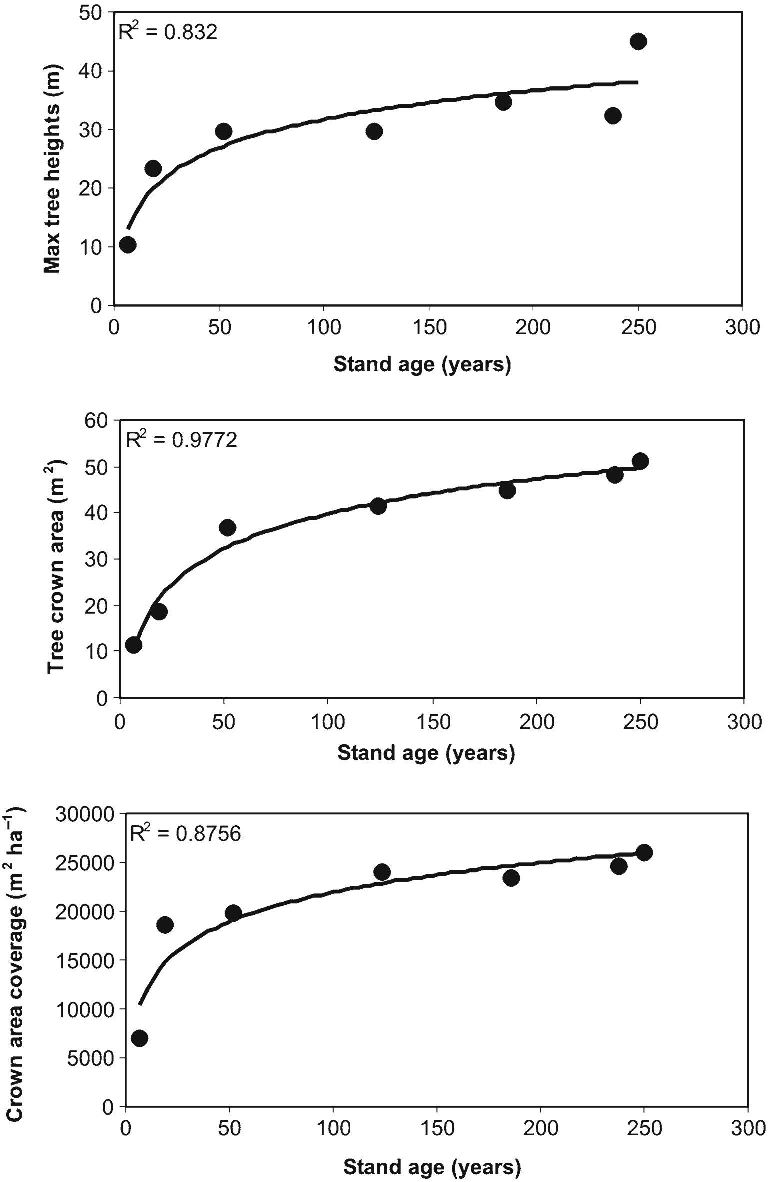

Fig. 4.6 Mean stand age of seven 1-ha forest plots plotted against mean tree heights of upper-canopy trees (**a**), mean crown area of upper-canopy trees (**b**), and mean crown area coverage of understorey and upper-canopy trees (ha^{-1}) (**c**). Data originate from Wittmann (2001) and Schöngart (2003)

traced back to the stratified canopies, different crown sizes, and lower crown area coverage resulting from the natural mortality of trees with partially extensive crowns. Consequently, the light reflectance patterns of the upper-canopy surfaces of these forests are more diffuse (Fig. 4.7; Wittmann et al. 2002a,b).

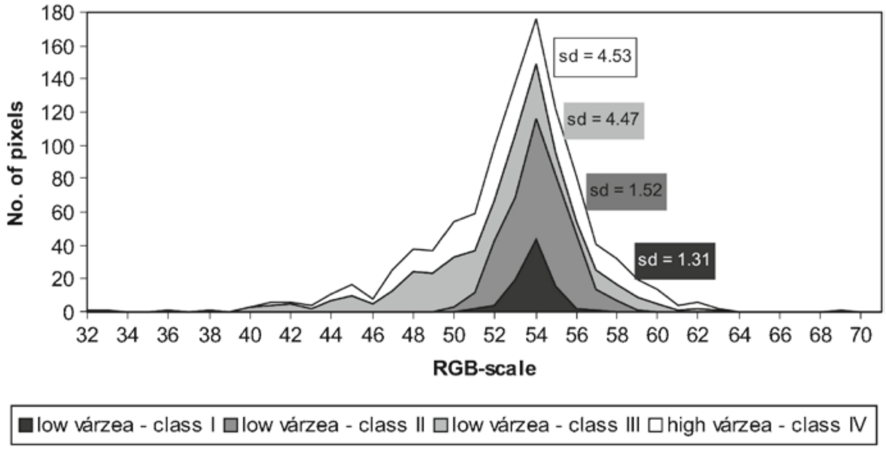

Fig. 4.7 Light reflectance patterns (RGB scale) of different várzea forest types scanned by LANDSAT TM image data. Low-várzea class I = early successional stage, low-várzea class II = early secondary stage, low-várzea class III = late-successional stage, high-várzea class IV = climax stage (Data modified from Wittmann et al. 2002b)

4.2.1.5 Population Structure and Regeneration Behaviour

The successional sequence is accompanied by different strategies regarding the dispersal, establishment, and growth of tree species. Wittmann (2001) investigated the spatial distribution of várzea species and associations along gradients of flooding, substrate texture, and incoming solar radiation on the forest floor. The author concluded that tree regeneration (<10 cm dbh) of many species show greater amplitudes of spatial distribution along these gradients than the mature tree population (≥10 cm dbh). The 96 mature individuals of *Pseudobombax munguba*, part of an inventory totaling 5 ha, for example, concentrated on an elevation with a mean inundation height of 4.63 ± 0.6 m, whereas the 158 individuals of tree regeneration in 40 aleatoric plots totaling 3,125 m^2 and located at the same sites concentrated on elevations where the mean inundation was 5.43 ± 1.8 m. This variation in species distribution patterns suggests that the mortality of already established seedlings or saplings of *P. munguba* is high, and that individuals are no longer competitive when establishing outside the optimal range of environmental conditions. In fact, the majority of the várzea's tree species are restricted to very small ecological amplitudes and habitats. Moreover, succession implies that for most várzea species the optimal range of conditions are present only during a restricted period within the successional sere. In early-successional stages, many of the trees do not successfully compete when regenerating at the same site as the parent trees.

Wittmann and Junk (2003) and Oliveira Wittmann et al. (2007b) investigated the structure and species composition of tree saplings (1–10 cm dbh) and tree seedlings (≤1 cm diameter; ≤1 m height) compared to the mature tree population (≥10 cm dbh)

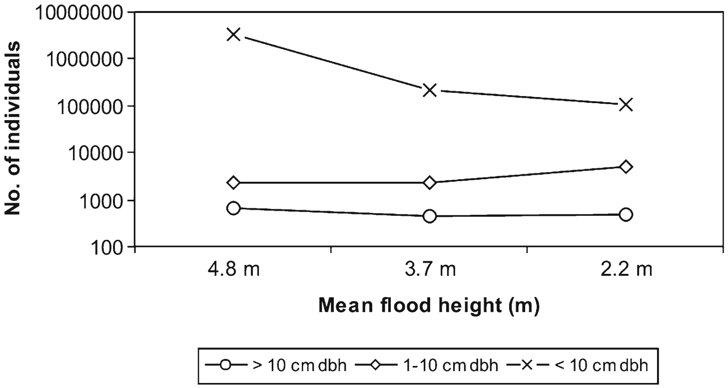

Fig. 4.8 Individual densities of várzea trees ≥10 cm dbh and tree regeneration (saplings = 1–10 cm dbh; seedlings = <1 cm dbh and <1 m height) in three várzea successional stages at different flood heights

in three várzea-forest types of different ages and inundation heights. The density of mature trees declined from 641 individuals ha^{-1} in a secondary forest (40 years, 4.8 m) to 434 individuals ha^{-1} in a late-successional forest (180 years, 3.7 m), and increased slightly, to 469 individuals ha^{-1}, in a high-várzea forest (>200 years, 2.2 m). By contrast, the density of saplings increased from 2,256 to 2,336 and 5,056 individuals ha^{-1}, respectively. The seedling density decreased from more than 3,000,000 individuals ha^{-1} in the secondary forest to about 210,000 individuals ha^{-1} in the late-successional plot and to about 110,000 individuals ha^{-1} in the high-várzea forest (Fig. 4.8). The majority of tree species in the secondary forest were represented by individuals at all community levels, i.e., the seedling, the saplings, and the mature tree community. This indicated that regeneration in these overall-dispersing species occurs frequently, despite the high impact of flooding. However, mortality rates in these species are high: the ratio seedlings-saplings-mature trees in this early stage of succession was 100–0.07–0.02. Thus, seedling mortality rates of at least 99.98% can be expected (in fact, they must be higher because both of the inventories mentioned above took place during a few weeks of the terrestrial phase, but many more seedlings may establish and die during a single vegetation period). The proceeding forest succession and decreasing impact of flooding lead to an increased number of tree species with low but more efficient reproduction strategies. Seedling densities in late-successional forests are low, but so are mortality rates. The ratio seedlings-saplings-mature trees were 100–1.1–0.2 in the late-successional low-várzea forest and 100–4.6–0.4 in the high-várzea forest (Oliveira Wittmann et al. 2007b).

