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# Leaf morphology and anatomy in eleven tree species from Central Amazonian floodplains (Brazil)*

by

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## Abstract

Leaf anatomy and morphology in eleven common arboreal species representing eleven families from Central Amazonian floodplain forests (Brazil) were analysed with SEM microscopy. Species differed in leaf-fall behaviour (evergreen, deciduous) as well as in the fate of submerged leaves (species either shed or keep their submerged leaves). Leaves of all species showed various traits generally related to leathery leaves and/or xeromorphism, e.g., large epidermal cells, thick outer epidermis walls, thick cuticula, compact spongy parenchyma with only few and small intercellular spaces, sunken stomata, and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath. We found no trend to differentiate evergreen from deciduous species by leaf morphology and anatomy. Species that shed their submerged leaves showed similar characteristics than species that keep their submerged leaves. A high level of screlophylly in most species suggests that the trees might experience water stress in their floodplain habitats, independent of leaf-fall behaviour. However, as leathery and/or xeromorphic leaf are the typical pattern in tropical trees, leaf structures found here are unlikely to represent adaptations to floodplain conditions. Keeping submerged leaves apparently does not require different or additional morphological or anatomical characteristics.

Keywords: **Amazon, leaf anatomy, leaf morphology, xeromorphism, cuticula, epidermis, sclerophylly**.

## Resumo

A anatomia e a morfologia foliar de onze espécies arbóreas representando onze familias das florestas inundáveis da Amazonia Central (Brasil) foram estudadas com um microscópio de varredura. As espécies diferenciaram-se no seu comportamento foliar (sempre-verdes e deciduas) assim como no "destino" das folhas submersas (mantê-las ou não). As folhas de todas as espécies apresentaram várias características descritas na literatura como coreaceas e/ou xeromórficas, como por exemplo células grandes na epiderme, paredes celulares exteriores da epidermis espessas, cutícula espessa, parênquima lacunoso compacto com alguns pequenos intercelulares, estômatos aprofundados na epiderme, feixes vasculares transcorrentes com cinto esclerenquimático forte em volta. Não foi encontrada uma tendência que pudesse diferenciar as

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espécies sempre-verdes das deciduas quanto a anatomia e morfologia foliar. Espécies que perdem as folhas submersas apresentam características foliares similares. O alto nível de sclerofilia na maioria das espécies indica um possível estresse de falta de água nos ambientes alagáveis, independente das árvores serem sempre-verdes ou deciduas ou perderem as folhas submersas ou não. Mas como folhas xeromórficas e/ou coreaceas são o padrão típico para florestas tropicais, as estruturas encontradas neste estudo provavelmente não representam adaptações às condições de inundação. Manter folhas submersas aparentemente não requer características morfológicas ou anatômicas adicionais ou diferentes.

## Introduction

Floodplain forests of Central Amazonia are inundated for up to 6.5 months every year, corresponding to a submersion depth of up to 8 m (JUNK et al. 1997; JUNK & KRAMBECK 2000). Tree species that do not shed their leaves during the whole year including the inundation period are generally classified as evergreen species whereas species that shed their leaves, usually during rising water levels, are referred to as deciduous. The latter flush new leaves between the high water peak and the end of the aquatic phase (WORBES 1986; WITTMANN & PAROLIN 1999; PAROLIN 2000; PAROLIN et al. 2001; SCHÖNGART et al. 2002). Most of the evergreen species even keep their submerged leaves and maintain their capacity for photosynthesis (FURCH 1984; SCHLÜTER & FURCH 1992; SCHLÜTER et al. 1993; WALDHOFF et al. 1998, 2000, 2002).

Leaves are the most exposed organs of the plant. Evolutionary changes in shape and structure are therefore interpreted as adaptations to specific environments (FAHN & CUTTLER 1992). Morphological and anatomical differences found in leaves within the same individual have been especially related to the extent of sun exposure or water availability (BARTHLOTT 1989; NIINEMETS & KULL 1994; SMITH et al. 1997).

The upper leaves of trees in tropical forests face high insolation and a scarce water supply. Correspondingly, their leaves are xeromorphic and of the so called sun-type: increased number of palisade layers (2-5 layers, in some cases the entire mesophyll is transformed into palisade cells) and elongated palisade cells (ROTH 1984; BOLHÀR-NORDENKAMPF & DRAXLER 1993). WALTER & BRECKLE (1984) emphasise the leathery consistence of leaves in tropical trees as a special form of xeromorphism. VARESCHI (1980), on the contrary, argues that leathery leaves may be xeromorphic in some species but are hygromorphic in others. A quantification of sclerophylly (relation of dry mass with surface area) indicates the extent of adaptation to potential water shortages. Several characteristics have been described as common in xeromorphic and/or leathery leaves, e.g., large-celled epidermis with water-storing cells, thick outer epidermis walls, thick cuticula, compact spongy parenchyma with few and small intercellular spaces, high stomata density, sunken stomata, and transcurrent vascular bundles with a strong sclerenchymatous bundle sheath (ROTH 1984; WALTER & BRECKLE 1984; BOLHÀR-NORDENKAMPF & DRAXLER 1993).

