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ARE THERE DIFFERENCES IN SPECIFIC WOOD GRAVITIES BETWEEN TREES IN VARZEA AND IGAPO (CENTRAL AMAZONIA)?

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Resumo. As florestas inundadas próximas a Manaus, Brasil, são divididas em dois tipos principais de acordo com o tipo de água dos rios que as inundam periodicamente. As florestas inundadas por rios de águas brancas (várzea) tem solos férteis, enquanto as florestas inundadas por rios de águas pretas (igapós) apresentam solos pobres em nutrientes. Neste estudo nós investigamos as diferenças na gravidade específica do tronco e o crescimento anual de 30 espécies de árvores na floresta de várzea e 35 espécies na floresta de igapó. As árvores na floresta de várzea apresentaram menor gravidade específica e maior incremento anual do que as árvores na floresta de igapó. A posição no gradiente de inundação e a duração da inundação não afetaram significativamente a gravidade específica das árvores nos dois tipos de florestas. Espécies pioneiras da floresta de várzea apresentaram uma gravidade específica significativamente menor e um incremento anual maior do que as espécies climax. A nível intraespecífico, duas das quatro espécies que ocorreram nas duas florestas ao mesmo tempo tiveram maior gravidade específica e menor incremento anual nas florestas de igapó do que nas florestas de várzea. As diferenças significativas na gravidade específica e no incremento anual entre os dois tipos de florestas, sugerem que o tipo de água relacionado diretamente com o nível de nutrientes, podem afetar diretamente o crescimento das árvores nestes ecossistemas. Nas florestas de igapó o menor incremento anual pode ser considerado uma adaptação aos baixos níveis de nutrientes e uma eficiente utilização dos nutrientes disponíveis.

Abstract. Central Amazonian floodplain forests near Manaus can be divided into two ecosystems, according to the principal flooding water types. Whitewater floodplains (várzea) have soils with high, blackwaters (igapó) with low nutrient content. Differences in wood specific gravities and annual increments were investigated in 30 tree species in várzea and 35 species in igapó. In várzea, trees had lower wood specific gravities and higher annual wood increments than in igapó. Elevation and flood duration showed no significant influences on wood specific gravities in both ecosystems. Pioneer species of whitewater floodplains had significantly lower mean wood specific gravities and higher annual increments than non-pioneer species. Intraspecifically, two of four species occurring in both systems showed significantly higher wood specific gravity and lower annual increments in blackwater than in whitewater floodplains. The significant differences in wood specific gravity and annual increments between the whitewater and blackwater floodplain systems suggest that the type of flooding water and the related nutrient input may directly affect tree growth. Slow growth in blackwater floodplain forests can be considered as an adaptation to the low nutrient status of the system and an efficient utilization of the available nutrients. *Accepted 16 March 1998.*

Key words: Wood specific gravity, wood density, wood increment, tree growth, floodplain forest, várzea, igapó, central Amazonia.

INTRODUCTION

In the central Amazon, two types of floodplain forests can be distinguished according to the origin and water quality of the flooding rivers (Prance 1979). Blackwater rivers originate in the geologically old Guyana Shields and are poor in sediment load (Sioli 1968). Their floodplains, igapó (Prance 1979), have soils with low nutrient content (Sombroek 1979). On the contrary, whitewater rivers, originating in the geologically younger Andes, carry a high sediment load and the floodplains (várzea, Prance 1979) are rich in nutrients.

Most environmental factors that can influence tree growth and wood production, such as water regime, light incidence, and temperature (Howe 1974), are almost identical in várzea and igapó forests near Manaus (Schmidt 1976). In both systems trees occur at different elevations along the flood gradient with vegetation zonations (Ferreira 1997, Ferreira & Stohlgren in press, Junk 1989). However, these two flooded systems are distinct with respect to nutrient availability (Furch 1984, 1997), floristic composition (Amaral *et al.* 1997, Ayres 1993, Ferreira 1997, Prance 1979), and plant growth and productivity (Adis *et al.* 1979). Várzeas have higher net productivity than igapós, presumably due to the higher nutrient availability in whitewaters (Furch & Klinge 1989).