The population structure of most of the várzea trees is a reverse-J-shaped curve (Fig. 4.9), which is characteristic for natural forests and well-known to be typical for many tropical forest types (Budowski 1965; Bazzaz and Pickett 1980; Denslow 1980; Whitmore 1989; Hubbell and Foster 1992). While most early-secondary

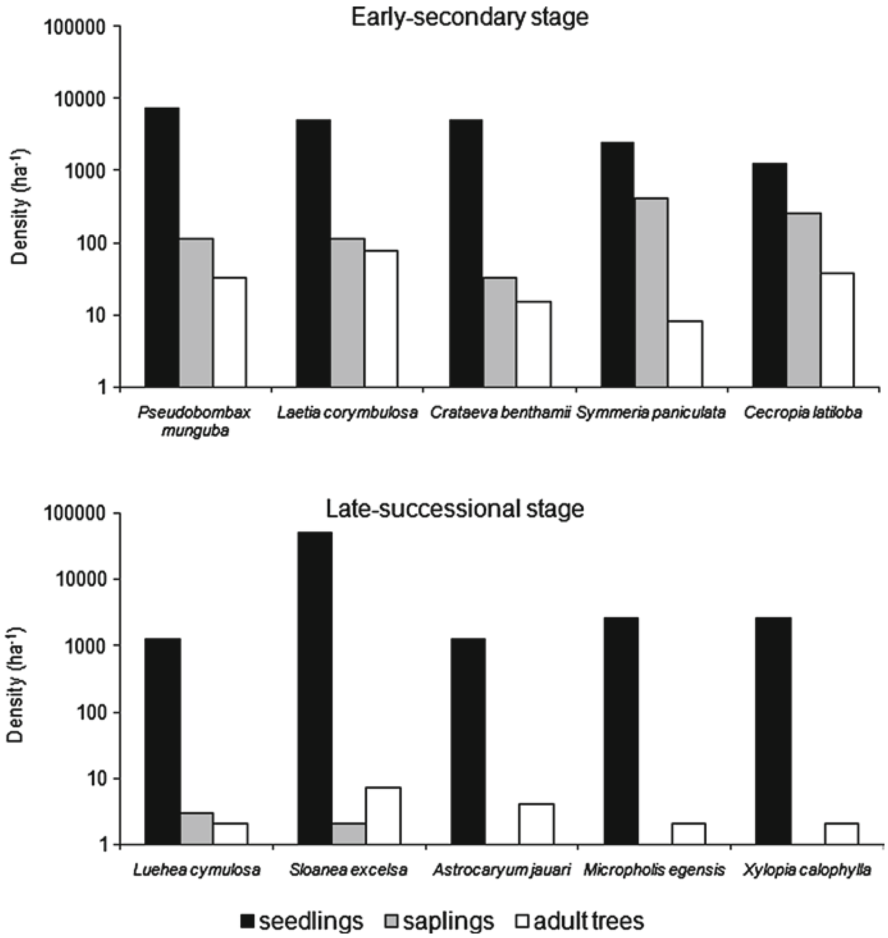

Fig. 4.9 Population structure of several várzea tree species in an early-secondary (**a**) and a late-successional (**b**) stage. Seedlings = <1 cm dbh and <1 m height; saplings = 1–10 cm dbh; mature trees = ≥10 cm dbh

species are represented in all community levels, seedling, sapling, and the mature tree community, most late-secondary and late-successional species lack individuals at the sapling level (Fig. 4.9). This indicates that many individuals of these species are eliminated after establishment and therefore may need exceptional environmental conditions to establish successfully, such as consecutive years with low inundations in less flood-tolerant species, or the creation of a gap by tree fall in light-demanding species or *opportunists* (*sensu* Bazzaz 1991).

Tree regeneration in várzea forests thus primarily depends on the flood pulse, but it is also linked to incoming solar radiation on the forest floor (Wittmann and Junk 2003). Early-successional tree regeneration is composed of light-requiring

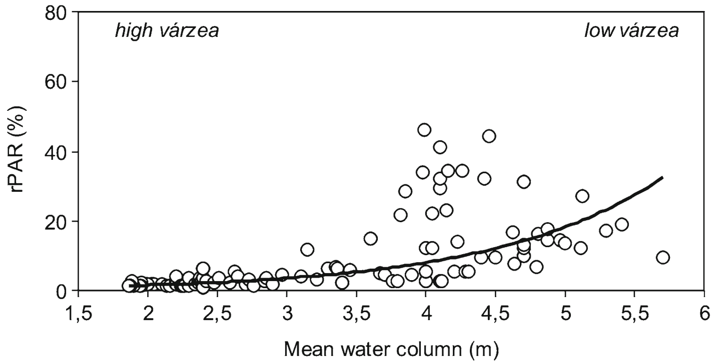

Fig. 4.10 Mean spatial distribution center (MDC, Ebdon 1998) of sapling species (1–10 cm dbh) along flooding and irradiation gradients on the forest floor in a várzea inventory of 24 plots totaling 1,875 m^2 (Wittmann and Junk 2003)

species, whereas the number of ecological niches with respect to radiation variability is low. Together with the decreasing impact of flooding, the more complex forest architecture in late-successional forests implies a high number of ecological niches at the seedling and sapling levels. Species richness and the density of saplings increase, resulting in shade-tolerant species groups that establish under closed forest canopies, and in light-tolerant species groups that establish near the forest borders and in gaps (Fig. 4.10). In the high várzea, the height and duration of flooding are reduced to the extent that regeneration during most of the year is terrestrial, and thus similar to that of non-flooded environments. However, the flood pulse in high-várzea forests probably remains a limiting factor influencing species composition with respect to tree regeneration. Kubitzki (1989a) stated that the origin of many várzea trees is the surrounding terra firme. When those trees immigrated to the floodplains, they gradually developed adaptations to the periodic inundations. For this reason, many high-várzea species have probably developed less pronounced adaptations to flooding than low-várzea species (Wittmann et al. 2002b) and may react very sensitively even to small flood-pulse variations.

4.2.2 Tree Species Composition and Diversity Gradients

Compared with the surrounding terra firme and despite the fact that fewer inventories and smaller databases are available, Amazonian floodplain forests are taxonomically relatively well-described. Of about 1,000 flood-tolerant tree species occurring in the white-water floodplains across the Amazon basin (Wittmann et al. 2006), 450 were already described during the first half of the nineteenth century by only eight botanists (with decreasing numbers of species descriptions: Bentham, Martius, Aublét, De Candolle, Spruce, Poeppig, Linné, and Willdenow). This emphasizes the easy accessibility of floodplain forests by these researchers; but it also demonstrates that

Amazonian várzea forests are a special ecosystem with a restricted number of tree species that are partially widely distributed.

4.2.2.1 Floristic Patterns at the Family Level

Representatives of nearly all plant families characterizing the neotropical flora of woody plants can be found within the floodplain forests – to some extent with the same relative importance as in the terra firme (Maas and Vestra 1993). Based on data from large-scale floristic inventories in terra firme forests, i.e., those described by Gentry (1992), Terborgh and Andresen (1998), Ter Steege et al. (2000, 2006), and Pitman et al. (2001), the most important tree families in neotropical terra firme forests are (with decreasing importance): Fabaceae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae, and Palmae. In a review of 44 floristic inventories (62.34 ha) of várzea forests scattered over the Amazon basin, Wittmann et al. (2006a) stated that the Fabaceae were the most important várzea tree family, followed by the Malvaceae (including former Bombacaceae, Sterculiaceae, and Tiliaceae), Euphorbiaceae, Moraceae, Palmae, and Salicaceae (including former Flacourtiaceae) (Table 4.1; the classification is the angiosperm phylogeny group, APG II 2003). The family importance, however, depends strongly on the location of the forest along the flood-level gradient, the successional stage, and the geographic location of the inventories.

Independent of vertical or geographic gradients the 18 most important tree families account for about 80–90% of all várzea tree species; however, the distribution of várzea tree families differs considerably between low-várzea and high-várzea forests. Specifically, the Fabaceae, Malvaceae, Salicaceae, Urticaceae, and Brassicaceae are more important in low-várzea forests, whereas Euphorbiaceae, Moraceae, Palmae, Annonaceae, Meliaceae, and Myristicaceae are more important in high-várzea forests (Table 4.1). Along the longitudinal gradient, Sapotaceae, Rubiaceae, Polygonaceae, and Clusiaceae are of increasing importance from eastern Amazonia to western Amazonia, whereas Malvaceae and Salicaceae show an opposite trend. Fabaceae, Euphorbiaceae, Urticaceae, Brassicaceae, Lauraceae, and Verbenaceae are more important in central Amazonia than in eastern and western várzea forests. Finally, there are also variations in family importance along the latitudinal gradient: Fabaceae, Euphorbiaceae, Urticaceae, and Lecythidaceae are more important in equatorial western Amazonia, whereas Malvaceae, Moraceae, Palmae, and Meliaceae are more important in the southern part of western Amazonia (Table 4.1).