Floodplain forests have to cope with an excessive amount of water in the ecosystem. WORBES (1986, 1997) reported on a water deficit in the canopy of Central Amazonian floodplain forests during the inundation period similar to the one found in trees on terra firme during the dry season. This is likely to be caused by reduced root activity and water conductance due to anaerobic conditions in flooded soils. Trees in Central Amazonian floodplain forests should additionally experience water stress during the dry season, especially those growing both at the higher and the very low along the flooding gradient (for climatological details cf. JUNK & KRAMBECK 2000). The latter are more exposed to insolation and often grow on sandy sediments. A xeromorphic leaf morphology and anatomy is therefore expected in these trees. FERNANDES-CÔRREA & FURCH (1992) and SCHLÜTER & FURCH (1992), although focussing on different topics, showed morphological features related to xeromorphism in selected tree species from these floodplain forests: sunken stomata, thick cuticula and wax layers, and large epidermal cells. WALDHOFF et al. (2002) reported on similar traits in leaves of *Symmeria paniculata* (Polygonaceae), a light-demanding tree species growing at the lowest part of the flooding gradient. Detailed investigations on leaf morphology and anatomy with respect to xeromorphism were not undertaken hitherto.

In this study we analyse the morphology and anatomy of the upper leaves in eleven common arboreal species from white- and blackwater floodplain forests (várzea and igapó, respectively; cf. PRANCE 1979, 2001) of Central Amazonia. We expect xeromorphic leaf structures. Deciduous species might show a lesser degree of xeromorphism whereas evergreen species that do not shed their submerged leaves are expected to show the highest degree of xeromorphism as they have to withstand the mechanical impact of the inundation and avoid influx of water (SCHLÜTER et al. 1993).

## Materials and methods

We selected eleven common species that differ in leaf-fall behaviour (Tab. 1) from eleven different species-rich families (cf. HALLÉ et al. 1978; WORBES 1997) to study leaf morphology and anatomy. Mature sun leaves (> 5 month, < 12 month) were collected in May 1996 (rising water levels) from trees located in floodplain forests on the Marchantaria Island (located in the Rio Solimões/Amazonas, várzea, 15 km from Manaus) and along the Tarumã River (igapó, 20 km north-east of Manaus). Surface cuttings and cross-sections of material were transported in 70 % alcohol from Manaus (Brazil) to Kiel (Germany). The samples were investigated with a scanning electron microscope (LEITZ SEM 1000). There they were dehydrated and transferred into acetone (steps 25 %, 50 %, 70 %, and 100 % acetone), dried using the critical-point method and then sputtered with gold. Stomata and glands were counted on several samples from the leaf lamina between the principal veins. The size of the cells and the thickness of cuticula and the epidermis wall were measured in typical cells on the photographs presented here and others of higher magnification. To describe the degree of sclerophylly the following index was determined from 1-5 leaves: (dry mass) / 2 (leaf surface). Leaf material was provided by the herbarium of the INPA/Manaus.

## Results

Cell sizes in different leaf components are summarized in Table 2. Two out of six species that keep submerged leaves showed a very thick cuticula and outer wall on the upper leaf side (*E. tenuifolia, R. brasiliensis*; Figs. 15, 27, 28). On the contrary, three out of five species that shed submerged leaves showed an upper epidermis with a thin outer wall/cuticula (*S. reticulata, S. guianensis, V. cymosa*; Figs. 7, 10, 12). All others presented either medium (*L. apetala, N. amazonum*; Figs. 19, 22) or thick (*E. inundata, H. spruceana, H. sucuuba, P. glomerata*; Figs. 1, 4, 17, 24) cuticula and outer walls. The outer walls and cuticula of the lower epidermis tended to be rather thin in all species. With the exception of *P. glomerata* (Fig. 21) all species showed medium (Figs. 7, 15), large (e.g., Figs. 1, 10) or even very large (Fig. 4) upper epidermal 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 *V. cymosa*. Those that do not shed submerged leaves showed more than one, some times even one additional layer at the lower leaf side, with the exception of *P. glomerata* (Tab. 3). In leaves with multiple palisade parenchyma layers the cell length decreased towards the inner layers (Tab. 2; Figs. 12, 15, 19, 22, 27).