Productivity studies and growth analyses of trees are often destructive and time consuming (Worbes 1995). Wood cores extracted with non-destructive methods can instead give fast information on annual wood increment (AWI) (Howe 1974) and wood specific gravity (WSG), a cardinal parameter determining wood properties (Wiemann & Williamson 1989).

Sixty-one tree species from várzea and igapó forests were selected for WSG determination to answer the following questions: (a) Do WSG and AWI differ in várzea and igapó? (b) Are differences in WSG and AWI between várzea and igapó related to elevation in the flood gradient? (c) Are there intraspecific differences in WSG and AWI in species occurring in both systems?

STUDY SITES, MATERIALS AND METHODS

Study area. The sites in the whitewater floodplains were located on the Ilha da Marchantaria, a river island 15 km upstream from the junction of the Amazon river with the Rio Negro (3°15'S, 58°58'W), and in the Xiborena channel, 20 km southeast of Manaus, Brazil. The two study sites in blackwater floodplains were located in the Jaú National Park 200 km northwest of Manaus, (1°90'S–3°00'S; 61°25'W–63°50'W), and in the lower course of the Rio Tarumã Mirim, 20 km Northeast of Manaus (3°02'S, 60°17'W).

The floodplain forests of these sites are seasonally inundated by whitewater and blackwater rivers respectively (Prance 1979). All sites are situated between 21 and 27 m above average sea level (AASL) and are subjected to an average high water level of 10 m, corresponding to a period of inundation of up to nine months per year (Junk 1989). Variation of river water level is markedly seasonal. The rising phase occurs between late December and early July, while the draining period occurs from the end of July to the end of November. The climate is hot and humid (Koeppen's Afi type). Mean monthly temperature ranges from 26.3°–27.2°C. Mean annual precipitation varies between 1700 mm and 2300 mm, with a marked dry season from June to November and a rainy season from December to May.

Species selection. For wood specific gravity (WSG) determinations, 61 common tree species of the two systems (30 from várzea, 35 from igapó, 4 of which occur in both systems) were chosen, based on inventories performed by Worbes (1983) in várzea and Ferreira (1991) in igapó. The selected species represent a wide array of taxa representative of different elevations along the flood gradient and different successional stages (Table 1). For annual wood increment (AWI), 12 species were chosen (Table 2).

To determine the influence of growth strategies, tree species in whitewater systems were categorized according to their ecological status: pioneer or non-pioneer species (*sensu* Swaine & Whitmore 1988). The successional criteria do not apply to blackwater forests because of the absence of fast-growing pioneer species (Ferreira 1991, Worbes 1992).

To determine the influence of elevation, tree species of both systems were categorized according to their occurrence along the flood gradient. Species growing mainly between 21 and 25 m AASL were classified as "low" elevation and those occurring between 25 and 28 m AASL were classified as "high" elevation.

Sample collection. Only healthy individuals were chosen. The number of sampled individuals per species varied from 1 to 19, totaling 383 trees. Wood samples were taken at 1.30 m above the ground, except for trees with buttresses which were sampled above the buttresses. In a few cases in which the trees were still flooded, the sample had to be taken above 1.30 m from the ground (e.g., *Eschweilera tenuifolia*).

Determination of WSG and AWI. WSG of one sample per tree was determined by calculating the ratio of oven dry mass to fresh volume. After removing the bark and phloem, a wood core was extracted with an increment borer according to Howe (1974) and Whitmore (1973) and cut into pieces of approximately 1.5 cm length. The volume of each sample was calculated by measuring the fresh sample with a vernier calliper: $\Pi r^2 h$, r being the radius of the core, and h being the length. Dry weight was measured after oven drying for four days at 105°C. The average WSG of the trees was calculated by the corrected mean of the 1.5 cm subsamples, where the subsample is multiplied by the percentage of the area of the respective part of the stem disk (Whitmore 1973).

