

2 Morphology, Anatomy, Life Forms and Hydraulic Architecture

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2.1 Hundreds of Species of One Morphotype

The 300 to 400 woody species of *Clusia* all display one typical morphotype (Lüttge 2000). *Clusias* are branched shrubs and trees with dichasial cymes and opposite leaves (see also Sect. 6.1). Among the various species leaves vary in absolute size. However, the leaves of all species are morphologically and anatomically very similar, always entire, leathery and somewhat succulent (Fig. 2.1). In view of the important effects of leaf form and structure on photosynthesis and ecophysiological performance (Niinemets and Sack 2005), this is remarkable particularly with respect to the large photosynthetic flexibility of some species of *Clusia*. However, this has not been much explored for *Clusia*. On the other hand, floral morphology of *Clusias* is rather variable (Sect. 6.5).

Leaf succulence of *Clusia* species is indicated by comparatively high fresh weight/dry weight and fresh weight or plant water/area ratios (Table 2.1). Although the data reveal some developmental influences (mature plants versus seedlings of *C. rosea*) and effects of nitrogen supply and irradiance (*C. minor*), the values obtained are rather homogenous. Two important exceptions are the conspicuously succulent *Clusia alata* Pl. et Tr. and *Clusia hilariana* Schlechtendal. These are obligate Crassulacean acid metabolism (CAM) plants. Succulence with highly vacuolated photosynthetically active cells is a general feature of CAM plants, which fix CO₂ in the dark period forming malate that is nocturnally accumulated in the vacuoles (see Chaps. 8 and 9). Another species, where comparatively high values of leaf succulence were obtained is *C. rosea*, which is also a CAM species.

Zotz et al. (1997) compared the leaf succulence attributes of *Clusia minor* L. with six other woody plants. *C. minor* is a C₃-photosynthesis/CAM-intermediate species. The ratios of fresh weight/dry weight of 4.7 and of plant water/area of 580 g m⁻² measured by Zotz et al. (1997) in *C. minor* (Table 2.1)