4.2.2.2 Floristic Patterns at the Species Level

With more than 1,000 recorded tree species, Amazonian várzea forests are the most species-rich floodplain forests worldwide and thus reflect the high diversity patterns generally characterizing the neotropical flora (Wittmann et al. 2006a). Species richness

Table 4.1 Family distribution of the 18 most important várzea tree families along vertical and geographic gradients. Numbers represent percentages of total importance values (TIV, Curtis and McIntosh 1951)

	Family	Vertical distribution		Longitudinal distribution			Latitudinal distribution in WA	
		LV	HV	EA	CA	WA	WAe	WAs
1	Fabaceae	12.46	8.45	7.62	12.23	8.79	10.05	6.9
2	Malvaceae	12.45	8.34	30.54	14.09	6.88	4.5	10.45
3	Euphorbiaceae	7.35	8.47	4.37	8.41	7.34	8.49	5.63
4	Moraceae	5.67	11.42	5.74	5.51	11.8	9.44	15.34
5	Arecaceae	5.09	12.33	5.58	0.71	11.42	9.36	14.5
6	Salicaceae	6.73	1.99	11.94	6.62	4.14	3.51	5.02
7	Urticaceae	5.23	2.53	4.63	5.69	3.21	4.68	1.02
8	Annonaceae	3.79	5.49	1.4	3.98	4.23	4.74	3.47
9	Brassicaceae	5.06	0.17	3.98	6.21	0.13	0.14	0.12
11	Lauraceae	3.92	1.24	2.18	4.72	1.16	1.62	0.47
12	Lecythidaceae	3.13	1.95	2.91	2.28	3.46	5.42	0.54
13	Verbenaceae	3.70	0.25	2.3	4.53	0.21	–	0.52
14	Meliaceae	1.41	5.09	1.02	0.52	4.99	3.65	6.99
15	Myristicaceae	0.9	4.76	1.75	1.08	3.8	4.64	2.53
16	Rubiaceae	1.7	2.28	1.16	1.78	2.36	2.93	1.52
17	Polygonaceae	2.48	2.19	2.06	2.44	2.77	2.77	1.77
18	Clusiaceae	1.89	1.28	1.11	1.15	2.28	1.25	3.82
Total		86.3	82.22	91.91	85.01	82.66	80.4	85.03
No. of families		63	64	35	48	64	56	44

LV, low várzea; HV, high várzea; EA, eastern Amazonia; CA, central Amazonia; WA, western Amazonia; WAe, equatorial western Amazonia; WAs, southern part of western Amazonia in the Amazonian várzea is at least 20 times higher than in the floodplains of the European temperate zone (Schnitzler et al. 2005) and about ten times higher than in the subtropical bottomland forests of North America (Johnson and Little 1967; Clark and Benforado 1981; Schnitzler et al. 2005). Compared with tropical floodplains, species richness in the Amazonian várzea is about ten times higher than in the forests of Cambodia (Tonle Sap; Campbell et al. 2006) and about three times higher than in the Brazilian Pantanal (Junk et al. 2006). One reason for the comparatively high tree species richness in várzea forests is the coexistence of species well-adapted to flooding and generalist species that also occur in the uplands.

At the species levels, the floristic similarity (SI, Sørensen's 1948 index) between várzea and adjacent terra firme forests amounts to about 30% for trees ≥10 cm dbh in all parts of the Amazon basin (see Terborgh and Andresen (1998) for the western part of the basin, Gama et al. (2005b) for the eastern part of the basin, and Wittmann et al. (2006a) for the central part of the basin) and to approximately 34% for trees ≥5 cm dbh (F. Wittmann, 2006, unpublished data; from terra firme originate from Oliveira and Mori 1999; Ribeiro et al. 1999; Pitman et al. 2001 and Gama et al. 2005b), because the latter comparison includes the mostly small trees and shrubs of families such as Melastomataceae, Theophrastaceae, and Burseraceae.

At the basin-wide scale (918 tree species in 62.34 ha), the 30 most important low-várzea species account for 42.3% of the overall importance (OI = sum of the importance value index (IVI; Curtis and McIntosh 1951) and the relative frequency [rF] in 44 inventories scattered over the Amazon basin [Wittmann et al. 2006a]), whereas the 30 most important high-várzea species account for only 24.9% of the OI (Table 4.2). Floristic similarity between low-várzea forests and high-várzea forests is 35% in eastern Amazonian várzea (data from Cattanio et al. 2002), but only 17.5% in central Amazonian várzea (Wittmann 2001; Wittmann et al. 2002b). For the western part of the basin, no data allowing for a comparison between low várzea and high várzea are available.

Low-várzea forests exhibit high floristic similarities, even when separated by large geographic distances. SI between adjacent low-várzea forest inventories may be as high as 70% (Wittmann et al. 2006a). With increasing distance between sites, floristic similarity decreases. Nevertheless, the SI between low-várzea forests >1,000 km apart still averages about 20% and exceeds 40% in several cases (Fig. 4.11), whereas comparative studies indicate that it averages less than 10% between low-várzea forests and the adjacent terra firme (Wittmann et al. 2002b, 2006; Fig. 4.12).

SI between adjacent high-várzea forests is about 30%, but decreases linearly to less than 10% in plots >1,000 km apart (Wittmann et al. 2006a; Fig. 4.13). We have estimated that species similarity of high-várzea forests and adjacent terra firme forests is between 25% and 32% (Fig. 4.12). Terborgh and Andresen (1998) previously concluded that geographic position is an important driver of floristic dissimilarity in both terra firme and alluvial floodplain forests. The authors found that within a region mean similarity between terra firme and flooded forests is larger than within forests of terra firme and floodplain respectively of two different regions. Thus, tree communities of inundated forests tend to more closely resemble those of terra firme forests within the same geographical region than those of inundation forests in

Table 4.2 Overall importances of the 30 most-important species in (a) low várzea and (b) high várzea. rIVI = relative importance value index (Curtis and McIntosh 1951), rF = relative frequency (a: n = 34 plots; b: n = 18 plots), OIV = overall importance value (= IVI + rF in 44 inventories scattered over the Amazon basin (Wittmann et al. 2006a)

	Family	Species	rIVI	rF	OIV
(a)					
1	Malvaceae	*Pseudobombax munguba* (Mart. & Zucc.) Dugand	8.48	1.47	9.95
2	Salicaceae	*Laetia corymbulosa* Spruce ex Benth.	5.33	1.18	6.51
3	Brassicaceae	*Crataeva benthamii* Eichler	5.13	0.97	6.10
4	Urticaceae	*Cecropia latiloba* Miq.	4.51	1.19	5.70
5	Fabaceae	*Pterocarpus amazonum* (Mart. ex Benth.) Amshoff	3.23	1.26	4.49
6	Verbenaceae	*Vitex cymosa* Bert. ex Spreng.	3.76	0.56	4.32
7	Lauraceae	*Nectandra amazonum* Nees	3.11	1.05	4.16
8	Euphorbiaceae	*Piranhea trifoliata* Baill.	2.73	0.98	3.71
9	Malvaceae	*Luehea cymulosa* Spruce ex Benth.	2.90	0.70	3.60
10	Arecaceae	*Euterpe oleracea* Mart.	2.67	0.56	3.23
11	Moraceae	*Ficus trigona* L.f.	2.40	0.42	2.82
12	Polygonaceae	*Triplaris surinamensis* Cham.	1.46	0.70	2.16
13	Bignoniaceae	*Tabebuia barbata* (E. Mey.) Sandwith	1.16	0.98	2.14
14	Fabaceae	*Macrolobium acaciifolium* (Benth.) Benth.	1.16	0.91	2.07
15	Aquifoliaceae	*Ilex inundata* Poepp. ex Reissek	1.67	0.29	1.96
16	Lecythidaceae	*Eschweilera albiflora* (DC.) Miers	1.37	0.56	1.93
17	Fabaceae	*Vatairea guianensis* Aubl.	1.13	0.77	1.90
18	Moraceae	*Maclura tinctoria* (L.) D. Don ex Steud.	1.20	0.63	1.83
19	Arecaceae	*Astrocaryum chonta* Mart.	1.18	0.42	1.60
20	Euphorbiaceae	*Mabea nitida* Spruce ex Benth.	0.96	0.56	1.52
21	Sapotaceae	*Pouteria elegans* (DC.) Baehni	1.02	0.42	1.44
22	Euphorbiaceae	*Hevea spruceana* (Benth.) Müll.Arg.	0.98	0.42	1.40
23	Rubiaceae	*Duroia duckei* Huber	0.83	0.56	1.39
24	Bignoniaceae	*Crescentia amazonica* Ducke	0.96	0.42	1.38

	Family	Species	rIVI	rF	OIV
25	Lecythidaceae	*Eschweilera parvifolia* Mart. ex DC.	0.90	0.42	1.32
26	Lecythidaceae	*Gustavia augusta* L.	0.40	0.91	1.31
27	Myrtaceae	*Calyptranthes crebra* Mc Vaugh	0.85	0.35	1.20
28	Clusiaceae	*Calophyllum brasiliense* Cambess	0.63	0.56	1.19
29	Salicaceae	*Casearia aculeata* Jacq.	0.61	0.56	1.17
30	Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	0.48	0.63	1.11
Σ			63.20	21.41	84.61
Σ 31–617			36.80	78.59	115.39
Total			100	100	200
(b)					
1	Moraceae	*Brosimum lactescens* (S. Moore) C.C. Berg	2.56	0.80	3.36
2	Malvaceae	*Theobroma cacao* L.	1.83	0.65	2.48
3	Euphorbiaceae	*Hura crepitans* L.	1.65	0.58	2.23
4	Meliaceae	*Trichilia septentrionalis* C. DC.	1.82	0.29	2.11
5	Anacardiaceae	*Spondias lutea* L.	1.59	0.51	2.10
6	Moraceae	*Maquira coriacea* (H. Karst.) C.C. Berg	1.53	0.51	2.04
7	Arecaceae	*Astrocaryum chonta* Mart.	1.64	0.36	2.00
8	Boraginaceae	*Cordia nodosa* Lam.	1.20	0.73	1.93
9	Arecaceae	*Iriartea deltoidea* Ruiz & Pav.	1.46	0.44	1.90
10	Euphorbiaceae	*Drypetes amazonica* Steyerm.	1.49	0.36	1.85
11	Arecaceae	*Euterpe oleracea* Mart.	1.04	0.65	1.69
12	Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	1.49	0.15	1.64
13	Malvaceae	*Ceiba samauma* (Mart.) K. Schum.	1.24	0.36	1.60
14	Dichapetalaceae	*Tapura acreana* (Ule) Rizzini	1.36	0.22	1.58
15	Myristicaceae	*Otoba parvifolia* (Markgr.) A.H. Gentry	1.40	0.15	1.55
16	Meliaceae	*Guarea macrophylla* Vahl	1.07	0.44	1.51

(continued)

Table 4.2 (continued)

