

Leaf structure in trees of Central Amazonian floodplain forests (Brazil)*

by

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Abstract

Leaf anatomy and morphology in 23 common arboreal species representing 20 families from Central Amazonian white- (várzea) and blackwater (igapó) floodplain forests (Brazil) were analyzed with SEM microscopy. Species differed in leaf-fall behavior (evergreen, deciduous) as well as in the fate of submerged leaves (species either shed or keep their submerged leaves). Leaves of all species showed various traits generally related to leathery leaves and/or xeromorphism, e.g., large epidermal cells, thick outer epidermis walls, thick cuticula, compact spongy parenchyma with only few and small intercellular spaces, sunken stomata, and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath. No trend was found to differentiate evergreen from deciduous species by leaf morphology and anatomy. Species that shed their submerged leaves showed similar characteristics than species that keep their submerged leaves, significant differences were found only in the leathery appearance and the thickness of the outer wall and cuticula. Keeping submerged leaves apparently does not require major morphological or anatomical modifications. Species from the nutrient rich várzea showed similar characteristics as species of the nutrient poor igapó. When the present data set was combined with data from a previous study (total of 34 species) the frequency of two leaf characters was significantly different between floodplain types with igapó species showing a somewhat higher degree of xeromorphism. As leathery and/or xeromorphic leaves are the typical pattern in tropical trees, leaf structures found here are unlikely to represent adaptations to floodplain conditions. The scarcity of similarities in confamilial or congeneric species also gives further evidence for this interpretation. The relation of xeromorphism with drought resistance and nutrient deficiency in Central Amazonian floodplains is discussed.

Keywords: **Amazon, várzea, igapó, leaf anatomy, leaf morphology, xeromorphism.**

Resumo

A anatomia e a morfologia foliar de 23 espécies arbóreas representando 20 famílias das florestas inundáveis de águas brancas (várzea) e pretas (igapó) da Amazonia Central (Brasil) foram estudadas com um microscópio de varredura. As espécies diferenciaram-se no seu comportamento foliar (sempre-verdes e deciduas) assim como no "destino" das folhas submersas (mantê-las ou não). As folhas de todas as espécies

*Dedicated to Prof. Dr. Wolfgang J. Junk on the occasion of his 60th anniversary.

apresentaram várias características descritas na literatura como xeromórficas, como por exemplo células grandes na epiderme, paredes celulares exteriores da epidermis espessas, cutícula espessa, parênquima lacunoso compacto com alguns pequenos intercelulares, estômatos aprofundados na epiderme, feixes vasculares transcorrentes com cinto esclerenquimático forte em volta. Não foi encontrada uma tendência que pudesse diferenciar as espécies sempre-verdes das decíduas quanto a anatomia e morfologia foliar. Espécies que perdem as folhas submersas apresentam características foliares similares a espécies que mantêm as folhas submersas, diferenças significantes apenas foram encontradas na aparência coreácea a na espessura das paredes celulares exteriores e da cutícula. Manter folhas submersas aparentemente não requer características morfológicas ou anatômicas adicionais ou diferentes. As espécies arbóreas da várzea (rica em nutrientes) apresentaram características similares às espécies do igapó (pobre em nutrientes). Foram encontradas diferenças significantes para duas características em uma avaliação deste estudo com um anterior (total de 34 espécies). As espécies do igapó parecem ter um grau de xeromorfismo um pouco mais alto do que as da várzea. Como folhas xeromórficas e/ou coreáceas são o padrão típico para florestas tropicais, as estruturas encontradas neste estudo provavelmente não representam adaptações às condições de inundação. A escassez de similaridades entre espécies confamiliares e congênicas confirma esta interpretação. Uma possível relação entre o xeromorfismo e uma resitência à secura e à uma deficiência de nutrientes nas áreas alagáveis da Amazônia Central é discutida.

Introduction

Floodplain forests of Central Amazonia are subjected to an annual inundation of up to 8 m depth and a duration of up to 6.5 months (JUNK et al. 1989; JUNK & KRAMBECK 2000). Tree species that do not shed their leaves during the whole year including the inundation period are generally classified as evergreen species whereas species that shed their leaves, usually during rising water levels, are referred to as deciduous. Most of the evergreen species even keep their submerged leaves and maintain their capacity for photosynthesis (FURCH 1984; SCHLÜTER & FURCH 1992; SCHLÜTER et al. 1993; WALDHOFF et al. 1998, 2000, 2002a).

Previous investigations on leaf anatomy and morphology in eleven common arboreal species from Central Amazonian floodplains demonstrated that all species showed leaf traits generally considered as leathery and/or xeromorphic, irrespective of leaf-fall behaviour (evergreen/deciduous) and the fate of submerged leaves (submerged leaves shed or kept)(WALDHOFF & FURCH 2002b). These findings were surprising as species that keep their submerged leaves were expected to show a higher degree of xeromorphism in leaves than those that shed them, as they have to withstand the mechanical impact of the inundation and avoid influx of water (SCHLÜTER et al. 1993). This contribution seeks to verify whether these findings hold when considering a greater species spectrum of Amazonian floodplain trees.