The compactness of the spongy parenchyma ranged from loose in *R. brasiliensis* and *S. guianensis*, regular in *E. inundata*, and compact to very compact in the other species (Tab. 3; Figs. 27, 10, 1, 4, 7, 15, 19, 24). The spongy parenchyma was completely missing in *V. cymosa* and *N. amazonum* (Figs. 12, 22). The extension of the vascular bundles as well as the form of the sclerenchymatous sheath varied between species in different combinations (Tab. 3). The degree of sclerophylly was high in seven out of eleven species as indicated by index values around 0.4 and higher.

Stomata density at the lower leaf side varied between 4 and 1188 $mm^{-2}$ (Tab. 4). In two species the stomata were sunken to an extent that made them invisible from the leaf surface (Tab. 4; *E. tenuifolia*, *L. apetala* (Fig. 21)). Three species showed amphistomatic leaves (Tab. 4). All species had sunken stomata at the lower side of the leaf, some even showed stomata buried in a cavity or pit-like hole (Tab. 4; Figs. 3, 6, 9, 14, 16, 18, 21, 23, 26, 29; cf.).

Glandular hairs where found in five species (Figs. 2, 11, 13, 16) whereas four species showed non-glandular hairs (Tab. 5; Figs. 8, 13, 23, 25). The lower leaf surface of *L. apetala* and *S. reticulata* was covered with papillas (Tab. 5; Figs. 8, 20). Four species exhibited wax deposits (Tab. 5; Figs. 6, 8, 9, 14, 23), seven showed cuticular ornamentations, mostly at the lower leaf side (Tab. 5; Figs. 2, 3, 5, 6, 11, 13, 18, 26, 29).

## Discussion

Corresponding to the taxonomic diversity, leaf morphology and anatomy varied greatly between the eleven investigated species. However, despite the differences in leaf-fall behaviour and fate of submerged leaves, all species showed leaf characteristics usually attributed to either leathery leaves and sclerophylly (VARESCHI 1980) or to xeromorphism (ROTH 1984; WALTER & BRECKLE 1984; BOLHÀR-NORDENKAMPF & DRAXLER 1993). Among the characteristics investigated no clear trend was found to differentiate deciduous from evergreen species by leaf morphology and anatomy. The same holds for species that either keep or shed their submerged leaves, with the possible exception of the thickness of cuticula and outer epidermal walls being thin in three out of five species that shed submerged leaves.

The stomata densities documented here lie well within the typical range of 100-600 $mm^{-2}$ reported for many tropical trees (ROTH 1984) which also holds for the few tree species form Central Amazonian floodplains studied so far (SCHLÜTER & FURCH 1992; WALDHOFF et al. 2002; WALDHOFF unpubl.). Stomata density was apparently not associated with a certain type of leaf-fall behaviour, which corresponds with the literature on the relation of stomata density with xeromorphism (WILKINSON 1979; ROTH 1984; BOLHÀR-NORDENKAMPF & DRAXLER 1993; CAO 2000; DONG & 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 (BOLHÀR-NORDENKAMPF & DRAXLER 1993). Amphistomatic leaves are commonly found in members of the family Caesalpiniaceae (ROTH 1984; METCALFE & CHALK 1950).

Sunken stomata are generally common in xeromorphic leaves because they reduce water losses through transpiration (ROTH 1984; BOLHÀR-NORDENKAMPF & DRAXLER 1993). WALDHOFF et al. (2002), FERNANDES-CÔRREA & FURCH (1992), and SCHLÜTER & FURCH (1992) also described sunken stomata in several tree species that do not shed submerged leaves from Central Amazonian floodplains. The latter two studies ascribed this structure to a postulated function they called "reverse plastron respiration" which would enable a "plastron photosynthesis". In analogy they interpreted the existence of wax layers as an adaptation to avoid water influx in submerged leaves.

Secretory canals in leaves of *R. brasiliensis* and *H. spruceana* represent peculiarities of the families, Clusiaceae and Euphorbiaceae, respectively, and do not seem to be related to xeromorphism (ROTH 1984). Most species showed either glandular or non-glandular hairs which is not in accordance with ROTH (1984) who reported that both hair types are very rare in the humid tropics. Papillas as found in two species are also reported to be scarce in the tropics (ROTH 1984). Cuticular ornamentations as found in this study are reported to be quite common in leaves of trees from tropical rainforests (ROTH 1984). The sculpturing of *H. spruceana* (Fig. 5) is very similar to that of *H. brasiliensis* from terra firme uplands (WILKINSON 1979; SENA GOMES & KOZLOWSKI 1988).

