

# Chapter 9

## Morphology and Anatomy of Leaves

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**Abstract** Leaves are among the most important organs of a plant, and they are indicators of the condition of a tree. Their morphology and anatomy shows adaptations and their functional traits reflect to some extent the constraints of the environments where the plants typically grow. However, despite the big differences in flooding intensity and nutrient availability, leaves of Amazonian floodplain trees are similar in their morphoanatomy and exhibit traits which are generally considered as xeromorph, just as the leaves of upland species. The xeromorphic leaf structure may represent a pre-adaptation resulting from the dry habitats most tree species originate from. It also helps to cope with insufficient water supply to the tree crowns

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during the aquatic phase which is caused by a decrease of root functioning due to waterlogging and submergence. The assimilation organs perform perfectly well despite the long periods of waterlogging or complete submergence in darkness. Leaf structure does not reflect the extreme environmental conditions to which trees in Amazonian floodplains are subjected. No patterns could be detected of a relationship of leaf functional traits with flooding intensity and nutrient availability.

## 9.1 Introduction

Long lasting inundations affect the physicochemical conditions in the soil, with oxygen deficiency in the rhizosphere and resulting stresses (Haase and Rättsch 2010) 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.

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.

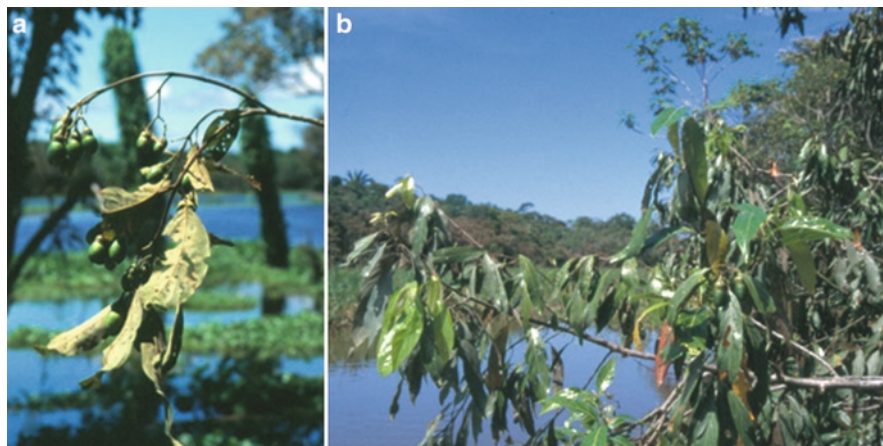
**Fig. 9.1** Submerged *Tabernaemontana juruana* in Manacapuru Lake (Parolin, August 1994)



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

## 9.2 Leaf Lifespan and Age

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



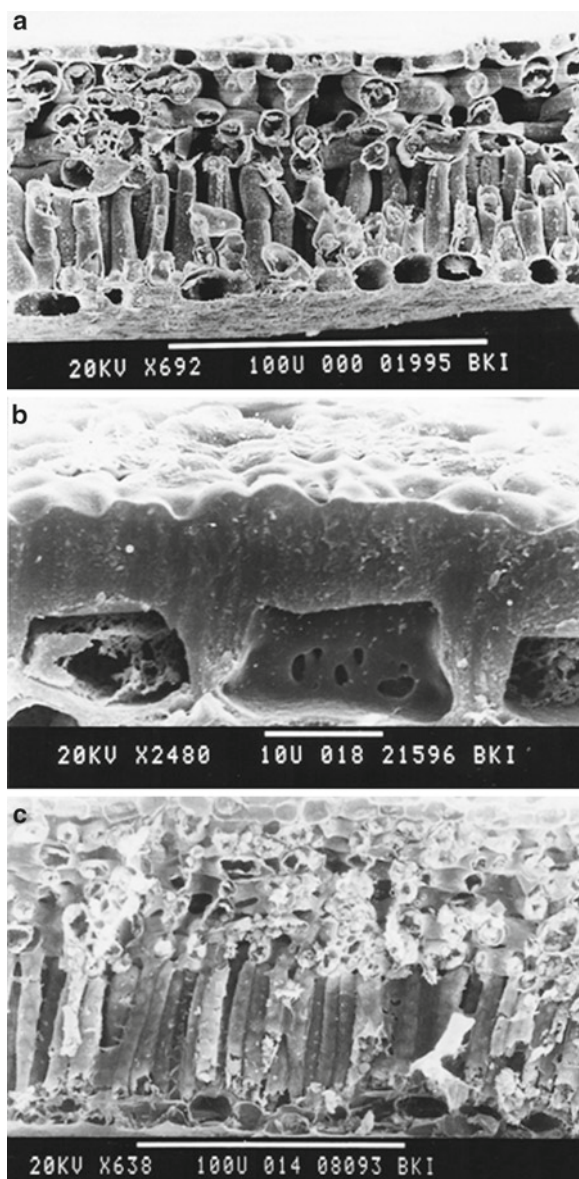
**Fig. 9.2** Branch of *Nectandra amazonum*: Leaf shedding and replacement occurs continuously, but a period with clearly senescent leaves (**a**) and fruit maturation dominates in the beginning of the aquatic period, whereas new leaves are flushed (**b**) at the highest water peak and towards the end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