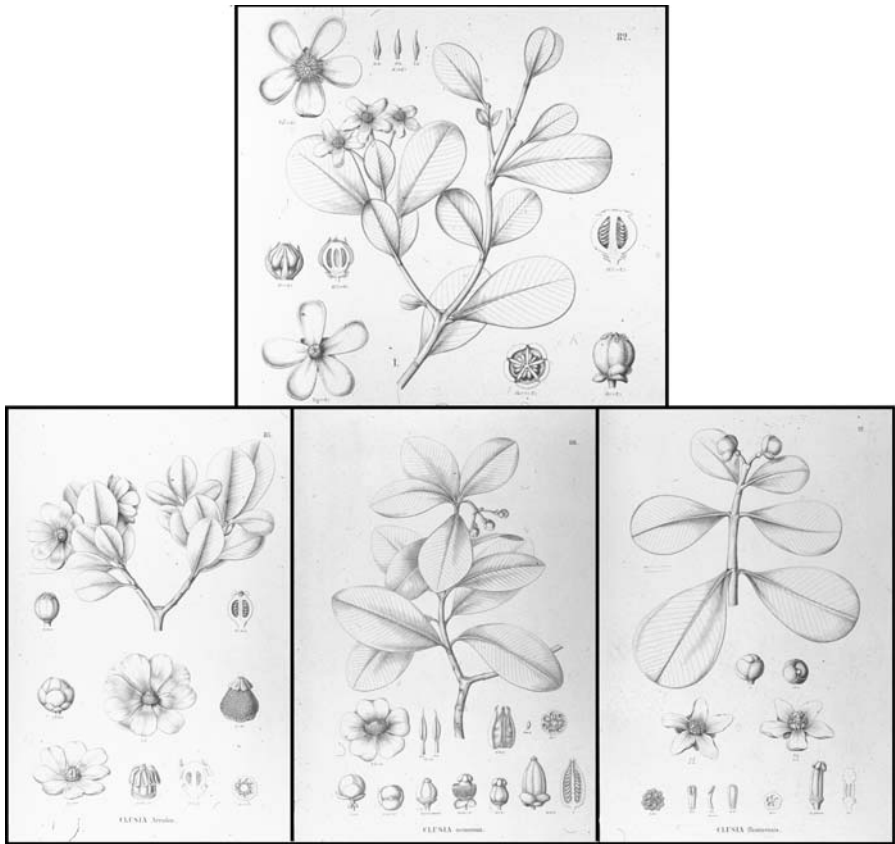


Fig. 2.1. Illustrations of *Clusias* in *Flora Brasiliensis* (Martii 1889). *Top*: *C. parviflora* Saldanha et Engl. *Bottom from left to right*: *C. arrudae* Planch. et Triana, *C. nemorosa* G. Mey., *C. fluminensis* Planch. et Triana

were the highest among the seven woody plants compared, where the lowest values were 1.6 and 150 g m⁻², respectively. All seven species were hemi-epiphytic life forms (see Sect. 2.3) in a tropical forest canopy. A comparison of evaporative loss of water and water storage showed that a net loss of 10 % of the leaf water in *C. minor* and *Clusia uvitana* Pittier, another C₃/CAM-intermediate plant, would sustain average transpiration rates for 7–9 h as compared to 0.2–0.8 h in the other species. In addition to leaf succulence this can be related to the performance of CAM as a water saving mode of photosynthesis (see Chaps. 8 and 9).

Table 2.1. Fresh weight (FW)/dry weight (DW) and plant water (PW, ml) or FW (g)/leaf area (m²) ratios of four CAM species of *Clusia* (*C. alata*, *C. hilariana*, *C. major* and *C. rosea*) and five C₃/CAM-intermediate species (*C. aripoensis*, *C. criuva*, *C. minor*, *C. uvitana*, *C. venosa*) that can switch between both modes of photosynthesis. ± N, with and without supply of nitrogen; PAR=photosynthetically active radiation

Species	Comments	FW/DW	PW ^a or FW ^b /area	Reference
<i>C. alata</i> Pl. et Tr.	dawn	4.1	750 ^a	Popp et al. 1987
	dusk	4.0	785 ^a	
<i>C. rosea</i> Jacq.	dawn	3.7	720 ^a	
	dusk	3.8	705 ^a	
<i>C. rosea</i> Jacq.	mature	3.8	795 ^b	Ball et al. 1991
	seedlings	5.2	465 ^b	
<i>C. venosa</i> Jacq.		4.5	375 ^a ; 480 ^b	Franco et al. 1990
<i>C. minor</i> L.		6.5	565 ^a ; 670 ^b	
<i>C. major</i> L.		5.3	505 ^a ; 625 ^b	
<i>C. alata</i> Pl. et Tr.		7.1	1 355 ^a ; 1 575 ^b	
<i>C. minor</i> L.		5.6		Holbrook and Putz 1996
<i>C. minor</i> L.		4.7	580 ^a	Zotz et al. 1997
<i>C. minor</i> L.			735 ^b	Borland et al. 1998
<i>C. rosea</i> Jacq.			805 ^b	
<i>C. aripoensis</i> Britt.			585 ^b	
<i>C. hilariana</i> Schl.			1 390 ^b	Berg et al. 2004
<i>C. minor</i> L.	-N, low PAR	6.8	640 ^a	Franco et al. 1991
	-N, high PAR	4.9	710 ^a	
	+N, low PAR	8.2	605 ^a	
	+N, high PAR	6.1	665 ^a	
<i>C. uvitana</i> Pittier	shade leaves	5.2	655 ^b	Zotz and Winter 1994
	sun leaves	4.3	780 ^b	
<i>C. criuva</i> Camb.			420 ^a	Herzog et al. 1999