AWI was determined by measuring the width of the increment rings which in the selected species

TABLE 1. Wood specific gravity of tree species from várzea and igapó, with successional status of whitewater species (pioneer or non-pioneer species, sensu Swaine & Whitmore 1988), elevation in the flood gradient (low = 21–25 m AASL, high = 25–28 m AASL), mean wood specific gravity (WSG, g x cm^{-3}), standard deviation (SD) and number of individuals sampled (N); in order by WSG.

Species	Family	Successional status	Elevation	Mean WSG	SD	N
Várzea						
Crudia amazonica	Caesalpiniaceae	non-pioneer	low	0.87	0.05	4
Piranhea trifoliata	Euphorbiaceae	non-pioneer	low	0.77	0	1
Psidium acutangulum	Myrtaceae	non-pioneer	low	0.74	0.02	4
Brothriospora corymbosa	Rubiaceae	non-pioneer	low	0.71	0.02	2
Genipa spruceana	Rubiaceae	non-pioneer	low	0.71	0.04	5
Eschweilera sp.	Lecythidaceae	non-pioneer	low	0.7	0.06	3
Pouteria glomerata	Sapotaceae	non-pioneer	low	0.68	0	1
Gustavia augusta	Lecythidaceae	non-pioneer	high	0.67	0.03	4
Casearia aculeata	Flacourtiaceae	non-pioneer	low	0.66	0.02	4
Laetia corymbulosa	Flacourtiaceae	non-pioneer	high	0.66	0.03	3
Tabebuia barbata	Bignoniaceae	non-pioneer	high	0.65	0.02	5
Acacia riparia	Mimosaceae	non-pioneer	high	0.63	0.09	6
Triplaris surinamensis	Polygonaceae	non-pioneer	high	0.63	0.06	11
Vitex cymosa	Celastraceae	non-pioneer	low	0.56	0.06	10
Nectandra amazonum	Lauraceae	non-pioneer	high	0.52	0.05	18
Crescentia sp.	Bignoniaceae	non-pioneer	low	0.5	0	1
Spondias lutea	Anacardiaceae	non-pioneer	high	0.5	0.01	2
Crateva benthami	Capparidaceae	non-pioneer	low	0.49	0.05	12
Macrolobium acaciifolium	Caesalpiniaceae	non-pioneer	low	0.49	0.07	5
Luehea cymulosa	Tiliaceae	non-pioneer	high	0.48	0.03	4
Senna reticulata	Caesalpiniaceae	pioneer	high	0.45	0.02	6
Salix humboldtiana	Salicaceae	pioneer	low	0.39	0.01	7
Ficus insipida	Moraceae	non-pioneer	high	0.38	0.03	7
Cecropia membranacea	Cecropiaceae	pioneer	low	0.36	0.03	13
Annona hypoglauca	Annonaceae	non-pioneer	low	0.35	0	1
Alchornea castaneifolia	Euphorbiaceae	pioneer	low	0.34	0.04	7
Cecropia latiloba	Cecropiaceae	pioneer	low	0.33	0.04	11
Erythrina fusca	Papilionaceae	non-pioneer	high	0.33	0.01	5
Solanum critino	Solanaceae	pioneer	high	0.24	0.03	4
Pseudobombax munguba	Bombacaceae	pioneer	low	0.22	0.03	11
Igapó						
Swartzia argentea	Papilionaceae	non-pioneer	high	0.87	0.08	3
Couepia paraensis	Chrysobalanaceae	non-pioneer	low	0.85	0.06	13
Crudia amazonica	Caesalpiniaceae	non-pioneer	low	0.85	0.04	11
Burdachia duckei	Malpighiaceae	non-pioneer	low	0.84	0.03	3
Amanoua oblongifolia	Euphorbiaceae	non-pioneer	low	0.83	0	1
Campsiandra comosa	Caesalpiniaceae	non-pioneer	low	0.81	0.01	2
Elvasia calophylla	Ochnaceae	non-pioneer	low	0.8	0.05	6
Caraipa grandiflora	Clusiaceae	non-pioneer	high	0.78	0.11	3
Eschweilera tenuifolia	Lecythidaceae	non-pioneer	low	0.77	0.04	6
Licania apetala	Chrysobalanaceae	non-pioneer	low	0.77	0.07	8
Alibertia edulis	Rubiaceae	non-pioneer	high	0.76	0.03	5
Aldina latifolia	Caesalpiniaceae	non-pioneer	high	0.75	0.06	12
Tabebuia barbata	Bignoniaceae	non-pioneer	low	0.75	0.06	16
Acosmium nitens	Caesalpiniaceae	non-pioneer	low	0.74	0.05	3
Vatairea guianensis	Papilionaceae	non-pioneer	high	0.74	0.05	4
Pouteria elegans	Sapotaceae	non-pioneer	low	0.73	0.11	9

