Aboveground Roots in Amazonian Floodplain Trees[1]

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ABSTRACT

Sediment-rich rivers seasonally flood central Amazonian várzea forests, leading to periodic anoxic conditions in the rhizosphere and requiring morphological and structural adaptations, such as aboveground root systems. We investigated some possible relationships between root types and environmental factors in forest plots covering 3.1 ha of várzea in the Mamirauá Sustainable Development Reserve, Brazil. Digital elevation models of the study sites were obtained; sedimentation and soil texture were investigated to check relationship between position of trees on the flood gradient, soil conditions, and aboveground root systems. Different types of aboveground roots were closely related to flooding duration and habitat dynamics. Species subjected to higher and more prolonged floods tended to produce more aboveground roots than species subjected to lower and shorter inundations. Plank-buttressing species increased with decreasing flood height and/or flood duration, and with increasing growth height and basal area. Habitats inundated for long periods were dominated by species with low growth heights and low basal areas, which formed stilt roots and aerial roots. Root system and sediment deposition showed a close relationship, plank buttressing being more common in sites subjected to lower sediment rates. In the disturbed sites close to the main river channel colonized by pioneer species, the occurrence of buttresses was lower than in less disturbed climax stages. No clear relationship was found between root systems and sediment grain sizes.

RESUMO

A várzea da Amazônia Central é inundada periodicamente por rios de água branca ricos em sedimentos. A fase terrestre e a fase aquática as quais a vegetação está sujeita, influenciam a fisiologia e a estrutura de espécies arbóreas. O pulso de inundação ocasiona um aumento da coluna de água e da sedimentação, o que resulta em condições anóxicas para a rizosfera, causando adaptações morfológicas e estruturais como raízes aéreas. Este trabalho investiga as possíveis relações entre a forma destas raízes e os fatores ambientais. Para o inventário das raízes foi selecionada uma área de 3.1 ha de várzea na Reserva de Desenvolvimento Sustentável Mamirauá. Foram feitos modelos digitais do terreno dos sítios, assim como medições da sedimentação e granulometria do solo, com o objetivo de investigar relações entre topografia, condições físicas do solo e a formação de raízes aéreas. Os resultados indicam, que a ocorrência de diferentes formas de raízes está relacionada com o tempo de inundação e a dinâmica geomorfológica dos habitats. Em geral, espécies situadas em cotas mais baixas, sofrendo inundações prolongadas, produzem mais freqüentemente raízes aéreas do que aquelas sujeitas a um menor período de inundação. Espécies que formam raízes tabulares ocorrem com mais freqüencia em áreas onde o período de inundação é mais curto, por outro lado, espécies com raízes adventícias e aéreas são mais comuns em áreas com inundação prolongada. Há ainda uma relação entre sedimentação e o sistema radicular, sendo que espécies com raízes tabulares ocorrem com maior freqüência em sítios com baixa sedimentação. Em áreas colonizadas por espécies pioneiras, adaptadas a altas taxas de sedimentação e solos arenosos, próximas aos rios principais, a ocorrência de raízes tabulares é menor do que em estágios clímax, onde o habitat é mais estável. Não houve relação entre as diferentes formas de raízes aéreas e a granulometria do solo.

THE VÁRZEA FORESTS OF CENTRAL AMAZONIA ARE SEASONALLY FLOODED by sediment- and nutrient-rich white-water rivers (Prance 1979), which occur along the Amazon River and its main tributaries. They are characterized by periodic floods, reaching average amplitudes of 10 m and lasting up to 230 d/yr (Junk 1989). The change between an aquatic and a terrestrial phase (Junk *et al.* 1989) influences tree species diversity and the structure of the floodplain forests (Junk 1989, Ayres 1993, Wittmann *et al.* 2002), resulting in a clear zonation along the flooding gradient: Low-várzea forests are influenced by annual inundations between 3 and 7 m, corresponding to 50–240 d/yr, whereas high-várzea forests establish at inundation levels of less than 3 m on an average (less than 50 d/yr, Wittmann *et al.* 2002).

Low-várzea forests are characterized by a successional sequence from early successional to late successional stages (Worbes *et al.* 1992). Early successional stages normally establish on the lowest levels next to the riverbanks. They often form monospecific, poorly

stratified stands. With proceeding forest succession, topography increases in height, because trees slow down water flow and favor sediment deposition. In undisturbed sites, species richness increases to about 50–100 species/ha and forests are multilayered stands (Worbes *et al.* 1992; Worbes 1997; Wittmann *et al.* 2002). High-várzea forests result in natural forest succession from low-várzea forests. Forest structure in the high várzea is similar to nonflooded forests and species richness is up to 90–150 species/ha (Nebel *et al.* 2001, Wittmann *et al.* 2002).

Tree ecophysiology is linked to the "flood pulse" (Junk *et al.* 1989), with a main growing season in the terrestrial phase, and growth reductions in the aquatic phase indicated by annual increment rings in the wood (Worbes 1985, 1997; Worbes & Junk 1989). The phenology of most species is triggered by the flood pulse, especially in the lower sites (Wittmann & Parolin 1999, Parolin *et al.* 2002a, Schöngart *et al.* 2002), and most trees shed their leaves during the high-water period (Worbes 1983, Worbes *et al.* 2001). Also, photosynthetic activity at the leaf-level is reduced during the aquatic phase (Parolin 2000, Parolin *et al.* 2001).