### 9.3 Xeromorphism

The leaves of Amazonian floodplain trees exhibit traits which are generally considered as xeromorph (Medina 1983; Roth 1984; Bolh  r-Nordenkampf and Draxler 1993; Waldhoff et al. 2002; Waldhoff 2003): large epidermal cells (*Hevea spruceana*, *Eugenia inundata*, Fig. 9.3a), thick outer epidermis walls (*Rheedia brasiliensis* Fig. 9.3b, *Himatanthus sucuuba*), thick cuticle (*Eschweilera tenuifolia*, *Simaba guianensis*), compact spongy parenchyma with only few and small intercellular spaces (*Senna reticulata* Fig. 9.3c, *Licania apetala*), 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



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

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.



The xeromorphic leaf structure may represent a pre-adaptation resulting from the dry habitats most tree species originate from (Kubitzki 1989a). 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. succuba*, *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.

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<sup>-2</sup> (Table 9.3) and did not differ significantly between species that keep or shed submerged leaves (Waldhoff 2003). Species with higher stomatal

**Table 9.1** Cell size in different leaf components (all measures in  $\mu\text{m}$ ). 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 Waldbhoff and Furch 2002; Waldbhoff 2003)

| Species                        | Epidermis cell size |           | Outer wall – cuticula |           | Palisade parenchyma cell size | Spongy parenchyma cell size |
|--------------------------------|---------------------|-----------|-----------------------|-----------|-------------------------------|-----------------------------|
|                                | ue                  | le        | ue                    | le        |                               |                             |
| <i>Aldina latifolia</i>        | Large               | Large     | Medium                | Thick     | Medium                        | Medium                      |
| <i>Alchornea</i> sp.           | Small               | Small     | Medium                | Thin      | Long/small                    | Medium                      |
| <i>Alibertia</i> sp.           | Large               | Small     | Thick                 | Thin      | Medium/small                  | Medium                      |
| <i>Baccharis bidentata</i>     | Small               | Small     | Thick                 | Thick     | Medium                        | Small                       |
| <i>Baccharis maraja</i>        | Medium+             | Medium    | Thick                 | Medium    | Not existing                  | Medium                      |
| <i>Calliandra amazonica</i>    | Medium              | Medium    | Thick                 | Thick     | Very long/small               | Small                       |
| <i>Cratogeomys benthami</i>    | Large               | Small     | Medium                | Thick     | Small                         | Small                       |
| <i>Cecropia latiloba</i>       | Large               | *         | Thin                  | *         | *                             | *                           |
| <i>Cassia leiandra</i>         | Medium              | Medium    | Thin                  | Thin      | Small                         | Small                       |
| <i>Couepia parensis</i>        | Large               | Medium    | Thick                 | Medium    | Medium/small                  | Not existing                |
| <i>Eugenia inundata</i>        | Large               | Small     | Thick                 | Thin      | Medium                        | Medium                      |
| <i>Eschweilera tenuifolia</i>  | Medium              | Small     | Very thick            | Thick     | Long/small/small              | Medium                      |
| <i>Hevea spruceana</i>         | Very large          | Large     | Thick                 | Thin      | Very long                     | Medium                      |
| <i>Himatanthus sucubus</i>     | Large               | Large     | Thick                 | Thin      |                               |                             |
| <i>Ilex inundata</i>           | Medium              | Small     | Thick                 | Thick     | Very long/small               | Small                       |
| <i>Licania apetala</i>         | Large               | (Papilla) | Medium                | (Papilla) | Long/small/small              | Medium                      |
| <i>Macarobium acaciifolium</i> | Large               | Medium    | Thick                 | Thin      | *                             | Medium                      |
| <i>Maprounea guianensis</i>    | Medium              | Large     | Thick                 | Thin      | Long                          | Small                       |
| <i>Mouriri guianensis</i>      | Small               | Small     | Thick                 | Thin      | Small                         | Large                       |
| <i>Nectandra amazonum</i>      | Large               | Large     | Medium                | Medium    | Long/small/small              | Not existing                |
| <i>Nectandra</i> sp.           | Large               | Large     | Thick                 | Thick     | Medium/small                  | Large                       |