2.2 Leaf Anatomy

Leaf anatomy was studied in *C. hilariana* and *Clusia spiritu-sanctensis* G. Mariz et Weinberg (Schneider 1985; da Silva et al. 2005), and in *Clusia rosea* Jacq. and *C. alata* (Popp et al. 1987; Borland et al. 1998) all of which are CAM species, in *Clusia mexicana* Vesque (Hartenburg 1937) and *Clusia minor* L. (Borland et al. 1998; Duarte 2006) which are C₃/CAM-intermediate and in *Clusia aripoensis* Britt. (Borland et al. 1998) which is weak CAM inducible. The succulent leaves of CAM plants are often uniformly composed of isodiametric and nearly spherical cells, e.g. in the genus *Kalanchoë* with an internal air space of 3 % of the total leaf volume in *K. daigremontiana* (Duarte et al. 2005). The large vacuoles of this succulent leaf tissue provide the storage capacity for nocturnal accumulation of malate, which in turn is related to the capacity for CAM. However, the leaves of all of the *Clusias* are clearly bifacial and differentiated into a palisade parenchyma of two to four cell layers and a spongy parenchyma with large intercellular air spaces (Fig. 2.2A–D) of, e.g., 9.3 % of the total leaf volume in *C. minor* (Duarte 2006). In the region of the major vein of leaves of *C. minor* there is no spongy parenchyma and there are one to four layers of palisade parenchyma on the adaxial side of the bundle which is thinner but continuous with the palisade parenchyma of the interveinal lamina tissue (Fig. 2.2F,G). The bundle is surrounded by isodiametric parenchyma cells which also have contact with the palisade parenchyma. In the tissue around the bundle in the major vein there are scarcely any intercellular spaces, and thus, lateral gas diffusion shall be highly limited in this part of the leaf (Fig. 2.2F,G). The size and the architecture of the internal air spaces of leaves are very important for lateral gas diffusion in leaves and the role and signalling functions of CO₂ and O₂ in synchronizing photosynthetic activities within leaves (Sects. 8.5 and 11.2.2), which have been studied in *C. minor* (Duarte and Lüttge 2007). *C. aripoensis* and *C. minor* have three to four adaxial hypodermal cell layers. *C. rosea* may have one to two adaxial and one abaxial hypodermal cell layers (Ting et al. 1985; Ball et al. 1991).

Dimensions were measured in leaves of *C. rosea* sampled in the field and in *C. rosea*, *C. minor* and *C. aripoensis* grown in a phytotron (Table 2.2). Leaves of seedlings of *C. rosea* were thinner than those of mature plants and in the latter sun exposed leaves were thicker than shaded leaves. These differences were due to differences in the thickness of the photosynthetically active mesophyll, i.e. the thickness of both palisade cell layers and spongy parenchyma (Table 2.2). Dimensions are also presented for *C. minor* by Holbrook and Putz (1996) but are not incorporated in Table 2.2 because these authors do not separate epidermis and hypodermis.

The high degree of vacuolization of the mesophyll cells with only a thin layer of cytoplasm along the walls seen in Fig. 2.2 is typical of CAM performing leaves.