	Family	Species	rIVI	rF	OIV
17	Rubiaceae	*Calycophyllum spruceanum* (Benth.) Hook.	1.06	0.44	1.50
18	Arecaceae	*Attalea phalerata* Mart. ex Spreng.	1.23	0.22	1.45
19	Moraceae	*Ficus maxima* Mill.	1.00	0.44	1.44
20	Euphorbiaceae	*Sapium marmieri* Huber	0.79	0.65	1.44
21	Arecaceae	*Astrocaryum jauari* Mart.	0.98	0.44	1.42
22	Annonaceae	*Unonopsis floribunda* Diels	0.73	0.58	1.31
23	Arecaceae	*Scheelea brachyclada* Burret	1.23	0.07	1.30
24	Polygonaceae	*Coccoloba densifrons* C. Mart. ex Meisn.	0.79	0.51	1.30
25	Malvaceae	*Ceiba pentandra* (L.) Gaertn.	0.81	0.44	1.25
26	Myristicaceae	*Virola calophylla* (Spruce) Warb.	0.72	0.51	1.22
27	Violaceae	*Leonia glycycarpa* Ruiz & Pav.	0.64	0.58	1.22
28	Myristicaceae	*Virola cuspidata* (Spruce ex Benth.) Warb.	0.60	0.58	1.18
29	Myristicaceae	*Virola surinamensis* (Rol. ex Rottb.) Warb.	0.81	0.36	1.17
30	Moraceae	*Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr.	0.73	0.44	1.17
Σ			36.49	13.46	49.94
Σ 31–686			63.51	86.54	150.06
Total			100	100	200

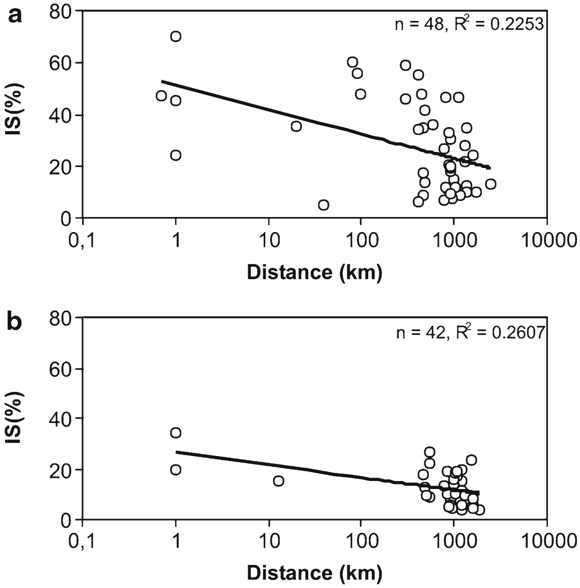

Fig. 4.11 Floristic similarity (IS = Sørensen's 1948 Index) between low-várzea forests (**a**) and high-várzea forests (**b**) over geographic distance (trees ≥10 cm dbh in floristic inventories totaling 62.34 ha (Wittmann et al. 2006a)

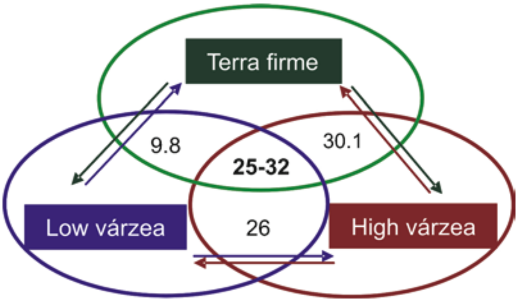

Fig. 4.12 Basin-wide floristic similarity (IS = Sørensen's 1948 Index) between low-várzea forests, high-várzea forests, and terra firme forests. Data from várzea originate from Wittmann et al. (2006a); data from terra firme originate from Ribeiro et al. (1999), Oliveira and Mori (1999), Oliveira and Nelson (2001), Pitman et al. (2001) and Duque et al. (2002)

adjacent regions. This holds true for the high várzea, where intense lateral species exchange between the high várzea and the terra firme is likely to occur (Wittmann and Junk 2003). Tree species of the terra firme migrate to the nutrient-rich floodplains and may establish in the high várzea, where inundations are short. The establishment of terra firme species in low-várzea forests, by contrast, requires long-term development of physiological or morphological adaptations to the periodic flooding events.

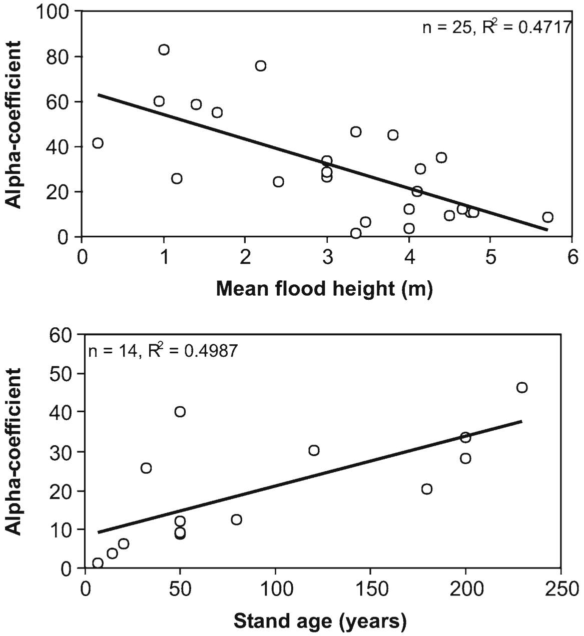

Fig. 4.13 Fisher's alpha-diversity coefficient (Fisher et al. 1943) plotted against mean flood height (**a**) and mean stand age (**b**) of várzea forest plots (Wittmann et al. 2006a)

The SI between várzea forests in eastern Amazonia and those in the western regions is approximately 20%. It increases to about 32% between central Amazonia and equatorial western Amazonia, about 31% between central Amazonia and the southern part of western Amazonia, and reaches the highest percentage between equatorial western Amazonia and the southern part of western Amazonia (about 36%, Wittmann et al. 2006a). The 30 overall most important tree species (OI = low-várzea + high-várzea forests) account for 30.4% and 46.0% of all species recorded in eastern Amazonia and central Amazonia, respectively, but only for 13.5% in equatorial western Amazonia and 20% in the southern part of western Amazonia (Wittmann et al. 2006a). This indicates that the floristic composition in the western Amazonian várzea is distinctly different from that in the eastern regions.

Tree species richness and alpha-diversity (Fisher et al. 1943) of várzea forests are significantly correlated with flood height and length as well as with the age of the forest stand (Fig. 4.13). The maximum species richness (≥10 cm dbh) recorded in high-várzea forests of eastern Amazonia is 84 species ha^{-1} (Cattanio et al. 2002), with 142 species ha^{-1} in central Amazonia (Wittmann et al. 2002b), and 157 species ha^{-1} in the southern part of western Amazonia (Dallmeier et al. 1996). These values show that maximum species richness in várzea forests is 60–70% of that of adjacent upland forests (117–120 species ha^{-1} in eastern Amazonia, 179–285 species ha^{-1} in central Amazonia, and up to 300 species ha^{-1} in western Amazonia (Gentry 1987; Valencia et al. 1994; data summarized from Oliveira and Nelson 2001; see also Ter Steege et al. 2003; Fig. 4.14).

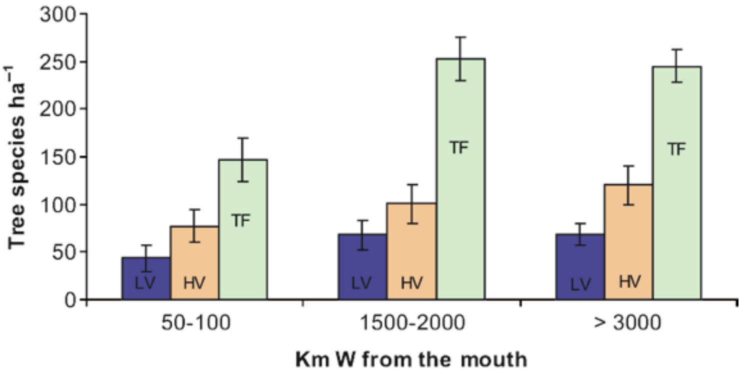

Fig. 4.14 Mean species richness in low-várzea forests (LV), high-várzea forests (HV), and terra firme forests (TF) as a function of the distance from the inventories to the mouth of the Amazon River. Data from várzea originate from Wittmann et al. (2006a), data from terra firme forests originate from Gentry (1987), Valencia et al. (1994), Ribeiro et al. (1999), Oliveira and Mori (1999), Oliveira and Nelson (2001), Pitman et al. (2001), and Ter Steege et al. (2003)

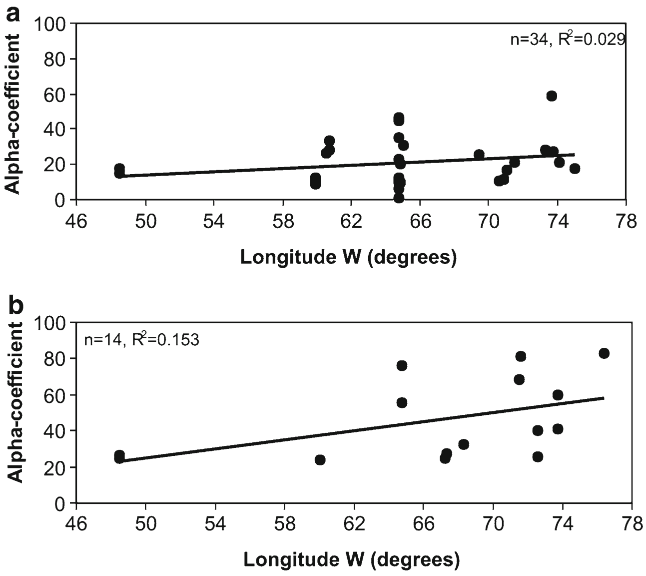

Fig. 4.15 Fisher's alpha-diversity coefficient (Fisher et al. 1943) plotted against the longitudinal location of the plots in low várzea (**a**) and high várzea (**b**) (Wittmann et al. 2006a)

Alpha-diversity and the longitudinal location of the forests are significantly correlated, indicating a trend of increasing diversity from east to west (Wittmann et al. 2006a). This trend is moderately pronounced in high-várzea forests but weak in low-várzea forests (Fig. 4.15). Within western Amazonian várzea forests, alpha-diversity decreases from equatorial western Amazonia to the southern part of western Amazonia. Again, this trend is more pronounced within high-várzea forests (n = 10 floristic inventories, $R^2 = 0.4898$, $P < 0.001$) than in low-várzea forests (n = 4 floristic inventories, $R^2 = 0.0223$, $P < 0.05$).

