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Abstract	<p>Long lasting inundations affect the physicochemical conditions in the soil, with oxygen deficiency in the rhizosphere and resulting stresses (Haase and Rättsch this volume) which have a strong influence on the whole metabolism of the trees. Continuous investigations of the rhizosphere are extremely difficult and hardly feasible for the entire yearly cycle in adult trees due to the high periodic water level fluctuations. Therefore other parameters have to be taken as indicators for the reactions of the trees to waterlogging. Clear indicators of the condition of a tree are its assimilation organs (Medina 1984). Several parameters can be easily measured directly on the living leaves, such as size and mass, water, chlorophyll and nitrogen contents, and anatomical characteristics for example of the surface structure, cuticle, parenchyma and stomata. Investigations from Parolin (2002c), indicate for Amazonian floodplain trees a periodicity in physiological leaf traits which changes with leaf phenology and consequently with leaf age. The phenological behaviour is linked to the flooding periodicity (Wittmann and Parolin 1999; Schöngart et al. 2002), and typical regular changes occur during the annual cycle. Many species shed their leaves in the first weeks to months of waterlogging or submergence, but the waterlogged trees resprout new leaves several weeks to months before the end of the high water period. Other species maintain all their leaves, also when completely submerged. Under experimental conditions, saplings were even able to produce new leaves under water (Waldhoff and Furch 2002; Waldhoff 2003) but in the field measurements to this respect are lacking.</p>	

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[AU1] Danielle Waldhoff and Pia Parolin3

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9.1 Introduction4

Long lasting inundations affect the physicochemical conditions in the soil, with oxygen deficiency in the rhizosphere and resulting stresses (Haase and Rättsch this volume) which have a strong influence on the whole metabolism of the trees. Continuous investigations of the rhizosphere are extremely difficult and hardly feasible for the entire yearly cycle in adult trees due to the high periodic water level fluctuations. Therefore other parameters have to be taken as indicators for the reactions of the trees to waterlogging. Clear indicators of the condition of a tree are its assimilation organs (Medina 1984). Several parameters can be easily measured directly on the living leaves, such as size and mass, water, chlorophyll and nitrogen contents, and anatomical characteristics for example of the surface structure, cuticle, parenchyma and stomata. Investigations from Parolin (2002c), indicate for Amazonian floodplain trees a periodicity in physiological leaf traits which changes with leaf phenology and consequently with leaf age. The phenological behaviour is linked to the flooding periodicity (Wittmann and Parolin 1999; Schöngart et al. 2002), and typical regular changes occur during the annual cycle. Many species shed their leaves in the first weeks to months of waterlogging

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or submergence, but the waterlogged trees resprout new leaves several weeks to months before the end of the high water period. Other species maintain all their leaves, also when completely submerged. Under experimental conditions, saplings were even able to produce new leaves under water (Waldhoff and Furch 2002; Waldhoff 2003) but in the field measurements to this respect are lacking.

The different parameters defining leaves may change in specific recurring patterns during the annual cycle. Since photosynthesis and the leaves' conditions are crucial for the energy balance of the trees, it is supposed that these parameters make statements possible about the physiological condition of the trees in situ.

Another striking feature when observing the leaves of Amazonian floodplain trees is that in many species at least some of the leaves are not shed when submerged, e.g. *Tabernaemontana juruana* (Fig. 9.1). Not only, but these leaves retain their structure and functional capability throughout the submerged period which can last as long as 7 months and leaves then can be in complete darkness for several weeks. Surprisingly, some of the plants do not display scotomorphogenesis induced by the lack of light during the flood periods (Fernandes-Corrêa and Furch 1992): their habitus, inner structures, metabolism and movements with respect to the ambient environment – called photomorphogenesis in light – are not optimized or changed with respect to the long period of darkness under water.

Thus, the aim of this chapter is to describe the leaf characteristics of Amazonian floodplain trees, to analyse the reactions to flooding of parameters related to the

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Fig. 9.1 Submerged *Tabernaemontana juruana* in Manacapuru Lake (Parolin, Au 1994)

assimilation organs and to discuss the variation in response to flooding. In the 41
whole chapter we deal with leaves which were not newly developed under water 42
but which were already present at the start of the flooding event. 43

9.2 Leaf Lifespan and Age 44

Leaf age appears to play a major role for changes of leaf characteristics in the annual 45
cycle. Leaf lifespan varies between the species, ranging from few months in *Senna* 46
reticulata to probably 2 years in *Nectandra amazonum* (Fig. 9.2) or even more (up to 47
5 years; Waldhoff, pers. comm.) in *Symmeria paniculata*. Most species have leaf 48
lifespan of about 1 year. New leaves are commonly flushed towards the end of the 49
flooded period, and leaf senescence occurs almost exclusively in the first waterlogged 50
months. Therefore average leaf age is higher in the aquatic than in the terrestrial 51
period, and might be responsible for higher average specific leaf mass. It was espe- 52
cially high in the months prior to leaf shedding. The same was due concerning leaf 53
water content, which in new leaves was higher than in adult and senescent leaves. 54

9.3 Xeromorphism 55

The leaves of Amazonian floodplain trees exhibit traits which are generally considered 56
as xeromorph (Medina 1983; Roth 1984; Bolh  r-Nordenkampf and Draxler 1993; 57
Waldhoff et al. 2002; Waldhoff 2003): large epidermal cells (*Hevea spruceana*, 58

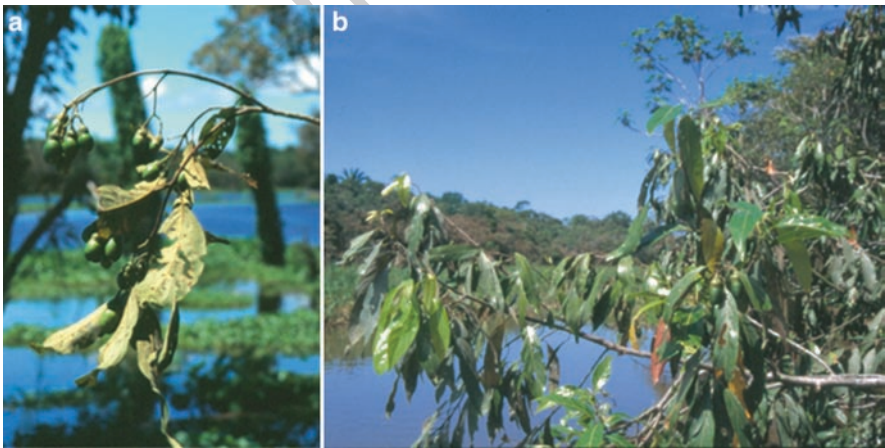


Fig. 9.2 Branch of *Nectandra amazonum*: Leaf shedding and replacement occurs continuously, but a period with clearly senescent leaves (a) and fruit maturation dominates in the beginning of the aquatic period, whereas new leaves are flushed (b) at the highest water peak and towards the end of the aquatic phase