Leaf morphology and anatomy were therefore analyzed in further 23 arboreal species, twelve from black- and eleven from whitewater floodplain forests of Central Amazonia (igapó and várzea, respectively; cf. PRANCE 1979, 2001). As indicated by the previous study (WALDHOFF & FURCH 2002b) leaves are expected to show xeromorphic traits typically found in tropical trees in general (ROTH 1984), and that the fate of submerged leaves is not reflected by specific morphological or anatomical characteristics. Unlike species from várzea forests igapó species originated mainly from woodland and savannah vegetation on oligotrophic white sand (KUBITZKI 1989a, b) which might be reflected in a higher degree of xeromorphism due to more severe drought conditions on white sand. A separate analysis was therefore performed to address this question. A combined data set of both studies (17 várzea and 17 igapó

species, representing 24 families) was additionally analyzed.

Material and methods

Leaf morphology and anatomy was studied in 23 selected species with different leaf-fall behaviour from várzea and igapó representing 20 species-rich families (cf. HALLÉ et al. 1978; WORBES 1997). Species differed in leaf-fall behaviour (evergreen, deciduous) as well as in the fate of submerged leaves (species either shed or keep their submerged leaves). Nine of the ten evergreen species keep their submerged leaves whereas all of the 13 deciduous species shed them (Table 1).

Mature sun leaves (6-11 months) were collected in May 1996 (rising water levels) from trees located in floodplain forests on Marchantaria Island (located in the Rio Solimões/Amazonas, várzea, 15 km southwest of Manaus) and along the Tarumã Mirim River (igapó, 20 km north-east of Manaus). They were investigated with a scanning electron microscope (LEITZ SEM 1000). Surface cuttings and cross-sections of material were transported in 70 % alcohol from Manaus (Brazil) to Kiel (Germany). There they were dehydrated and transferred into acetone (steps 25 %, 50 %, 70 %, and 100 % acetone), dried using the critical-point method and then sputtered with gold. Stomata and glands were counted on several samples from the leaf lamina between the principal veins. The size of the cells and the thickness of cuticula and the epidermis wall were measured in typical cells on the photographs presented here and others of higher magnification.

Results

A leathery appearance of the leaves was significantly associated with the character of keeping submerged leaves (Tables 1, 6). Size of the upper and lower epidermis cells varied irrespectively of leaf-fall behavior (Tables 2, 6). A medium to very thick outer wall and cuticula was more frequent among species that keep submerged leaves (Fig. 11) than in those that shed them (Fig. 9), although differences were significant for the lower epidermis only (Tables 2, 6). Most of the species showed medium or small cells in the palisade parenchyma and the spongy parenchyma without apparent relation to leaf fall behavior or fate of submerged leaves (Tables 2, 6; Figs. 3, 11).

Eight out of the 23 species showed more than one layer of palisade parenchyma and another three species showed one layer on both sides of the leaf (Fig. 7). In the former species cell length decreased towards the inner layers (Table 2). No association was found between leaf-fall behavior or fate of submerged leaves and the number of layers of the palisade parenchyma (Table 6).

Leaves of the palm species *Bactris bidentula* showed palisade parenchyma cells densely filled with unidentified organelles (Fig. 5). The compactness of the spongy parenchyma ranged from loose and regular in four species (Figs. 7, 11), to compact to very compact in the other species (Table 3; Figs. 3, 5). It was not associated with leaf-fall behavior or fate of submerged leaves (Table 6). The spongy parenchyma was completely missing in *Couepia paraensis* and *Salix humboldtiana*.

The extension of the vascular bundles as well as the form of the sclerenchymatous sheath varied between species in different combinations (Table 3) and showed no association with leaf-fall behavior or fate of submerged leaves (Table 6). *Bactris bidentula* and *Bactris maraja* presented fibres between the bundles (Figs. 3, 5).

Six species had stomata level with the other epidermis cells. All other species had sunken stomata, some even showed stomata buried in a cavity or pit-like hole (Table 4; Figs. 1, 2, 4, 8, 12-14). In four species the stomata were sunken to an extent that made them invisible from the leaf surface (Table 4). Stomata form varied irrespectively of leaf-fall behavior or fate of submerged leaves (Table 6). Six species showed amphisto-

matic stomata. In *Cecropia latiloba* stomata were found on the upper leaf side only. Stomata density at the lower leaf side varied between 25 and 2339 mm⁻² (Table 4) and did not differ significantly between species that keep or shed submerged leaves (Table 6).

Glandular hairs were found in three species whereas seven species showed non-glandular hairs (Table 5; Figs. 9, 10). The lower leaf surface of *Cassia leiandra*, and *Quiinia shytidopus* was covered with papillas (Fig. 14). Six species exhibited wax deposits, 13 showed cuticular ornamentations, mostly at the lower leaf side (Table 5; Figs. 5, 6, 8, 12).

No significant differences in leaf appearance, size of epidermis cell and outer cell walls, palisade parenchyma, sclerenchyma and stomata properties were found between species with regard to their habitat (várzea or igapó) (Table 7).

Discussion

Leaf anatomy and morphology varied greatly between the 23 species reflecting their taxonomic diversity. All species showed a varying number of leaf characters generally associated with xeromorphism, e.g., large-celled epidermis with water-storing cells, thick outer epidermis walls, thick cuticula, compact spongy parenchyma with few and small intercellular spaces, sunken stomata, and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath (cf. ROTH 1984; FAHN & CUTLER 1992; BOLHÅR-NORDENKAMPF & DRAXLER 1993; LINDORF 1993).