Seven out of eleven floodplain tree species showed a high degree of sclerophylly which suggest that they might experience water stress in their environment. A relation of sclerophylly with nutritional limitation which might be the case for the species from the nutrient poor igapó is not evident from the present data as species from the nutrient rich várzeas showed similar levels of sclerophylly. The lack of a clear trend differentiating deciduous from evergreen species might be due to the fact that deciduous species face the same conditions as evergreen species at least during part of the aquatic phase because the leafless period is only 2 month (SCHÖNGART et al. 2002) while flooding lasts up to 7 months. Apparently keeping submerged leaves does not require different or additional morphological or anatomical traits. Overall, the xeromorphic and/or scleromorphic features found here are unlikely to be adaptations selected under floodplain conditions but rather represent wide spread and common traits in tropical trees both from terra firma and floodplain habitats alike.

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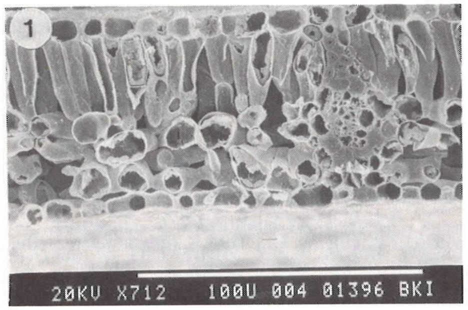
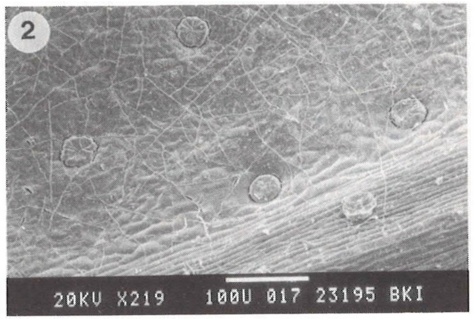
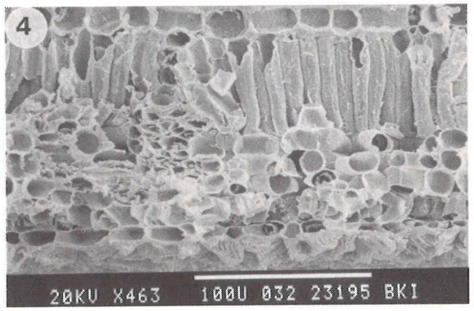
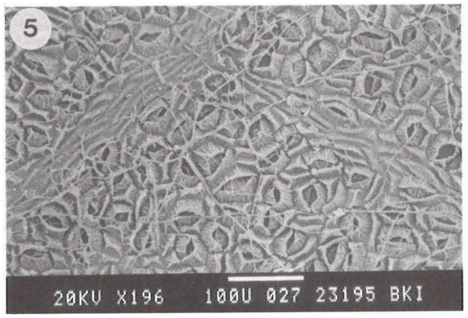
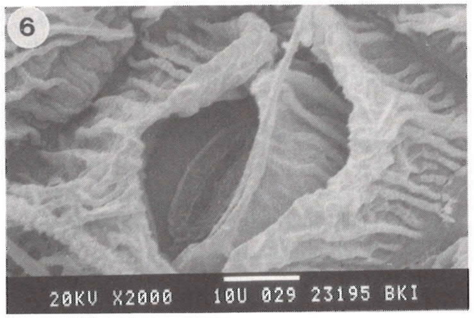










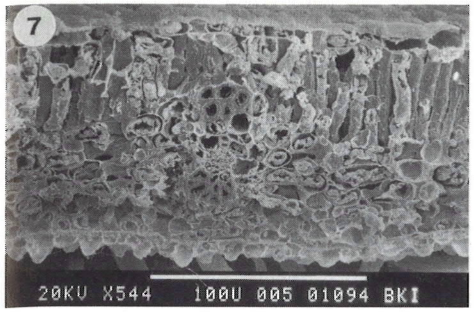
Figs. 1-6:

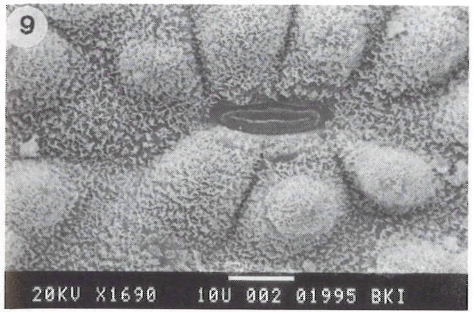
**1-3**: *Eugenia inundata.*

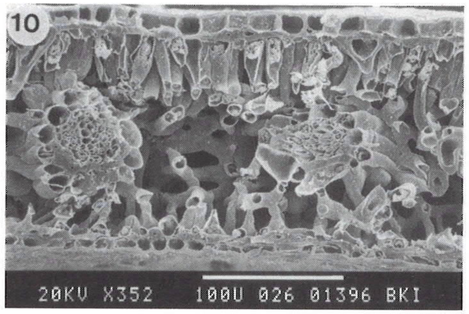
**1**: Cross section through leaf. **2**: Lower epidermis with stomata and glandular hairs. **3**: Stomata sunken in cavity formed by the raised stomatal rim, and extended wings of striae.