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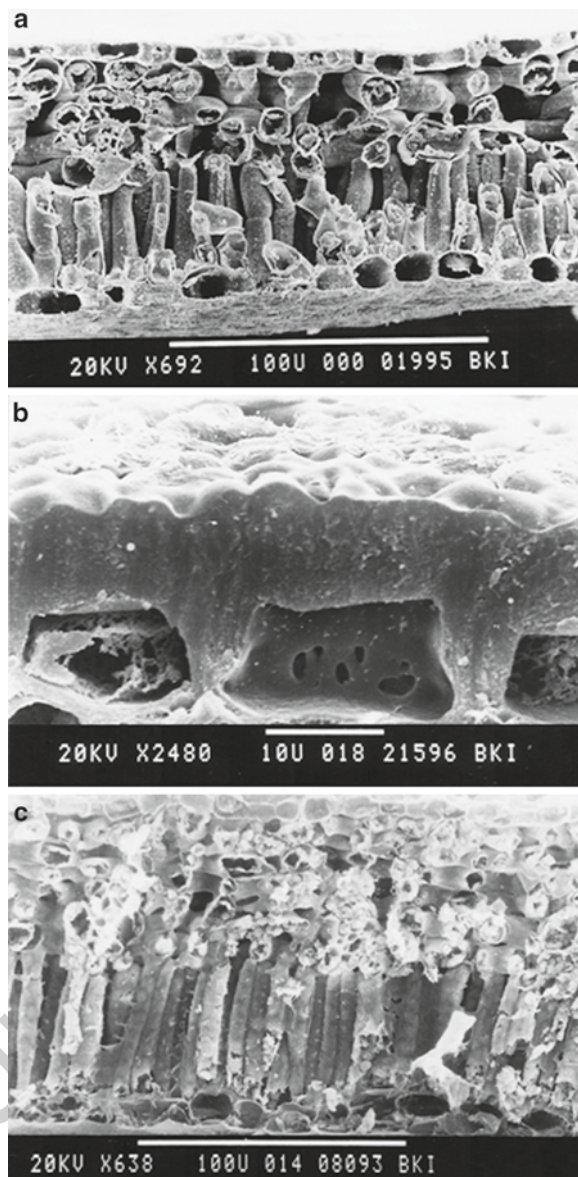


Fig. 9.3 Leaf anatomy: (a) *Eugenia inundata* cross section with large epidermal cells; (b) *Rheedia brasiliensis* thick outer epidermis walls; (c) *Senna reticulata* compact spongy parenchyma with only few and small intercellular spaces

Eugenia inundata, Fig. 9.3a), thick outer epidermis walls (*Rheedia brasiliensis* Fig. 9.3b, *Himatanthus sucuiba*), thick cuticle (*Eschweilera tenuifolia*, *Simaba guianensis*), compact spongy parenchyma with only few and small intercellular spaces (*Senna reticulata*

Fig. 9.3c, *Licania apetalata*), sunken stomata (*Vitex cymosa*, *Pouteria glomerata*), and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath (*Nectandra amazonum*, *Eugenia inundata*).

Xeromorphic characters may be associated to high efficiency mechanisms for nutrient cycling that compensates for low soil nutrient contents (Medina 1984) which is surely not the case in nutrient-rich Amazonian white-water floodplains. Xeromorphic characters also can be a result of defense responses against herbivores. Pressure of herbivores is severe in tropical systems, and supposedly also in the floodplains (Turner 1994).

Xeromorphism can also be a response to drought (Medina 1983; Medina et al. 1990). Xeromorphic characters of all leaf types indicate that the trees experience drought stress in their floodplain habitats, independent of leaf-fall behaviour. This at a first glance is astonishing, because the trees grow during several months in flooded or waterlogged soils and during the remaining time drought stress seems to be moderate because of a high groundwater table in the floodplain and/or sporadic rainfall. However, 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 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.

[AU2] The xeromorphic leaf structure may represent a pre-adaptation resulting from the dry habitats most tree species originate from (Kubitzki 1987). It helps to cope with insufficient water supply to the tree crowns during the aquatic phase which is caused by a decrease of root functioning due to waterlogging and submergence. It also is an adaptation against the periods of drought which occur occasionally in the terrestrial phase. Secretory canals in leaves of *Rheedia brasiliensis* and *Hevea spruceana* represent peculiarities of the families, Clusiaceae and Euphorbiaceae, respectively, and do not seem to be related to xeromorphism (Roth 1984; Waldhoff and Furch 2002).

9.4 Anatomy of Leaves

When analysing cell sizes in different leaf components (Table 9.1) Waldhoff and Furch (2002) found that several species that keep submerged leaves showed a very thick cuticula and outer wall on the upper leaf side (e.g. *Eschweilera tenuifolia*, *Rheedia brasiliensis*). On the contrary, other species that shed submerged leaves showed an upper epidermis with a thin outer wall/cuticula (e.g. *Senna reticulata*, *Simaba guianensis*, *Vitex cymosa*). Others presented either medium (*Licania apetalata*, *Nectandra amazonum*) or thick (*Eugenia inundata*, *Hevea spruceana*, *v. sucuuba*, *Pouteria glomerata*) cuticula and outer walls. The outer walls and cuticula of the lower epidermis tended to be rather thin in all analysed species. With the exception of *Pouteria glomerata* all species showed medium, large or even very large upper epidermis cells, long palisade parenchyma cells, and medium to small spongy parenchyma cells.

Table 9.1 Cell size in different leaf components (all measures in μm). Epidermis cells, width \times length, small: $<10 \times 5$, medium: $>10 \times 5$, large: $>15 \times 10$, very large: $>30 \times 15$. 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 (From Waldhoff and Furch 2002; Waldhoff 2003)