(continued)

Table 9.1 (continued)

| Species                        | Epidermis cell size |        | Outer wall – cuticula |        | Palisade parenchyma cell size | Spongy parenchyma cell size |
|--------------------------------|---------------------|--------|-----------------------|--------|-------------------------------|-----------------------------|
|                                | ue                  | le     | ue                    | le     |                               |                             |
| <i>Ouratea hexasperma</i>      | Large               | Medium | Very thick            | Medium | Very long                     | Medium                      |
| <i>Psidium acutangulum</i>     | Large +             | Small  | Thick                 | Thin   | Medium/small                  | Medium                      |
| <i>Pouteria glomerata</i>      | Small               | Small  | Thick                 |        | Medium                        | Small                       |
| <i>Pseudobombax munguba</i>    | Large               | Medium | Thin                  | Medium | Long/small                    | Small                       |
| <i>Quinia rhytidopus</i>       | Medium              | Small  | Thick                 | Thin   | Medium                        | Medium                      |
| <i>Rheedia brasiliensis</i>    | Large               | Large  | Very thick            | Thick  | Medium/small                  | Medium                      |
| <i>Simaba guianensis</i>       | Large               | Small  | Thin                  | Thick  | Medium                        | Small                       |
| <i>Salix humboldtiana</i>      | Medium +            | Medium | Thin                  | Thin   | Small/small etc.              | Not existing                |
| <i>Senna reticulata</i>        | Medium              | Medium | Thin                  | Thin   | Long                          | Medium                      |
| <i>Tabebuia barbata</i>        | Medium +            | Large  | Thin                  | Thin   | Long-very long                | Medium                      |
| <i>Tabernaemontana juruana</i> | Large               | Large  | Thick                 | Thick  | Small                         | Large                       |
| <i>Tovomitia macrophylla</i>   | Large               | Large  | Thick                 | Thick  | Small                         | Small                       |
| <i>Vitex cynosa</i>            | Large               | Large  | Thin                  | Thin   | Long/small/small              | Not existing                |

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



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

| Species                         | No. of layers of palisade parenchyma | Compactness of spongy parenchyma | Canals       | Vascular bundles    |                                       |
|---------------------------------|--------------------------------------|----------------------------------|--------------|---------------------|---------------------------------------|
|                                 |                                      |                                  |              | Extension           | Sclerenchyma                          |
| <i>Aldina 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>Bactris bidentula</i>        | 1                                    | Compact                          |              | Not transcurrent    | Sheath surrounding the bundle, fibres |
| <i>Bactris maraja</i>           | Not existing                         | Compact                          |              | Not transcurrent    | Sheath surrounding the bundle, fibres |
| <i>Calliandra amazonica</i>     | 1 up, 1 low                          | Loose                            |              | Not transcurrent    | Weekly developed                      |
| <i>Cratava benthami</i>         | 1–2                                  | Loose                            |              | Not transcurrent    | No sclerenchyma                       |
| <i>Cecropia latiloba</i>        | *                                    | *                                |              | *                   | *                                     |
| <i>Cassia leiandra</i>          | 1                                    | Compact                          |              | Transcurrent        | Strong sheath surrounding the bundle  |
| <i>Couepia paraensis</i>        | 4                                    | –                                |              | Transcurrent        | Capping bundles on both sites         |
| <i>Eugenia inundata</i>         | 1                                    | Regular                          |              | Transcurrent        | Capping bundles on both sites         |
| <i>Eschweilera tenuifolia</i>   | 1 up, 1 low                          | Very compact                     |              | Mostly transcurrent | Sheath surrounding the bundle         |
| <i>Hevea spruceana</i>          | 1                                    | Compact                          | Laticiferous | Not transcurrent    | Weekly developed                      |
| <i>Himatanthus sucuba</i>       | *                                    | *                                |              | *                   | *                                     |
| <i>Ilex inundata</i>            | 2                                    | Regular                          |              | Not transcurrent    | Capping bundles on one site           |
| <i>Licania apetala</i>          | 2                                    | Very compact                     |              | Not transcurrent    | Strong sheath surrounding the bundle  |
| <i>Macrolobium acaciifolium</i> | *                                    | Regular                          |              | *                   | *                                     |
| <i>Maprounea guianensis</i>     | 1                                    | Regular                          |              | Transcurrent        | Strong sheath surrounding the bundle  |
| <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>Quinia 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>Tovomita macrophylla</i>    | 1–2                                  | Regular                          |           | Not transcurrent    | Weekly developed                     |
| <i>Vitex cymosa</i>            | 2–3                                  | Not existing                     |           | Transcurrent        | Capping bundles on both sites        |