Besides flooding, the highly dynamic geomorphology in the várzea influences tree growth and establishment (Salo *et al.* 1986, Kalliola *et al.* 1991, Terborgh & Petren 1991). Low topographic variations in combination with high content of sediments and suspended materials in the white-water rivers result in aquatic–terrestrial landscapes with a high variety of microhabitats (Campbell *et al.* 1992). Sedimentation on highly eroding stream-banks of the main river channels can reach 0.3–1 m/yr (Junk 1989, Campbell *et al.* 1992). Fine-coarse sediments, which are deposited primarily in oxbows with reduced water velocity, worsen the physical soil properties because of the increasing lack of oxygen at the root level (Wittmann 2002). Flooding itself also reduces the diffusion of oxygen into the soil because of the pressure of the water column, and the anaerobic soil conditions caused by the accumulation of organic matter that lead to reduced physiological activities (Sioli 1954, Crawford 1983, Kozlowski 1984, Ernst 1990, Larcher 1994).

Thus, root forms, their function to plant support, and oxygen and nutrient uptake in the inundation forests of Amazonia may play key roles for plant establishment and survival. The formation of aerial roots, for example, in *Salix* spp., may compensate for respiration losses (Kozlowski 1971, 1984; Schlüter & Furch 1992).

Richards (1952) mentioned the high abundance of buttresses and stilt roots in tropical freshwater swamp forests, as compared to nonflooded habitats. Segal *et al.* (1987) stated that buttressing served as a reliable indicator of inundation in a study where wetland boundaries were delimited by abrupt and obvious changes in ecosystem structure. Ayres (1993) noted that in várzea forests near Tefé, Amazonia, frequency of tree species forming buttresses was linked to the flood-level gradient. He suggested that many species in low várzea develop buttresses to increase plant support as an adaptation to water velocity, high sedimentation rates, or erosion. According to Whitford (1906), Senn (1923), and Navez (1930), buttress formation is the direct response of the tree to the mechanical stimulation of strains set up by gravity and wind. In fact, buttressed roots are effective as structural members, supporting large trees on substrates that offer poor anchorage, since they reduce the danger of tree failure (Henwood 1973, Crook *et al.* 1997). Plank buttressing in tropical trees may also be related to a competitive mechanism, since the physical presence of buttresses presumably hinders the neighbor establishment of other large trees and of soil-rooted woody vines (Black & Harper 1979, Sloover & Fagnant 1994).

Some várzea tree species produce more root biomass in the primary root system during the aquatic phase: Meyer (1991) showed that the amount of fine roots increased with increasing length of the inundation period. In seedlings of *Senna reticulata* (Caesalpiniaceae) and *Himatanthus sucuuba* (Apocynaceae), the production of belowground and aboveground root systems increased with waterlogging (Ferreira 2000; Parolin 2001, 2002).

Although a high number of species are endemic to Amazonian flood plains and the formation of aerial roots has been mentioned by various authors for várzea tree species (Hueck 1966; Worbes 1983, 1997; Kozlowski 1984; Kubitzki 1989; Meyer 1991; Parolin 1998, 2001; Oliveira 1998), detailed information about the types of aboveground root systems, their functions, and the biotic and abiotic conditions responsible for their formation is scarce. The present study describes the aboveground root systems of Amazonian floodplain trees, recorded in forest plots covering 3.1 ha of várzea in the Mamirauá Sustainable Development Reserve, Brazil. Digital elevation models of the study sites were obtained, and sedimentation and soil texture were investigated to check for correlations between height and duration of inundation, soil grain size distribution, and the aboveground root systems of trees.

METHODS

STUDY AREA.—The study was carried out in the focal area of the Mamirauá Sustainable Development Reserve (MSDR) (2°51′S, 64°55′W), approximately 70 km NW of the city of Tefé and 50 km upstream from the mouth of the Japurá river into the Solimões (Amazon) river, in western Central Amazonia, Brazil (Fig. 1). The study area is influenced by annual inundations of the Japurá and Solimões rivers. Mean monthly temperature vary little over the year and range between 25°C and 28°C. Mean annual rainfall at MSDR is about 3000 mm (1996–2000, Institute for Sustainable Development Research Mamirauá-ISDRM, Tefé). Annual water-level fluctuations of the Solimões river ranged between 6.6 and 10.1 m during 1993–2000 (Fig. 2).

INVENTORIES.—To study the root systems of trees in the main várzea forest communities, five plots were investigated in the MSDR, four located in different microhabitats of the low várzea, and one located in the high várzea (Fig. 1). Within the low várzea, two square plots (I, II) of 625 m^2 were installed which were influenced by annual flooding about 6.5 m. This flooding depth corresponds to a submersion of 220 d/yr at the study sites (Fig. 2). Plot I was installed at a recently deposited sand bar next to the Japurá river bank, covered by an early successional stage (classification of Worbes *et al.* 1992). Plot II was installed in a *chavascal*-formation, which is a dense swamp forest that establishes in the marginal zone of still-water lakes or in ancient, silted-up river-arms that do not drain (Ayres 1993, Wittmann *et al.* 2002). Three rectangular plots (III, IV, and V), each of 1 ha in size (50 m × 200 m) and each divided into 16 square plots of 625 m^2 in size were installed, differing in elevation and thus flood depth and duration of flooding. Plots III and IV (low várzea) were subjected to an average height of submersion of 4.5 m (122 d/yr), representing a secondary and a late successional stage (Worbes *et al.* 1992). Plot V was installed inside a climax stage of high várzea, subjected to an average inundation of 2.3 m (43 d/yr, Fig. 2).