A trend of increasing alpha-diversity from east to west was also documented for equatorial Amazonian terra firme, where it seems to be linked to tree density and rainfall seasonality (e.g., Condit et al. 2000, 2002; Pitman et al. 2002; Ter Steege et al. 2003). Nonetheless, a recent study instead indicated that the nutrient status of the soil is the most important factor influencing diversity gradients from eastern to western terra firme (Ter Steege et al. 2006). Within várzea forests, increasing diversity from east to west is especially pronounced within the high várzea. We have argued that, in addition to the intense lateral species exchange between high várzea and terra firme, the high alpha-diversity in western Amazonian várzea is the result of the high nutrient status originating from poorly weathered alluvial substrates compared with that further east. The strong floristic resemblance between high várzea and terra firme is especially pronounced in western Amazonia, because of the more accentuated topography compared to the relief of floodplains further east. Inundations in western Amazonia are higher but shorter than those in central and eastern Amazonia (Terborgh and Andresen 1998). Therefore, trees without specific adaptations to flooding might establish more readily in western Amazonian várzea.

4.2.2.3 Species Oligarchies, Endemism and the Tree Species Colonization Concept

The periodic flood pulse associated with the hydrogeomorphologic dynamism of várzea floodplains implies that the ecological factors important for the establishment and distribution of tree species in várzea forests are relatively constant over thousands of kilometers along the river courses. Describing the abundance patterns of tree species at different scales in Peru and Ecuador, Pitman et al. (2001) stated that the majority of the most abundant tree species found in floristic inventories in Amazonian terra firme belong to a small set of ubiquitous, common tree species that combine high frequency with local abundance, thus forming predictable oligarchies that dominate over vast areas (several thousand square kilometers) of forest at each site. The authors further argued that these species distribution patterns are more indicative of regulation of relative abundances by ecological factors than by non-equilibrium chance-based dynamics (*sensu* Hubbell and Foster 1986; Hubbell 1995) or by the patchiness and unpredictability of tropical forest landscapes, as described by Denslow (1987), Gentry (1988), and Clark et al. (1995, 1998).

We have proposed that species oligarchies in várzea forests are even more evident than in the terra firme, where edaphic changes at different spatial scales may influence species distribution patterns (e.g., Tuomisto et al. 1995; Terborgh and Andresen 1998). Despite the small-scale heterogeneity of the alluvial landscape, the high connectivity of riparian corridors leads to similar, vertically arranged ecological niches across remote várzea forests and, consequently, to a restricted number of highly dominant tree species across the Amazon basin (Wittmann et al. 2006a). Godoy et al. (1999)

noted that the Amazon and Orinoco basins show marked similarities in habitats and tree species, which the authors interpreted as being the result of the high connectivity between the riparian corridors of the two basins and the effective operation of dispersal mechanisms. Long-distance dispersal by currents and fish is common for many low-várzea trees (Gottsberger 1978; Goulding 1983; Pires and Prance 1985; Ziburski 1991; Kubitzki and Ziburski 1994; Lopez 2001; Moegenburg 2002; Mannheimer et al. 2003; Scarano et al. 2003; Oliveira Wittmann et al. 2007a) and thus contributes to randomly distributed tree species that dominate several thousands of square kilometers in Amazonian várzea.

Kubitzki (1989) stated that many floodplain tree species are ecotypes originating from the surrounding terra firme. When the species immigrated to the floodplains, they gradually developed adaptations to the periodic inundations. The colonization of episodically flooded margins of small rivers (igarapés) in the terra firme, or general high precipitation with persistent soil saturation might be an important prerequisite in the provision of a transitional habitat for terra firme species migrating to the floodplains. Once they tolerate and/or create specific adaptations to episodic inundations, these species are able to colonize the higher parts of the floodplains, where inundations are low, sometimes occasional, and do not exceed about 50 days year^{-1}. Wittmann and Junk (2003) stated that the number of immigrant species from the adjacent terra firme is highest within the low-flooded high várzea. Some of these species developed to species able to colonize the lower parts of the floodplains, where periodic waterlogging of roots, parts of the above-ground organs, or the entire plant is unavoidable. With an increasing water column and inundation period, natural selection led to only a few species, i.e., those able to tolerate the extreme inundations near the forest border. At this stage, we have argued, species colonization is driven by the selection pressure provided by flooding and the associated hydrogeomorphologic factors. Effective competitive mechanisms lead to a stage in which an ecotype reaches a ‘point of no return’, which means that it has developed adaptations to the periodic inundations that no longer allow successful competition in non-flooded environments. Following our tree species colonization concept (Fig. 4.16), the ecotype thus became endemic to the floodplains.

Despite the fact that distribution maps of most Amazonian tree species are incomplete due to the patchiness of botanical collecting and the scarcity of forest inventories in combination with the huge geographic area, some authors have concluded that Amazonian floodplain forests are characterized by a high degree of endemic tree species (Prance 1979; Kubitzki 1989; Junk 1989). Endemism can be defined as ‘the restriction of a genotype to a defined geographic region, without taking into consideration its size’ (Ricklefs 1990; Schroeder 1998). Haeupler (1983) suggested the term ‘micro-scale endemism’ for species with a restricted occurrence in very small areas, such as islands or inselbergs. For tropical forests, Gentry (1986) proposed the term ‘local endemism’ to describe genotypes restricted to areas <75,000 km^2.

We investigated the occurrence and distribution of the 186 most common tree species of central Amazonian várzea, using the species samples available in the literature (62.34 ha scattered over the Amazon basin, Wittmann et al. 2006a), herbaria (Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Brazil;

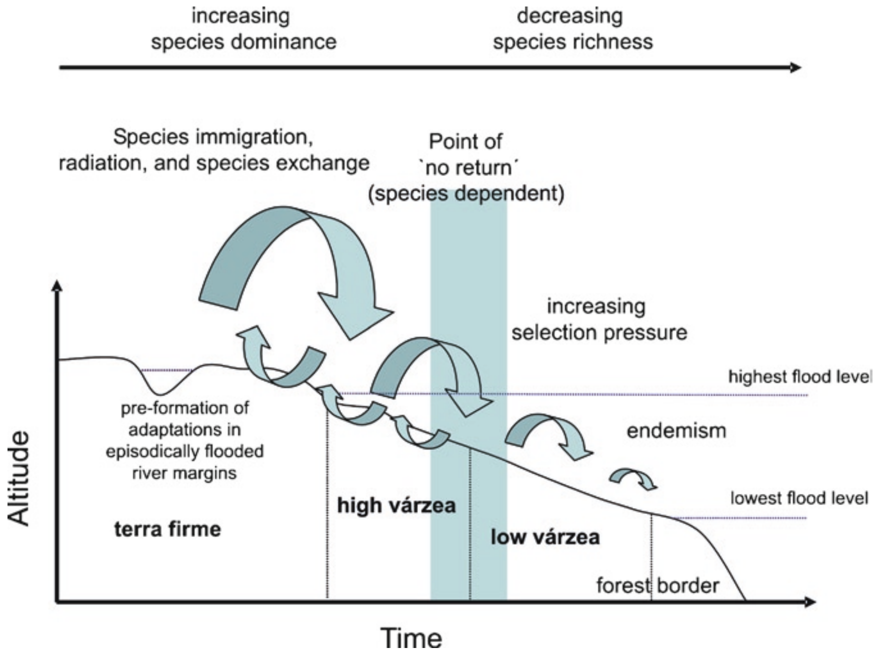

Fig. 4.16 Species colonization concept in várzea floodplains

Missouri Botanical Garden (MBG), USA; New York Botanical Garden (NYBG), USA; Royal Botanical Gardens, Kew, Great Britain), and the Internet (including specimens available in digital herbaria databases such as the *Flora Brasiliensis* (Martius 1840–1906), the National Herbarium of Utrecht, the Netherlands, the International Legume database (Ildis), etc.). The results indicated that 74 (39.78%) of the 186 most common central Amazonian várzea tree species can be classified as endemics following the definition of Ricklefs (1990). Of these endemic tree species, the occurrence of 50 (67.56%) of them was restricted to the low várzea, while 11 (14.86%) were present in both low-várzea and high-várzea forests, and only 13 (17.57%) were restricted to high-várzea forests (Table 4.3).