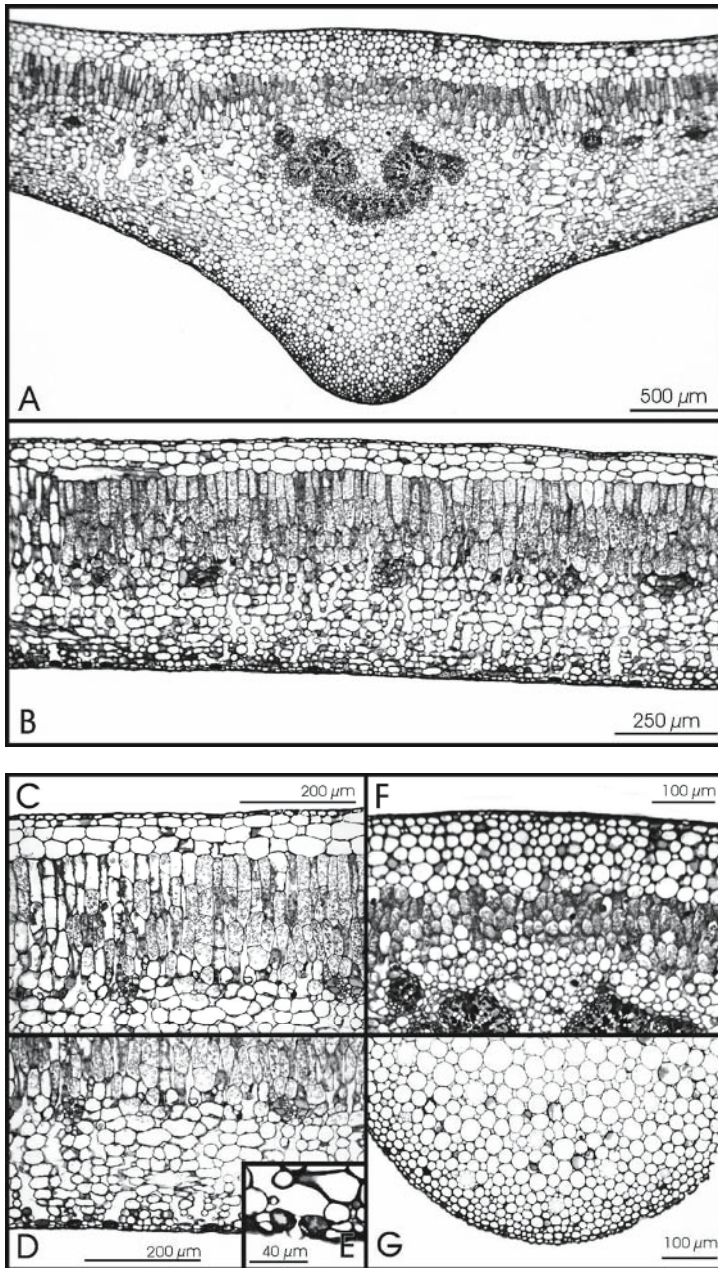


Fig. 2.2A–G. Leaf anatomy of *C. minor*: **A** cross section at the main vein; **B** cross section at an intercostal portion of the leaf; **C** detail of the adaxial epidermis, hypodermis and palisade parenchyma; **D** detail of the abaxial epidermis and spongy parenchyma; **E** stoma in the adaxial epidermis; **F** detail of the adaxial tissue of the main vein, there is collenchyma directly under the epidermis, the palisade parenchyma is not interrupted by the vein but there is no spongy parenchyma (see **G**) and the cells are tightly packed; **G** detail of the abaxial tissue of the main vein

Table 2.2. Thickness of cell layers measured in cross sections of leaves (A) of *C. rosea* sampled in the field on St. John Island, Lesser Antilles, and (B) of *C. rosea*, *C. minor* and *C. aripoensis* grown in a phytotron. Summarized and rounded from detailed analyses of (A) Ball et al. (1991) and (B) Borland et al. (1998)

(A) <i>C. rosea</i>	Shaded (μm)	Exposed (μm)	Seedlings (μm)
Adaxial epidermis	20	15	15
Hypodermis 1	15	15	25
Hypodermis 2	30	30	25
Palisade 1	125	130	75
Palisade 2	105	130	80
Palisade 3	70	110	–
Spongy parenchyma	440	500	330
Hypodermis	20	25	20
Abaxial epidermis	20	20	20
Sum	845	975	590
(B)	<i>C. rosea</i>	<i>C. minor</i>	<i>C. aripoensis</i>
	(% of total leaf thickness)		
Hypodermis	5	12	21
Palisade parenchyma	36	42	24
Spongy parenchyma	59	46	55

Table 2.3. Stomatal densities (number mm^{-2}) of *C. rosea* and *C. minor* in comparison to other woody hemi-epiphytes

Plants	Stomatal density	Reference
<i>C. rosea</i>	55	Ball et al. 1991
<i>C. minor</i>	186	Holbrook and Putz 1996
	180	Duarte 2006
<i>C. minor</i>	90	Zotz et al. 1997
Others	110 to 1035	

The leaves of *Clusia* contain many secretory ducts filled with a latex-type secretion.