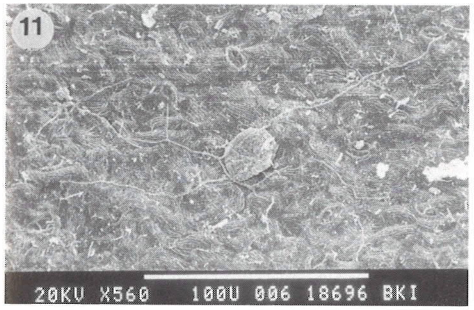
**4-6**: *Hevea spruceana*

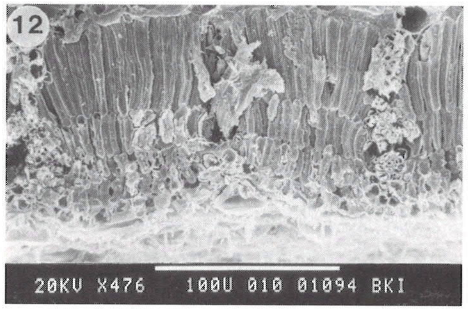
**4**: Cross section through leaf. **5**: Lower epidermis with stomata. **6**: Sunken stomata with reticulum of crests and but tressed ridges.

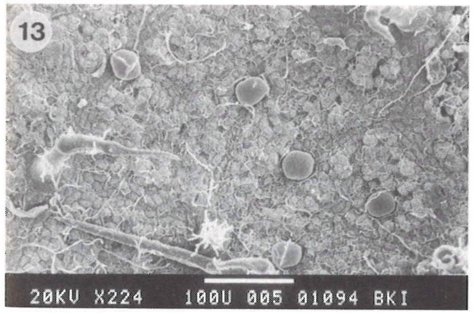


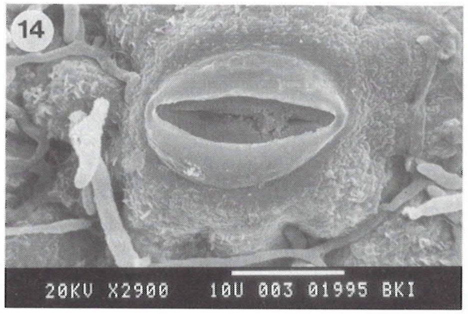






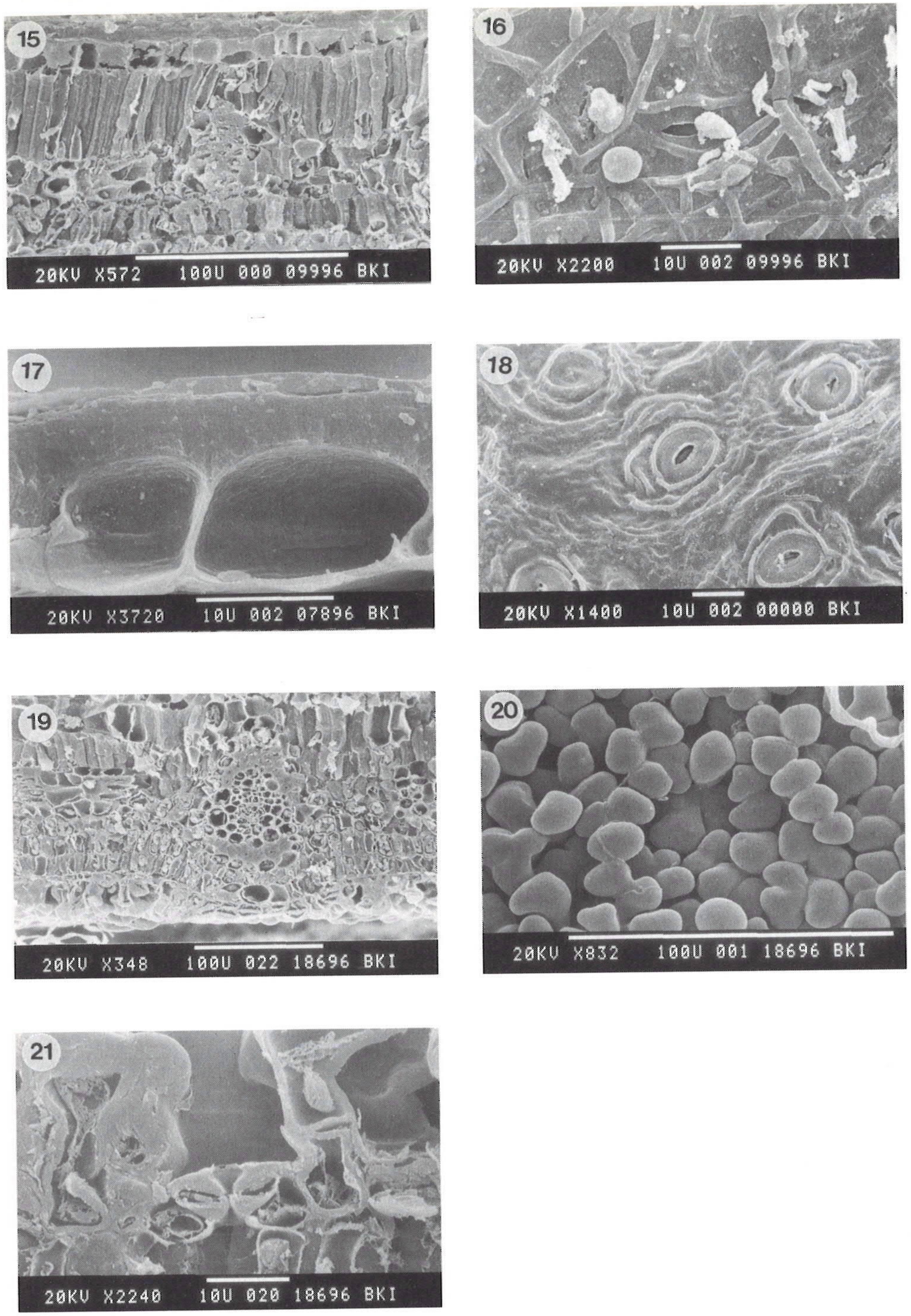




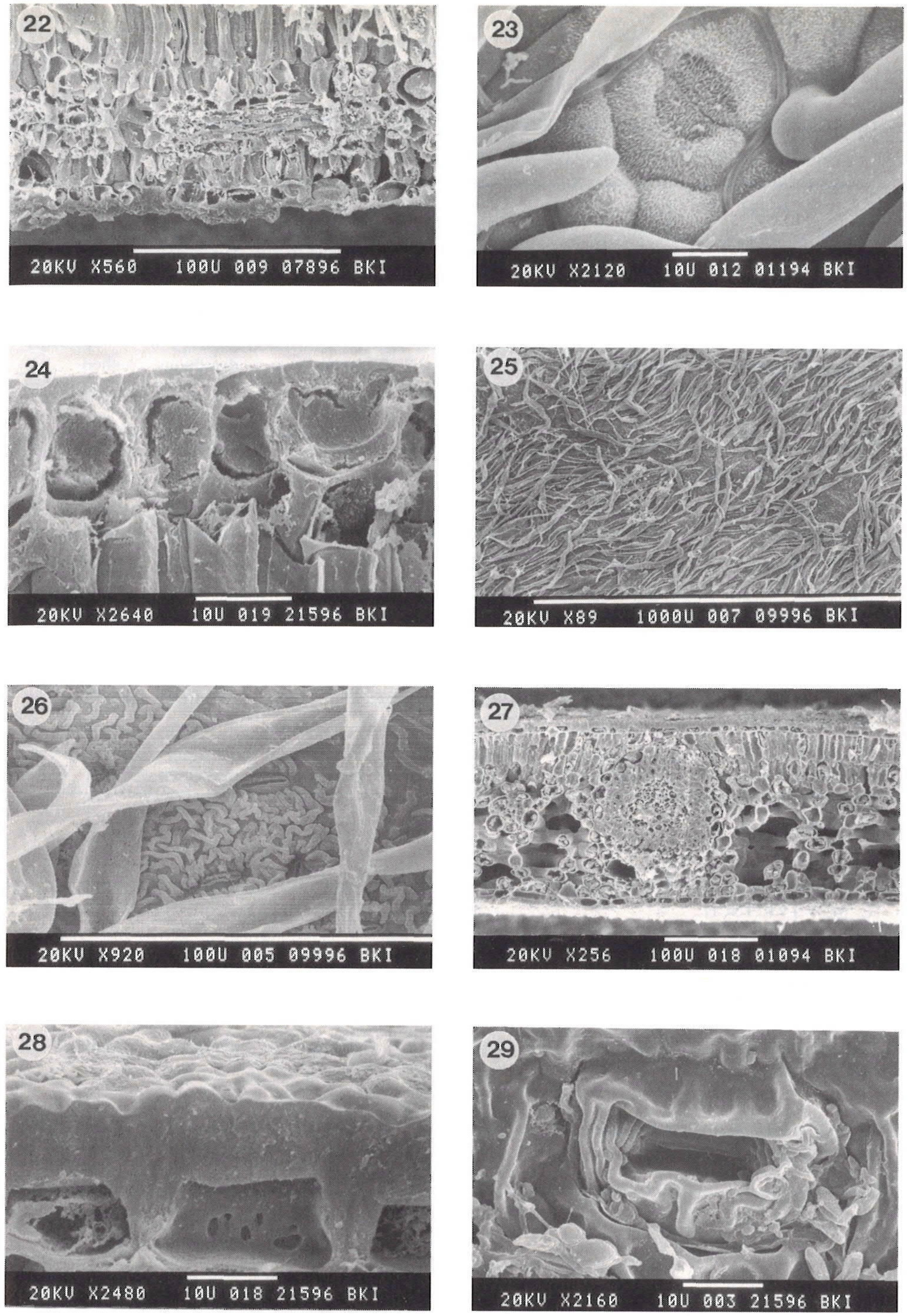


Figs. 7-14:

**7-9**: *Senna reticulata*; **7**: Cross section through leaf. **8**: Lower epidermis with simple, cone-like papillas, unicellular hairs, and stomata. **9**: Sunken stomata, papillas and upright wax scales. **10-11**: *Simaba guianensis*. **10**: Cross section through leaf. **11**: Lower epidermis with sunken stomata, extended wings of striae and one gland. **12-14**: *Vitex cymosa*; **12**: Cross section through leaf. **13**: Lower epidermis with sunken stomata, glandular and non-glandular hairs, and epicuticular wax. **14**: Stomata sunken in cavity formed by the raised stomatal rim.



Figs. 15-21:
**15-16**: *Eschweileria tenuifolia*; **15**: Cross section through leaf. **16**: Lower epidermis with sunken stomata. **17-18**: *Himatanthus sucuuba*; **17**: Cross section through the lower epidermis with very thick outer wall and cuticula. **18**: Lower epidermis with sunken stomata, and concentric rings of striae. **19-21**: *Licania apetala* **19**: Cross section through leaf. **20**: Lower epidermis with papillose hairs and sunken stomata. **21**: Cross section through a stomata sunken in deep pits formed by papillose cells.



Figs. 22-29:
**22-23**: *Nectandra amazonum*; **22**: Cross section through leaf. **23**: Sunken stomata in the lower epidermis, rods of wax and unicellular hairs. **24-26**: *Pouteria glomerata*; **24**: Cross section through leaf. **25**: Lower epidermis with hairs. **26**: Sunken stomata with raised stomatal rim and long, narrow aperture, complex network of undulated striae, lower epidermis. **27-29**: *Rheedia brasiliensis*; **27**: Cross section through leaf. **28**: Cross section through the lower epidermis with a very thick outer wall and cuticula. **29**: Stomata sunken in pit formed by thick cuticula, concentric rings of striae.

Table 1: Tree species investigated: scientific name, family, local name, occurrence, leaf-fall behaviour, and fate of submerged leaves.