Among the characters investigated only three allowed a differentiation of species that keep from those that shed their submerged leaves by leaf morphology and anatomy: leathery leaves and thick outer wall and cuticula on the upper as well as the lower epidermis were associated with keeping submerged leaves. However, a leathery appearance is at least in part due to a thick outer wall and cuticula, i.e. these characters might in fact represent just one trait (but see also VARESCHI 1980).

Sunken stomata is a common feature in xeromorphic leaves (ROTH 1984; BOLHÅR-NORDENKAMPF & DRAXLER 1993). FAHN & CUTLER (1992) reported that only 34 % of xeromorphic species (35 dicotyledons, 33 monocotyledons, 3 gymnosperms) from arid and semi-arid environments possess sunken stomata. LINDORF (1993) studied 17 tree species from Venezuelan tropical rainforests and found no species with sunken stomata. From this perspective the presence of sunken stomata in 17 out of 23 species studied seems remarkable. Two of the species that showed stomata level with the other epidermis cells (*Tabernaemontana juruana* and *Tovomita macrophylla*) keep submerged leaves which is the first record of this type of leaf-fall behavior (cf. WALDHOF et al. 2002a, b; FERNANDES-CORRÊA & FURCH 1992; SCHLÜTER & FURCH 1992). It is doubtful whether *Cecropia latiloba* had epistomatic leaves, as the lower epidermis was covered by long, filamentous hair, concealing the epidermis surface. The lower epidermis is likely to present stomata as well, which might additionally be hidden in crypts, as described for the congeneric *Cecropia sciadophylla* (ROTH 1984), and which is common in leaves of some xerophytes (BOLHÅR-NORDENKAMPF & DRAXLER 1993).

The stomata densities lie in the typical range described for tropical trees (ROTH 1980, 1984) and other species from Amazonian floodplain studied so far (SCHLÜTER & FURCH 1992; WALDHOF et al. 2002a, b). Species with higher stomata densities tended to show small epidermis cells (e.g. *Mouriri guianensis*, *Ouratea hexasperma*,

Quiinia rhytidopus) and vice versa (e.g. *Acmanthera latifolia*, *Tabernaemontana juruana*, *Tovomita macrophylla*). According to ROTH (1980) this phenomenon might have a spatial origin.

The palisade parenchyma cells in *Bactris bidentula* were densely filled with presumably chloroplasts. Such a high density of chloroplasts in palisade parenchyma had not been described hitherto. It might be helpful for a possible photosynthesis under the water when light is the limiting factor (FURCH et al. 1985).

About half of the species showed glandular or not-glandular hairs, two species presented papillas, and six species showed wax layers. Cuticular ornamentations, mostly well-developed striations, were found in most species. These have been interpreted in the literature as assisting water to channel off the leaf surface (BARTHLOTT 1990; CARPENTER 1994).

Similarities between species pairs of the same family were scarce (data of the present study pooled with WALDHOFF & FURCH 2002b): Similar cuticular ornamentations were found in *Senna reticulata* and *Cassia leiandra* (Caesalpiniaceae), and *Alchornea* sp. and *Maprounea guianensis* (Euphorbiaceae). On the contrary, *Eugenia inundata* and *Psidium acutangulum* (Myrtaceae), *Himatanthus sucuuba* and *Tabernaemontana juruana* (Apocynaceae), *Licania apetala* and *Couepia paraensis* (Chrysobalanaceae), and *Rheedia brasiliensis* and *Tovomita macrophylla* (Clusiaceae) presented distinct leaf morphology and/or anatomy.

Even species of the same genus, e.g. *Nectandra amazonum* and *Nectandra* sp. (Lauraceae), and *Bactris bidentula* and *Bactris maraja* (Arecaceae) differed in cuticular ornamentations and stomata as well as in arrangements and size of cells in the cross sections. *Bactris maraja*, e.g., showed little differentiation between palisade and spongy parenchyma whereas *Bactris bidentula* exhibited a clear differentiation in palisade and spongy parenchyma. Both kinds of cellular arrangements are common in Arecaceae (NAPP-ZINN 1973).

The present findings are in good agreement with the results of a similar study on eleven arboreal species from Central Amazonian floodplains (WALDHOFF & FURCH 2002b). An analyses of the pooled data sets reveals the same trends: no association of morphological and anatomical leaf characters with leaf-fall behavior except for the character complex of leathery leaves and thick outer walls and cuticula (Table 6).

It remains open whether the association of the character complex of leathery leaves with keeping submerged leaves represent an ecological/evolutionary trend. Alternatively it might simply reflect the higher frequency of leathery leaves in evergreen species (WALTER & BRECKLE 1984). It seems plausible to assume that only evergreen species acquired the strategy of keeping submerged leaves, which is confirmed by the present finding that only evergreen species keep submerged leaves. Leathery leaves might therefore represent the plesiomorphic state of evergreen species rather than a specific adaptation to conditions under water, although they are certainly more suited to withstand submergence.

