

WOOD SPECIFIC GRAVITY OF TREES IN AMAZONIAN WHITE-WATER FORESTS IN RELATION TO FLOODING

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SUMMARY

Wood specific gravity (SG) was analysed from wood cores of 180 individuals belonging to 58 common upper canopy tree species of late successional white water (várzea) forests in the Mamirauá Sustainable Development Reserve, Central Amazon Basin. We tested for a SG gradient of trees along the flood gradient. Mean SG in the low várzea was 0.62 g cm^{-3} , in the high várzea 0.57 g cm^{-3} . SG tended to increase with height and duration of flooding. In the two species that occurred in both forest types (*Hevea spruceana*, *Tabebuia barbata*) SG was significantly lower in the high várzea trees. Therefore, height and duration of flooding seem to be important factors influencing growth and wood properties in várzea trees. In addition, SG variation depended on the core section and to a lesser extent on tree diameter and height. Compared to trees in Amazonian upland ecosystems, SG of the várzea trees was lower than SG in Central and Eastern Amazonian terra firme, but was within the same range reported for Western Amazonian terra firme.

Key words: Amazon, flooding, high várzea, low várzea, wood specific gravity, wood cores.

INTRODUCTION

In Amazonian floodplain forests, water-level fluctuations result in an aquatic and a terrestrial phase during the course of the year (Junk *et al.* 1989). During the aquatic phase, trees are subjected to annual inundations, which can reach heights up to 7 m and periods up to nine months. Flood duration has a strong influence on tree growth, tree physiology, species distribution and forest structure (Junk 1989; Wittmann *et al.* 2002). In nutrient-rich seasonal várzea (*sensu* Prance 1979), species diversity increases with decreasing impact of flooding from monospecific stands at the lowest elevations to 150 species ha^{-1} on high elevations, and forests develop from mono-layered to multi-layered, stratified stands. In low-várzea forests (LV), where the inundation of trees averages heights of more than 3 m (inundation period $>50 \text{ d year}^{-1}$), common species are *Vitex cymosa*

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Bert. *ex* Spreng., *Tabebuia barbata* (E. Mey.) Sandwith and *Piranhea trifoliata* Baill. Those species usually reach maximum heights of about 25–30 m. In high-várzea forests (HV), inundation of trees averages less than 3 m (Wittmann *et al.* 2002). Common species are *Pouteria procera* (Mart.) K. Hammer, *Homalium guianense* (Aubl.) Oken and *Aspidosperma riedelii* Muell. Arg., which can reach heights up to 40 m.

Wood specific gravity (SG) is a reliable index of wood quality (Yao 1970) given the strong correlations with the wood anatomical features, mechanical properties of wood and pulp yield (Panshin & De Zeeuw 1980). SG reflects the amount of wood biomass accumulated per unit volume of living tree trunk, thus representing a measure of forest wood biomass (Wiemann & Williamson 1989; Woodcock 2000). In várzea trees, SG is reported to range between 0.24–0.72 g cm⁻³ (Martius 1992) and 0.22–0.87 g cm⁻³ (Parolin *et al.* 1998; Parolin 2002a). This indicates that SG range and mean SG is lower compared to non-flooded terra firme forests (0.05–1.08 g cm⁻³, Rueda & Williamson 1992; 0.14–1.21 g cm⁻³, Fearnside 1997). Worbes (1988) and Parolin & Worbes (2000) reported on correlation between SG and flood duration, which could have been caused by a) different durations of the growth period and b) the high wood increments and comparatively low SG of young successional stages in LV. The coexistence of fast growing pioneer species and slow growing late-successional species that can reach ages up to 400 years (Worbes 1997) complicates direct comparisons of SG and flood duration in these forests.

To date, SG from the várzea has not been analysed with standardised methods permitting a comparable determination of SG means along the flood gradient, or between different forest types. Furthermore, no HV stands have been analysed yet. The present study investigates the SG of 58 common high canopy tree species along the flood gradient. This study focused on the following questions: a) does SG vary among late successional upper canopy species in LV and HV? b) is there a SG variation along the flood gradient? c) is there intraspecific SG variation? and d) are várzea SG means comparable to those of other Amazonian forest ecosystems?

MATERIAL AND METHODS

Study area

The study was conducted 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, in the Western Brazilian Amazon. The focal area of MSDR covers an area of approximately 2600 km² and is located between the confluence of the Solimões and the Japurá Rivers (Fig. 1). Mean monthly temperatures in the MSDR vary little over the year, ranging from 25 to 28 °C. Between 1996 and 2002, mean annual rainfall was about 3000 mm (Institute for Sustainable Development Research Mamirauá – ISDM, Tefé). Annual water-level fluctuations of the Solimões and Japurá Rivers averaged 11.38 m during 1993–2002 (ISDM, Tefé).