	Species	Epidermis cell size		Outer wall – cuticula		Palisade parenchyma cell size	Spongy parenchyma cell size
		ue	le	ue	le		
t1.1		Large	Large	Medium	Thick	Medium	Medium
t1.2	<i>Aldina latifolia</i>	Small	Small	Medium	Medium	Long/small	Medium
t1.3	<i>Alchornea</i> sp.	Large	Small	Thick	Thin	Medium/small	Medium
t1.4	<i>Alibertia</i> sp.	Small	Small	Thick	Thick	Medium	Small
t1.5	<i>Bacris bidentata</i>	Medium+	Medium	Thick	Medium	Not existing	Medium
t1.6	<i>Bacris maraja</i>	Medium	Medium	Thick	Thick	Very long/small	Small
t1.7	<i>Calliandra amazonica</i>	Large	Small	Medium	Thick	Small	Small
t1.8	<i>Cratava benthami</i>	Large	*	Thin	*	*	*
t1.9	<i>Cecropia latiloba</i>	Medium	Medium	Thin	Thin	Small	Small
t1.10	<i>Cassia leiandra</i>	Large	Medium	Thick	Medium	Medium/small	Not existing
t1.11	<i>Couepia paraensis</i>	Large	Medium	Thick	Thin	Medium	Medium
t1.12	<i>Eugenia inundata</i>	Large	Small	Very thick	Thick	Long/small/small	Medium
t1.13	<i>Eschweilera tenuifolia</i>	Medium	Small	Thick	Thin	Very long	Medium
t1.14	<i>Hevea spruceana</i>	Very large	Large	Thick	Thin		
t1.15	<i>Himatanthus sucuba</i>	Large		Thick	Thin		
t1.16	<i>Ilex inundata</i>	Medium	Small	Thick	Thick	Very long/small	Small
t1.17	<i>Licania apetala</i>	Large	(Papilla)	Medium	(Papilla)	Long/small/small	Medium
t1.18	<i>Macrobolium</i>	Large	Medium	Thick	Thin	*	Medium
t1.19	<i>Macrobolium acaciifolium</i>						
t1.20	<i>Maprounea guianensis</i>	Medium	Large	Thick	Thin	Long	Small
t1.21	<i>Mouriri guianensis</i>	Small	Small	Thick	Thin	Small	Large
t1.22	<i>Nectandra amazonum</i>	Large	Large	Medium	Medium	Long/small/small	Not existing
t1.23	<i>Nectandra</i> sp.	Large	Large	Thick	Thick	Medium/small	Large
t1.24	<i>Ouratea hexasperma</i>	Large	Medium	Very thick	Medium	Very long	Medium

t1.31	<i>Psidium acutangulum</i>	Large +	Small	Thick	Thin	Medium/small	Medium
t1.32	<i>Pouteria glomerata</i>	Small	Small	Thick		Medium	Small
t1.33	<i>Pseudobombax munguba</i>	Large	Medium	Thin	Medium	Long/small	Small
t1.34	<i>Quinia rhytidopus</i>	Medium	Small	Thick	Thin	Medium	Medium
t1.35	<i>Rheedia brasiliensis</i>	Large	Large	Very thick	Thick	Medium/small	Medium
t1.36	<i>Simaba guianensis</i>	Large	Small	Thin	Thick	Medium	Small
t1.37	<i>Salix humboldtiana</i>	Medium +	Medium	Thin	Thin	Small/small etc.	Not existing
t1.38	<i>Senna reticulata</i>	Medium	Medium	Thin	Thin	Long	Medium
t1.39	<i>Tabebea barbata</i>	Medium +	Large	Thin	Thin	Long-very long	Medium
t1.40	<i>Tabernaemontana</i>	Large	Large	Thick	Thick	Small	Large
t1.41	<i>juruana</i>						
t1.42	<i>Tovomita macrophylla</i>	Large	Large	Thick	Thick	Small	Small
t1.43	<i>Vitex cymosa</i>	Large	Large	Thin	Thin	Long/small/small	Not existing

le, lower epidermis; ue, upper epidermis; *, missing data; cells not visible (see text).

All species that shed submerged leaves showed only one layer of palisade parenchyma except for *Vitex cymosa*. Those that do not shed submerged leaves showed more than one layer of palisade parenchyma at the lower leaf side, with the exception of *Pouteria glomerata* (Table 9.2). In leaves with multiple palisade parenchyma layers cell length decreased towards the inner layers (Table 9.1).

The compactness of the spongy parenchyma ranged from loose in *Rheedia brasiliensis* and *Simaba guianensis*, regular in *Eugenia inundata*, and compact to very compact in other species (Table 9.2). The spongy parenchyma was completely missing in *Couepia paraensis*, *Nectandra amazonum*, *Salix martiana* and *Vitex cymosa* (Waldhoff 2003). Neither the spongy parenchyma was associated with leaf-fall behaviour or fate of submerged leaves nor the extension of the vascular bundles as well as the form of the sclerenchymatous sheath (Waldhoff 2003). Both the extension of the vascular bundles and the form of the sclerenchymatous sheath varied between species in different combinations (Table 9.2) (Waldhoff and Furch 2002).

9.5 Stomata

Stomatal density at the lower leaf side of 34 analysed tree species varied between 25 and 2,339 mm⁻² (Table 9.3) and did not differ significantly between species that keep or shed submerged leaves (Waldhoff 2003). Species with higher stomatal densities tended to show small epidermal cells (e.g. *Mouriri guianensis*, *Ouratea hexasperma*, *Quiinia rhytidopus*) and vice versa (e.g. *Acmanthera latifolia*, *Tabernaemontana juruana*, *Tovomita macrophylla*). Stomatal densities were apparently not associated with a certain type of leaf-fall behaviour, which corresponds with the literature on the relation of stomatal density with xeromorphism (Wilkinson 1979; Roth 1984; Bolh  r-Nordenkampf and Draxler 1993; Cao 2000; Dong and Zhang 2000). While hypostomatic leaves represent the usual pattern among dicotyledonous trees, additional stomata at the upper leaf side may have emerged as an adaptation to dry habitats in some species (Bolh  r-Nordenkampf and Draxler 1993), e.g. *Rheedia brasiliensis* (Fig. 9.4a), *Bactris maraj  *, *Pouteria glomerata*, and *Psidium acutangulum* (Fig. 9.5). Amphistomatic leaves are commonly found in members of the family Caesalpinaceae (Roth 1984; Metcalfe and Chalk 1950).

Most of the analysed species had sunken stomata at the lower side of the leaf (Fig. 9.4b; Waldhoff 2003), some even had stomata that are not visible because they are buried in a cavity or pit-like hole, sunken between waxy elevation or cuticular folds (Table 9.3).

Waldhoff et al. (2002), Fernandes-Corr  a and Furch (1992), and Schl  ter and Furch (1992) also described sunken stomata in several tree species that do not shed submerged leaves. The latter two studies ascribed this structure to a postulated function they called "reverse plastron respiration" which would enable a "plastron photosynthesis".

Sunken stomata are common in xeromorphic leaves (Roth 1984; Bolh  r-Nordenkampf and Draxler 1993). On the other hand Fahn and Cutler (1992) reported that only 34% of xeromorphic species (35 dicotyledons, 33 monocotyledons, 3 gymnosperms) from arid and semi-arid environments possess sunken stomata.