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

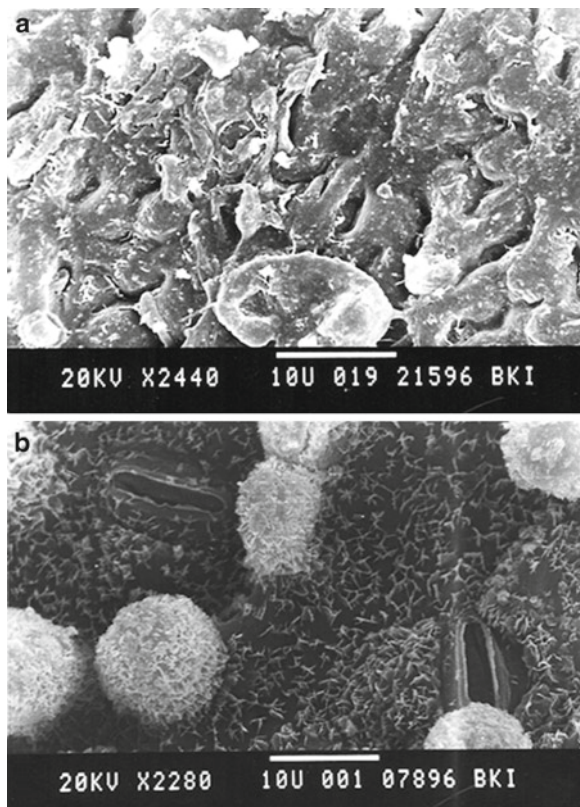
**Table 9.3** Density and form of stomata (from Waldhoff and Furch 2002; Waldhoff 2003)

| Species                         | Density (number mm <sup>-2</sup> ) |       | Form  |
|---------------------------------|------------------------------------|-------|---|
|                                 | ue                                 | le    |   |
| <i>Aldina latifolia</i>         |                                    | 25    | Sunken in thick cuticula  |
| <i>Alchornea</i> sp.            | 309                                | 233   | Not sunken  |
| <i>Alibertia</i> sp.            |                                    | 696   | Not sunken  |
| <i>Bactris bidentula</i>        |                                    | nv    | Completely sunken in cuticular folds  |
| <i>Bactris maraja</i>           | 63                                 | 248   | Sunken  |
| <i>Calliandra amazonica</i>     |                                    | 643   | Sunken in thick cuticula  |
| <i>Crateva benthami</i>         |                                    | 582   | Not sunken  |
| <i>Cecropia latiloba</i>        | 69                                 | ?     | Not sunken  |
| <i>Cassia leiandra</i>          |                                    | 814   | Sunken  |
| <i>Couepia paraensis</i>        |                                    | nv    | Sunken in cuticular folds, hidden by hairs                                    |
| <i>Eugenia inundata</i>         |                                    | 620   | Sunken in cavity formed by the raised stomatal rim                            |
| <i>Eschweilera tenuifolia</i>   |                                    | nv    | Sunken in very thick cuticula   |
| <i>Hevea spruceana</i>          |                                    | 369   | Sunken  |
| <i>Himatanthus sucuuba</i>      |                                    | 675   | Sunken, with raised stomatal rim  |
| <i>Ilex inundata</i>            |                                    | 601   | Sunken with raised stomatal rim   |
| <i>Licania apetala</i>          |                                    | nv    | Sunken in deep pit formed by papillose subsidiary cells                       |
| <i>Macrolobium acaciifolium</i> | nv                                 | nv    | le: sunken between elevations of wax  |
| <i>Maprounea guianensis</i>     |                                    | nv    | Sunken in cuticular folds   |
| <i>Mouriri guianensis</i>       |                                    | 1,952 | Sunken in holes formed by cuticular folds                                     |
| <i>Nectandra amazonum</i>       |                                    | 1,188 | Sunken  |
| <i>Nectandra</i> sp.            |                                    | 318   | Sunken in cuticula  |
| <i>Ouratea hexasperma</i>       |                                    | 913   | Sunken in cavity formed by the raised stomatal rim                            |
| <i>Psidium acutangulum</i>      | 149                                | 837   | Sunken in cavity formed by the raised stomatal rim                            |
| <i>Pouteria glomerata</i>       | 177                                | 449   | ue: not sunken, le: sunken with raised stomatal rim and long, narrow aperture |
| <i>Pseudobombax munguba</i>     | nv                                 | 284   | Sunken with raised stomatal rim   |
| <i>Quiinia rhytidopus</i>       |                                    | 2,339 | Sunken in deep pit formed by papillose subsidiary cells                       |
| <i>Rheedia brasiliensis</i>     | nv                                 | 178   | Sunken in pit formed by very thick cuticula                                   |
| <i>Simaba guianensis</i>        |                                    | 4     | Sunken  |
| <i>Salix humboldtiana</i>       | 393                                | 343   | Sunken with raised stomatal rim   |
| <i>Senna reticulata</i>         | 141                                | 84    | Sunken  |
| <i>Tabebuia barbata</i>         |                                    | 287   | Sunken with raised stomatal rim   |
| <i>Tabernaemontana juruana</i>  |                                    | 716   | Not sunken  |
| <i>Tovomita macrophylla</i>     |                                    | 201   | Not sunken  |
| <i>Vitex cymosa</i>             |                                    | 176   | Sunken in cavity formed by the raised stomatal rim                            |