About 90% of the focal area of MSDR is covered by closed-canopy forests (Sociedade Civil Mamirauá *et al.* 1996). Due to the small-scale irregular topography of the landscape, they form a patchwork of different forest types. About 92% of the closed-

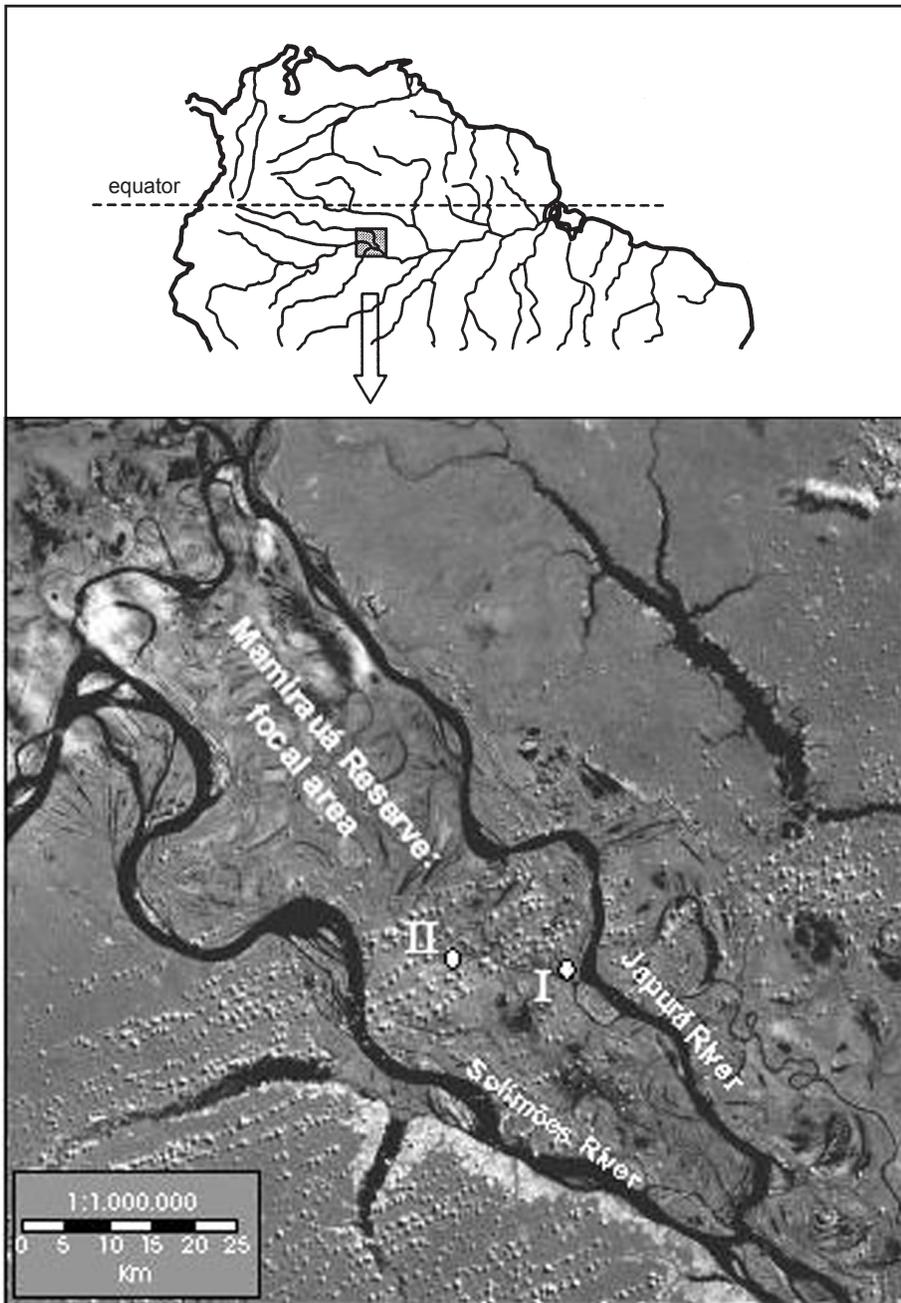


Fig. 1. Studied sites within the focal area of the Mamirauá Sustainable Development Reserve, located between the Japurá and the Solimões Rivers. Plot I: late successional stage, low várzea; plot II: late successional stage of the high várzea.

canopy forests in the focal area of MS DR comprise different successional stages of the LV type, whereas about 8% of the forests are of the HV type (Wittmann *et al.* 2002).