| **Species** | **Family** | **Local name** | **Floodplain type** | **Leaf-fall behaviour** | **Submerged leaves** |
|---|---|---|---|---|---|
| *Eugenia inundata* DC. | Myrtaceae | araçá | igapó | deciduous | shed |
| *Hevea spruceana* (BENTH.) MUELL.-ARG. | Euphorbiaceae | seringa barriguda | igapó | deciduous | shed |
| *Senna reticulata* (WILLD.) IRWIN & BARN | Caesalpiniaceae | mata-pasto | várzea | evergreen | shed |
| *Simaba guianensis* AUBL. | Simaroubaceae | cajurana | várzea | deciduous | shed |
| *Vitex cymosa* BENTH. EX. SPRENGL. | Verbenaceae | tarumã | várzea | deciduous | shed |
| *Eschweilera tenuifolia* (BERG.) MIERS | Lecythidaceae | macacaricuia | igapó | evergreen | kept |
| *Himatanthus sucuuba* (SPRUCE EX MUELL.-ARG.) WOOD. | Apocynaceae | sucuúba | igapó | evergreen | kept |
| *Licania apetala* (E. MEY.) FRITSCH. | Chrysobalanaceae | uchirana | igapó | evergreen | kept |
| *Nectandra amazonum* NEES | Lauraceae | louro | várzea | evergreen | kept |
| *Pouteria glomerata* (MIQ.) RADKL. | Sapotaceae | abiurana | várzea | evergreen | kept |
| *Rheedia brasiliensis* (MART.) TR. & PL. | Clusiaceae | bacurí | várzea | evergreen | kept |