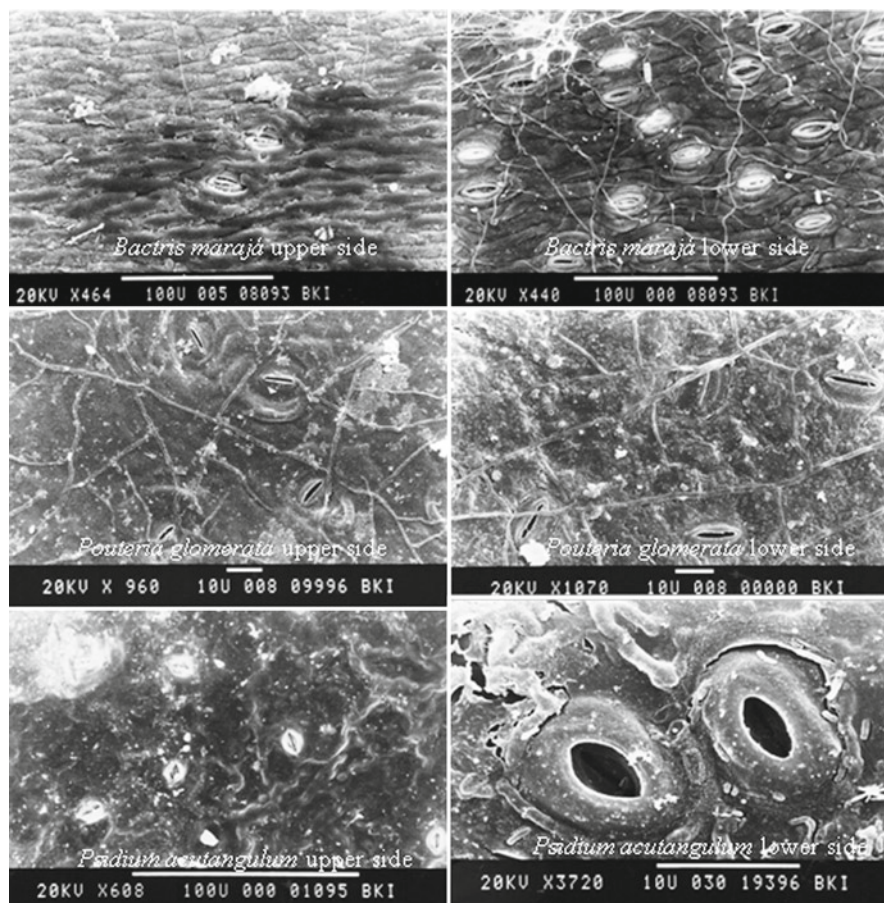
le, lower epidermis; nv, not visible; ue, upper epidermis

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-Nordenkamp 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-Nordenkamp and Draxler 1993), e.g. *Rheedia brasiliensis* (Fig. 9.4a), *Bactris maraja*, *Pouteria glomerata*, and *Psidium acutangulum* (Fig. 9.5). Amphistomatic leaves are commonly found in members of the family Caesalpiniaceae (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



**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)



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

are buried in a cavity or pit-like hole, sunken between waxy elevation or cuticular folds (Table 9.3).

Waldhoff et al. (2002), Fernandes-Corrêa and Furch (1992), and Schlüter 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”.