Within the focal area of the MS DR, we selected two long-term rectangular plots each of the size of 1 ha and divided into 16 subplots with an area of 625 m². Species composition of trees ≥ 10 cm diameter at breast height (dbh) was formerly inventoried (Wittmann *et al.* 2002). The forests of both plots are late successional stages, one located in LV and one in HV. The flooding regime and structural data of both plots are listed in Table 1.

Table 1. Differences between the low várzea (LV) and the high várzea (HV) forest stands at the Mamirauá Sustainable Development Reserve (MS DR, Wittmann *et al.* 2002). ⁽¹⁾Worbes *et al.* (1992), ⁽²⁾Ayres (1993).

	LV	HV
Synonym designations	<i>Piranhea trifoliata</i> - forest type ⁽¹⁾	Restinga alta ⁽²⁾
Mean inundation height (m)	4.1	2.2
Mean inundation period between 1993–2002 (d year ⁻¹)	111	36
No. of species ≥ 10 cm dbh (ha ⁻¹)	91	168
No. of individuals ≥ 10 cm dbh (ha ⁻¹)	434	469
Successional stage ⁽¹⁾	Late	Late
Upper canopy height (m)	25–30	35–40
Basal area (m ² ha ⁻¹)	40	33
Mean SG (g cm ⁻³)	0.62 \pm 0.15	0.57 \pm 0.13

Species selection

For SG analysis we selected three individuals of 30 tree species (90 trees ≥ 10 cm dbh) in each study plot. Two of the investigated species (*Hevea spruceana* Muell. Arg., *Tabebuia barbata* (E. Mey.) Sandwith) occurred in both forest types (LV and HV). The selection was restricted to species that occurred with at least three individuals per plot, each of them placed in the upper canopy, thus minimising SG variations caused by different light environments. In late successional várzea forests, upper canopy trees represent 58–65% of the total aboveground wood biomass (Schöngart 2003). The selected species represent to about 33% and 18% of all species in the LV and the HV plots, respectively (≥ 10 cm dbh). A detailed list of the studied species in both plots is presented in the Appendix.

Measured parameters

Fieldwork was performed during the terrestrial phase in 2002/2003. Dbh of all trees was recorded. For buttressed trees, diameters were measured above the buttresses. Tree heights were measured using the altimeter function of a theodolite (Zeiss Ni2, Jena, Germany).

The vertical position of individual trees relative to the water level was determined from maximum flood marks of the last inundation (July 2002) on trunks relative to water levels recorded in Tefé (ISDM). For flooding–SG relationships we calculated the length of the terrestrial phase for the study site from the daily water-level records (1993–2000) at the port of Manaus, because data of water-level fluctuations of the study area are only available since 1993. Despite the long distance of ~550 km, the available data sets (1993–2000) of water-level fluctuations of the Japurá River in the MSDR and the lower Solimões River at Manaus show a strong correlation ($R^2 = 0.80$, $p < 0.001$), with a difference of only 9 cm in the mean amplitude (Schöngart *et al.* 2005).

In non-buttressed trees, two wood cores to the pith were extracted at breast height using an increment borer with a sharpened point (inner diameter 5 mm, length 500 mm, Haglöf Inc., Sweden). In buttressed trees, the cores were taken above the buttresses. Due to the different diameters of the sampled trees, the cores were separated to stretches between bark and pith after extraction. Samples of 2 cm length were drawn from the inner (pith), central, and outer (bark) sections of the wood cores using a caliper rule to the nearest 0.1 mm. The fresh volume of the samples was estimated multiplying their length with the core diameter. SG of each sample was calculated after 72 h oven drying at a temperature of 105 °C as the ratio between dry weight and volume of the green wood (Fearnside 1997; Nogueira *et al.* 2005). Due to the different wood properties of the sampled species, the core borer possibly caused minuscule damage at the core margins, which might result in a slight underestimation of the precise volume in some samples, and which could not have been quantified in the context of this study.

Data analysis

SG within the wood cores, between the cores of the same individual and between different individuals of the same species was calculated to derive mean, minimum and maximum SG for each species. Multiple regression analysis was calculated between the SG of the species as dependent variable, and mean water level at the tree site, tree diameters and tree heights as independent variables. Differences in the SG-variations between the sampled LV and HV trees were analysed by a T-test. Data available in literature were used to compare our SG values to those in other várzea inventories and to those in other Amazonian forest ecosystems.