TABLE 1. Continued.

Species	Family	Successional status	Elevation	Mean WSG	SD	N
Sclerolobium hypoleucum	Caesalpiniaceae	non-pioneer	low	0.71	0.01	3
Mabea nitida	Euphorbiaceae	non-pioneer	high	0.7	0.09	4
Buchenavia ochnopnuma	Combretaceae	non-pioneer	low	0.69	0.08	5
Erisma calcaratum	Vochysiaceae	non-pioneer	high	0.68	0.07	2
Parkia discolor	Mimosaceae	non-pioneer	low	0.64	0.06	8
Pentaclethra macroloba	Mimosaceae	non-pioneer	high	0.64	0	1
Swartzia laevicarpa	Papilionaceae	non-pioneer	high	0.63	0.06	9
Caryocar microcarpum	Caryocaraceae	non-pioneer	high	0.62	0.02	4
Swartzia polyphylla	Papilionaceae	non-pioneer	high	0.62	0.04	10
Virola sp.	Myristicaceae	non-pioneer	high	0.62	0.06	4
Ormosia excelsa	Caesalpiniaceae	non-pioneer	low	0.61	0.02	4
Laetia suaveolens	Flacourtiaceae	non-pioneer	high	0.59	0	1
Nectandra amazonum	Lauraceae	non-pioneer	low	0.58	0.06	6
Maprounea guianensis	Euphorbiaceae	non-pioneer	low	0.57	0.04	7
Himatanthus attenuatus	Apocynaceae	non-pioneer	high	0.48	0	2
Leopoldinia pulchra	Arecaceae	non-pioneer	high	0.48	0.09	3
Macrolobium acaciifolium	Caesalpiniaceae	non-pioneer	high	0.45	0.08	6
Simaba orinocense	Simaroubaceae	non-pioneer	high	0.42	0.05	3
Hevea spruceana	Euphorbiaceae	non-pioneer	low	0.4	0.05	19

are formed annually (Worbes 1988, 1995). AWI was measured on stem disks or on samples taken with the increment borer.

Data analysis. We used t-test to test differences in WSG between the different floodplain ecosystems. Kolomogorov-Smirnov was used to test differences in species distribution of WSG between the two floodplain ecosystems; the Cronquist System of classification in the taxonomic treatment was employed for this study (Nee 1995).

TABLE 2. Annual wood increment (AWI): mean and standard deviation, sample size (N), and mean wood specific gravity (WSG); in order by AWI.

Species	AWI (mm x year^{-1})	N	WSG (g x cm^{-3})
Várzea			
Senna reticulata	21.4 ± 0.6	3	0.45
Cecropia latiloba	15.0	1	0.33
Crateva benthami	10.0	1	0.49
Crudia amazonica	8.6	1	0.87
Vitex cymosa	6.1	1	0.56
Macrolobium acaciifolium	5.3	1	0.49
Tabebuia barbata	4.4	1	0.65
Igapó			
Acosmium nitens	2.9	1	0.74
Licania apetala	2.6 ± 0.5	2	0.77
Elvasia calophylla	2.0	1	0.80
Buchenavia ochnopnuma	1.8	1	0.69
Maprounea guianensis	1.8	1	0.57
Tabebuia barbata	1.7 ± 0.1	3	0.75