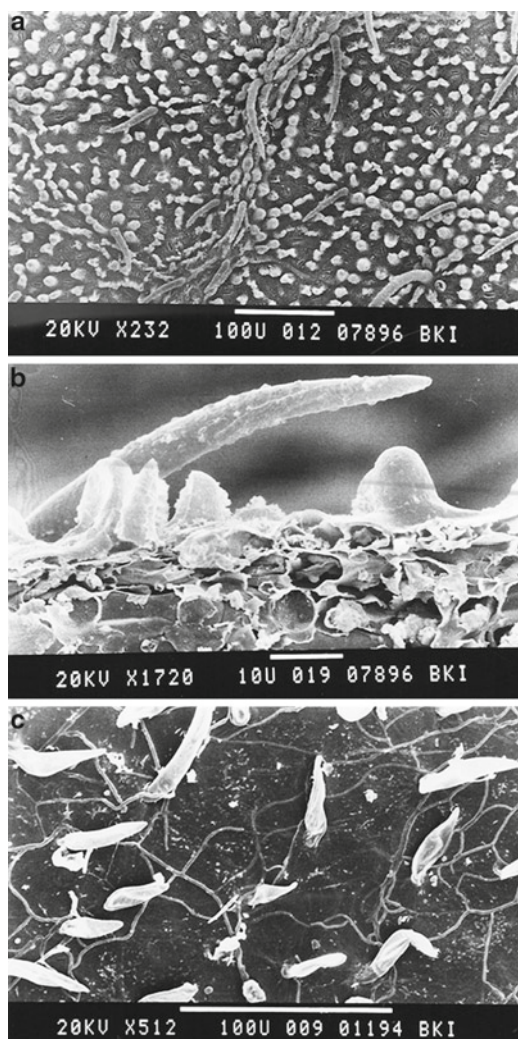
Sunken stomata are common in xeromorphic leaves (Roth 1984; Bolhàr-Nordenkamp and Draxler 1993). On the other hand Fahn and Cutler (1992) reported that only 34% of xeromorphic species (35 dicotyledons, 33 monocotyledons, 3 gymnosperms) from arid and semi-arid environments possess sunken stomata. Lindorf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

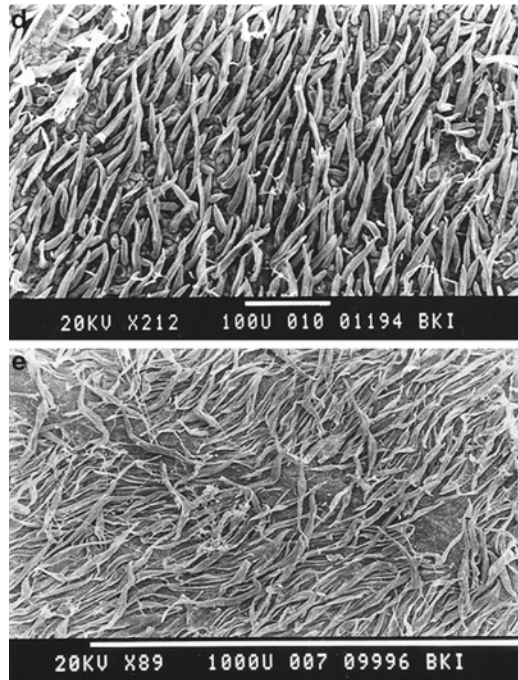
Glandular and non-glandular hairs were found in leaves from several species studied in the floodplain forests, e.g. *Cassia leiandra*, *Nectandra amazonum*, and *Pouteria glomerata* (Fig. 9.6, Table 9.4; Waldhoff and Furch 2002; Waldhoff 2003). The lower leaf surface of *Licania apetalata*, *Senna reticulata*,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

Ten analysed species exhibited wax deposits (Fig. 9.7), twenty showed cuticular ornamentations, mostly on the lower leaf side (see Table 9.4). These ornamenta-



**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)

tions 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 1990). The sculpturing of *Hevea spruceana* is very similar to that of *Hevea brasiliensis* from terra firme uplands (Wilkinson 1979; Sena Gomes and Kozłowski 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).