RESULTS

Inundation, dbh and tree height

In the studied LV and HV forest plots, mean annual inundation was 4.1 m (min. 3.72, max. 5.81 m) and 2.2 m (min. 1.28, max. 3.02 m), corresponding to a mean inundation period of 111 d year⁻¹ and 36 d year⁻¹, respectively (Table 1). Mean dbh of the trees was 34.6 ± 17.8 cm in LV, and 35.5 ± 12.7 cm in HV. Tree height averaged 23.7 ± 4.4 m in LV and 28.4 ± 5.5 m in HV (see Appendix).

Relation between SG, flooding, dbh, tree height and core section

Mean SG in the LV species was 0.62 g cm^{-3} , whereas it was 0.57 g cm^{-3} in the HV species (Table 1). Highest and lowest SG was recorded in LV for *Piranhea trifoliata*

Table 2. Multiple regression analysis between mean SG as dependent variable, and mean dbh, mean tree height and mean flood height (1993–2002) at the study sites as independent variables. Beta values (standardised regression coefficients) measure how well each independent variable predicts the dependent variable when the other independent variable is held constant. The T-test examines whether the beta coefficient is significantly different from zero.

	Beta	Std. err. (Beta)	t (56)	p-level
Intercept			2.615	0.011
Tree dbh	-0.251	0.137	-1.828	0.072
Tree height	0.247	0.154	1.606	0.113
Flood height	0.366	0.142	2.568	0.012

Regression summary: $R^2 = 0.132$, $F(3.56) = 2.830$, $p < 0.046$

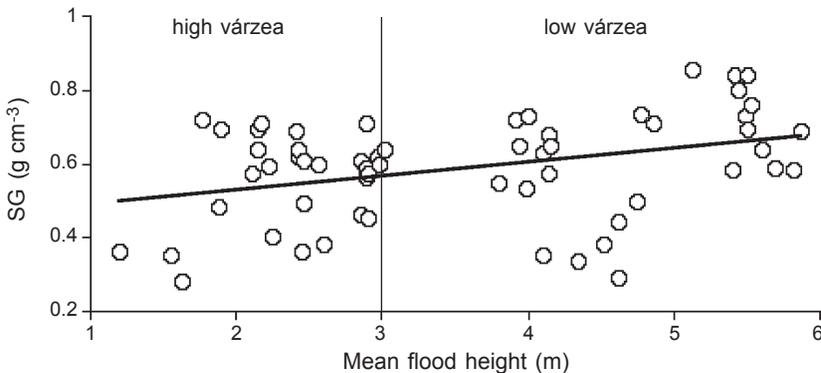


Fig. 2. Mean SG and location of the sampled upper canopy tree species along the flood-level gradient.

Baill. at 0.86 g cm^{-3} , and *Pseudobombax munguba* (Mart. & Zucc.) Dugand at 0.29 g cm^{-3} (Appendix). The multiple regression analysis indicated a significant relationship between SG and the position of trees along the flood gradient ($R^2 = 0.13$, $p = 0.046$, Table 2, Fig. 2). Despite significant correlation between dbh and tree heights in both plots (LV: $R^2 = 0.23$, $p < 0.001$; HV: $R^2 = 0.25$, $p < 0.001$), multiple regression analysis showed no significant relation between SG, tree diameters and heights. Nevertheless, at the interspecific level, a positive trend of increasing mean SG with increasing mean dbh was detected among the HV tree species. In the LV species, this trend was negative (Fig. 3).

Variance in SG between the LV and HV plots was considerably greater than variance within plots (T-value = 1.22, $F = 1.34$, $p = 0.22$). In the two species that occurred in both LV and HV plots, SG was lower in the HV trees. Mean SG in *Hevea spruceana* was 0.35 g cm^{-3} in LV, but it was 0.33 g cm^{-3} in HV. In *Tabebuia barbata*, mean SG was 0.83 g cm^{-3} in LV and 0.79 g cm^{-3} in HV.

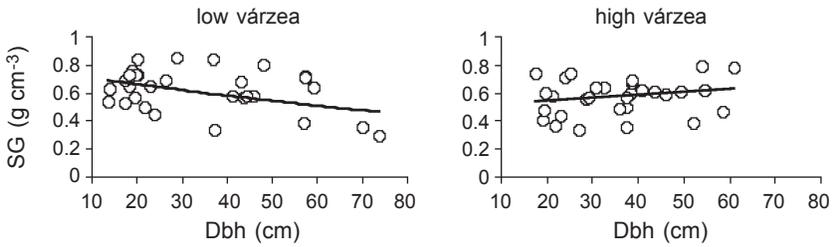


Fig. 3. Interspecific relation between mean SG of the sampled upper canopy tree species and mean dbh (non-significant).

