SAPWOOD AREA IN SEVEN COMMON TREE SPECIES OF CENTRAL AMAZON FLOODPLAINS

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Abstract

The sapwood area of seven common tree species in Amazonian floodplains (*Albizia multiflora, Crateva benthamii, Laetia corymbulosa, Nectandra amazonum, Pseudobombax munguba, Tabebuia barbata, Vitex cymosa*) was analysed in field measurements. A borehole was inserted in the stem on two opposite positions and filled with pigment dye crimson red by syringe. After one hour a core sample was extracted with an increment borer exactly 10 cm above the point of injection. Tree diameter and the length of the core sample coloured red were measured, and the total sapwood area of the individual was calculated. A total of 138 trees was sampled, with 14 to 30 individuals per species. Mean sapwood area ranged from 73 cm² in *Crateva benthamii* to 139 cm² in *Pseudobombax munguba*. There was no significant difference between the average sapwood area in the deciduous and the evergreen species. Correlations between sapwood area and stem diameter were high in all species with the exception of *Laetia corymbulosa*.

Key words: sapwood thickness, sapwood area, hydroactive xylem, Amazonian floodplain trees, várzea.

Resumo

A área do alburno foi determinada para sete espécies de árvores comuns nas planícies de inundação da Amazônia (*Albizia multiflora, Crateva benthamii, Laetia corymbulosa, Nectandra amazonum, Pseudobombax munguba, Tabebuia barbata, Vitex cymosa*). Com o auxílio de um trado foram feitas duas perfurações em lados opostos nos troncos das árvores a serem analisadas. Em cada orifício foi injetada uma tintura vermelha. Após uma hora foi extraída, com o auxílio de um trado, uma amosta do lenho 10 cm acima do ponto de injeção. Para cada amostra colorida de vermelho foi determinado o diâmetro e o comprimento e, com base nesses dados, foi calculada a área total do lenho ativo de cada espécie. A área média variou entre 73 cm² *em Crateva benthamii* e 139 cm² em *Pseudobombax munguba.* Não foram constatadas diferenças significativas entre a média das espécies decíduas e perenifólias. As correlações entre a área do alburno e o diámetro do tronco, com exceçao de *Laetia corymbulosa,* foram sempre altas.

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Palavras-chave: espessura do alburno, área do alburno, lenho hidroativo, árvores das planícies de inundação da Amazônia, planície de inundação, várzea.

Introduction

Large areas of Amazonia are covered by floodplains (300.000 km^2; Junk, 1997). This ecosystem harbours several hundred endemic tree species (Worbes, 1997; Wittmann & Junk, 2003; Parolin *et al.,* in press), many of them with commercial value. They have various adaptations and life history strategies (Parolin *et al.*, 2004) which allow them to cope with periods of waterlogging or even submergence which exceed 7 months per year, with water columns of up to 8 m (Junk, 1989; Junk *et al.*, 1989). The functioning of the ecosystem and specifically of the trees are still poorly understood. The present paper aims at giving insight into one aspect of tree characteristics and function, the active sapwood area, determined with a simple method.

Trees exhibit very different patterns of water transfer within the sapwood (Granier *et al.,* 1996a). In temperate oak trees (*Quercus petraea*), 80% of the sapflow circulates in the outer 1 cm of sapwood of the trunk – the sapwood total thickness is about 19 mm in that species (Granier *et al.,* 1996a). Sapwood thickness increases with increased age of the tree and maintains a relatively constant width after a specified time, which is species-specific, through the life of the tree. After this species-specific time, most of the heartwood is formed annually (Yang & Benson, 1997).

Failure to recognize that not all sapwood is functional in water transport regularly introduces systematic bias into estimates of both tree and stand water use (Wullschleger & King, 2000). Therefore, the correct determination of active sapwood is fundamental for extrapolations to transpiration (Granier *et al.,* 1996b), and to calculate actual sap flow (Granier, 1996), i.e. the amount of water transported in a tree which in this way can be measured without felling. Estimating sap flux through sapwood area decides the precision of heat pulse application for detailed measurements of sap flux density, radial variation in sap flux density being a function of sapwood thickness (Zhou *et al.,* 2002). As Granier *et al.* (1996a) suggest, preliminary measurements on the path of water transfer and on the variations of sapflow within a tree stem are necessary before further analysing water supply and transport, and other parameters which base on the size of the water-transporting stem section.