During the terrestrial phases 1999/2000 and 2000/2001 (September–February), all trees ≥10 cm dbh (diameter at breast height) present in the five plots defined above were measured in DBH and identified to the species level. Determinations of floristic equitability ("evenness," Shannon & Weaver 1949) were performed. Each individual was measured in height using the clinometer function of the theodolite (Carl Zeiss Ni2, Jena, Germany) and classified based on its crown position. Thus, there was a stratification into A- (upper canopy), B- (middle canopy) and C-story (lower canopy).
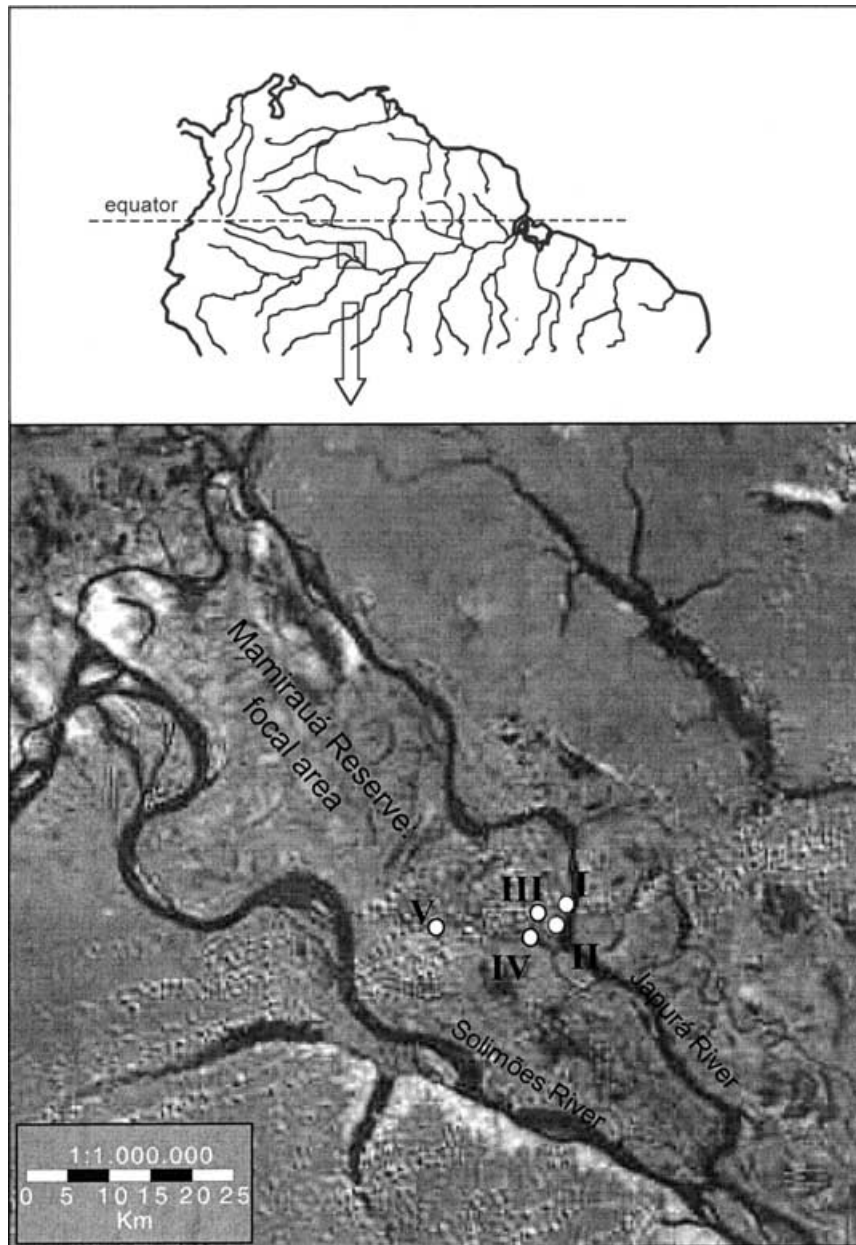
FIGURE 1.   Studied sites within the focal area of the Mamirauá Sustainable Development Reserve, located between the Japurá and the Solimões rivers. Plot I: early successional stage, plot II: chavascal, plot III: secondary stage, plot IV: late successional stage, all low várzea; plot V: climax stage of the high várzea.

The forests of plots I and II were mono-layered (only A-story). For each individual, the visible, aboveground root form was recorded using the definition of root systems by Oldeman (1990), which distinguishes between belowground roots (primary and secondary root system, not visible) and specialized roots: aerial roots (as outgrowth on stem, without contact to the soil), pneumatophores, stilt roots, and plank buttresses (tabular roots).

To determine a possible zonation of root systems and species along the flooding gradient, each individual tree within the research plots was entered into a three-dimensional coordinate system (position: x, y, height: z) using a theodolite (Carl Zeiss Ni2, Jena,

Germany). The vertical position of individual trees was derived comparing 1999 flood marks on trunks with water levels recorded in Tefé (ISDRM, Tefé). For each plot, a high-resolution Digital Elevation Model was generated by Triangulated Irregular Network. Sedimentation was recorded with the aid of measuring slats, put up at the end of the terrestrial phase in March 2000, and read at the end of the aquatic phase, in August/September 2000. The woody slats (3 cm × 3 cm × 200 cm) with a millimeter scale were dug right-angled into the ground to a depth of 60 cm. In each square plot (I, II), one measuring slat was installed, while in each of the rectangular plots (II–V), two slats were installed.
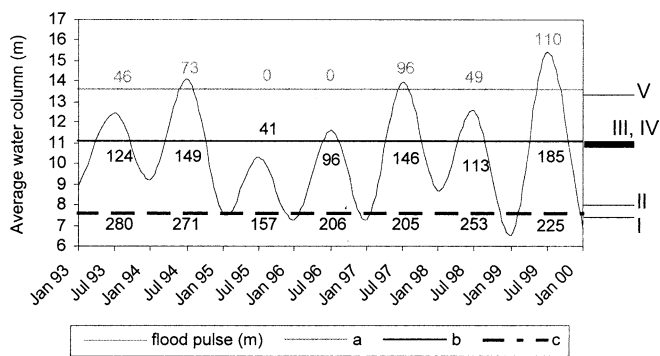
FIGURE 2. Location of the study sites (plots I–V, right side) in relation to average height (m) of the water column of the flooding river, with days of submersion per year in (a) high várzea, (b) low várzea, and (c) closed forest borderline.