## 9.7 Chloroplasts

In the palm *Bactris bidentula*, palisade parenchyma cells are densely filled with chloroplasts (Waldhoff 2003). Such a high density of chloroplasts in palisade parenchyma had not been described hitherto. It might be helpful for a possible photosynthesis under water when light is the limiting factor (Furch et al. 1985). Although light can be an important limiting factor under water, presumably  $\text{CO}_2$  is

**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                |                       |                        |   |
| <i>Aldina latifolia</i>       | le                        |                          |                       |                        | le: rough surface with irregular elevations<br>ue: radiating striae around stomata<br>le: rough surface<br>ue, le: the whole surface is structured by many cuticular folds<br>ue, le: the whole surface is structured by some cuticular folds |
| <i>Alchomea</i> sp.           |                           |                          |                       |                        |   |
| <i>Alibertia</i> sp.          |                           |                          |                       |                        |   |
| <i>Bactris bidentula</i>      |                           |                          |                       | le                     |   |
| <i>Bactris maraja</i>         | le                        |                          |                       |                        |   |
| <i>Calliandra amazonica</i>   | ue                        |                          |                       |                        | ue, le: the whole surface is structured by many cuticular folds   |
| <i>Crateva benthami</i>       |                           |                          |                       |                        |   |
| <i>Cecropia latiloba</i>      | ue; le: filamentous hairs | ue                       |                       |                        |   |
| <i>Cassia leiandra</i>        | le                        |                          | le: simple, corn-like | ue, le: upright scales |   |
| <i>Couepia paraensis</i>      | le                        |                          |                       |                        | le: cuticular folds; ue: very large cuticular folds<br>le: concentric rings of striae around stomata and radiating striae around concentric rings<br>ue: striae random and very dense   |
| <i>Eugenia inundata</i>       |                           | ue, le: glandular scales |                       |                        |   |
| <i>Eschweilera tenuifolia</i> |                           | ue, le: glandular scales |                       |                        |   |

|                                 |        |                     |  |
|---------------------------------|--------|---------------------|--|
| <i>Hevea spruceana</i>          |        | le                  | ue, le: reticulum of crests and buttressed ridges around stomata<br>le: concentric rings of striae around stomata<br>le: concentric rings of striae around the stoma |
| <i>Himatanthus sucuuba</i>      |        |                     |  |
| <i>Ilex inundata</i>            |        | ue                  |  |
| <i>Licania apetala</i>          |        |                     | le: with dense papillose hairs   |
| <i>Macrolobium acaciifolium</i> | ue     | ue: many elevations |  |
| <i>Maprounea guianensis</i>     |        | ue: many elevations | le: dense network of radiating striae around the stoma and between them<br>le: dense network of cuticular folds  |
| <i>Mouriri guianensis</i>       |        |                     |  |
| <i>Nectandra amazonum</i>       | ue, le | le: rods of wax     |  |
| <i>Nectandra</i> sp.            |        |                     |  |
| <i>Ouratea hexasperma</i>       | le     | ue, le              | le: elevations formed by cuticula<br>ue, le: cuticula forms puzzle like structures   |
| <i>Psidium acutangulum</i>      |        |                     | le: dense and complex network of undulate striae   |
| <i>Pouteria glomerata</i>       | le     |                     | le: concentric rings of striae around the stoma, and radiating striae around concentric rings  |
| <i>Pseudobombax munguba</i>     |        | le: nectaries       |  |

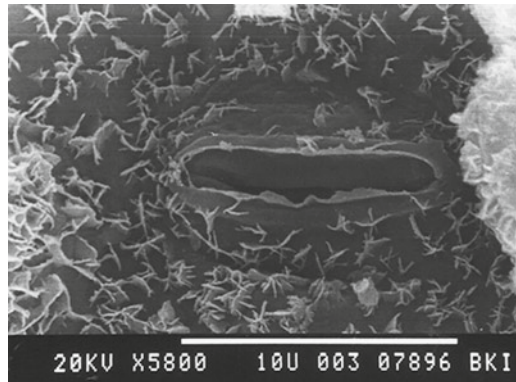
(continued)

Table 9.4 (continued)