Table 9.2 Parenchyma characteristics (From Walldhoff and Furch 2002; Walldhoff 2003)

	Species	No. of layers of palisade parenchyma	Compactness of spongy parenchyma	Canals	Vascular bundles	
					Extension	Sclerenchyma
t2.1	<i>Aldina latifolia</i>	1	Very compact		Some transcurrent	Weekly developed
t2.2	<i>Alchornea</i> sp.	1 up, 1 low	Very compact		Some transcurrent	Weekly developed
t2.3	<i>Alibertia</i> sp.	2	Compact		Not transcurrent	Weekly developed
t2.5	<i>Bactris bidentula</i>	1	Compact		Not transcurrent	Sheath surrounding the bundle, fibres
t2.6	<i>Bactris maraja</i>	Not existing	Compact		Not transcurrent	Sheath surrounding the bundle, fibres
t2.7	<i>Calliandra amazonica</i>	1 up, 1 low	Loose		Not transcurrent	Weekly developed
t2.8	<i>Cratava benthami</i>	1-2	Loose		Not transcurrent	No sclerenchyma
t2.9	<i>Cecropia latiloba</i>	*	*		*	*
t2.10	<i>Cassia leiandra</i>	1	Compact		Transcurrent	Strong sheath surrounding the bundle
t2.11	<i>Couepia paraensis</i>	4	-		Transcurrent	Capping bundles on both sites
t2.12	<i>Eugenia inundata</i>	1	Regular		Transcurrent	Capping bundles on both sites
t2.13	<i>Eschweilera tenuifolia</i>	1 up, 1 low	Very compact		Mostly transcurrent	Sheath surrounding the bundle
t2.14	<i>Hevea spruceana</i>	1	Compact	Laticiferous	Not transcurrent	Weekly developed
t2.15	<i>Himatanthus sucuba</i>	*	*		*	*
t2.16	<i>Ilex inundata</i>	2	Regular		Not transcurrent	Capping bundles on one site
t2.17	<i>Licania apetala</i>	2	Very compact		Not transcurrent	Strong sheath surrounding the bundle
t2.18	<i>Macrolobium acaciifolium</i>	*	Regular		*	*
t2.19	<i>Maprounea guianensis</i>	1	Regular		Transcurrent	Strong sheath surrounding the bundle
t2.20	<i>Mouriri guianensis</i>	1	Regular		Not transcurrent	Strong sheath surrounding the bundle

(continued)

Table 9.2 (continued)

Species	No. of layers of palisade parenchyma	Compactness of spongy parenchyma	Canals	Vascular bundles	
				Extension	Sclerenchyma
<i>Nectandra amazonum</i>	2 up, 1 low	Not existing		Transcurrent	Capping bundles on both sites
<i>Nectandra</i> sp.	1 up, 1 low	Compact		Transcurrent	Capping bundles on both sites
<i>Ouratea hexasperma</i>	1	Very compact		Not transcurrent	Capping bundles on both sites
<i>Psidium acutangulum</i>	1–3	Compact		Not transcurrent	Sheath surrounding the bundle
<i>Pouteria glomerata</i>	1	Very compact		*	*
<i>Pseudobombax munguba</i>	2	Loose		Transcurrent	Capping bundles on both sites
<i>Quiinitia rhytidopus</i>	1	Regular		*	*
<i>Rheedea brasiliensis</i>	2	Loose	Resin	Mostly transcurrent	Strong sheath surrounding the bundle
<i>Simaba guianensis</i>	1	Very loose		Not transcurrent	Weekly developed
<i>Salix humboldtiana</i>	5–6	Not existing	Oil cells	Transcurrent	Weekly developed
<i>Senna reticulata</i>	1	Compact		Transcurrent	Capping bundles on both sites
<i>Tabebuia barbata</i>	1	Regular		Transcurrent	Capping bundles on both sites
<i>Tabernaemontana juruana</i>	1	Loose		Not transcurrent	Weekly developed
<i>Tovomitia macrophylla</i>	1–2	Regular		Not transcurrent	Weekly developed
<i>Vitex cymosa</i>	2–3	Not existing		Transcurrent	Capping bundles on both sites

t2.30 up, upper side of leaf; low, lower side of leaf; *, missing data.

Table 9.3 Density and form of stomata (from Waldhoff and Furch 2002; Waldhoff 2003) t3.1

Species	Density (number mm ⁻²)		Form	t3.2
	ue	le		
<i>Aldina latifolia</i>		25	Sunken in thick cuticula	t3.3
<i>Alchornea</i> sp.	309	233	Not sunken	t3.4
<i>Alibertia</i> sp.		696	Not sunken	t3.5
<i>Bactris bidentula</i>		nv	Completely sunken in cuticular folds	t3.6
<i>Bactris maraja</i>	63	248	Sunken	t3.7
<i>Calliandra amazonica</i>		643	Sunken in thick cuticula	t3.8
<i>Crateva benthami</i>		582	Not sunken	t3.9
<i>Cecropia latiloba</i>	69	?	Not sunken	t3.10
<i>Cassia leiandra</i>		814	Sunken	t3.11
<i>Couepia paraensis</i>		nv	Sunken in cuticular folds, hidden by hairs	t3.12 t3.13
<i>Eugenia inundata</i>		620	Sunken in cavity formed by the raised stomatal rim	t3.14 t3.15
<i>Eschweilera tenuifolia</i>		nv	Sunken in very thick cuticula	t3.16
<i>Hevea spruceana</i>		369	Sunken	t3.17
<i>Himatanthus sucuuba</i>		675	Sunken, with raised stomatal rim	t3.18
<i>Ilex inundata</i>		601	Sunken with raised stomatal rim	t3.19
<i>Licania apetala</i>		nv	Sunken in deep pit formed by papillose subsidiary cells	t3.20 t3.21
<i>Macrolobium acaciifolium</i>	nv	nv	le: sunken between elevations of wax	t3.22 t3.23
<i>Maprounea guianensis</i>		nv	Sunken in cuticular folds	t3.24
<i>Mouriri guianensis</i>		1,952	Sunken in holes formed by cuticular folds	t3.25
<i>Nectandra amazonum</i>		1,188	Sunken	t3.26
<i>Nectandra</i> sp.		318	Sunken in cuticula	t3.27
<i>Ouratea hexasperma</i>		913	Sunken in cavity formed by the raised stomatal rim	t3.28 t3.29
<i>Psidium acutangulum</i>	149	837	Sunken in cavity formed by the raised stomatal rim	t3.30 t3.31
<i>Pouteria glomerata</i>	177	449	ue: not sunken, le: sunken with raised stomatal rim and long, narrow aperture	t3.32 t3.33 t3.34
<i>Pseudobombax munguba</i>	nv	284	Sunken with raised stomatal rim	t3.35 t3.36
<i>Quinia rhytidopus</i>		2,339	Sunken in deep pit formed by papillose subsidiary cells	t3.37 t3.38
<i>Rheedia brasiliensis</i>	nv	178	Sunken in pit formed by very thick cuticula	t3.39 t3.40
<i>Simaba guianensis</i>		4	Sunken	t3.41
<i>Salix humboldtiana</i>	393	343	Sunken with raised stomatal rim	t3.42
<i>Senna reticulata</i>	141	84	Sunken	t3.43
<i>Tabebuia barbata</i>		287	Sunken with raised stomatal rim	t3.44
<i>Tabernaemontana juruana</i>		716	Not sunken	t3.45 t3.46
<i>Tovomita macrophylla</i>		201	Not sunken	t3.47
<i>Vitex cymosa</i>		176	Sunken in cavity formed by the raised stomatal rim	t3.48 t3.49