Intraspecific SG variation between the sampled cores of the same individual was low ($6.0 \pm 2.9\%$), and showed a non-significant trend of increasing SG with increasing dbh among the three individuals of the same species ($23.1 \pm 16.0\%$). Generally, SG increased from bark to pith in all investigated species (see Appendix). Within LV, this increment averaged $11.9 \pm 7.3\%$, showing highest increases in *Paramachaerium ormosioides* Ducke (38.7%). In HV, increasing SG from bark to pith averaged $11.7 \pm 6.6\%$, being highest in *Pachira insignis* Gaertn. (26.6%).

DISCUSSION

Relation between SG and flooding

The results of the present study confirm that SG in Amazonian late successional várzea forests is linked to the location of trees along the flood gradient. Trees in highly inundated forests have higher mean SG than trees in shortly and low-flooded forests. Due to increased flood stress, tree growth in many LV trees is reduced during the high water period (Parolin *et al.* 2002). The different hydric conditions induced by the 'flood pulse' (Junk *et al.* 1989) lead to the reduction of growth in the aquatic phase, and to accelerated growth during the terrestrial phase. This leads to the formation of annual growth rings in the wood of many tree species (Worbes 1989, 1995, 1997; Schöngart *et al.* 2002; Schöngart 2003).

Depending on the environmental site conditions, trees within tropical forests can exhibit high growth plasticity. In general, tree growth is affected by several factors, such as climatic periodicity, edaphic conditions, tree architecture and competition for light (*e.g.*, Phillips *et al.* 1994; Silva *et al.* 1995; Ter Steege *et al.* 1995; Suzuki 1999; Clark & Clark 1999; Muller-Landau 2004). However, in Amazonian floodplain forests, periodical inundations become the most important driving factor influencing tree physiology and growth (Junk 1989; Worbes 1995). Due to the annually refreshed nutrient input by the rivers, the alluvial várzea soils are nutrient-rich in comparison to the surrounding uplands (Furch & Klinge 1989; De Oliveira *et al.* 2000). Local soil nutrient variations are low, and their influence on SG can possibly be neglected.

Our study indicates an increasing SG with increasing inundation time or depth for late successional canopy species. Depending on the location of trees along the flood gradient, the inundation period in HV trees hardly reaches more than two months per

year, and may fail completely during exceptional dry years with low floods (*e.g.*, during El Niño-events, Schöngart *et al.* 2004, 2005). Worbes *et al.* (1992) and Schöngart (2003) stated, that SG and mean diameter increment in várzea trees are negatively correlated. Due to the shorter aquatic phase, HV trees have a longer vegetation period compared to trees in LV, resulting in higher increment rates. This would explain the significantly lower SG mean in the HV trees in our study.

Comparing SG and mean diameter increment (MDI) in trees of *Macrobium acaciifolium* (Benth.) Benth. in nutrient-rich white-water and nutrient-poor black-water floodplain forests of the central Amazon, Schöngart *et al.* (2005) demonstrated that intraspecific SG and MDI variations are linked to current ecological processes, such as length of the terrestrial phase and nutrient supply. The results of the present study indicate that intraspecific SG variations in *Hevea spruceana* and *Tabebuia barbata* are determined by height and length of the annual inundations. However, phylogenetic effects may also play a role in determining the SG differences between LV and HV. Kubitzki (1989) mentioned that many várzea tree species are ecotypes originating from the surrounding terra firme. The ability of some species to develop different survival strategies to flooding favoured them to colonise the deeper flooded LV (Wittmann & Junk 2003). In fact, LV communities in central Amazonia show comparatively low floristic resemblance to the surrounding terra firme (floristic similarity less than 15%, own obs.), and many LV species seem to be endemic. Thus, a higher SG in LV trees might be the result of evolutionary induced long-term adaptations to high inundations.

SG in relation to core section, dbh and growth height

In all extracted wood cores, SG increased from bark to pith. These radial SG variations sometimes occur in late successional stages in contrast to light demanding and fast growing pioneer trees, which normally are characterised by bark to pith decreases (Wiemann & Williamson 1989). The vast majority of várzea late successional species are typical mature forest species, which regenerate below a dense and multi-layered canopy and which often persist several decades with low growth rates before reaching the upper canopy (Wittmann & Junk 2003). Besides low-light induced growth limitations, the periodical inundations may affect growth especially in late successional LV seedlings and saplings. In LV, species with comparatively small trees had higher SG than species represented by trees with large diameters, whereas in HV, an opposite trend was observed. Differences in life history certainly influence interspecific SG differences. However, we believe that current ecological processes may also explain the opposite SG-diameter trends found in LV and HV. Based on height measurements in seedlings from 31 várzea tree species, Parolin *et al.* (2002b) stated that there are different growth strategies of várzea tree seedlings along the flood-level gradient. Where submergence of tree seedlings is unavoidable, on the lower sites in the flooding gradient, seedlings had significantly lower shoot extension than on the higher elevated sites. LV species dispose of a complex system of adaptations to the high inundations, which is necessary because even rapid height increases would not lead to an escape from total submergence during the first years following establishment. The consequently slow growth results in comparatively high SG during the juvenile phase. When LV species reach