The results of our investigation further indicated that 112 (60.21%) of the most frequent central Amazonian várzea tree species are generalist species that also occur in other neotropical ecosystems. Prance (1979) and Worbes (1997) stated that some of these generalist tree species (e.g., *Pseudobombax munguba*, *Leonia glycycarpa* Ruiz & Pav., and *Duroia duckei*) are widely distributed throughout the neotropics and occur particularly in semi-deciduous forests and savannas. Our investigation, however, showed that, of the 186 most common tree species of the central Amazonian várzea, only 12 (6.45%; mostly Malvaceae and Fabaceae) occur in ecosystems with climatic- and/or edaphic-induced aridity, such as the Cerrado, the Caatinga, or the Pacific (western) slope of the Andes. Twenty-seven (12.90%) várzea species also occur in southeastern Brazilian Atlantic rainforests. The majority of Amazonian várzea tree species are found in adjacent moist terra firme forests

Table 4.3 Number of endemic species (*sensu* Ricklefs 1990) and generalist species within the 186 most common várzea tree species of the Amazon basin. (*sensu* Wittmann et al. 2006a; see text for explanation and data source)

	Number of species	(%)
Investigated várzea tree species	186	100.00
Endemic to Amazonian várzea	74	39.78
Endemic to Amazonian low várzea	50	26.88
Endemic to Amazonian high várzea	13	6.99
Occurrence in other neotropical ecosystems	112	60.22
Occurrence in moist terra firme	100	53.76
Occurrence in moist terra firme and igapó	36	19.35
Occurrence in Amazonian igapó	21	11.29
Occurrence in Central America and the Caribbean	59	31.72
Ocurrence in savanna (Cerrado, Caatinga, Llanos, Chaco)	12	6.45
Occurrence in Atlantic rainforest	27	14.52
Occurrence in the Paleotropis	6	3.23

(100 tree species, 53.76%). Only 21 (18.75%) are restricted to várzea and igapó, whereas 36 (32.14%) occur in all Amazonian ecosystems, i.e., várzea, igapó, and moist terra firme forests (Table 4.3).

Our data thus indicate that species oligarchies *sensu* Pitman et al. (2001) are common in Amazonian várzea forests. The oligarchies are the feature of two different species groups: (1) generalist species of high-várzea forests that also occur in the surrounding terra firme, and to a lesser extent in other neotropical ecosystems, e.g., the igapó, the Atlantic rainforest, and cerrados and caatingas [many of these species, inlcuding *Ceiba pentandra* (L.) Gaertn. and *Leonia glycycarpa*, are included in Pitman's list of ubiquitous species]; and (2) endemic species (*sensu* Ricklefs 1990) of low-várzea forests, which dominate thousands of square kilometers along the river courses. We estimated that about one-third of these endemic low-várzea tree species (e.g., *Crescentia amazonica* Ducke, *Clitoria amazonum* Mart. ex Benth.) are present in spatially restricted areas along the main tributaries of the Solimões and Amazon Rivers and thus can be classified as local endemics *sensu* Gentry (1986).

A discussion of species oligarchies and endemism in várzea forests must also focus on the floristic evolution of neotropical floodplain and upland forests. Evidence of the occurrence of tropical rainforests in South America dates from at least the early Paleocene (Burnham and Graham 1999; Rull 1999; Johnson and Ellis 2002; Burnham and Johnson 2004). Pollen data from Colombia, Guyana, and Venezuela lend support for warm, equable climates at low altitudes in the early Paleocene (Van der Hammen and Wymstra 1964; Van der Hammen and Garcia 1966; Colmenares and Teran 1993; Jaramillo and Dilcher 2000, 2001), while climatic reconstructions for the Eocene, based on global climate modeling (Frakes et al. 1992; Beerling and Woodward 2001; Ziegler et al. 2003), indicate tropical temperatures encompassing from one-third to two-thirds of the South American continent. Paleobotanically based reconstructions have shown that tropical rainforests in the Eocene extended uninterruptedly from southern Bolivia to New Mexico (Frakes et al. 1992; Burnham and Johnson 2004).

Theoretically, the tropical climate in equatorial Amazonia together with the continuous uplift of the Andes would have already created the physical conditions for the development of várzea forests beginning in at least the early Paleocene. This geological time span certainly was sufficiently long enough to allow for specific adaptations of ecotypes to important ecological factors in floodplain forests and thus to species dominance and oligarchy. With respect to Neogene and Quaternary landscape histories, and despite the impact of climatic changes especially during the last glacial maximum (LGM) and the controversially discussed refugia hypothesis, there is no evidence for forest fragmentation in equatorial Amazonia during the glacial periods (Colinvaux et al. 2000; Van der Hammen and Hooghiemstra 2000; Colinvaux and De Oliveira 2001; Anhuf et al. 2006). Instead, the impact of a drier climate during the LGM affected the equatorial lowland forest on the species level rather than on the community level, i.e., by shifting species sensitive to soil-moisture seasonality to comparatively wet refuges, and by the occurrence of now montane species in the lowlands (Bush et al. 1990; Colinvaux et al. 2000; Oyama and Nobre 2004; Hutyra et al. 2005).

It is, nonetheless, indubitable that climatic changes during the tertiary and quaternary directly affected the sea level and thus the size of floodplain forests by periodic reductions (during the LGM) and enlargements (during the interglacials, formation of the Lago Amazonas) of their areas (Vuilleumier 1971; Van der Hammen 1974; Frailey et al. 1988; Tuomisto et al. 1992; Irion et al. 1995, 1997; Oliveira and Mori 1999). The postulated species shift from dry to moist climatic conditions combined with a spatial reduction of flooded areas, however, affected floodplain species to a lesser extent than upland species, because the flooded ecosystems persisted, at smaller scales, even during glacial maximums. The riparian connectivity and the highly adapted dispersal mechanisms of floodplain trees would have reduced species losses at regional scales (Wittmann 2001), with the floodplains themselves acting as linear refuges for sensitive terra firme species during periods with postulated dryer climatic conditions (Pires 1984). Due to the constant habitat availability even through tertiary and quaternary climatic changes, species oligarchies in várzea forests are evident.

4.3 The Igapó Forest

Much less phytogeographic knowledge is available for the Amazonian igapó than for the várzea floodplains. The majority of floristic inventories in igapó forests were carried out in central Amazonia, at the lower Negro River near Manaus (Rodrigues 1961; Takeuchi 1962; Keel and Prance 1979; Revilla 1981; Worbes 1986; Ferreira 1991; Parolin et al. 2004; Ferreira and Almeida 2005), or at the same river, about 150 km NW in the Jaú National Park (Ferreira 1997, 2000; J. Schöngart et al. 2005, unpublished). Further central Amazonian igapó inventories were done by Ayres (1993) and Inuma (2006) in the Amanã Sustainable Development Reserve, near the city of Tefé, and by Haugaasen and Peres (2006) at small blackwater rivers near the confluence with the lower Purús River. From the eastern Amazonian igapó, there are three floristic inventories, one by Campbell et al. (1986) at the Xingú River, one by Ferreira and Prance (1998) at the lower Tapajós River, and one by Ferreira et al. (2005) at the Curuá River, about 400 km east of the city of Belém. From the western and northwestern Amazon basin, no published floristic inventories in igapó forests are available.

Tree species composition and diversity in igapó forests are linked to the location of forest types along the flooding gradient in the same range as in várzea forests. The closed forest border, however, occurs at sites where mean inundation is 9.0–9.5 m (corresponding to an inundation period of 280–290 days year^{-1}; Schlüter 1989; Ferreira 1997). The establishment of the forest border at different flood levels in the várzea and igapó can be explained through photon flux under water during aquatic phases. Sunlight is transmitted in black-water and clear-water to depths of 2.0–2.5 m, whereas in white-water it is transmitted only to depths of 0.3–0.5 m (Sioli 1984b; Furch and Junk 1997a). The duration and height of flooding as well as the water chemistry thus form a light-incidence threshold for tree seedlings and define the elevations where trees can successfully establish. Furthermore, smaller amounts of easily degradable organic material result in anoxic conditions in the water, near the bottom, for shorter periods in igapó forests than in the várzea.

Several authors noted different patterns of tree species composition and richness along the flooding gradient in igapó forests of the lower Negro River (Worbes 1986, 1997; Ferreira 1997, 2000). In a floristic inventory of 1 ha of each of several igapó forests of the Jaú National Park, at elevations where the mean inundation height is 8.6 ± 0.5 m, 4.8 ± 0.3 m, and 2.1 ± 0.7 m, Ferreira (1997) recorded 44, 103, and 137 tree species ≥10 cm dbh, respectively. J. Schöngart et al. (2005, unpublished) noted seven tree species ≥10 cm dbh in an area of 625 m^2 in an igapó forest of the Jaú National Park subjected to a mean inundation of 6.55 m, whereas in plots of the same sizes but where the inundation height was 1 m and 1.9 m, 12 and 14 tree species, respectively, were reported. Investigating tree species richness and diversity of trees ≥5 cm dbh in inventories of 0.2-ha areas in three different elevations (4.8, 2.2, and 1.0 m) at the lower Rio Negro near Manaus, Ferreira (2000) described a significant increase of species richness and diversity with decreasing height of inundation. Inuma (2006) confirmed this relationship in floristic inventories at three different inundation levels, each with an area of 0.75 ha, in igapó forests of the Lago Amanã. Tree species richness ≥10 cm increased from 26 species at inundation levels between 7 and 5 m, to 35 and 44 species at inundation levels of 5–3 m and 3–1 m, respectively.

The zonation of tree species along the flooding gradient and the increase of species richness with decreasing impact of flooding appear also to be linked to the physical conditions of the soil. In general, igapó soils are coarser than várzea soils (Irion et al. 1997; Haugaasen and Peres 2006). Several authors observed white-sand soils in low-lying igapó tree communities (Piedade 1985; Worbes 1986; Ferreira 1997), while the soils of higher-lying communities consisted of at least 50% clay (Worbes 1986, 1997). Highly flood-tolerant tree species that dominate white-sand igapó soils in central Amazonia include *Borreria capitata* (Ruiz & Pav.) DC., *Dalbergia inundata* Spruce ex Benth., *Pithecellobium* spp., and *Eugenia* spp., while those of higher elevations and clayish soils include *Couepia paraensis* (Mart. & Zucc.) Benth. ex Hook f., *Leopoldinia insignis* Mart., and *Licania* spp. (Worbes 1997; Ferreira 2000). Detailed species lists of igapó forests on the different soil types, as recorded in inventories carried out by Keel and Prance (1979), Revilla (1981), Piedade (1985), Worbes (1986), and Ferreira (1991), were provided by Worbes (1997).