le, lower epidermis; nv, not visible; ue, upper epidermis t3.50

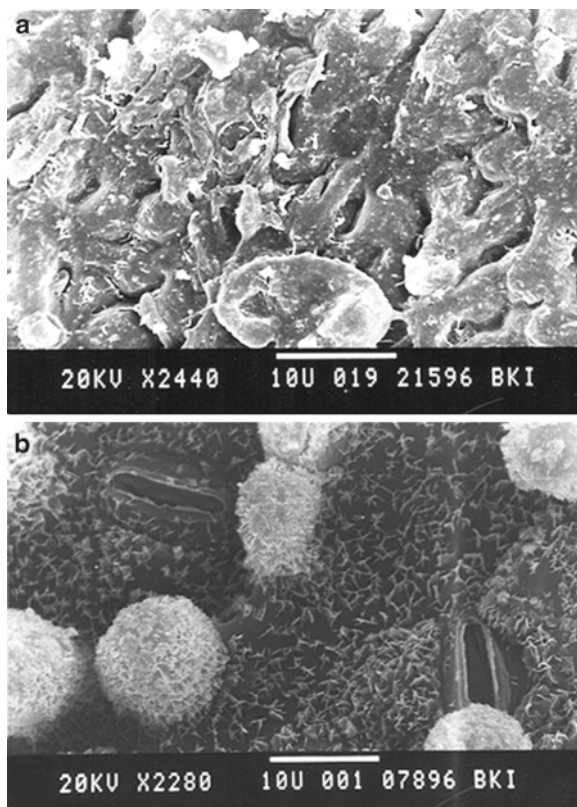


Fig. 9.4 *Rheedia brasiliensis* stomata on the upper leaf side (a); sunken stomata on the lower side of the leaf in *Cassia leiandra*, with wax crystals (b)

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 27 out of 34 species studied seems remarkable.

9.6 Surface Structures

Glandular and non-glandular hairs were found in leaves from several species studied in the floodplain forests, e.g. *Cassia leiandra*, *Nectandra amazonum*, and *Pouteria glomerata* (Fig. 9.6, Table 9.4; Waldhoff and Furch 2002; Waldhoff 2003). The lower leaf surface of *Licania apetala*, *Senna reticulata*, *Cassia leiandra*, and *Quinia shytidopus* is covered with papillae (Fig. 9.6a). Roth (1984) reported that both hair types and papillae are scarce in the humid tropics.

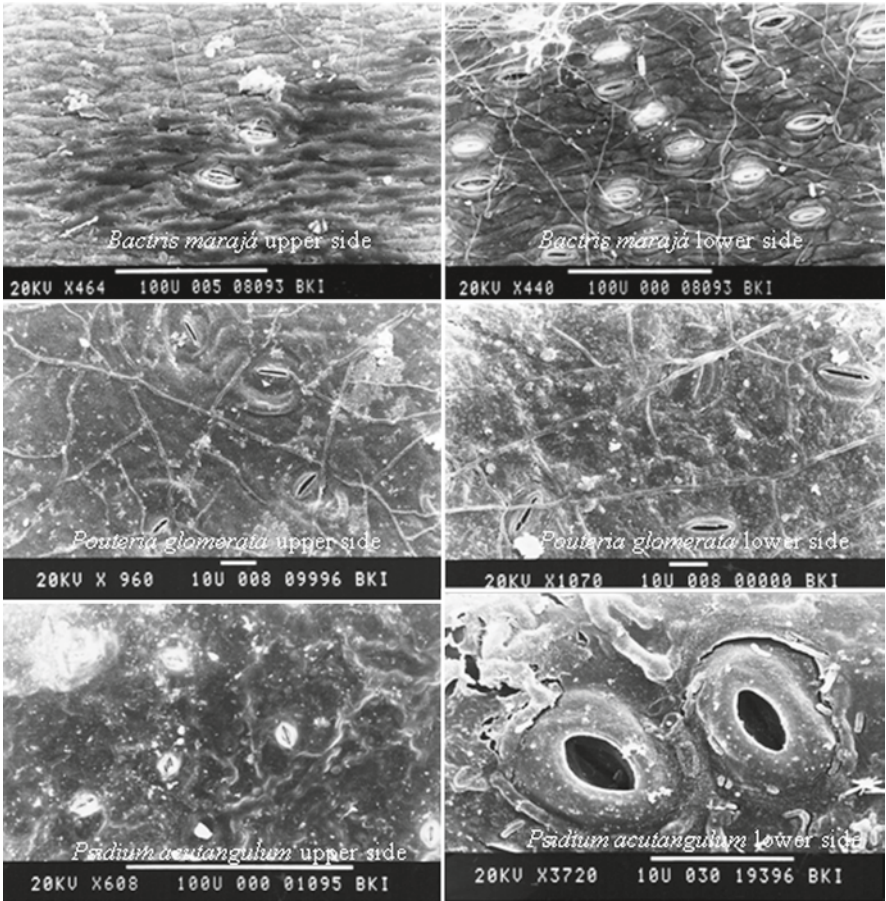


Fig. 9.5 Upper (left) and lower (right) leaf side of *Bactris marajá*, *Pouteria glomerata*, and *Psidium acutangulum*

Ten analysed species exhibited wax deposits (Fig. 9.7), twenty showed cuticular ornamentations, mostly on the lower leaf side (see Table 9.4). These ornamentations are reported to be quite common in leaves of trees from tropical rainforests (Roth 1984). These have been interpreted in the literature as assisting water to channel off the leaf surface (Barthlott 1996; Carpenter 1996). The sculpturing of *Hevea spruceana* is very similar to that of *Hevea brasiliensis* from terra firme uplands (Wilkinson 1979; Sena Gomes and Kozlowski 1988).

In analogy to the sunken stomata ascribed to the postulated function called “reverse plastron respiration” mentioned above which would enable a “plastron photosynthesis” the existence of wax layers may be interpreted as an adaptation to avoid water influx in submerged leaves (Fernandes-Corrêa and Furch 1992; Schlüter and Furch 1992).

166 9.7 Chloroplasts

167 In the palm *Bactris bidentula*, palisade parenchyma cells are densely filled with
 168 chloroplasts (Waldhoff 2003). Such a high density of chloroplasts in palisade
 169 parenchyma had not been described hitherto. It might be helpful for a possible
 170 photosynthesis under water when light is the limiting factor (Furch et al. 1985).
 171 Although light can be an important limiting factor under water, presumably CO₂ is
 172 much more limiting (Mommer and Visser 2005), but no studies are available to this
 173 respect in Amazonian floodplain trees.