The significance of xeromorphism as an adaptation to drought and/or nutrient deficiency in Central Amazonian floodplains remains elusive. Xeromorphic leaves are reported to be a general feature in tropical forests (ROTH 1984). WORBES (1986, 1997) reported on a water deficit in the canopy of Central Amazonian floodplain forests during the inundation period similar to the one found in trees on terra firme during the dry season. On the contrary, studies on tropical forests from Jamaica and Malaya

present evidence that xeromorphism may not be related to drought resistance (BUCKLEY et al. 1980; KAPOŠ & TANNER 1985). SMALL (1973) and HILL (1998) reported that xeromorphic structures are frequently present in plants both from arid and nutrient deficient habitats in the Australian Proteaceae. They concluded that xeromorphic structures evolved independently in response to aridity and nutrient deficiency, and that such a preadaptation may facilitate occupation of the reciprocal habitat.

SOBRADO & MEDINA (1980) related scleromorphic leaves in trees of the "bana" vegetation from the Upper Rio Negro basin with oligotrophic white sand soils and its widely fluctuating water table. As species from the nutrient-poor igapó are generally related to woodland and savannah vegetation on oligotrophic white sand soils (KUBITZKI 1989a, b) one might therefore expect a higher degree of xeromorphism in igapó species as in those from the nutrient-rich várzea. The analysis of the pooled data sets of the present and the previous study (WALDHOFF & FURCH 2002b), however, revealed significant differences between igapó and várzea species for two leaf characters only: thickness of the outer wall and cuticula of the upper epidermis and the compactness of the spongy parenchyma (Table 7) suggesting a somewhat higher degree of xeromorphism in igapó species. This could well be a trend, but a much greater number of species and an analysis of the closely related species from non-flooded upland habitats are needed to address this question.

Conclusions

From the present study as well as the combined analysis with WALDHOFF & FURCH (2002b) it appears that all 34 species had xeromorphic leaves. Given that xeromorphism is related to water stress the lack of a clear trend differentiating deciduous from evergreen species might be due to the fact that deciduous species face the same conditions as evergreen species at least during part of the aquatic phase because the leafless period is only 2 months (SCHÖNGART et al. 2002) while flooding last up to 7 months, and the drought conditions in the terrestrial phase are equal for all species. Keeping submerged leaves apparently does not require specific morphological or anatomical modifications apart from the plesiomorphic trait of leathery leaves typical for evergreen species. When compared to várzea species, igapó species showed a somewhat higher degree of xeromorphism in two specific leaf characters only, although this needs further investigations of a wider range of species. From the above it appears that the xeromorphic features found in Central Amazonian floodplain trees are unlikely to be adaptations selected under floodplain conditions but rather represent wide spread and common traits in tropical trees both from floodplain or terra firme habitats. The scarcity of similarities in confamilial or congeneric species likewise indicates that the leaf characters do not represent specific responses to the floodplain conditions.