Clusia leaves are hypostomatic. The stomata of *C. mexicana* are at the bottom of an external cavity formed by a pair of peripheral horns (Hartenburg 1937). The guard cells of *C. minor* have an inner and an outer pair of horns (Fig. 2.2E). The stomatal apparatus of *C. rosea* forms several cavities by means of an outer pair of horns on the subsidiary cells and an outer and inner pair of horns on the guard cells (Popp et al. 1987). Stomatal densities are rather low. In comparison to a range of stomatal densities of other woody species in tropical forests values of *Clusia* are at the lowest end (Table 2.3).

2.3 Life Forms

As noted above, with respect to leaf morphology and anatomy all species of *Clusia* are very uniform and constitute one single morphotype. However, a large diversity between species as well as plasticity within species is apparent in other respects. These include the ecological amplitude of *Clusia* (Chap. 9), the different photosynthetic physiotypes (Chap. 8) and biochemical reactions of CAM (Chap. 8). Morphological diversity and plasticity are given by expression of different life forms. Seeds of given species of *Clusia* can facultatively germinate both terrestrially and epiphytically in small accumulations of humus in forks of tree branches, within the tanks of bromeliads and in epiphyte nests (Figs. 2.3 and 2.4). Terrestrial seedlings directly develop free standing shrubs and trees (Fig. 2.4). Epiphytic seedlings produce many adventitious aerial roots. Some of these adventitious roots serve as holdfasts and at the same time strangle the bark of their host trees. Some of the adven-

Aus dem Leben eines Baumwürgers

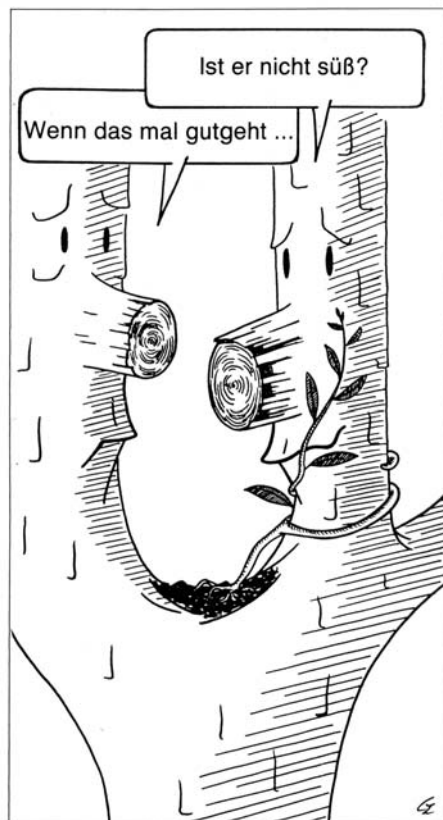


Fig. 2.3 Cartoon unexpectedly added to Lüttge (1991) by the publisher, headed "From the life of a strangler" where the right hand branch of the phorophyte says "isn't he sweet?" but the left hand branch replies "if this may go well ...". Drawing by J. Czichos, www.joachim-czichos.de



Fig. 2.4A–L. Life forms of *Clusias*: A terrestrial seedlings of *C. multiflora* H.B.K. (area of Instituto Venezolano de Investigaciones Científicas, IVIC, Caracas, Venezuela); B terrestrial seedlings of *C. spiritu sanctensis* Mariz et Weinberg (Estação Biológica de Santa Lúcia, Santa Teresa, Espírito Santo State, Brazil); C seedling of *C. spec.* rooting between the bark and the wood of a rotting tree (Serrania de San Luis, Falcon State, Venezuela); D seedling of *C. rosea* Jacq. in a tree fork (St. John, US-Virgin Islands); E seedling of *C. rosea* in the tank of the bromeliad *Aechmea lingulata* (St. John); F tank of *A. lingulata* cut open to show the roots of *C. rosea* (St. John);