RESULTS

Influence of floodplain type. Mean WSG was significantly lower in tree species of whitewater (X = 0.53 g cm^{-3}, SD = 0.16, N = 30) than of blackwater floodplains (X = 0.68 g cm^{-3}, SD = 0.12, N = 35) (t = 10.34, P = 0.0001). WSG ranged from 0.22 to 0.87 g cm^{-3} in whitewater floodplains, and from 0.40 to 0.87 g cm^{-3} in blackwater (Table 1). Nine species from várzea had WSG below the lowest WSG (0.40 g cm^{-3}) found in igapó.

AWI, i.e., the mean width of annual growth rings, was higher in the chosen whitewater species (X = 12.5 mm x $year^{-1}$, SD = 5.6) than in the blackwater species (X = 2.1 mm x $year^{-1}$, SD = 0.5) (Table 2).

Influence of successional status. WSG was significantly lower (t = 14.05, P = 0.0001) in pioneer species (X = 0.34 g cm^{-3}, SD = 0.072, N = 59) than in non-pioneer species (X = 0.57 g cm^{-3}, SD = 0.135, N = 97) in whitewater forests.

AWI was higher in the pioneers *Senna reticulata* and *Cecropia latiloba* (X = 18.2 mm x $year^{-1}$, SD = 3.2) than in the non-pioneers (X = 6.8 mm x $year^{-1}$, SD = 2.1) of whitewater floodplains.

Influence of elevation. There were no significant differences in mean WSG between tree species growing in high and low elevations, in both ecosystems (Fig. 1). In whitewater forests, mean WSG in high elevations was 0.54 g cm^{-3} (SD = 0.13, N = 12 species) and in low elevations 0.45 g cm^{-3} (SD = 0.172, N = 18 species). In blackwater forests, mean WSG in high elevations was 0.64 g cm^{-3} (SD = 0.12, N = 17 species) and in low elevations 0.72 g cm^{-3} (SD = 0.12, N = 18 species).

Instraspecific comparisons. Of the four species occurring in both floodplain ecosystems, two had significantly higher WSG in blackwaters, *Nectandra amazonica* (t = 2.42, P = 0.04) and *Tabebuia barbata* (t = 19.00, P = 0.0001), whereas the other two, *Crudia amazonica* (t = -1.04, P = 0.35) and *Macrolobium acaciaefolium* (t = -0.24, P = 0.82) were not significantly different. AWI of *Tabebuia barbata* was more than twice as much in whitewater forests (4.4 mm x $year^{-1}$) as in individuals growing in blackwater floodplains (1.7 mm x $year^{-1}$).

DISCUSSION

The significant differences in WSG in the whitewater and blackwater floodplain systems suggest that the type of flooding water, and the related nutrient input, directly affect tree growth. One factor for the diffe-