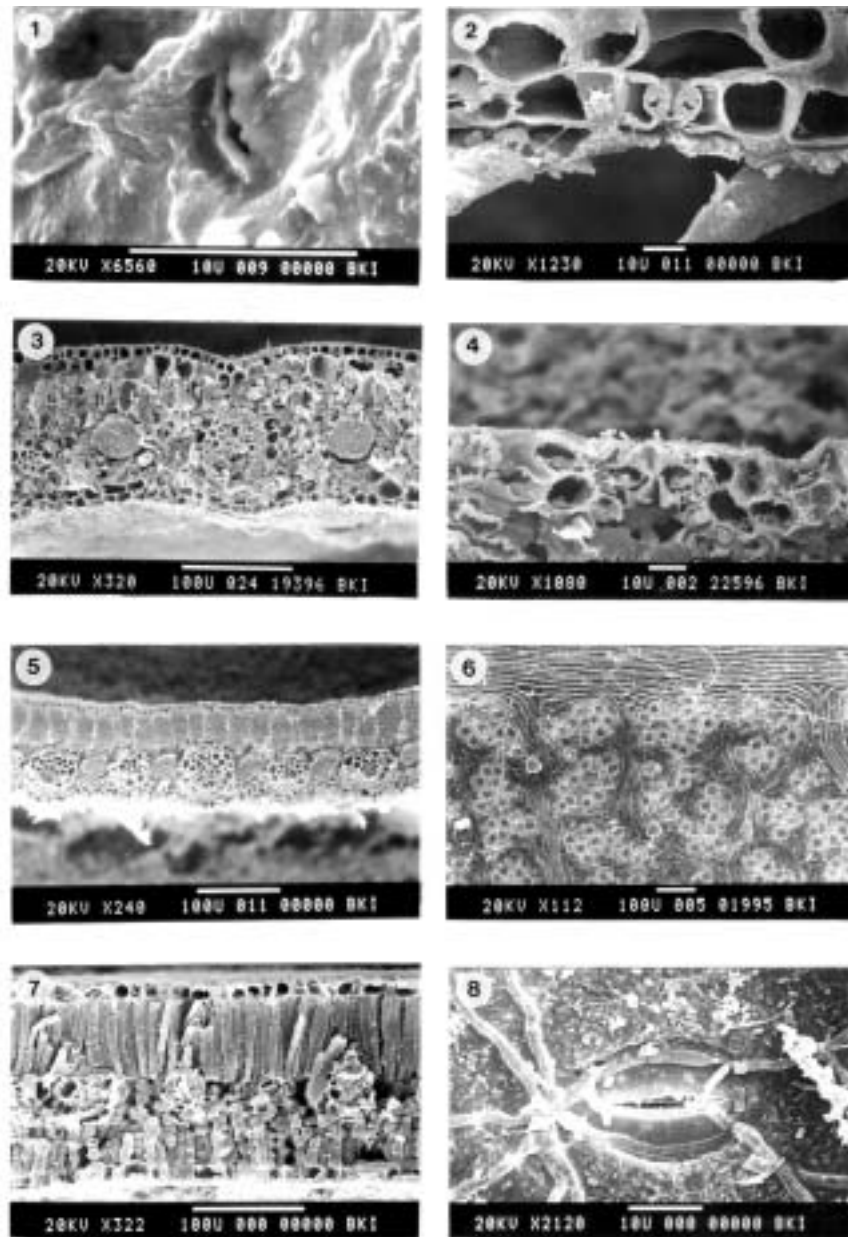
Acknowledgments

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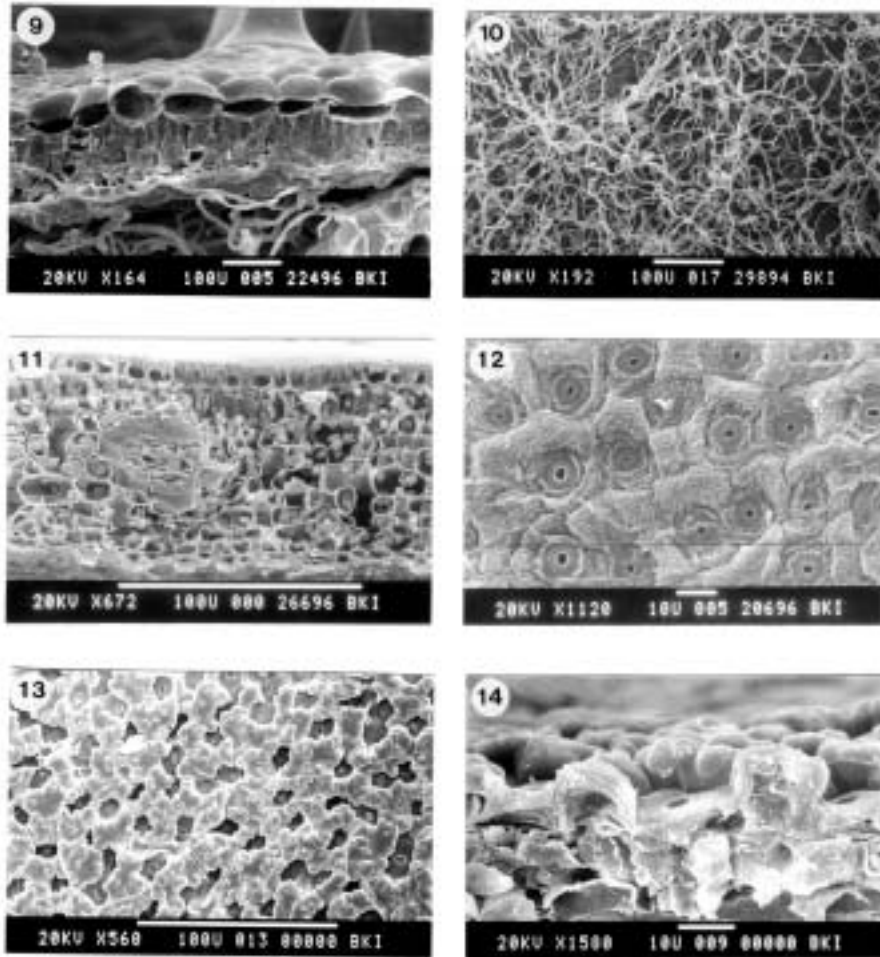
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Figs. 1-8:

1-2: *Acmanthera latifolia*; **1:** Stomata sunken in thick cuticula, rough surface with irregular elevations. **2:** Cross section through leaf with view of sunken stomata. **3-4:** *Bactris maraja*; **3:** Cross section through leaf. **4:** Cross section through leaf with view of sunken stomata. **5:** *Bactris bidentula*: Cross section through leaf. **6:** *Pseudobombax munguba*: Lower epidermis with stomata, nectaries, and cuticular striae. **7-8:** *Calliandra amazonica*; **7:** Cross section through leaf. **8:** Stomata sunken in thick cuticula.



Figs. 9-14:

9-10: *Cecropia latiloba*; **9:** Cross section through leaf. **10:** Lower epidermis with filamentous hairs. **11-12:** *Mouriri guianensis*; **11:** Cross section through the lower epidermis with very thick outer wall and cuticula. **12:** Lower epidermis with stomata sunken in holes formed by cuticular folds. **13-14:** *Quinia shitidopus*; **13:** Lower epidermis with papilla and sunken stomata. **14:** Cross section through leaf with stomata sunken in deep pit formed by papillose subsidiary cells.