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

| **Species** | **Epidermis cell size** | | **Outer wall - cuticula** | | **Palisade parenchyma cell size** | **Spongy parenchyma cell size** |
|---|---|---|---|---|---|---|
| | **ue** | **le** | **ue** | **le** | | |
| *E. inundata* | large | small | thick | thin | medium | medium |
| *H. spruceana* | very large | large | thick | thin | very long | medium |
| *S. reticulata* | medium | medium | thin | thin | long | medium |
| *S. guianensis* | large | small | thin | thick | medium | small |
| *V. cymosa* | large | large | thin | thin | long/small/small | not existing |
| *E. tenuifolia* | medium | small | very thick | thick | long/small/small | medium |
| *H. sucuuba* | large | thick | thin | | | |
| *L. apetala* | large | + | medium | + | long/small/small | medium |
| *N. amazonum* | large | large | medium | medium | long/small/small | not existing |
| *P. glomerata* | small | small | thick | | medium | small |
| *R. brasiliensis* | large | large | very thick | thick | medium/small | medium |

Table 3: Parenchyma characteristics. up: upper side of leaf, low = lower side of leaf, * = missing data. Sclerophylly index: cf. text.

| Species | No. of layers of palisade parenchyma | Compactness of spongy parenchyma | Canals | Vascular bundles | | Sclerophylly index |
|---|---|---|---|---|---|---|
| | | | | Extension | Sclerenchyma | |
| *E. inundata* | 1 | regular | | transcurrent | capping bundles on both sites | 0,41 |
| *H. spruceana* | 1 | compact | laticifirous | not transcurrent | weekly developed | 0,19 |
| *S. reticulata* | 1 | compact | | transcurrent | capping bundles on both sites | 0,12 |
| *S. guianensis* | 1 | very loose | oil cells | not transcurrent | weekly developed | 0,38 |
| *V. cymosa* | 2-3 | not existing | | transcurrent | capping bundles on both sites | 0,41 |
| *E. tenuifolia* | 1 up, 1 low | very compact | | mostly transcurrent | sheath surrounding the bundle | 0,42 |
| *H. sucuuba* | * | * | | * | * | 0,44 |
| *L. apetala* | 2 | very compact | | not transcurrent | strong sheath surrounding the bundle | 0,37 |
| *N. amazonum* | 2 up, 1 low | not existing | | transcurrent | capping bundles on both sites | 0,40 |
| *P. glomerata* | 1 | very compact | | * | * | 0,22 |
| *R. brasiliensis* | 2 | loose | resin | mostly transcurrent | strong sheath surrounding the bundle | 0,47 |

Table 4: Density and form of stomata. le = lower epidermis, nv = not visible, ue = upper epidermis.

| Species | Density (number mm$^{-2}$) | | Form |
|---|---|---|---|
| | ue | le | |
| *E. inundata* | | 620 | sunken in cavity formed by the raised stomatal rim |
| *H. spruceana* | | 369 | sunken |
| *S. reticulata* | 141 | 84 | sunken |
| *S. guianensis* | | 4 | sunken |
| *V. cymosa* | | 176 | sunken in cavity formed by the raised stomatal rim |
| *E. tenuifolia* | | nv | sunken in very thick cuticula |
| *H. sucuuba* | | 675 | sunken, with raised stomatal rim |
| *L. apetala* | | nv | sunken in deep pit formed by papillose subsidiary cells |
| *N. amazonum* | | 1188 | sunken |
| *P. glomerata* | 177 | 449 | ue: not sunken, le: sunken with raised stomatal rim and long, narrow aperture |
| *R. brasiliensis* | nv | 178 | sunken in pit formed by very thick cuticula |

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

| Species | Hairs | | Papillas | Wax layer | Cuticular ornamentation |
|---|---|---|---|---|---|
| | not glandular | glandular | | | |
| *E. inundata* | | ue, le: glandular scales | | | le: concentric rings of striae around stomata and radiating striae around concentric rings ue: striae random and very dense |
| *H. spruceana* | | | | le | ue, le: reticulum of crests and buttressed ridges around stomata |
| *S. reticulata* | ue, le | | ue, le: simple, cone-like | ue, le: upright scales | |
| *S. guianensis* | | ue, le glandular scales | | | le: concentric rings of striae around stomata and radiating striae around concentric rings, ue: striae random and very dense |
| *V. cymosa* | le | le, flattened glandular scales | | le | le: rough surface of bulbous-like elevations |
| *E. tenuifolia* | | ue, le: glandular scales | | | |
| *H. sucuuba* | | | | | le: concentric rings of striae around stomata |
| *L. apetala* | | | le: with dense pappilose hairs | | |
| *N. amazonum* | ue, le | | | le:rods of wax | |
| *P. glomerata* | le | | | | le: dense and complex network of undulate striae |
| *R. brasiliensis* | | le | | | le: concentric rings of striae around stomata and radiating striae around concentric rings |