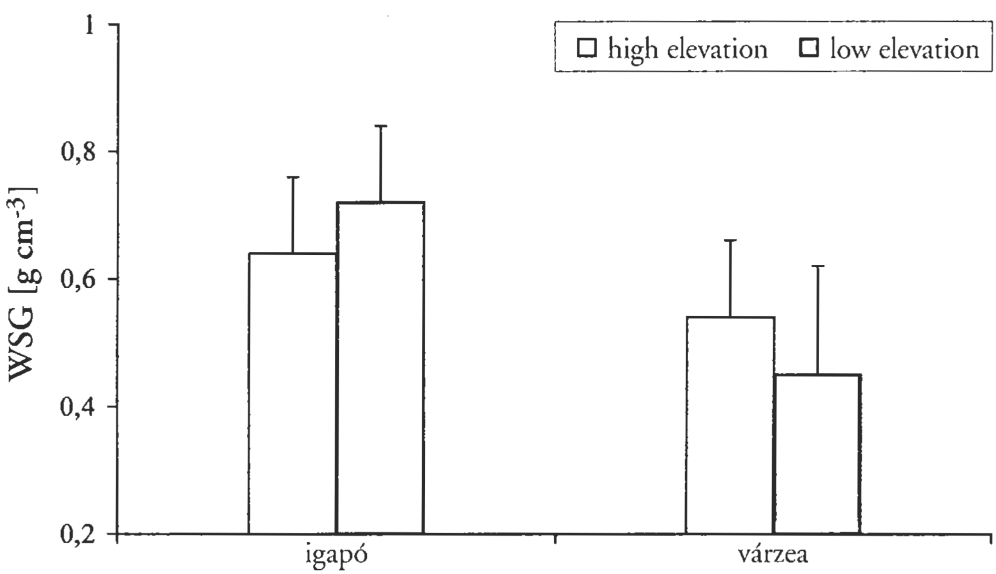

FIG. 1. Wood specific gravity of tree species growing in high and low elevations, in whitewater (várzea) and blackwater (igapó) floodplain forests.

rences in average WSG between várzea and igapó is the absence of species with inherently low WSG in igapó, in particular fast-growing pioneers. Nutrients carried by whitewater rivers allow the presence of classical pioneers, which are typically fast growing and light-demanding species (Swaine & Whitmore 1988). Pioneer species of whitewater floodplains have significantly lower wood density in relarion to non-pioneer species. This justifies the common use of wood density to classify successional stages and growth strategies of trees (Worbes *et al.* 1992). Some typical representatives of this category analyzed in this study are *Cecropia latiloba, Pseudobombax munguba, Salix humboldtiana, Senna reticulata*, and *Solanum critino* which are common in whitewater floodplain forests (Worbes *et al.* 1992).

Nutrient rich whitewater floodplains may allow fast growth or make the presence of pioneer trees possible. Both mechanisms may be operating, as pioneers are absent from blackwaters. Eliminating all whitewater pioneer species from the data analysis still leaves significantly lower WSG of species in whitewaters (X = 0.57 g cm^{-3}, SD = 0.13) compared to blackwaters (X = 0.69 g cm^{-3}, SD = 0.13).

Intraspecific comparisons should explan the relationship between soil quality and WSG. The higher WSG of species growing in blackwater floodplains may be accompanied by smaller wood increments. Although AWI was calculated in only a few species, and no inverse correlation between AWI and WSG could be detected (Table 2), the results indicate that AWI is lower in igapó. Intraspecific comparisons of *Tabebuia barbata* showed high WSG and low AWI in igapó, and the opposite in várzea. Worbes (1988) describes the capacity of *Tabebuia barbata* to adapt its wood growth to the edaphic conditions and light environment. Individuals which grow in várzea built 'wood with low density and high storage capacity', i.e., with a high amount of storage tissue (parenchyma) and little fiber wood. In nutrient poor igapó, more supporting tissue (fiber wood) was produced, leading to lower growth rates (Worbes 1988: 86).

Two of four tree species occurring in both ecosystems showed higher WSG in the blackwater floodplains. Lower WSG in várzea than in igapó (*N. amazonica* and *T. barbata*), and larger increments (*T. barbata*), can mean that these species are able to use higher nutrient levels for higher growth rates. *C.*