To date, the comparatively few floristic inventories available in igapó forests do not allow for a reliable classification of different stand age classes and/or successional stages or forest types, which complicates, among other things, comparisons of forest structure between várzea and igapó. Ferreira (1997) reported a significant increase in tree densities (≥10 cm dbh), from 796 to 941 and 1,130 trees ha^{-1}, with decreasing impact of flooding, from 8.6 to 4.8 and 2.1 m, respectively, in igapó forests of the Jaú National Park. However, the basal area of the three elevations appears to be characterized by the same distribution as in várzea forests (for comparison with várzea, see Fig. 4.6). Highly flooded igapó forests show comparatively low basal areas (20–22 m^2 ha^{-1}, 8.6 m flood height). The highest basal areas were recorded in mid-level flood communities (about 41 m^2 ha^{-1}, 4.8 m flood height), whereas in higher-located communities basal areas declined again (about 34 m^2 ha^{-1}, 2.1 m flood height; Ferreira 1997).

The increase in densities of trees ≥10 cm dbh with decreasing impact of flooding in igapó forests contrasts with the situation in várzea forests, where tree densities generally decline from highly flooded to low flooded sites, becoming highest in early-secondary stages (Worbes et al. 1992; Schöngart 2003; Wittmann et al. 2004). Other authors found no significant differences in tree densities ≥10 cm dbh in comparative studies of várzea and igapó forests at the lower Purús River and the Amanã Sustainable Development Reserve (Haugaasen and Peres 2006; Inuma 2006). Increasing tree densities with decreasing flood height were later described by Ferreira (2000) at the lower Negro River, near Manaus, for trees ≥ 5 cm dbh. An increase in the tree density of small trees and saplings with increasing topographic elevation of the forested sites was also documented for várzea forests (Wittmann and Junk 2003).

Species richness comparisons between várzea and igapó forests in the vicinity of the city of Manaus (Worbes 1986, 1997) and at the Floresta National de Caxiuanã (Caruá River, Ferreira et al. 2005) indicated higher species richness in igapó forests. These studies, however, compared forest communities of different successional stages and topographic levels, but gave no information about the degree of anthropogenic disturbance, particularly in the várzea. By contrast, Prance (1979, 1987) and Ayres (1993) stated that igapó forests are generally poorer in tree species than várzea forests. The highest species richness (≥10 cm dbh) reported from igapó was 137 species ha^{-1} in a forest subjected to inundations of 2.1 m (Ferreira 1997). This value is below the maximum species richness described by Balslev et al. (1987), Dallmeier et al. (1996), Nebel et al. (2001), and Wittmann et al. (2002a,b) in western and central Amazonian high-várzea forests. That species richness is lower in the igapó than in the várzea was recently confirmed by comparative floristic studies from Haugaasen and Peres (2006) at the lower Purús River and from Inuma (2006) in the Amanã Sustainable Development Reserve. Ongoing floristic inventories in the igapó forests of the Amanã Reserve also indicate lower species richness in the igapó than in the várzea of the nearby located Mamirauá Sustainable Development Reserve (Schöngart et al. 2005) (Figs. 4.17 and 4.18).

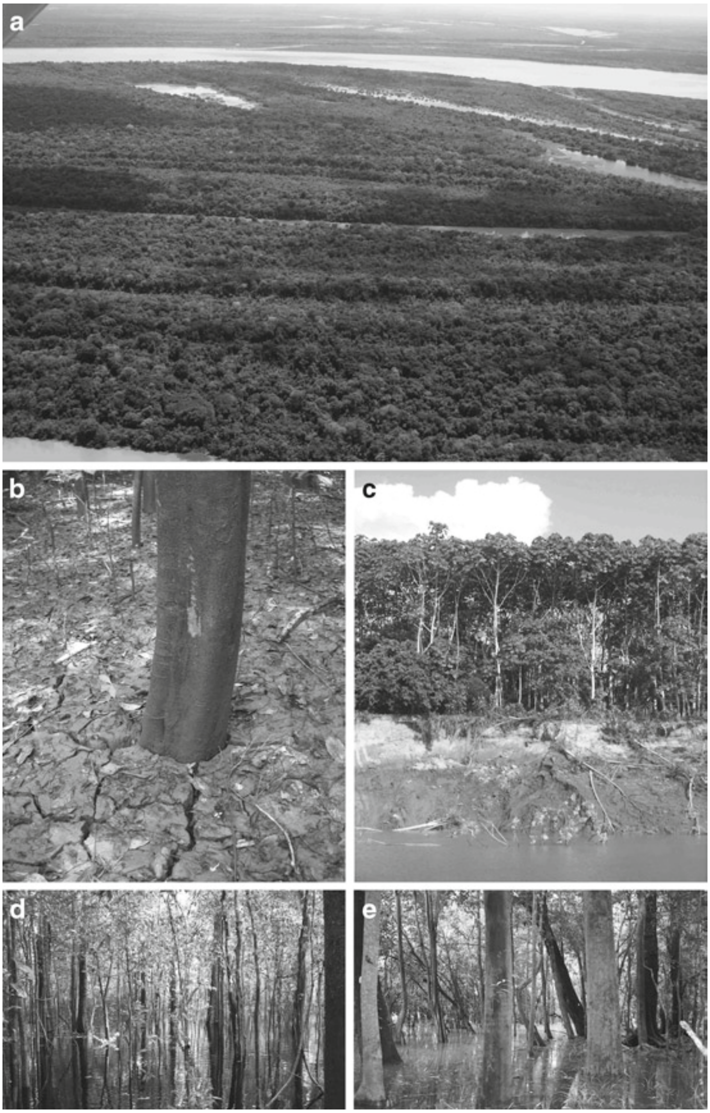

Fig. 4.17 (**a**) Mamirauá Sustainable Development Reserve, between the Japurá (*top*) and the Solimões Rivers: The sediment of the major Amazonian white-water rivers is deposited in form of meanders, channel-bars, depressions, and lakes, which partially loose connection to the main-river channels during the low-water periods. (**b**) High annual sedimentation rates cover the superficial root layer of an individual of *Pseudobombax munguba* at a fluvial island next to the Japurá River bank. Besides the creation of anoxia at the root level of mature trees, the sediment destroys tree regeneration at these sites. (**c**) Solimões River near the city of Tefé: Independent of the successional stage of the forest stand, fluvial erosion can destroy several hectares of forest during one high-water period. (**d**) Lower Purús River near the city of Beruri: Late-secondary stages are composed by tree species with maximum ages between 80 and 150 years. These forests are characterized by densities of 500–600 individuals ha^{-1}, belonging to 20–50 tree species. (**e**) Mamirauá Sustainable Development Reserve, near the community of São Raimundo do Jarauá: Low-várzea late-successional stages are well-stratified and colonized by trees with maximum ages of up to 400 years. Due to annual inundations of up to 3 m in height, the sub-canopy stratum is characteristically poor in individuals

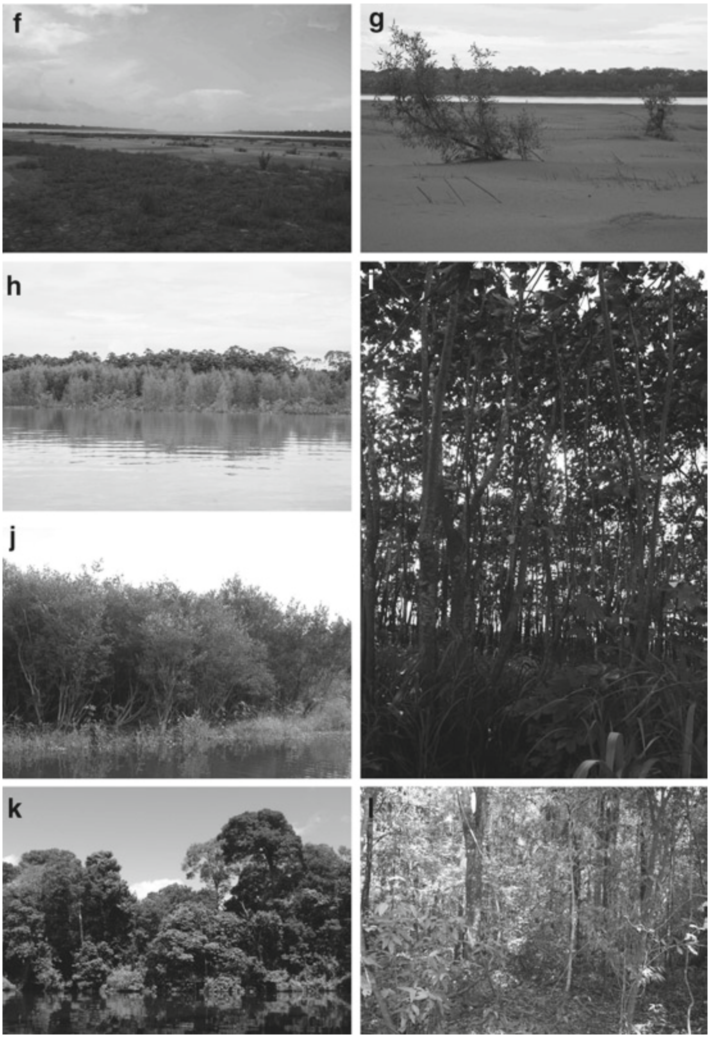

Fig. 4.18 (**f**) Japurá River, Mamirauá Sustainable Development Reserve: Large-scale new-site colonization by annual grasses that establish during the terrestrial phases. These grasses are frequently replaced by perennial grasses (mainly *Paspalum respens* and *Echinochloa polystachya*), which in turn decrease water energy and favour the deposition of sediment, allowing for the establishment of pioneer tree species. (**g**) Solimões River near the city of Manaus: When sediment is deposited at topographic levels subjected to less than 7.5 m of inundation (corresponding to a flooded period of <270 days year^{-1}), first pioneer trees like *Alchornea castaneifolia* establish without prior colonization by grasses. (**h**): Solimões River near the city of Manaus: Monospecific stand of the pioneer tree *Salix martiana*. Besides inundations of up to 7 m in height, and 100% of rPAR, this species tolerates high sedimentation rates due to the formation of secondary root layers above the annual sediment deposits. (**i**) Japurá River, Mamirauá Sustainable Development Reserve: The perennial grasses *Paspalum repens* and *Echinochloa polystachya* are replaced by the