Methods

Seven common tree species of Central Amazonian floodplain forests were analysed in this study: *Albizia multiflora* (Kunth) Barneby & J.W. Grimes (Fabaceae, paricarana), *Crateva benthamii* Eichler (Capparaceae, catoré), *Laetia corymbulosa* Spruce ex Benth. (Flacourtiaceae, sardinheira), *Nectandra amazonum* Nees (Lauraceae, louro), *Pseudobombax munguba* (Mart. & Zucc.) Dugand (Bombacaceae, munguba), *Tabebuia barbata* (E. Mey.) Sandwith (Bignoniaceae, capitari), and *Vitex cymosa* Bertero ex Spreng. (Verbenaceae, tarumã).

The seven species were chosen basing on their frequent occurrence at the study site on the Ilha de Marchantaria, a river island 15 km upstream from the confluence of the Amazon (Solimões) River with the Rio Negro, northeast of Manaus, Brazil (03°15´S, 59°58´W). A total of 138 a dult trees was sampled, with 14 to 30 individuals per species (Table 1). Two species were evergreen, four deciduous and one stem-succulent / deciduous (Schöngart *et al.,* 2002). They were subjected to a mean inundation height of 5.5-6.8 m measured on the tree stems.

Measurements were performed between 27.5.99 (highest river water levels) and 6.10.99 (lowest river water levels). Since sapwood thickness generally remains constant at the base of the tree, but increases near the base of the live crown, and decreases near the top of the tree (as was stated for cedar trees, www.yale.edu/edex/cedar/growth/growth.htm), all samples were taken at the same height (1.30 m from the ground). A borehole of 3 mm diameter and 5 cm depth was inserted in the stem on two opposite positions. The borehole was completely filled with pigment dye crimson red by syringe. The outer diameter of the syringe lock fitted exactly into the borehole and the syringe remained in the stem during the experiment tightening the hole. After one hour a core sample was extracted with an increment borer exactly 10 cm above the point of injection. Tree diameter and the length of the core sample coloured red (b) were measured, and the total sapwood area of the individual was calculated with the formula $A = 2 \Pi r b + \Pi b^2$, where r is the tree radius and b the coloured distance of the sampled core (Goldstein *et al.,* 1998; Motzer, 1998; Dünisch & Morais, 2002).

Results and discussion

Sapwood thickness (hydroactive xylem, or active xylem depth) ranged from 16 mm to 38 mm (Table 1). It lies in the range of other tropical (20-35 mm in Venezuelan tropical forest; Anhuf *et al.,* 1999) and temperate forest species (19-36 mm; Granier *et al.,* 1994). It is lower than in Brazilian savanna trees where the sapwood depth ranged between 30-60 mm in six tree species (Bucci *et al.,* 2004). In most species analysed in the present study, sapwood thickness did not vary much between individuals, with the exception of *Pseudobombax munguba* and *Albizia multiflora*, which had a high standard deviation. The reason for this might be the social position in the tree stand or tree height (Motzer, pers. comm.). It was observed that the relation between leaf area and sapwood area sinks with increasing tree height (Phillips *et al.,* 2001). Perhaps

Pseudobombax munguba and *Albizia multiflora* are higher and have more exposed crowns than other species with the same dbh, which – if there is a comparable leaf area – means higher water loss through transpiration, and this again might have lead to the formation of a more efficient water conducting system.

Also in temperate trees sapwood thickness can be extremely variable, e.g. in sugar maple (Wiemann *et al.,* 2004) or in *Liriodendron tulipifera* where sapwood thickness ranged from 21 to 148 mm (Wullschleger & King, 2000).

Mean active sapwood area ranged from 73 cm² in *Crateva benthamii* to 139 cm² in *Pseudobombax munguba* (Table 1). These values are in the range or lower than in trees of upland tropical (Granier *et al.,* 1996b; Andrade *et al.,* 1998; Goldstein *et al.,* 1998; Anhuf *et al.,* 1999; Table 2), temperate (Lu *et al.,* 1995), or mediterranean forests (Granier *et al.,* 1990). They are higher than trees of tropical early successional forests (Goldstein *et al.,* 1998), Brazilian cerrado (Meinzer *et al.,* 1999), or mediterranean forests (Loustau *et al.,* 1996).