Soil samples were obtained in a total of eight sites, one in the center of each square plot (I, II), and two in each rectangular plot, localized near the small sides of the plots (III, IV, and V). The samples were taken at the ground surface and depths of 40, 100, and 200 cm below the ground surface. The samples were dried, sieved, and their particle size distribution was determined.

For statistical comparisons, we calculated correlations (Pearson) between the amount of trees producing aboveground roots, their DBH, and their location at the flood gradient.

RESULTS

SPECIES NUMBER.—Field inventory yielded, on the entire research area of 3.1 ha, a total of 1626 individual trees ≥10 cm dbh, belonging to 222 species. Tree species density increased with increasing successional stage of the forests, and also with decreasing depth of inundation and length of the flooded period. Simultaneously, species evenness decreased (Table 1). Within the low várzea, plot I represented the early successional stage. Only four species were recorded, forming an open forest on the sand bars close to the river margin. Plot II, representing the *chavascal* next to a lake margin, was characterized by six tree species, but a higher density of individuals (Table 1). The secondary stage (plot III) showed also a high number of individuals, belonging to 45 species/ha. The late successional stage of low várzea (plot IV) showed a decreasing number of individuals, but higher species density, with 91 species/ha. Within the high várzea (plot V), the 469 individual trees ≥10 cm dbh belonged to 168 species/ha (Table 1).

SEDIMENTATION AND SOIL TEXTURE.—We recorded a decrease of sediment deposition with increasing elevation of the sites during the high water period in 2000, excepting the *chavascal* (plot II). However, sedimentation height also depended on the geomorphology and distance of the sites to the main river channel. On the sand bar of the Japurá river (plot I), sedimentation amounted to 15.1 cm during the submersion period in 2000. In spite of the high inundation level, sedimentation in the *chavascal* (plot II) amounted to only 0.2 cm, due to its short contact with sediment-loaded water of the main river channel. In the secondary stage (plot III), sediment deposition ranged between 1.2 and 1.1 cm, whereas sedimentation in the plot covered by the late successional stage (plot IV) ranged from 0.6 to 0.4 cm. In the high-várzea plot (plot V), sediment deposition averaged 0.1 cm.

Soil texture was also related to the time of inundation and to the deposit location in relation to the main river channel. On the sand bar next to the Japurá river margin (plot I), we observed relatively high water velocity during the aquatic phase, which probably favored the deposition of coarse grain sizes. The clay content of soil averaged 55 percent (Fig. 3). In the *chavascal* (plot II), water energy within the lake margin slows down, and the soil clay content amounted to 88 percent. In the secondary and late successional stages of low várzea (plots III and IV), the soil clay content averaged 65–78 percent, while in the high-várzea plot (plot V) the value was about 66 percent (Fig. 3).

ROOT SYSTEMS.—In total, we recorded the formation of visible, aboveground roots in 86 tree species (38.7%). Plank-buttressing species prevailed with a total of 25.2 percent, stilt-rooted species amounted to 11.8 percent, and species producing aerial roots amounted to 2.7 percent. No pneumatophores were found. Within the species producing specialized roots, most produced more than one root system (Appendix).

TABLE 1. *Plot characteristics. Species evenness = Shannon & Weavers equitability index: $(J) = H (\ln S)^{-1}$, where H = Shannon's diversity index ($H = -\Sigma P_1 \ln P_1$, where P_1 = no. individuals of species A/total number of individuals of all species), S = total number of species.*

| Plot	Habitat	Forest type	Mean flood height (m)	Inventoried area (m²)	Number of individuals	Number of species	Species evenness
I	Low várzea	Early successional stage	6.5	625	27	4	0.71
II	Low várzea	Chavascal	6.5	625	55	6	0.59
III	Low várzea	Secondary stage	4.5	10,000	641	45	0.43
IV	Low várzea	Late successional stage	4.5	10,000	434	91	0.46
V	High várzea	Climax stage	2.3	10,000	469	168	0.42
Total				31,250	1626	222	
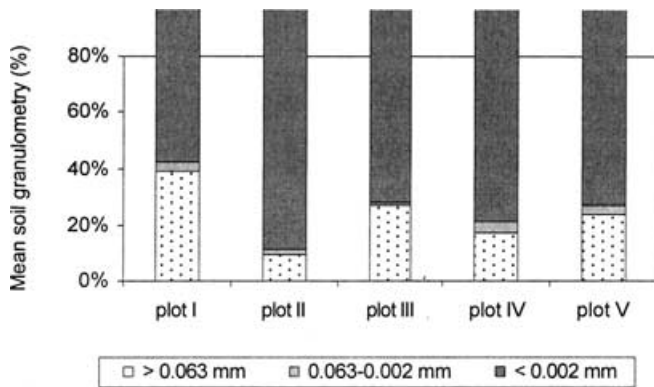
FIGURE 3.   Mean soil particle size distribution in samples from 0, 40, 100, and 200 cm below ground surface.