Table 1: Tree species investigated: scientific name, family, local occurrence, leathery leaves (yes-no), leaf-fall behavior, and fate of submerged leaves.

Species	Family	Local name	Floodplain type	Leathery leaves	Leaf-fall behaviour	Submerged leaves
<i>Acmathera latifolia</i> (ADR. JUSSIEU) GRISEB.	Malpighiaceae		igapó	y	evergreen	kept
<i>Alchornea</i> sp.	Euphorbiaceae	oerana	várzea	n	deciduous	shed
<i>Alibertia</i> sp.	Rubiaceae	apurui	várzea	y	deciduous	shed
<i>Bactris bidentata</i> SPRUCE	Arecaceae	marajá	igapó	y	evergreen	kept
<i>Bactris maraja</i> MART.	Arecaceae		igapó	y	evergreen	kept
<i>Calliandra amazonica</i> BENTH.	Mimosaceae		igapó	n	deciduous	shed
<i>Cecropia latiloba</i> MIQ.	Cecropiaceae	embauba	várzea	n	evergreen	shed
<i>Cassia leiandra</i> BENTH.	Caesalpinaceae	mari-mari	várzea	n	deciduous	shed
<i>Cratava benthami</i> EICHLER	Capparaceae	catoré	várzea	y	deciduous	shed
<i>Couepia paraensis</i> (MART. & ZUCC.) BENTH. EX HOOK. F.	Chrysobalanaceae	uxirana	igapó	y	evergreen	kept
<i>Ilex inundata</i> POEPP. EX REISSEK	Aquifoliaceae	chumbinho	várzea	y	deciduous	shed
<i>Macarobium acaciifolium</i> (BENTH.) BENTH.	Caesalpinaceae	arapari	igapó	n	deciduous	shed
<i>Maprounea guianensis</i> AUBL.	Euphorbiaceae		igapó	n	deciduous	shed
<i>Mouriri guianensis</i> AUBL.	Melastomataceae	araçá	igapó	y	deciduous	shed
<i>Nectandra</i> sp.	Lauraceae	louro	várzea	y	evergreen	kept
<i>Ouratea hexasperma</i> (A. ST.-HIL.) BAILL.	Ochnaceae		igapó	y	evergreen	kept
<i>Pseudobombax munguba</i> (MART. & ZUCC.) DUGAND	Bombacaceae	munguba	várzea	n	deciduous	shed
<i>Psidium acutangulum</i> DC.	Myrtaceae	goiaba-araçá	várzea	y	deciduous	shed
<i>Quinia rhytidopus</i> TUL.	Quinaceae	quinarana	igapó	y	evergreen	kept
<i>Salix humboldtiana</i> WILLD.	Salicaceae	oerana	várzea	n	deciduous	shed

Table 1: Continuation.

Species	Family	Local name	Floodplain type	Leathery leaves	Leaf-fall behaviour	Submerged leaves
<i>Tabebuia barbata</i> (E. MEY.) SANDWICH	Bignoniaceae	capitari	igapó	n	deciduous	shed
<i>Tabernaemontana juruana</i> (MARKGR.) SCHUMANN EX J.F. MACBRIDE	Apocynaceae	bonafusia	várzea	y	evergreen	kept
<i>Tovomitia macrophylla</i> (POEPP.) WALP.	Clusiaceae	sapateiro	igapó	y	evergreen	kept

Table 2: Cell size in different leaf components (all measures in μm). Epidermis cells, width*length, small: $<10*5$, medium: $>10*5$, large: $>15*10$, very large: $>30*15$. Thickness of cuticula including outer cell wall, thin: <2 , medium: >2 , thick: >3 , very thick: >9 . Length of palisade parenchyma cells, small: <30 , medium: >30 , long: >40 , very long: >70 . Width of spongy parenchyma cells, small: <10 , medium: >10 , large: >15 . le = lower epidermis, ue = upper epidermis, x = missing data: cells not visible (see text), + = hypodermis.

Species	Epidermis cell size		Outer wall - cuticula		Palisade parenchyma cell size	Spongy parenchyma cell size
	ue	le	ue	le		
<i>A. latifolia</i>	large	large	medium	thick	medium	medium
<i>Alchornea</i> sp.	small	small	medium	medium	long/small	medium
<i>Alibertia</i> sp.	large	small	thick	thin	medium/small	medium
<i>B. hidetula</i>	small	small	thick	thick	medium	small
<i>B. maraja</i>	medium ⁺	medium	thick	medium	not existing	medium
<i>C. amazonica</i>	medium	medium	thick	thick	very long/small	small
<i>C. latiloba</i>	large	x	thin	x	x	x
<i>C. leiandra</i>	medium	medium	thin	thin	small	small
<i>C. benthami</i>	large	small	medium	thick	small	small
<i>C. paraensis</i>	large	medium	thick	medium	medium/small	not existing
<i>I. inundata</i>	medium	small	thick	thick	very long/small	small
<i>M. acaciifolium</i>	large	medium	thick	thin	x	medium
<i>Ma. guianensis</i>	medium	large	thick	thin	long	small
<i>Mo. guianensis</i>	small	small	thick	thin	small	large
<i>Nectandra</i> sp.	large	large	thick	thick	medium/small	large
<i>O. hexasperma</i>	large	medium	very thick	medium	very long	medium
<i>P. munguba</i>	large	medium	thin	medium	long/small medium/small/	small
<i>P. acutangulum</i>	large ⁺	small	thick	thin	small	medium
<i>Q. rhytidopus</i>	medium	small	thick	thin	medium	medium
<i>S. humboldtiana</i>	medium ⁺	medium	thin	thin	small/small etc.	not existing
<i>T. barbata</i>	medium ⁺	large	thin	thin	long-very long	medium
<i>T. juruana</i>	large	large	thick	thick	small	large
<i>T. macrophylla</i>	large	large	thick	thick	small	small

Table 3: Parenchyma characteristics. up: upper side of leaf, low = lower side of leaf, x = missing data.