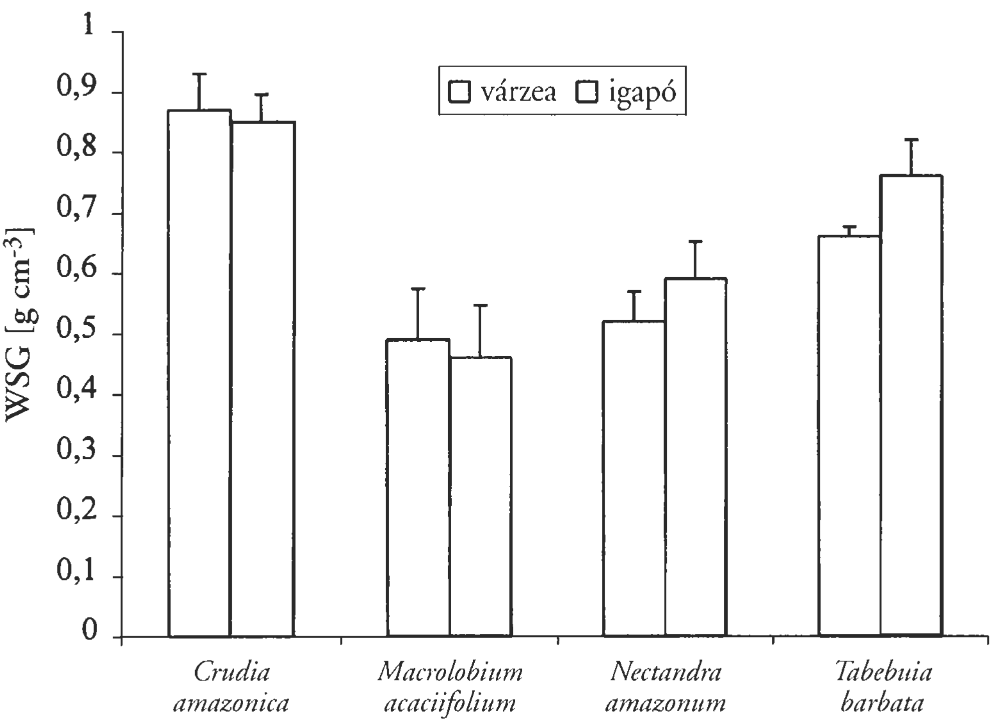

FIG. 2. Intraspecific differences in WSG in whitewater (várzea) and blackwater (igapó) floodplain forests.

amazonica and *M. acaciaefolium*, which showed no difference in wood density in the two forest types (Fig. 2), exhibit constant growth, to a certain degree, independent of nutrient supply. Thus, in some species, nutrient supply may be a limiting factor for growth, but has little or no effect on growth in others. These results suggest that trees in Amazonian floodplains can have a high growth plasticity, allowing some species to exhibit higher growth rates under more favorable growth conditions. Similar results have been found in Costa Rica, where lower wood densities were found in individuals growing in less seasonal environments (Wiemann & Williamson 1989). On the other hand, slow growth in blackwater floodplains, which can result in high WSG, can be considered as an adaptation to the low nutrient status of the system and efficient utilization of the available nutrients.

The reported variations in mean WSG can be additionally linked to differences in the cellular structure and chemical composition of the wood. Analyses of wood properties are needed here.

In blackwater and whitewater floodplains, we differentiated between species growing at low and high elevations in the flooding gradient. Some studies have shown that Amazonian tree species vary in their sensibility to flooding (Ferreira & Stohlgren in press; Kozlowski 1982, 1984) and that a longer period of inundation causes smaller annual increments (Worbes 1997). They are subjected to a longer period of inundation and suffer higher flood stress than trees situated in high positions (Junk 1989). Higher WSG should thus be expected at low elevations (Worbes 1988). In the species studied here, trees of the igapó exhibited higher mean WSG in low elevations, but the differences were not significant. In várzea, WSG was lower in low elevations. This can be explained by the high number of pioneers which are highly flood resistant and grow along the whole flood gradient. The effect of flood duration on tree growth could not be shown with the measured parameters.

CONCLUSIONS

The type of flooding water and the related nutrient input may directly affect wood specific gravity and annual increment of the species chosen. Fast-growing pioneers occur exclusively in whitewater floodplains, contributing to a lower mean WSG. Also considering non-pioneers alone, mean WSG was significantly lower in várzea than in igapó. Elevation in the flood gradient and related flood duration had no effect on WSG. WSG and AWI tend to be inversely correlated, however not consistently. The corresponding mechanisms, production of stronger cellular structures and consequential slower growth, are therefore not exclusive determinants for the differences between várzea and igapó. Further analyses of wood anatomical properties and intraspecific differences between the two floodplain ecosystems, as well as between different elevations, should provide explanations for the WSG found in várzea and igapó trees.

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