Plank-buttressing trees were mainly those with crowns reaching the A-story (Fig. 4). Accordingly, DBH of all plank-buttressing trees averaged 32 cm (SD = 16.4), in the late successional stages up to 40 cm (SD = 13.1), with single emergents reaching diameters of up to 100 cm (*Conceveiba* sp., *Couepia paraensis*). Stilt roots were produced mainly by smaller B- and C-story trees with relative low basal areas (Fig. 4). DBH of all stilt-rooted trees averaged 16.2 cm (SD = 5.8).

RELATIONSHIP BETWEEN SUCCESSIONAL STAGE AND ABOVEGROUND ROOTS: I. LOW VÁRZEA.—*Early successional stage (plot I).*—Three of the four species colonizing the sand bar next to the Japurá river bank showed the production of aboveground roots. From the 16 recorded individuals of *Alchornea castaneifolia*, 14 produced stilt roots, whereas all individuals of *Salix martiana* showed the production of aerial roots as outgrowth on stems. The single individual of *Ficus anthelmintica* also produced stilt roots.

Chavascal (plot II).—Four of the six recorded species produced aboveground roots among six recorded species. The most abundant species *Buchenavia* sp. produced stilt roots up to a height of 6 m on tree stems, often almost reaching the treecrowns. In some cases, stilt roots of *Buchenavia* showed the formation of buds and young shoots, characterizing the capacity of vegetative reproduction. Stilt roots also were recorded in all individuals of *Symmeria* sp., whereas the palm trees (*Bactris maraja*, *Astrocaryum jauari*) showed aerial roots as outgrowth on stems.

Secondary forest (plot III).—From the 639 trees recorded, 74.5 percent showed no formation of aboveground roots; 22.7 percent of the studied individuals produced stilt roots. Stilt roots were recorded on all trees of *Tococa* sp. and on trees of *Cecropia latiloba* and *Cecropia membranacea* with stem diameters above *ca* 15 cm. *Cecropia latiloba* was the most frequent species in this successional stage, and thus responsible for the high percentage of stilt roots in the plot. Buttress-producing individuals were scarce with 2.8 percent (*Tabebuia barbata*, *Sapium* sp., and *Luehea cymulosa*). These species
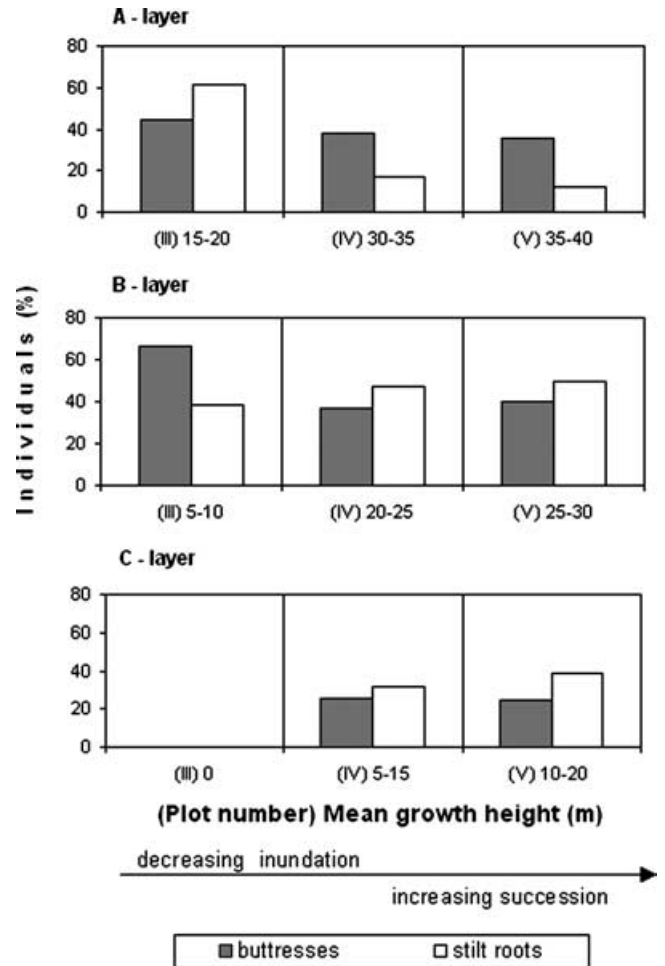

FIGURE 4.   Relationship between aboveground root system of trees and stratification. With relative frequency and growth height of individuals within the A- (upper canopy), B- (middle canopy), and C- (lower canopy) stratum. Roman number in brackets: plot number, Arabic numbers: canopy height (m).

were characterized by low individual frequencies in this early stage of succession, although not all individuals of *L. cymulosa* produced buttresses.

Late successional stage (plot IV).—From the 434 trees recorded, 67.7 percent showed no production of aboveground roots. Buttresses were produced in 20 percent of all individuals, stilt roots in 12.3 percent, respectively. Plank buttressing was mainly concentrated on frequent high-canopy trees with extensive basal areas, such as *Duroia duckei*, *Etaballia dubia*, *Piranhea trifoliata*, and *Terminalia dichotoma*. In some species (*e.g.*, *Pterocarpus amazonum*, *D. duckei*), no visible aboveground roots were recorded in young individuals of low basal areas in the subcanopy, whereas mature individuals produced buttresses when reaching the upper canopy. Only B- and C-story species or pioneer species with low basal areas formed stilt roots. *Cecropia latiloba* and *Tovomita rostrata* produced stilt roots in the mature phase, mainly in gaps where they were abundant.