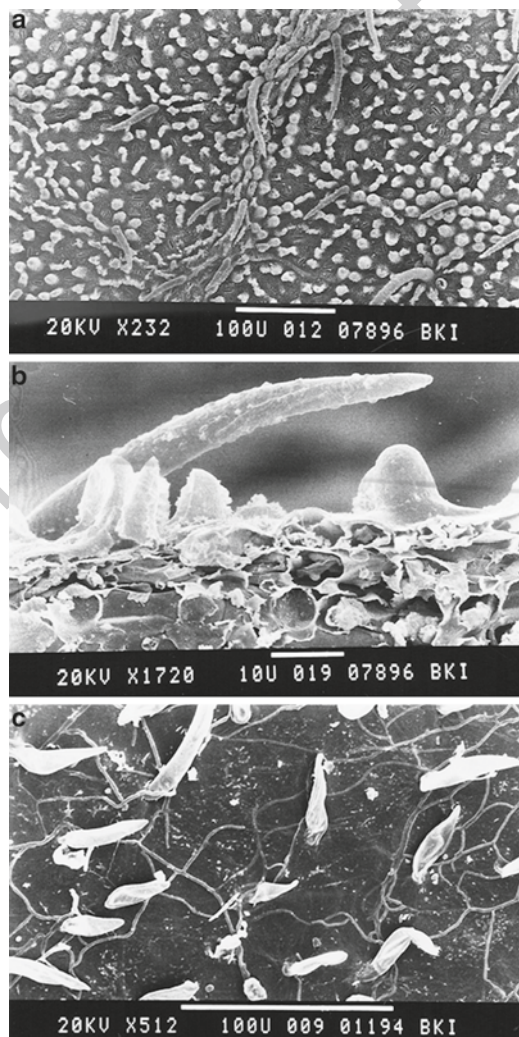


Fig. 9.6 Leaf surface structures: hairs and papillae (a, cross section b) on lower leaf surface of *Cassia leiandra*, hairs on upper (c) and lower (d) leaf side of *Nectandra amazonum*, and lower leaf side (e) of *Pouteria glomerata*

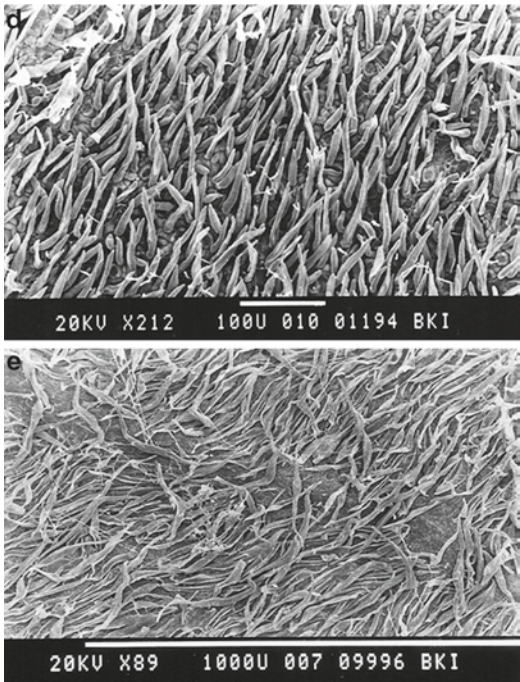


Fig. 9.6 (continued)

Transmission electron microscope (TEM) analyses of leaves from *Symmeria* 174
paniculata at 1 m depth showed that short-term submergence did not affect neither 175
chloroplast shape nor the interior structures of chloroplasts with thylakoids, stacks, 176
and starch grains (Waldhoff et al. 2002). The leaves have big epidermis cells with 177
thick outer walls followed by the first row of palisade parenchyma, which show 178
chloroplasts along the cell walls filled with stroma and grana thylakoid-forming 179
stacks and starch grains (Fig. 9.8). These stacks are responsible for the tolerance of 180
extreme low light in this species. On the other hand, chloroplast shape and starch 181
content may change with long-term submergence as was found in *Laetia corymbu-* 182
losa and *Pouteria glomerata* (Waldhoff et al. 2002). 183

9.8 Specific Leaf Mass

Specific leaf mass was higher in waterlogged months in many species, e.g. *Cecropia* 185
latiloba, *Nectandra amazonum*, *Senna reticulata*, *Tabebuia barbata*, and *Vitex* 186
cymosa, in adult trees in the field as well as in seedlings under experimental conditions 187

Table 9.4 Occurrence and characteristics of epidermal and cuticular structures: hairs, papillae, wax layer, and cuticular ornamentations (From Waldhoff and Furch 2002; Waldhoff 2003)

	Species	Hairs		Papillae	Wax layer	Cuticular ornamentation
		Not glandular	Glandular			
t4.3						
t4.4	<i>Aldina latifolia</i>	le				le: rough surface with irregular elevations
t4.5						
t4.6	<i>Alchomea</i> sp.					ue: radiating striae around stomata
t4.7	<i>Alibertia</i> sp.					le: rough surface
t4.8	<i>Bactris bidentula</i>				le	ue, le: the whole surface is structured by many cuticular folds
t4.9						
t4.10						
t4.11	<i>Bactris maraja</i>	le				ue, le: the whole surface is structured by some cuticular folds
t4.12						
t4.13						
t4.14	<i>Calliandra amazonica</i>	ue				ue, le: the whole surface is structured by many cuticular folds
t4.15	<i>Cratva benthami</i>					
t4.16						
t4.17						
t4.18	<i>Cecropia latiloba</i>	ue; le: filamentous hairs	ue			
t4.19						
t4.20	<i>Cassia leiandra</i>	le		le: simple, corn-like	ue, le: upright scales	
t4.21						
t4.22	<i>Couepia paraensis</i>	le				le: cuticular folds; ue: very large cuticular folds
t4.23						
t4.24	<i>Eugenia inundata</i>		ue, le: glandular scales			le: concentric rings of striae around stomata and radiating striae around concentric rings
t4.25						ue: striae random and very dense
t4.26						
t4.27						
t4.28						
t4.29	<i>Eschweilera tenuifolia</i>		ue, le: glandular scales			
t4.30						

t4.31	<i>Hevea spruceana</i>		le	ue, le: reticulum of crests and buttressed ridges around stomata
t4.32				
t4.33				
t4.34	<i>Himatanthus sucuuba</i>			le: concentric rings of striae around stomata
t4.35				
t4.36	<i>Ilex inundata</i>		ue	le: concentric rings of striae around the stoma
t4.37				
t4.38	<i>Licania apetala</i>			le: with dense papillose hairs
t4.39				
t4.40	<i>Macrobium</i>	ue		ue: many elevations
t4.41	<i>acaciifolium</i>			
t4.42	<i>Maprounea guianensis</i>			le: dense network of radiating striae around the stoma and between them
t4.43				le: dense network of cuticular folds
t4.44				
t4.45	<i>Mouriri guianensis</i>			
t4.46				
t4.47	<i>Nectandra amazonum</i>	ue, le		le: rods of wax
t4.48	<i>Nectandra</i> sp.			
t4.49	<i>Ouratea hexasperma</i>		ue, le	le: elevations formed by cuticula
t4.50	<i>Psidium acutangulum</i>	le		ue, le: cuticula forms puzzle like structures
t4.51				le: dense and complex network of undulate striae
t4.52	<i>Pouteria glomerata</i>	le		le: concentric rings of striae around the stoma, and radiating striae around concentric rings
t4.53				
t4.54	<i>Pseudobombax munguba</i>		le: nectaries	
t4.55				
t4.56				