Species	No. of layers of palisade parenchyma	Compactness of spongy parenchyma	Vascular bundles	
			Extension	Sclerenchyma
<i>A. latifolia</i>	1	very compact	some transcurrent	weekly developed
<i>Alchornea</i> sp.	1 up, 1 low	very compact	some transcurrent	weekly developed
<i>Alibertia</i> sp.	2	compact	not transcurrent	weekly developed
<i>B. bidentula</i>	1	compact	not transcurrent	sheat surrounding the bundle, fibres
<i>B. maraja</i>	not existing	compact	not transcurrent	sheat surrounding the bundle, fibres
<i>C. amazonica</i>	1 up, 1 low	loose	not transcurrent	weekly developed
<i>C. latiloba</i>	x	x	x	x
<i>C. leiandra</i>	1	compact	transcurrent	strong sheat surrounding the bundle
<i>C. benthami</i>	1-2	loose	not transcurrent	no sclerenchyma
<i>C. paraensis</i>	4	-	transcurrent	capping bundles on both sides
<i>I. inundata</i>	2	regular	not transcurrent	capping bundles on one side
<i>M. acaciifolium</i>	x	regular	x	x
<i>Ma. guianensis</i>	1	regular	transcurrent	strong sheat surrounding the bundle
<i>Mo. guianensis</i>	1	regular	not transcurrent	strong sheat surrounding the bundle
<i>Nectandra</i> sp.	1 up, 1 low	compact	transcurrent	capping bundles on both sides
<i>O. hexasperma</i>	1	very compact	not transcurrent	capping bundles on both sides
<i>P. munguba</i>	2	loose	transcurrent	capping bundles on both sides
<i>P. acutangulum</i>	1-3	compact	not transcurrent	sheat surrounding the bundle
<i>Q. rhytidopus</i>	1	regular	x	x
<i>S. humboldtiana</i>	5-6	not existing	transcurrent	weekly developed
<i>T. barbata</i>	1	regular	transcurrent	capping bundles on both sides
<i>T. juruana</i>	1	loose	not transcurrent	weekly developed
<i>T. macrophylla</i>	1-2	regular	not transcurrent	weekly developed

Table 4: Density (middle of five leaves) and form of stomata. le = lower epidermis, nv = not visible, ue = upper epidermis.

Species	Density (number mm ⁻²)		Form
	ue	le	
<i>A. latifolia</i>		25	sunken in thick cuticula
<i>Alchornea</i> sp.	309	233	not sunken
<i>Alibertia</i> sp.		696	not sunken
<i>B. bidentula</i>		nv	completely sunken in cuticular folds
<i>B. maraja</i>	63	248	sunken
<i>C. amazonica</i>		643	sunken in thick cuticula
<i>C. latiloba</i>	69	?	not sunken
<i>C. leiandra</i>		814	sunken
<i>C. benthami</i>		582	not sunken
<i>C. paraensis</i>		nv	sunken in cuticular folds, hidden by hairs
<i>I. inundata</i>		601	sunken with raised stomatal rim
<i>M. acaciifolium</i>	nv	nv	le: sunken between elevations of wax
<i>Ma. guianensis</i>		nv	sunken in cuticular folds
<i>Mo. guianensis</i>		1952	sunken in holes formed by cuticular folds
<i>Nectandra</i> sp.		318	sunken in cuticula
<i>O. hexasperma</i>		913	sunken in cavity formed by the raised stomatal rim
<i>P. munguba</i>	nv	284	sunken with raised stomatal rim
<i>P. acutangulum</i>	149	837	sunken in cavity formed by the raised stomatal rim
<i>Q. rhytidopus</i>		2339	sunken in deep pit formed by papillose subsidiary cells
<i>S. humboldtiana</i>	393	343	sunken with raised stomatal rim
<i>T. barbata</i>		287	sunken with raised stomatal rim
<i>T. juruana</i>		716	not sunken
<i>T. macrophylla</i>		201	not sunken

Table 5: Occurrence and characteristics of epidermal and cuticular structures: hairs, papillas, wax layer, and cuticular ornamentations. ue = upper epidermis, le = lower epidermis.