RELATIONSHIP BETWEEN SUCCESSIONAL STAGE AND ABOVEGROUND ROOTS: II. HIGH VÁRZEA.—*Climax stage (plot V).*—From the 469 trees recorded, 72.8 percent showed no production of aboveground roots, whereas 19.5 percent produced plank buttresses and 7.7 percent produced stilt roots. Due to the high species diversity, the majority of tree species occurred with only one single individual, so that no information about the formation of different root systems is available at the population level. Plank buttresses occurred mainly on high-canopy trees, like *Tabebuia barbata*, *Zygia caracterae*, and *Sloanea guianensis*. Smaller trees within the subcanopy, such as *Sterculia frondosa*, *Hirtella hispidula*, and *Iryanthera juruensis*, produced stilt roots.

PRODUCTION OF DIFFERENT ROOT SYSTEMS.—In about 21 percent of all species, different individuals of the same species showed the production of more than one root system. Buttressing in most species was correlated to the trunk diameters ($r = 0.66$, $P = 0.001$). Frequently, buttressing species developed buttresses only when getting large stem diameters. For example, DBH of *Tabebuia barbata*, which is frequent in the low and high várzea, amounted to 25 cm (SD = 10.4) on all individuals without buttresses, but amounted to 40.2 cm (SD = 8.8 cm) on all buttressed individuals. In *Luehea cymulosa* (low várzea), DBH averaged 15.5 (SD = 7) in nonbuttressed and 57.9 (SD = 13.2 cm) in buttressed individuals. Larger diameters of stems were also recorded in most buttressing individuals of the high-várzea species.

The production of buttresses and the location of individuals along the flood gradient were highly correlated ($r = 0.73$, $P = 0.001$). Buttressed individuals in most of the species were subjected to higher and more prolonged periods of inundation than individuals without buttresses. In *Tabebuia barbata*, buttressed individuals within the low várzea averaged inundations about 4.4 m (SD = 0.21), no buttress-producing individuals 3.9 m (SD = 0.24). In *Luehea cymulosa* (low várzea), the average inundation of individuals producing buttresses was 4.3 m (SD = 0.32), whereas inundation averaged 3.8 m (SD = 0.63) in nonbuttressed trees. Within the high várzea, only few tree species showed high abundances, so that sufficient data about different root types is not available. However, in species characterized by the production of buttresses, such as *Homalium guianense*, *Xylopia calophylla*, or *Aspidosperma riedelii*, buttressing individuals were subjected to higher inundations of at least 0.3 m than the nonbuttressed individuals of the same species. In *T. barbata*, difference of elevation between buttressed and nonbuttressed individuals averaged more than 1 m.

The production of stilt roots was also correlated with average DBH ($r = 0.51$, $P = 0.01$) and average height of inundation ($r = 0.12$, $P = 0.05$). In *Cecropia latiloba* (low várzea; Fig. 5), DBH of stilt root producing individuals averaged 21.9 cm (SD = 6.5), and inundation of these individuals amounted to 4.4 m (SD = 0.21). In nonstilt rooting individuals, average DBH was 13.5 cm (SD = 4.7), and inundation amounted to 4.1 m (SD = 0.33). *Nectandra amazonum* showed the production of aerial roots mainly on mature individuals (mean dbh = 43.2 cm), subjected to average inundations of 4.7 m, whereas no aerial roots producing individuals (mean dbh = 26.7 cm) were subjected to inundations of 3.5 m.

FIGURE 5.   Stilt roots in *Cecropia latiloba*.

From all species recorded in this study, 2.7 percent showed the production of more than one aboveground root system. Most of these species occurred with low frequencies in the high várzea, such as *Aniba terminalis*, *Etaballia dubia*, and *Tovomita* sp. Within the low várzea, only *Sloanea excelsa* produced stilt roots in some individuals, buttresses in other individuals, or no specialized root system in a third category of individuals.

DISCUSSION

The production of different types of aboveground roots is common in many várzea tree species, and more frequent than in upland forests (Richards 1952, Salomão *et al.* 1988, Sanford & Cuevas 1996). Flooding height, duration, and related habitat dynamics seem to be the most important factors influencing the production of aboveground roots in Amazonian flood plains. Most tree species analyzed in this study had the capacity to produce different aboveground root types. The variety of aboveground roots may be linked to the patchwork of microhabitats in the várzea (Campbell *et al.* 1992), which includes sites with extremely unstable environmental conditions next to the main rivers on the one hand, and sites with relatively stable conditions on the other hand, such as the high várzea or *chavascal* (Ayres 1993, Wittmann *et al.* 2002). Species subjected to high and prolonged floods tended to produce more aboveground roots than species subjected to lower inundations.