The scarcity of floristic inventories in clear-water floodplain forests do not allow reliable comparisons with black-water and white-water floodplain forests concerning species composition, richness, and diversity. Ferreira and Prance (1998) recorded 21, 24, and 30 tree species ha^{-1} (≥ 5 cm dbh) in a floristic inventory totaling 3 ha in clear-water forests at the lower Tapajós River near Santarém. Campbell et al. (1986) recorded 40 tree species ≥ 10 cm dbh in an area of 0.5 ha in clear-water forests of the Xingú River. Both inventories were done in forests on white-sand soils and were thus comparable to inventories of highly flooded igapó forests of the Negro River (Ferreira 1997). Besides flooding and nutrient scarcity, Ferreira and Prance (1998) argued that the low species richness found at the lower Tapajós River could be the result of the surrounding savanna vegetation, which is generally poorer in tree species than is the case for the upland forests surrounding the igapó of the Negro River. Kubitzki (1989) and Ferreira and Prance (1998) noted high floristic similarities between Amazonian clear-water and black-water forests, and cited several tree species that are found on white-sand soils in both forest ecosystems (e.g., *Swartzia polyphylla* DC., *Campsiandra laurifolia* Benth., *Cynometra spruceana* Benth., *Leopoldinia insignis*, *Burdachia prismatocarpa* A. Juss., and *Macrolobium multijugum* (DC.) Benth.). However, 16 of the 36 tree species found by Ferreira and Prance (1998) at the lower Tapajós River also were reported to occur in Amazonian white-water floodplains (data from Wittmann et al. 2006a). More detailed comparisons can only be obtained when data from additional floristic inventories in black-water and clear-water igapó forests are available.

The igapó forests of the lower Negro River are characterized by a distinct species composition. Differences between igapó of the Negro River and the central Amazonian várzea already can be detected at the family level. Fabaceae, Euphorbiaceae, Sapotaceae, and Lecythidaceae are important families in both forest ecosystems, but with significantly greater importance in the igapó. Malpighiaceae, Combretaceae, and Ochnaceae, which are among the ten most important families in igapó, are of very little importance in várzea forests. By contrast, Malvaceae,

Fig. 4.18 (continued) tree species *Cecropia latiloba*, which form monospecific and dense stands with densities of up to 1,000 individuals ha^{-1}. After the creation of a closed canopy, the light-demanding C_4-grasses swiftly loose competition by shading. When the trees reach ages of about 20 years, *C. latiloba* itself no longer regenerates at this site, and will be replaced by species of late-secondary stages. (**j**) Maciel lake, Mamirauá Sustainable Development Reserve: *Eugenia ochrophloea* is one of highly flood-tolerant tree species that colonizes the margin of still-water systems in oxbows and lakes. At these sites, sedimentation rates are reduced, and the fine-grained substrate and the accumulated organic material often cause anaerobic site conditions during the most part of the year. (**k**) Secondary-river channel Paracuúba, Mamirauá Sustainable Development Reserve: With more than 100 species ha^{-1}, high-várzea forests are the most species-rich várzea forest type, which is characterized by emergent trees with maximum heights of up to 40 m. These forests establish along the elevated banks of rivers and river channels. (**l**) Secondary-river channel Paracuúba, Mamirauá Sustainable Development Reserve: The lower stratum of high-várzea forests is densely covered by shrubs, small trees, and tree regeneration competing for light

Table 4.4 Comparison of importance (FIV = relative abundance + relative dominance) of the 17 most important families (trees ≥10 cm dbh) in central Amazonian igapó (mean values of inventories totaling 3 ha in the Jaú National Park, Rio Negro; Ferreira 1997) and central Amazonian várzea (mean values of inventories totaling 3 ha in the Mamirauá Sustainable Development Reserve, Solimões River, Wittmann et al. 2002b).

	Igapó	Várzea
Fabaceae	28.14	12.23
Euphorbiaceae	20.89	8.41
Malvaceae	<1	14.09
Sapotaceae	6.46	3.06
Salicaceae	2.19	6.62
Moraceae	2.48	5.51
Malpighiaceae	7.44	<1
Lecythidaceae	4.46	2.28
Combretaceae	6.13	<1
Brassicaceae	<1	6.21
Annonaceae	1.93	3.98
Urticaceae	<1	5.69
Myrtaceae	3.45	2.14
Lauraceae	<1	4.72
Chrysobalanaceae	3.32	1.31
Verbenaceae	<1	4.53
Ochnaceae	2.81	<1

Salicaceae, Moraceae, Brassicaceae, Urticaceae, and Lauraceae belong to the ten most important várzea families, but are not particularly important within igapó forests (Table 4.4).

At the species levels, floristic similarities between central Amazonian várzea and the igapó of the lower Negro River amount to about 32%. Parolin et al. (2004) found that, based on two inventories performed at the lower Negro River near the confluence with the Solimões River, one 0.1 ha (trees ≥3.2 cm dbh), and the other 1.5 ha (trees ≥32 cm dbh), only about 30% of the 44 tree species had restricted occurrence in igapó. The majority of species occurred in igapó, várzea, and the surrounding terra firme.

Using floristic data from central Amazonian várzea, summarized by Wittmann et al. (2006a), and from our species list of the 186 most common tree species in central Amazonian várzea (see Section 2.2), and from the igapó species lists summarized by Worbes (1997), Ferreira (1997), Ferreira and Prance (1998) and Parolin et al. (2004), we compiled a species list of common tree species in igapó and várzea (Table 4.5). The greater portion of species found in both ecosystems also was reported in the surrounding uplands.

Table 4.5 Most common tree species occurring in igapó forests of the lower Negro River and of the lower Tapajós River, and in Amazonian várzea forests. Data from our study concerns the 186 most common várzea tree species found in central Amazonian várzea; data from Wittmann et al. (2006a) concern species in 44 inventories (62.34 ha) across the Amazon basin. (1) Ferreira (1997), (2) Ferreira and Prance (1998), (3) Ferreira (2000), (4) Parolin et al. (2004), (5) Worbes (1997), (6) Haugaasen and Peres (2006), (7) Wittmann et al. (2006a), and (8) our study

Species	Ocurrence in igapó	Occurrence in várzea
Acosmium nitens (Vogel) Yakovlev	2	8
Alibertia edulis (Rich.) A. Rich. ex DC.	1	8
Buchenavia oxycarpa (Mart.) Eichler	1	8
Byrsonima amazonica Griseb.	3	8
Caryocar microcarpum Ducke	4	8
Couepia paraensis (Mart. & Zucc.) Benth.	2, 5	8
Crudia amazonica Spruce ex Benth.	1	8
Eschweilera albiflora (DC.) Miers	4	7, 8
Eschweilera parvifolia Mart. ex DC.	3	7, 8
Hevea spruceana (Benth.) Müll.Arg.	1, 3	7, 8
Inga punctata Willd.	1, 3	8
Licania apetala (E. Mey.) Fritsch	2	8
Licania heteromorpha Benth.	4	8
Mabea nitida Spruce ex Benth.	3	7, 8
Macrolobium acaciifolium (Benth.) Benth.	1, 2	7, 8
Malouetia tamaquarina (Aubl.) A.DC.	1, 3	8
Mouriri guianensis Aubl.	1	8
Myrciaria dubia (Kunth) McVaugh	2	8
Ormosia excelsa Benth.	1	8
Piranhea trifoliata Baill.	5, 6	7, 8
Pouteria elegans (A.DC.) Baehni	1, 3, 4	7, 8
Quiina rhytidopus Tul.	3	8
Swartzia polyphylla DC.	1, 3	8
Tabebuia barbata (E. Mey.) Sandwith	2, 5	7, 8
Unonopsis guatterioides (A. DC.) R.E. Fries	3	8

4.4 Conclusions

The information provided in this chapter demonstrates that Amazonian floodplain forests belong to special ecosystems with a partial highly adapted and endemic vegetation. The flood pulse and the ecologic connectivity created by the vast and dynamic Amazonian river system allow for simultaneous ecological processes and predictable aggregations of tree species over huge geographic distances. Tree species richness and diversity variations and species oligarchies in Amazonian floodplains seem to follow environmental gradients and rules similar to those of Amazonian terra firme. Although increasing attention has been focused on the floristic variation within forests of the Amazon Basin, species composition and diversity variations are still poorly understood. There are large Amazonian floodplain areas for which no floristic information is available, i.e., along the tributaries of the Solimões/Amazon Rivers and in Amazonian igapó. We are thus still at the beginning of our efforts to describe the Amazonian floodplain flora and to understand the evolutionary and ecological interactions between floodplains and their surrounding uplands.

Slight changes of the atmospheric water content beginning in the early Paleocene were probably crucial factors triggering the evolution of both Amazonian floodplain and terra firme forests. More comparative studies between floodplain and terra firme forests thus would not only close local gaps in species distribution maps, but might also reveal important results that allow for interpretations of the evolution and current state of Amazonian flora as a whole. We are therefore convinced that these kinds of studies will substantially contribute to an understanding and modeling of the Amazonian flora with respect to present and future climate changes.