Species	Hairs		Papillas	Wax layer	Cuticular ornamentation
	not glandular	glandular			
<i>A. latifolia</i>	le				le: rough surface with irregular elevations ue: radiating striae around stomata le: rough surface
<i>Alchornea</i> sp.					
<i>Alibertia</i> sp.					
<i>B. bidentula</i>				le	ue, le: the whole surface is structured by many cuticular folds
<i>B. maraja</i>	le				ue, le: the whole surface is structured by many cuticular folds
<i>C. amazonica</i>	ue				ue, le: the whole surface is structured by some cuticular folds
<i>C. latiloba</i>	ue, le:	ue			
	filamentous hairs				
<i>C. leiandra</i>	le		le: simple, horn-like	ue, le: upright scales	
<i>C. benthami</i>					ue, le: the whole surface is structured by many cuticular folds
<i>C. paraensis</i>	le				le: cuticular folds; ue: very large cuticular folds
<i>I. inundata</i>				ue	le: concentric rings of striae around the stoma
<i>M. acaciifolium</i>		ue		ue: many elevations	

Table 5: Continuation.

<i>Ma. guianensis</i>		ue: many elevations	le: dense network of radiating striae around the stoma and between them le: dense network of cuticular folds
<i>Mo. guianensis</i>			
<i>Nectandra</i> sp.			
<i>O. hexasperma</i>			
<i>P. munguba</i>	le: nectaries	ue, le	le: elevations formed by cuticula le: concentric rings of striae around the stoma, and radiating striae around concentric rings ue, le: cuticula forms puzzle like structures
<i>P. acutangulum</i>	le		
<i>Q. rhytidopus</i>			
<i>S. humboldtiana</i>			le: concentric rings of striae around the stoma, and radiating striae around concentric rings le: radiating striae around stomata
<i>T. barbata</i>			
<i>T. juruana</i>	le		
<i>T. macrophylla</i>			ue: dense network of cuticular elevations

Table 6: Association and comparison of selected morphological and anatomical characteristics of leaves with the fate of submerged leaves (see text for explanations); p-values of Fishers' exact tests and Mann-Whitney-U-test (*). Leaf data of present study except for leathery appearance derived from Tables 2-4. Bold face: association significant ($p < 0.05$); n-s = number of species that shed submerged leaves; n-k = number of species that keep submerged leaves; ** = re-examined for the present study.

Characters	Present study		Present study pooled with data from WALDHOFF & FURCH 2002	
	p (two-tailed)	n-s, n-k	p (two-tailed)	n-s, n-k
Leaf appearance (leathery vs. not leathery)	0.003	14, 9	0.000**	19, 15**
Size of upper epidermis cells (small vs. medium-large)	1.0	14, 9	1.0	19, 15
Size of lower epidermis cells (small vs. medium-large)	0.380	13, 9	0.442	18, 12
Thickness of outer wall and cuticula, upper epidermis (thin vs. medium-very thick)	0.116	14, 9	0.049	19, 15
Thickness of outer wall and cuticula, lower epidermis (thin vs. medium-very thick)	0.031	13, 9	0.009	18, 13
Palisade parenchyma: number of layers (1 layer vs. >1 layer) (Species with p. p. at the lower leaf side omitted).	0.335	10, 7	1.0	15, 10
Compactness of spongy parenchyma (loose vs. regular-very compact)	0.619	12, 8	0.673	16, 12
Extension of vascular bundles (transcurrent vs. not transcurrent)	0.670	12, 8	1.0	17, 12
Sclerenchyma (without or weak vs. strong or capping bundles)	1.0	11, 8	0.190	16, 10
Stomata (sunken vs. even)	1.0	14, 9	0.672	19, 15
Stomata density at lower epidermis and fate of submerged leaves (shed vs. keep)*	0.618	11, 7	0.693	16, 11

Table 7: Association and comparison of selected morphological and anatomical characteristics of leaves from várzea and igapó: p-values of Fishers' exact tests and Mann-Whitney-U-test (*). Leaf data of present study except for leathery appearance derived from Tables 2-4. Bold face: association significant ($p < 0.05$); n-v = number from species of the várzea; n-i = number from species of the igapó; ** = re-examined for the present study.

Characters	Present study		Present study pooled with data from WALDHOFF & FURCH 2002	
	p (two-tailed)	n-v, n-i	p (two-tailed)	n-v, n-i
Leaf appearance (leathery vs. not leathery)	0.680	11, 12	1.0**	17, 17**
Size of upper epidermis cells (small vs. medium-large)	1.0	11, 12	1.0	17, 17
Size of lower epidermis cells (small vs. medium-large)	0.084	10, 12	0.285	16, 15
Thickness of outer wall and cuticula, upper epidermis (thin vs. medium-very thick)	0.155	11, 12	0.039	17, 17
Thickness of outer wall and cuticula, lower epidermis (thin vs. medium-very thick)	1.0	10, 12	0.738	15, 19
Palisade parenchyma: number of layers (1 layer vs. >1 layer) (Species with p. p. at the lower leaf side omitted)	0.335	8, 9	0.411	13, 12
Compactness of spongy parenchyma (loose vs. regular-very compact)	0.087	9, 10	0.039	13, 12
Extension of vascular bundles (transcurrent vs. not transcurrent)	1.0	10, 10	0.466	15, 14
Sclerenchyma (without or weak vs. strong or capping bundles)	0.650	10, 10	0.7	15, 14
Stomata (sunken vs. even)	0.069	17, 17	0.085	17, 17
Stomata density at lower epidermis (várzea vs. igapó)*	0.929	11, 8	0.430	16, 11