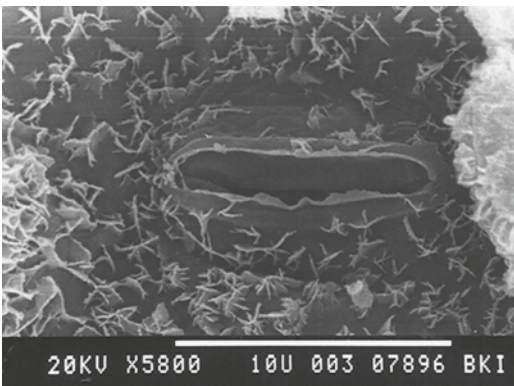
(continued)

Table 9.4 (continued)

Species	Hairs		Papillae	Wax layer	Cuticular ornamentation
	Not glandular	Glandular			
<i>Quinia rhytidopus</i>			le: with dense papillose hairs		le: concentric rings of striae around stomata and radiating striae around concentric rings
<i>Rheedia brasiliensis</i>		le			le: concentric rings of striae around stomata and radiating striae around concentric rings, ue: striae random and very dense
<i>Simaba guianensis</i>		ue, le glandular scales			le: concentric rings of striae around the stoma, and radiating striae around concentric rings
<i>Salix humboldtiana</i>					
<i>Senna reticulata</i>	ue, le		ue, le: simple, cone-like scales	ue, le: upright scales	
<i>Tabebuia barbata</i>		le			le: radiating striae around stomata
<i>Tabernaemontana juruana</i>					
<i>Tovomita macrophylla</i>					
<i>Vitex cymosa</i>	le	le, flattened glandular scales		le	ue: dense network of cuticular elevations le: rough surface of bulbous-like elevations

t4.57 ue, upper epidermis; le, lower epidermis

Fig. 9.7 Leaf surface structures: wax crystals and stoma on lower leaf surface of *Cassia leiandra*



(Parolin 2002d). Specific leaf mass in the non-flooded period varied between 48.8 gm⁻² for the pioneer *Senna reticulata* and 118.9 gm⁻² for the evergreen non-pioneer *Nectandra amazonum* (Table 9.5). In waterlogged months, specific leaf mass in an average was 5–33% higher than in non-flooded months. Only *Crateva benthami* had significantly lower specific leaf mass with waterlogging. This was due to the fact that the new leaves – which were mainly produced in the aquatic period – had higher specific leaf mass than older leaves. In *Cecropia latiloba*, *Crateva benthami*, *Tabebuia barbata* and *Vitex cymosa* there was a constant increase of specific leaf mass in the first months after leaf expansion, which occurs in the last months of the flooded period.

9.9 Leaf Size

The size of single leaves varied between few cm² for *Salix* and more than 2,380 cm² for *Cecropia latiloba* (Table 9.5). The pioneer *Senna reticulata* and two deciduous non-pioneers (*Crateva benthami*, *Tabebuia barbata*) had highly significant reductions of leaf area (25–37%) in the aquatic period, compared to the terrestrial period (Table 9.5). *Cecropia latiloba* and *Nectandra amazonum* produced leaves with a more or less constant size throughout the year.

Reductions of leaf size were caused by leaf senescence and a subsequent loss of leaflets. Only in *Senna reticulata* leaf size reduction was a direct response to water stress: in waterlogged months, the newly produced leaves and leaflets were smaller than in the terrestrial period (Parolin 2001c) (Fig. 9.9). Data in this study indicate a periodicity in several leaf traits which changes parallel to the flooding periodicity, but which is determined primarily by leaf age and senescence and only indirectly by flooding. The timing of the changes of specific leaf mass and leaf size was similar between species and was concentrated in the aquatic period, but the degree of changes differed among the species. Leaves of pioneer and non-pioneer species,

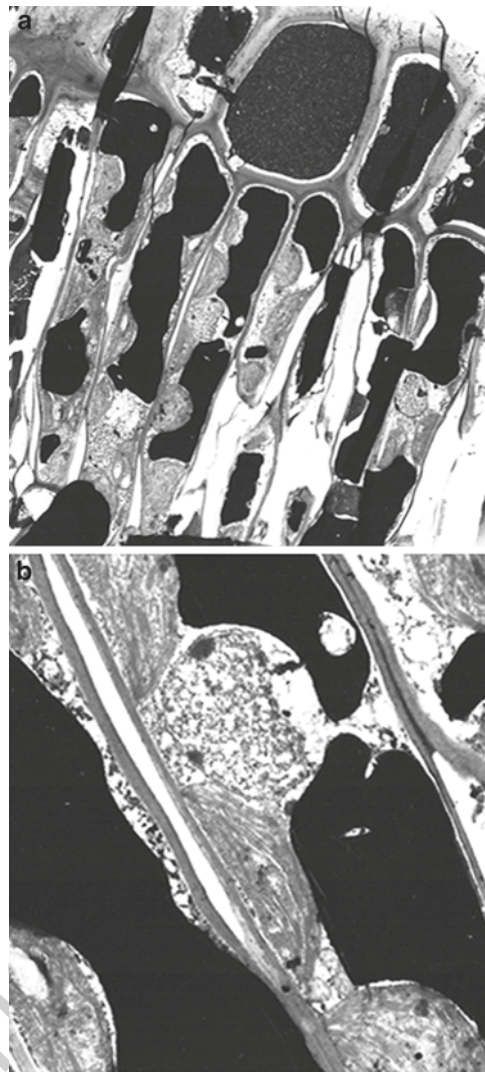


Fig. 9.8 Cross-sections from a leaf of *Symmeria paniculata* submerged at 1m depth: (a) Epidermis cells (upper row) and palisade parenchyma (lower row; arrow: starch grain); (b) chloroplast (upper organelle) and nucleus (middle organelle) from palisade parenchyma cell (transmission electron microscopy photographs, from Waldhoff et al. 2002)

214 and leaves of deciduous and evergreen species did not show a uniform trend, characteristic
 215 for certain growth strategies, as response to flooding. Apparently differences were
 216 closely linked to leaf age and cannot be considered as adaptive to the changing
 217 hydricological conditions.