heights where part of the tree remains above the floodwaters, height and diameter growth are accelerated, resulting in lower SG during the mature phase. In HV, flooding is comparatively low and short, and less predictable. The occurrence of many immigrant species from the surrounding terra firme is expected, and establishment in many species might be restricted to consecutive years with comparatively low floods (Wittmann & Junk 2003). Floristic resemblance between central Amazonian HV and the surrounding terra firme could reach up to 30% (own obs.). Many of the immigrant species try to escape complete submergence by rapid height growth. After one or two years, they already dispose of heights permitting that the vegetation cone and part of the leaves remain above the highest flood levels. Consequently, comparatively low SG reflects this growth strategy in the juvenile phase. Once reaching heights where parts of the tree are established above the floodwaters, the low-light conditions below a dense overstorey reduce height and diameter increment, leading to a positive trend of SG increases over life span in the HV tree species.

SG in comparison to other Amazonian ecosystems

Several authors have stated that mean SG in várzea forests is low in comparison with non-flooded terra firme forests, which can be traced back to the high nutrient levels of the várzea (Parolin *et al.* 1998; Parolin & Worbes 2000). Due to the annual input of nutrients from the white waters, net productivity of várzea trees is high (Furch & Klinge 1989). The aboveground wood increment (AWI) in várzea forests (6.8–16.7 Mg ha⁻¹, Schöngart 2003) is significantly higher than in Amazonian terra firme forests (3.8 Mg ha⁻¹, Clark *et al.* 2001; 3.2–6.1 Mg ha⁻¹, Chambers *et al.* 2000). Prior studies comparing SG between várzea and other Amazonian ecosystems always included the fast growing pioneer species from LV forests (*e.g.* *Alchornea castaneifolia* A. Juss., *Salix martiana* Leyb. and *Cecropia latiloba* Miq.) that colonise freshly deposited sand bars and form monospecific stands at the highest flood levels (Worbes *et al.* 1992). These pioneers typically have low SG (0.30–0.39 g cm⁻³, Schöngart 2003), fast growth and short life cycles. In the present study, we excluded these species from our samples because they distort direct comparisons of SG means with those of other Amazonian ecosystems, where monospecific pioneer stands rarely occur.

Mean SG in the present study (0.59 g cm⁻³) was lower than mean SG reported in Central Amazonian black-water inundation forests (0.67 g cm⁻³ at lower Rio Negro, Parolin & Worbes 2000), Central Amazonian terra firme forests (0.67 g cm⁻³ in plots near Manaus, Chambers *et al.* 2000; 0.71 g cm⁻³ in plots near Manaus, Muller Landau 2004) and East Amazonian terra firme forests (0.70 g cm⁻³ in plots near Belém, Baker *et al.* 2004). However, it is well within the range of the estimated pantropical SG mean of 0.58 g cm⁻³ (Brown 1997) and to those SG means reported from Bolivian (Cerro Pelao), Peruvian (Tambopata and Cuzco Amazonico) and Ecuadorian (Jatun Sacha) lowland terra firme forests (0.62 g cm⁻³, 0.61 g cm⁻³ and 0.59 g cm⁻³, respectively; Baker *et al.* 2004).

Comparing SG and forest structure of 56 mature forest plots across Amazonia, Baker *et al.* (2004) derived a gradual increase of SG from Western to Eastern Amazonian terra firme. The authors traced this pattern to the high relative abundance of genera

with high wood density in Central and Eastern Amazonia, and the greater abundance of low wood density genera in Western Amazonia. We cannot confirm a possible spatial SG gradient across Amazonian várzea, until more data are available. SG means from western várzea forests (Bolivia, Peru and Ecuador) vary between 0.57–0.68 g cm⁻³ (Baker *et al.* 2004), whereas they range between 0.49–0.67 g cm⁻³ in eastern várzea forests near Manaus (Martius 1992; Parolin *et al.* 1998; Parolin & Worbes 2000).

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For the Appendix, see the next pages

Appendix – Mean dbh, mean tree height (n = 3) and mean SG of the sample species (n = 3 individuals, 6 cores) from outer (bark), central, and inner (pith) position of the cores.