THE ROLE OF SEDIMENTATION.—Sediment deposition played a major role (Fig. 6): the highest amount of stilt roots occurred in places with high sediment deposition like the low várzea, whereas plank buttressing was more common in sites which were subjected to minor sediment rates. There also seemed to be a relationship between root system and soil grain size. Coarse soils showed a high number of stilt-rooted trees, but these belonged to few species only. Stilt roots were frequent in the *chavascal*, characterized by the highest content
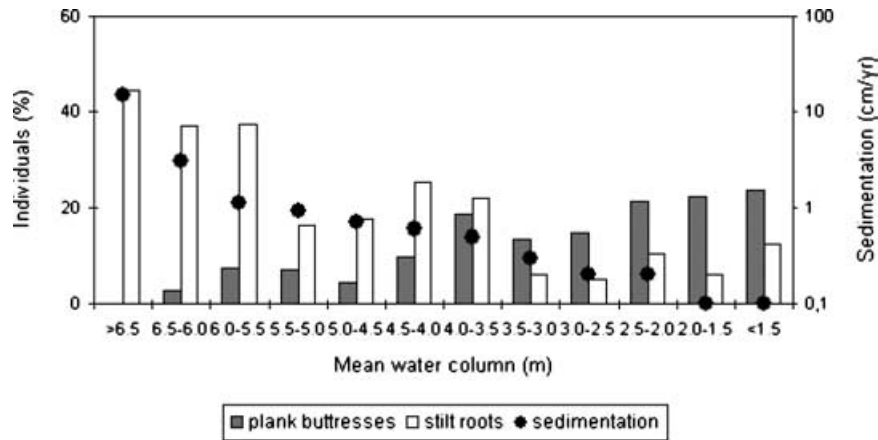
FIGURE 6.   Relative frequency of buttressing and stilt-rooting trees ($N = 755$ in 3.1 ha) along the flood and sedimentation gradient.

of clay among the plots analyzed in this study. Plank-buttressing trees were absent from the coarse soil next to the main river channel and the loamy soil of the *chavascal*. Most species with plank buttresses were found on the high várzea with medium grain size (Fig. 6).

THE ROLE OF FLOOD HEIGHT AND/OR DURATION.—There was a proportional increase of species with plank buttressing with decreasing flood height and/or flood duration. In contrast to observations made by Ayres (1993), indicating a higher number of species with buttresses in the low várzea, we recorded an opposite trend: buttressing prevailed in high várzea, whereas habitats inundated for long periods were dominated by species with stilt roots and aerial roots. Near the forest border, with average flooding heights of 6.5–7 m/yr, plank-buttressing trees were absent. Species that are able to produce different root types, or that also present individuals without aerial roots, produced buttresses more frequently on higher levels in the flooding gradient (*e.g., Eschweilera ovalifolia*, Fig. 7).

FUNCTION OF ABOVEGROUND ROOTS: AERATION.—Stilt roots and/or aerial roots are essential to compensate for constant anaerobic soil conditions under flooding. According to Lüttge (1997), the increase in aboveground root surface brought about by these root types may facilitate aeration, especially in wet tropical soils. In fallen individuals of *Buchenavia* and *Symmeria*, we observed that primary and specialized roots hardly reached depths of more than 1 m below the ground surface. The production of deeper roots may be strongly inhibited under such unfavorable aeration conditions, and new root layers formed with increasing sediment deposit on the tree stem may be needed. This was observed in pioneer species like *Salix martiana* (Fig. 8a), where the primary belowground root reaches depth of up to 6 m, but several well-defined layers of fine secondary roots stacked up along the main root with a space of 30–40 cm. The same was found in *Alchornea castaneifolia* (Fig. 8b), which also produced stilt roots of up to 40 cm above the ground surface.

The primary function of stilt roots in the analyzed species seems to be the facilitation of aeration, which is extremely important in

this environment with mostly hypoxic to anoxic conditions in the rhizosphere. Pneumatophores as typical adaptations to enhance root aeration are absent in várzea trees (Junk 1984), and were not found in the present study. According to Kubitzki (1988), their formation is impeded because of the high amplitudes of water-level fluctuations and the periodic high water column in central Amazonian flood plains. On the other hand, aeration through pneumathodes is potentially possible: under experimental conditions several várzea species produced these negatively geotropic aerial roots (K. Haase, pers. comm.) as described for the mangrove species *Laguncularia racemosa* (Geissler *et al.* 2002).

FUNCTION OF ABOVEGROUND ROOTS: MECHANICAL SUPPORT.— According to Benzing (1991), the primary function of stilt roots and buttresses is the mechanical support of trees. The results of the present study showed that the distribution of both root types was correlated with the gradient of flooding, sedimentation, and

FIGURE 7.   Buttresses in *Eschweilera ovalifolia*.

FIGURE 8.   Adventitious roots in *Salix martiana* (A) and stratified roots in *Alchornea castaneifolia* (B).

soil properties. This indicates that the production of stilt roots or buttresses seems to depend on the growth strategies related to the environmental conditions of the microhabitat the trees live in. Buttresses seem to offer better anchorage especially in high-canopy trees, which are more exposed to wind loads, whereas the function of stilt roots is better aeration. Richards (1952) mentioned that the function of stilt roots as mechanical support of trees is doubtful because it is surprising that stilt roots should be more common in small trees growing mainly in the sheltered undergrowth than in tall trees with heavy crowns to support. Since most stilt-rooted trees were small-to-medium-sized and belonged to the C-story, we suppose that the mechanical support of stilt roots—which increases the aboveground root surface more than buttresses—is at best a secondary function in várzea trees.

FUNCTION OF ABOVEGROUND ROOTS: *OTHER FACTORS*.—Buttressing was more frequent in the late successional stages in low and high várzea, where upper canopy trees reach heights of up to 30–40 m. In the study plots, tree density was low in late successional stages, and soil-rooted woody vines were observed with more frequency in high-várzea sites. The production of buttresses may be linked to interspecific competition, or to the defense against the establishment of soil-rooted woody vines, as described by Black and Harper (1979) and Sloover and Fagnant (1994). However, since no replicates in other sites could be performed to date, further studies are necessary to better understand the function of buttresses as related to competition.