Table 9.5 Specific leaf mass and leaf area of six species in the non-flooded and waterlogged months (From Parolin 2002c): minimum and maximum measured values, average of the measurements in the terrestrial phase, average of the measurements in the aquatic phase, with standard deviations, difference between terrestrial (= 100%) and aquatic phase

Specific leaf mass				
Species	Min-max (gm ⁻²)	Terrestrial phase (gm ⁻²)	Aquatic phase (gm ⁻²)	Difference (%)
15.5				
15.6				
15.7				
15.8				
15.9				
15.10				
15.11				
15.12				
15.13				
15.14				
15.15				
15.16				
15.17				
15.18				
15.19				

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Fig. 9.9 *Senna reticulata* with different leaf size in non-waterlogged (control) and waterlogged conditions



9.10 Leaf Water Content

Leaf water content varies between 49% and 74% (Parolin 2002c). Evergreen pioneer species had the highest water contents, and evergreen non-pioneer *Nectandra amazonum* the lowest (Table 9.6). In the flooded period, leaf water content was lower in all analysed species, probably as a result of new leaf expansion during this time. While differences were neglectable in *Cecropia latiloba* and *Nectandra amazonum*, where leaf water content was rather constant throughout the year, it changed significantly in the deciduous species and in the pioneer *Senna reticulata*. In all species, the new leaves had higher water contents than the adult and senescent leaves in the subsequent months. The absolute highest water contents were measured in newly developed leaves during the flooded period, but overall means were lower in this period.

9.11 Discussion and Conclusions

Most measured parameters and their changes in the annual cycle do not reflect the extreme environmental conditions to which trees in Amazonian floodplains are subjected. The hydrological conditions in the floodplains are unfavourable for tree growth for several months every year, as indicated by regular growth reductions in the wood

Table 9.6 Leaf water content of six species in the non-flooded and waterlogged months (from Parolin 2002c): minimum and maximum measured values, average of the measurements in the terrestrial phase, average of the measurements in the aquatic phase, with standard deviations, difference between terrestrial (= 100%) and aquatic phase, and statistical probability p

Species	Min–max (g m ⁻²)	Terrestrial phase (g m ⁻²)	Aquatic phase (g m ⁻²)	Difference (%)	P
<i>C. latiloba</i>	55.2–83.3	73.6 ± 5	71.8 ± 5	–2.6	n.s.
<i>S. reticulata</i>	57.0–84.4	71.0 ± 5	64.5 ± 4	–9.2	***
<i>N. amazonum</i>	30.9–59.0	48.6 ± 4	48.5 ± 4	–0.2	n.s.
<i>C. benthami</i>	49.4–81.4	67.6 ± 5	61.5 ± 6	–9.1	***
<i>T. barbata</i>	30.3–80.8	62.7 ± 5	54.7 ± 11	–12.8	***
<i>V. cymosa</i>	44.8–90.8	62.7 ± 9	55.0 ± 7	–12.3	***

*p ≥ 0.05; **p ≥ 0.01; ***p ≥ 0.001; n.s. not significant

(Worbes 1989). A relationship between leaf parameters and flooding periodicity was not found in the study species, and the measured variations, e.g. in leaf mass and size, are not understood as adaptations against flooding. If we take for example leaf size, we find that it has evolved to regulate leaf temperature, keeping it near an optimum for photosynthesis when the leaf is active and preventing thermal damage or death when the leaf is under stress (Givnish and Vermeij 1976). The reduction of the transpirational surface, i.e. leaf size, in periods of unfavorable hydric conditions could be an adaptation to the reduced tree water status induced by flooding (Borchert 1994a). It enables the plant to maintain high photosynthetic activity despite prolonged waterlogging. Only in *Senna reticulata* the reductions of 37% were a direct response to water stress: in the waterlogged months, the newly produced leaves and leaflets were smaller than those produced in the terrestrial period. Evidence for a reaction to waterlogging with the production of smaller leaves was given in an experiment with seedlings of *Senna reticulata* (Parolin 2001c). Since this species constantly produces new leaves, the production of smaller leaves under unfavourable conditions can be seen as adaptation against waterlogging. In other species, leaf production was not as fast as in *Senna reticulata*, and the newly produced leaves were not smaller. On the contrary, in *Nectandra amazonum*, and to a lesser extent in *Cecropia latiloba* and *Vitex cymosa*, in the flooded period a higher average leaf area was measured. This can be typical for highly flood tolerant species which have other physiological, morphological and anatomical adaptations to waterlogging than the regulation of leaf size (Angelov et al. 1996). A reduction of mean size of the single leaves in *Crateva benthami* and *Tabebuia barbata* was also related to leaf senescence and a consequent loss of leaflets in old leaves.




Concluding, leaf parameters make statements possible about the physiological condition of the trees in situ but the reactions to flooding are not as astonishing as could have been expected given the extreme flooding conditions the trees are subjected to. Most parameters indicate that the assimilation organs perform perfectly well despite the long periods of waterlogging or complete submergence in darkness. The high diversity of species is reflected in a high diversity of life strategies (evergreen/deciduous, fast-/slow-growing, high/low annual wood increments, high/low wood specific gravity, etc.) to cope with flooding, and leaf types differ to a certain extent (perhaps also due to taxonomic differences). However, the reactions of the leaves' functions are not as manifold as the extreme environment could suggest.

Leaf anatomy is not particularly divergent between species. Common to most species are a xeromorphic character, large upper epidermis cells, long palisade parenchyma cells, small spongy parenchyma cells, sunken stomata, hairs and wax layers on the leaf surface.

Amazonian floodplains show all characteristics of extreme sites. A very long uninterrupted period of flooding with a high amplitude, rapid changes of water level, anoxic conditions in the rhizosphere, high sedimentation in várzea, lack of nutrients in sediment-poor igapó, high mechanical stress and even drought lead to difficult conditions for growth of all organisms living in this ecosystem. Nevertheless, the high diversity of species and life strategies may result from the fact that this extreme site has only a reduced number of factors representing stress for the trees, and the regular disturbances may even represent a driving force for resistance and adaptive evolution. The high complexity of the system and the short but regular occurrence of factors enhancing tree growth allow the formation of highly diverse survival strategies. The species are seldom highly specialized – most have high ecological amplitudes. In these floodplains, specialization is low enough to allow the trees to react to changing environmental conditions, and is high enough to allow a high diversity along the hydric and edaphic gradient.

Author Queries

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Queries	Details Required	Author's Response
AU1	Please provide affiliations.	
AU2	Please specify a, b or c in Kubitzki (1989).	
AU3	'Barthlott 1990' is cited in text but not given in the reference list. Please provide details in the list.	
AU4	'Carpenter 1994' is cited in text but not given in the reference list. Please provide details in the list.	

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