Family	Low várzea species	Flood height (m)	Dbh (cm)	Tree height (m)	Mean SG (g cm ⁻³)			
					Outer	Central	Inner	Mean
Leguminosae	<i>Albizia subdimidiata</i> (Splitg.) Barn. & Gr.	4.4	59.4	28	0.60	0.64	0.67	0.64
Combretaceae	<i>Buchenavia oxycarpa</i> (Mart.) Eichl.	4.8	19.1	25	0.65	0.76	0.93	0.77
Polygonaceae	<i>Coccoloba</i> sp.	4.6	41.2	26	0.49	0.58	0.74	0.58
Combretaceae	<i>Combretum</i> sp.	4.0	57.1	30	0.33	0.38	0.44	0.37
Capparaceae	<i>Crataeva benthamii</i> Eichl.	5.1	48.2	23	0.70	0.80	0.88	0.78
Lecythidaceae	<i>Eschweilera albiflora</i> Miers	4.2	22.9	19	0.59	0.65	0.73	0.66
Lecythidaceae	<i>Eschweilera pedicellata</i> (Rich.) S.A. Mori	4.4	20.1	18	0.65	0.73	0.82	0.73
Leguminosae	<i>Etaballia dubia</i> (H.B. & K.) Rudd.	4.2	18.5	29	0.62	0.65	0.69	0.66
Rubiaceae	<i>Genipa americana</i> L.	4.3	45.9	24	0.54	0.58	0.61	0.57
Lecythidaceae	<i>Gustavia augusta</i> DC.	4.1	19.5	27	0.54	0.57	0.59	0.56
Euphorbiaceae	<i>Hevea spruceana</i> Muell. Arg.	3.9	37.2	18	0.31	0.33	0.38	0.35
Apocynaceae	<i>Himatanthus attenuatus</i> (Benth.) Wood.	4.3	17.3	24	0.48	0.53	0.57	0.52
Flacourtiaceae	<i>Homalium guianense</i> (Aubl.) Oken	4.2	26.4	31	0.63	0.69	0.76	0.69
Leguminosae	<i>Inga laterifolia</i> Miq.	3.7	43.7	26	0.54	0.57	0.59	0.56
Flacourtiaceae	<i>Laetia corymbulosa</i> Spruce <i>ex</i> Benth.	5.3	17.3	23	0.63	0.69	0.73	0.67
Tiliaceae	<i>Luehea cymulosa</i> Spruce <i>ex</i> Benth.	4.6	70.1	24	0.29	0.35	0.41	0.35
Euphorbiaceae	<i>Mabea nitida</i> Spruce <i>ex</i> Benth.	4.3	13.8	19	0.5	0.54	0.57	0.54
Lauraceae	<i>Nectandra amazonum</i> Nees	5.2	23.8	23	0.35	0.44	0.49	0.44
Annonaceae	<i>Oxandra riedeliana</i> R.E. Fries	4.9	21.6	24	0.45	0.49	0.54	0.51
Leguminosae	<i>Paramachaerium ormosioides</i> Ducke	4.6	43.0	21	0.49	0.68	0.78	0.66
Euphorbiaceae	<i>Piranhea trifoliata</i> Baill.	4.6	28.8	28	0.77	0.85	0.90	0.86
Sapotaceae	<i>Pouteria elegans</i> (A. DC.) Baehni	4.5	20.0	26	0.65	0.73	0.79	0.72
Bombacaceae	<i>Pseudobombax munguba</i> Dug.	5.0	73.8	24	0.17	0.29	0.31	0.29
Elaeocarpaceae	<i>Sloanea excelsa</i> Ducke	4.9	57.3	19	0.66	0.72	0.79	0.71
Polygonaceae	<i>Symmeria paniculata</i> Benth.	5.6	18.5	14	0.64	0.73	0.82	0.73
Bignoniaceae	<i>Tabebuia barbata</i> (E. Mey) Sw.	4.7	37.1	28	0.73	0.84	0.94	0.83
Clusiaceae	<i>Tovomita spruceana</i> Planch. & Triana	4.4	20.1	22	0.82	0.84	0.87	0.84
Leguminosae	<i>Vatairea guianensis</i> Aubl.	4.4	57.5	31	0.65	0.71	0.77	0.71
Verbenaceae	<i>Vitex cymosa</i> Bert. <i>ex</i> Spreng.	4.9	44.4	16	0.51	0.58	0.66	0.57
Leguminosae	<i>Zygia ampla</i> (Spruce <i>ex</i> Benth.) Pitt.	4.3	14.0	22	0.57	0.63	0.74	0.61
	Mean	4.5	34.6	23.7	0.55	0.62	0.69	0.62