In conclusion, the environment does not act alone to influence tree structure and functioning; tree establishment and successional sequences change the environmental conditions. *Salix* spp. occur mainly at low sites subjected to long periods of inundation and high sedimentation rates. Once *Salix* formed dense forest stands, sedi-mentation and water currents are reduced at these sites and *Cecropia latiloba* may take over (Parolin *et al.* 2002b). Thus, tree establishment and perhaps buttressing may play a role for the modification of the processes of riverbank erosion by altering bank hydrology, flow hydraulics, and bank geotechnical properties (Abernethy & Rutherfurd 2000).

ACKNOWLEDGMENTS

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APPENDIX. *Recorded species producing aboveground roots; with occurrence in lv = low várzea, hv = high várzea, and root systems: pb = plank buttresses, st = stilt roots, and ae = aerial roots.*

Species	Distribution		Root form		
	lv	hv	pb	st	ae
Acacia loretensis Machr.		o	x		
Albizia subdimidiata (Splitg.) Barneby & Grimes	o	o	x		
Alchornea castaneifolia A. Juss.	o			x	
Aldina sp.		o	x		
Aniba guianensis Aubl.	o			x	
Aniba riparia Mez.	o			x	

APPENDIX. *Continued.*

Species	Distribution		Root form		
	lv	hv	pb	st	ae
Aniba sp.		o	x	x	
Apeiba membranacea Spruce ex Bentham.	o		x		
Aspidosperma riedelii Muell. Arg.	o		x		
Astrocaryum jauari Mart.	o	o			x
Bactris maraja Mart.	o			x	x
Banara sp.	o			x	
Banisteriopsis sp.		o	x		
Bombacopsis sp.		o	x		
Boraginaceae sp.	o			x	
Buchenavia sp.	o			x	
Byttneria coriacea Britton.		o	x		
Byrsonima amazonica Griseb.	o	o	x		
Cecropia latiloba Miq. S.	o	o		x	
Cecropia membranaceae Trec.	o	o		x	
Cedrela odorata Blanco.		o	x		
Chomelia sp.		o	x		
Conceveiba sp.2	o	o	x		
Coussarea hirticalyx Standley.		o	x		
Discocarpus brasiliensis Klotzsch		o	x		
Duroia duckei Huber	o	o	x		
Eschweilera ovalifolia Nied.	o	o	x		
Etaballia dubia (H.B. & K.) Rudd.	o	o	x	x	
Ficus anthelmintica Mart.	o		x	x	
Ficus insipida (Willd.) S. Carvajal.	o		x	x	
Guarea sp.		o	x		
Guatteria pteropus Benth.		o	x		
Guatteriopsis paraensis R.E. Fries		o	x		
Hirtella hispidula Miq.		o		x	
Homalium guianense (Aubl.) Oken	o	o	x		
Homalium sp.		o	x		
Ilex innundata Poepp. ex Reiss.	o		x		
Ilex sp.	o	o	x		
Inga splendens Benth.		o		x	
Iryanthera juruensis Warb.		o		x	
Licaria armeniaca (Nees) Kosterm.	o	o	x		
Luehea cymulosa Spruce ex Bentham.	o		x		
Margaritaria sp.		o		x	
Marlierea sp.	o		x		
Matayba sp.	o		x		
Naucleopsis ternstroemiiflora (Mildbr.) C.C. Berg.		o	x		

APPENDIX.   *Continued.*

Species	Distribution		Root form		
	lv	hv	pb	st	ae
Nectandra amazonum Nees	o				x
Neea ovalifolia Spruce ex J.A. Schmidt	o	o		x	
Ocotea aciphylla Mez.		o	x	x	
Ocotea floribunda Benth. & Hook. f.	o	o		x	
Ocotea megaphylla Mez.		o	x	x	
Ocotea parvifolia (Ducke) Kosterm.		o		x	
Oxandra polyanthea R.E. Fries		o	x		
Pachira insignis Gaertn.		o	x	x	
Paramachaerium ormosioides Ducke	o	o	x		
Parinari montana Aubl.		o	x		
Piranhea trifoliata Baill.	o		x		
Pouteria elegans (A.DC.) Baehni	o		x		
Pouteria ephedrantha (A.C. Smith) T.D. Pennington.		o	x		
Pouteria gomphiaefolia Radlk.	o	o	x		
Pterocarpus amazonum Huber		o	x		
Pterocarpus sp.1	o		x		
Salix martiana Leyb.	o			x	x
Sapium sp.1	o		x		
Sapium sp.2		o	x		

APPENDIX.   *Continued.*

Species	Distribution		Root form		
	lv	hv	pb	st	ae
Sloanea excelsa Ducke	o		x		
Sloanea guianensis Benth.		o	x		
Sloanea laurifolia Benth.		o	x		
Sloanea poryphrocarpa Ducke		o	x	x	
Symmeria sp.	o			x	
Tabebuia barbata (E. Mey.) Sandwith	o	o	x		
Tapura juruana (Ule) Rizzini		o	x		
Terminalia dichotoma E. Mey.	o	o	x		
Tococa sp.	o	o		x	
Tovomita acutiflora M.S. de Barros & G. Mariz		o		x	
Trichilia lecointei Ducke	o		x		
Trichilia sp.1		o	x		
Trichilia sp.2	o			x	
Trichilia sp.3	o	o	x		
Trichilia sp.4		o	x		
Vatairea guianensis Aubl.	o		x		
Virola calophylla Warb.		o		x	
Xylopia calophylla		o	x		
Xylopia sp.	o	o	x		
Zygia caracterae (Kunth) M.de L. Rico-Arce.		o	x		
Zygia latifolia Fawcett & Rendle.		o	x		