The fact that the only stem-succulent (deciduous) tree, *Pseudobombax munguba* (Schöngart *et al.,* 2002), has the highest active sapwood area and thickness (139 cm², Table 1) might state the hypothesis that this species possesses different adaptive strategies than other deciduous species (Schöngart pers. comm.), their growth rhythm being triggered by different external factors than in other deciduous species (Worbes, 1999; Borchert & Rivera, 2001). In the case of *Pseudobombax munguba*, phenology is triggered by precipitation and not by the floodpulse (Schöngart *et al.*, 2002).

The replicate cores taken from the trees revealed that sapwood thickness was mostly uniform around the circumference of the trees. Although some authors state that the sapwood area depends on the amount of available water and transpirational acitivities (Lu *et al.,* 1995; Drake & Franks, 2003; Motzer, 1998), in our study we could not detect these differences between the period of highest and lowest water levels. The differences found in *Pinus pinaster* in two different studies (Table 2; Granier *et al.,* 1990, 1996a; Loustau *et al.,* 1996) indicate that site conditions may play a role for sapwood area in this species.

Sapwood thickness generally increases with tree diameter (Wiemann *et al.,* 2004). Correlations between sapwood area and stem diameter were high in all species with the exception of *Laetia corymbulosa* (r^2 0.54) (Figure 1). As other studies have shown, this correlation was to be expected (Zhou *et al.,* 2002).

The sapwood portion of the species chosen here ranged between 54 and 92% of total stem cross sectional area (Table 1). In Amazonian terra firme trees Dünisch & Morais (2002) found 36% for *Swietenia macrophylla*, 78% in *Cedrela odorata* and 93% in *Carapa guianensis*. In temperate *Liriodendron tulipifera* the fraction of functional sapwood averaged 0.66 ± 0.13 (Wullschleger

& King, 2000). However, sapwood area may cover almost 100% of the cross sectional area in some tropical forest trees (Goldstein *et al*., 1998; Phillips *et al*., 2001; Motzer, pers. comm.).

Sapwood changes to heartwood over time (Coyea *et al.,* 1990) so that clear delimitations of the boundary were sometimes difficult to find. Only in two species (*Crateva benthamii, Tabebuia barbata*; Table 1) all measured individuals reacted to the treatment, whereas in the other species a percentage of up to 23% did not show a measureable reaction to the colouring. This problem appeared also in other Amazonian species of the non-flooded terra firme (Dünisch & Morais, 2002).

The data give an insight into the range of sapwood area in some common tree species of Amazonian floodplains. We hope that in the near future more data are available to allow the estimation of correlations with leaf area data by measuring sapwood area with the methods described above. In temperate trees, total sapwood area was consistently more highly correlated with foliar weight and leaf area than were other stem dimensions (e.g. stem cross-sectional area, and current sapwood area at breast height; Meadows & Hodges, 2002). The speculation that more of the sapwood than just the most recent one or two growth rings may be active in water conduction in bottomland species in warm climates (Meadows & Hodges, 2002) should also be analysed in Amazonian floodplain trees.