Continued on the next page

Appendix – continued

Family	High várzea species	Flood height (m)	Dbh (cm)	Tree height (m)	Mean SG (g cm ⁻³)			
					Outer	Central	Inner	Mean
Lauraceae	<i>Aniba terminalis</i> Ducke	2.4	28.7	19	0.53	0.56	0.60	0.57
Tiliaceae	<i>Apeiba aspera</i> Aubl.	2.1	19.1	27	0.33	0.40	0.50	0.42
Moraceae	<i>Brosimum rubescens</i> Taub.	2.2	41.0	34	0.56	0.62	0.69	0.62
Malpighiaceae	<i>Byrsonima</i> sp.	2.4	46.0	30	0.57	0.59	0.61	0.59
Meliaceae	<i>Cedrela odorata</i> Blanco	2.7	49.3	41	0.53	0.61	0.79	0.62
Euphorbiaceae	<i>Discocarpus brasiliensis</i> Klotzsch	2.3	32.5	24	0.53	0.64	0.74	0.63
Lecythidaceae	<i>Eschweilera parvifolia</i> Mart. ex DC.	2.4	24.0	26	0.68	0.71	0.76	0.71
Annonaceae	<i>Guatteria pilosula</i> Planch & Lind.	1.8	23.0	23	0.31	0.43	0.51	0.42
Moraceae	<i>Helicostylis scabra</i> (Macbr.) C.C. Berg	2.1	25.2	24	0.68	0.74	0.87	0.76
Euphorbiaceae	<i>Hevea spruceana</i> Muell. Arg.	2.3	27.1	29	0.31	0.33	0.36	0.33
Euphorbiaceae	<i>Hura crepitans</i> L.	2.0	52.3	35	0.29	0.38	0.47	0.38
Aquifoliaceae	<i>Ilex</i> sp.	2.6	61.2	35	0.74	0.78	0.84	0.78
Leguminosae	<i>Inga pilosula</i> (L.C. Rich) Macbr.	2.8	21.4	22	0.47	0.58	0.68	0.61
Leguminosae	<i>Inga splendens</i> Benth.	2.3	54.6	38	0.57	0.62	0.68	0.61
Apocynaceae	<i>Malouetia tamaquarina</i> A. DC.	1.9	58.7	32	0.43	0.46	0.48	0.45
Moraceae	<i>Naucleopsis kruckovii</i> (Std.) C.C. Berg	2.4	19.8	27	0.53	0.60	0.71	0.61
Lauraceae	<i>Ocotea cymbarum</i> Kunth	2.8	43.7	27	0.55	0.61	0.66	0.61
Annonaceae	<i>Oxandra polyanthera</i> R.E. Fries	2.4	29.3	26	0.53	0.57	0.61	0.56
Bombacaceae	<i>Pachira insignis</i> Gaertn.	2.0	37.6	30	0.34	0.49	0.6	0.47
Sapotaceae	<i>Pouteria procera</i> (Mart.) K. Hammer	2.1	30.9	29	0.58	0.64	0.71	0.64
Euphorbiaceae	<i>Sapium marmieri</i> Huber.	1.8	37.4	27	0.30	0.35	0.41	0.36
Elaeocarpaceae	<i>Sloanea guianensis</i> Benth.	2.8	17.7	20	0.72	0.74	0.78	0.74
Sterculiaceae	<i>Sterculia frondosa</i> Spruce ex Benth.	2.1	36.0	32	0.40	0.48	0.53	0.47
Bignoniaceae	<i>Tabebuia barbata</i> (E. Mey) Sw.	2.6	54.1	35	0.74	0.79	0.85	0.79
Dichapetalaceae	<i>Tapura juruana</i> (Ule) Rizz.	2.6	38.4	24	0.57	0.60	0.71	0.62
Combretaceae	<i>Terminalia dichotoma</i> E. Mey.	2.4	38.6	26	0.61	0.67	0.72	0.66
Myristicaceae	<i>Virola calophylla</i> Warb.	2.4	38.8	33	0.63	0.69	0.75	0.7
Clusiaceae	<i>Vismia macrophylla</i> H.B. & K.	2.2	37.4	21	0.53	0.57	0.62	0.57
Annonaceae	<i>Xylopia calophylla</i> R.E. Fries	1.9	21.8	23	0.34	0.36	0.38	0.35
Annonaceae	<i>Xylopia ocantra</i> R.E. Fries	2.2	19.6	33	0.45	0.47	0.49	0.47
	Mean	2.3	35.5	28.4	0.51	0.57	0.64	0.57