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

ue, upper epidermis; le, lower epidermis

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

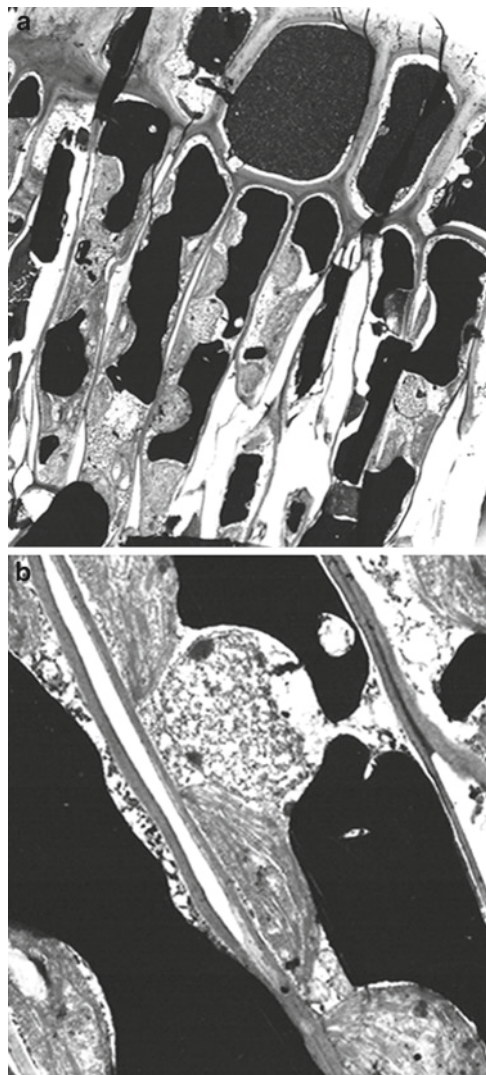


much more limiting (Mommer and Visser 2005), but no studies are available to this respect in Amazonian floodplain trees.

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

## 9.8 Specific Leaf Mass

Specific leaf mass was higher in waterlogged months in many species, e.g. *Cecropia latiloba*, *Nectandra amazonum*, *Senna reticulata*, *Tabebuia barbata*, and *Vitex cymosa*, in adult trees in the field as well as in seedlings under experimental conditions (Parolin 2002d). Specific leaf mass in the non-flooded period varied between 48.8 gm<sup>-2</sup> for the pioneer *Senna reticulata* and 118.9 gm<sup>-2</sup> 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.



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

## 9.9 Leaf Size

The size of single leaves varied between few cm<sup>2</sup> for *Salix* and more than 2,380 cm<sup>2</sup> for *Cecropia latiloba* (Table 9.5). The pioneer *Senna reticulata* and two deciduous non-pioneers (*Crateva benthami*, *Tabebuia barbata*) had highly significant



**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

| Species                   | Specific leaf mass          |                                       |                                   |                |
|---------------------------|-----------------------------|---------------------------------------|-----------------------------------|----------------|
|                           | Min-max (gm <sup>-2</sup> ) | Terrestrial phase (gm <sup>-2</sup> ) | Aquatic phase (gm <sup>-2</sup> ) | Difference (%) |
| <i>Cecropia latiloba</i>  | 43.8–112.7                  | 74.6 ± 16                             | 78.0 ± 17                         | 4.6            |
| <i>Senna reticulata</i>   | 25.3–86.7                   | 48.8 ± 11                             | 64.8 ± 12                         | 32.7           |
| <i>Nectandra amazonum</i> | 95.0–163.9                  | 118.9 ± 14                            | 140.1 ± 17                        | 17.7           |
| <i>Cratava benthami</i>   | 38.2–126.9                  | 94.3 ± 24                             | 80.5 ± 28                         | –14.6          |
| <i>Tabebuia barbata</i>   | 33.4–133.5                  | 76.3 ± 19                             | 96.5 ± 23                         | 26.4           |
| <i>Vitex cymosa</i>       | 50.8–143.4                  | 83.3 ± 19                             | 106.9 ± 20                        | 28.4           |
| Leaf area                 |                             |                                       |                                   |                |
|                           | Min-max (cm <sup>2</sup> )  | Terrestrial phase (cm <sup>2</sup> )  | Aquatic phase (cm <sup>2</sup> )  | Difference (%) |
| <i>Cecropia latiloba</i>  | 605–2,380                   | 1,051.9 ± 113                         | 1,090.3 ± 122                     | 3.7            |
| <i>Senna reticulata</i>   | 660–1,588                   | 805.4 ± 218                           | 504.3 ± 262                       | –37.0          |
| <i>Nectandra amazonum</i> | 12–101                      | 42.0 ± 12                             | 52.3 ± 18                         | 24.6           |
| <i>Cratava benthami</i>   | 49–531                      | 209.0 ± 81                            | 131.7 ± 47                        | –37.4          |
| <i>Tabebuia barbata</i>   | 89–670                      | 371.1 ± 105                           | 278.9 ± 122                       | –24.9          |
| <i>Vitex cymosa</i>       | 88–663                      | 262.1 ± 133                           | 232.9 ± 93                        | 11.1           |

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



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

**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 <sup>-2</sup> ) | Terrestrial phase (g m <sup>-2</sup> ) | Aquatic phase (g m <sup>-2</sup> ) | 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

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 (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.