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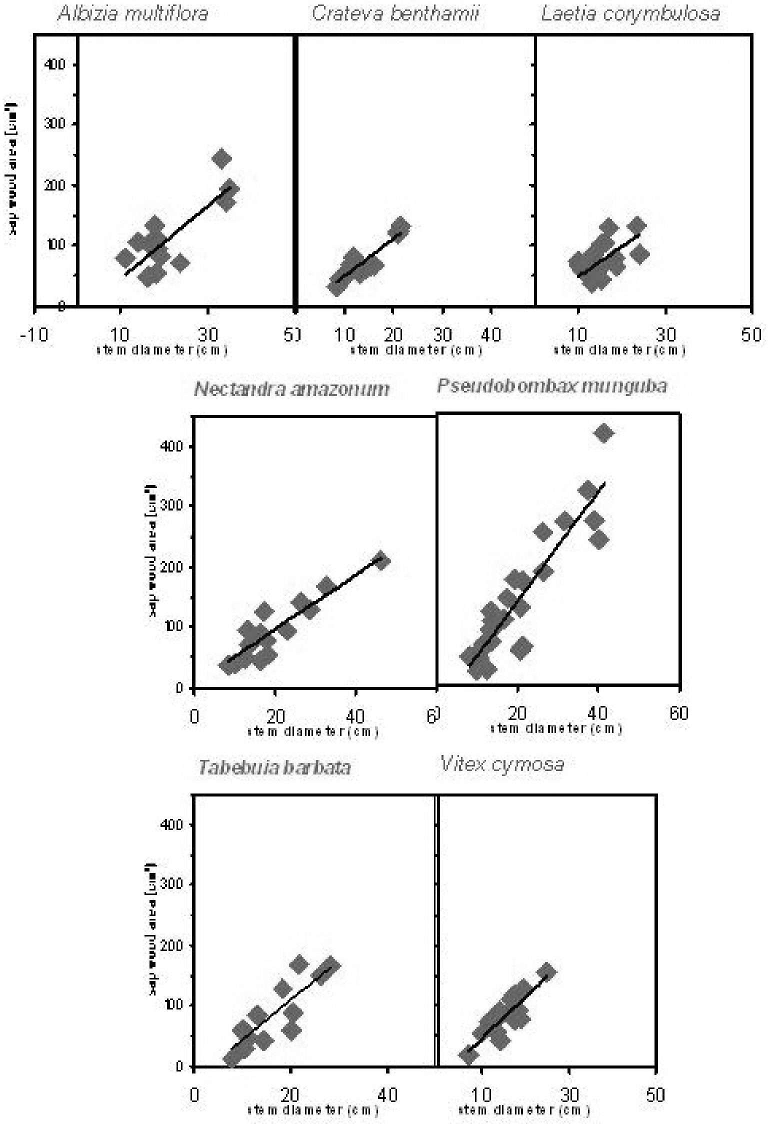

Figure 1: Correlation between sapwood area and stem diameter in the seven study species.

Table 1: Species analysed (in alphabetical order), with tree phenology (Schöngart *et al.,* 2002), number of sampled individuals (n), tree diameter (mean and standard deviation), sapwood area (mean and sd), percentage of sapwood area on total stem diameter, and percentage of trees that did not show a measureable reaction to the colouring treatment.

Species	phenology	n	mean tree diameter (cm)	sd	mean sapwood thickness (mm)	sd	mean sapwood area (cm²)	sd	% sapwood area / stem diameter	correlation r² sap wood area / stem diameter	indiv. with no reaction (%)
Laetia corymbulosa	evergreen	22	15.1	4	16	6	76.1	29	42.5	0.54	22.7
Nectandra amazonum	evergreen	18	19.6	9	29	36	94.9	49	31.5	0.90	11.1
Crateva benthamii	deciduous	16	13.7	4	17	3	72.9	28	49.5	0.92	0.0
Tabebuia barbata	deciduous	14	15.9	6	16	6	81.9	51	41.3	0.86	0.0
Vitex cymosa	deciduous	20	15.2	4	17	4	83.2	33	45.9	0.85	10.0
Albizia multiflora	deciduous	18	20.1	7	30	52	109.0	56	34.4	0.81	16.7
Pseudobombax munguba	stem-succulent	30	19.8	9	38	57	138.6	99	45.0	0.91	6.7

Table 2: Mean sapwood cross-sectional area in trees of different studies.

Study	Environment	Range of mean sapwood cross-sectional area (cm^2)
Present study	tropical floodplain forest	73 -139
Granier *et al.,* 1996b	tropical rain forest, French Guiana	103-796
Anhuf *et al.,* 1999	tropical forest, Venezuela	26-646
Andrade *et al.,* 1998, Goldstein *et al.,* 1998	tropical forest, Panama	2-51
Meinzer *et al.,* 1999	Brazilian cerrado	6-39
Loustau *et al.,* 1996	Mediterranean forest, Portugal	32-67
Granier *et al.,* 1994	Mediterranean forest, France	147-293
Granier *et al.,* 1990	Mediterranean forest, France	181-533
Lu *et al.,* 1995	temperate forest, Norway	99-275