G *C. rosea* in an epiphyte nest (St. John); H *C. rosea* strangling the phorophyte (St. John); I free standing shrubs of *C. minor* L. (narrow leaves) and *C. multiflora* (broad leaves) (area of IVIC); J free standing shrub of *C. spiritus sanctensis* (Santa Teresa); K *C. rosea* strangler getting a free standing tree (St. John); L *C. rosea* free standing tree (St. John)



titious roots grow positively gravitropically and eventually establish contact with the soil. The strangled host trees may die from interruption of the stream of assimilates in the phloem of their bark, and with their dead trunks rotting away the originally epiphytic *Clusias* become free standing trees. This life form is therefore called hemi-epiphytic.

Holbrook and Putz (1996) have compared several morphological/anatomical traits in rooted trees and epiphytes of *C. minor*. Specific leaf area (area per weight) was 30 % larger in the epiphytes compared to the trees. Leaf thickness, stomatal density and the diameter and length of stomata were similar in both life forms. The bulk elastic modulus was larger, i.e. leaves were more rigid in the rooted trees. The differences between the rooted trees and the epiphytes with respect to these traits were larger in species of *Ficus* than in *C. minor*, and the authors conclude that it is a physiological rather than a morphological/anatomical plasticity that is a more important attribute in *Clusia*. It is notable in this context that *Ficus* species are obligate C_3 -plants (Ting et al. 1987) while *Clusias* have the CAM-option, and therefore, although hemi-epiphytic species of both genera are very similar life forms, in the absence of any CAM option *Ficus* must adapt differently in the epiphytic stage. In fact *Clusias* are the only known hemi-epiphytic stranglers having CAM (Ting et al. 1987).

2.4 Hydraulic Architecture

The physiological morphology and anatomy in relation to water transport in plants, i.e. the hydraulic architecture, among others is governed by parameters such as:

- Specific conductivity of stem segments, K_s , providing information about the hydraulic efficiency of xylem on a cross-sectional area basis
- Leaf specific conductivity of stem segments, K_l , providing information about the hydraulic sufficiency of a stem segment on a leaf area basis
- Ratio of wood cross section invested per unit leaf area, H_v , the so-called Huber-value

Hydraulic architecture relates to (i) life form as well as (ii) mode of photosynthesis. With respect to *Clusia* these are (i) free standing trees vs hemi-epiphytes and (ii) C_3 -photosynthesis vs CAM. Hemi-epiphytes potentially need a smaller wood cross section than free standing trees to support their foliage and crown as they have the mechanical support of their host trees or phorophytes. CAM is a water saving variation of photosynthesis and CAM plants may operate with lower water conductivities than C_3 -plants. Since species of *Clusia* are the only woody dicotyledonous plants performing CAM (Chap. 1) this may distinguish their hydraulic architecture from all other woody species in tropical forests.

Hence, variants of desirable comparison are:

1. Free standing trees vs hemi-epiphytes both with C_3 -photosynthesis
2. Free standing trees vs hemi-epiphytes both with CAM
3. Free standing trees with C_3 -photosynthesis vs CAM
4. Hemi-epiphytes with C_3 -photosynthesis vs CAM

where 1 and 2 would indicate the role of hemi-epiphytism and 3 and 4 that of the mode of photosynthesis.

A comparison of various tropical trees and woody hemi-epiphytes including species of *Clusia* led to the general suggestion (Zotz et al. 1997) that:

- Hemi-epiphytes show significantly higher specific stem conductivity, K_s , compared to trees
- Hemi-epiphytes invest less wood cross-section per unit leaf area, H_v , compared to trees
- Hemi-epiphytes tend to have less conductive stems per unit leaf area, K_l , compared to trees

Table 2.4 shows a comparison of the hemi-epiphytic C_3 /CAM-intermediate *C. uvitana* with a number of other tropical tree species (Zotz et al. 1994). In terms of hydraulic architecture the K_s values are rather similar, i.e. the xylem of *Clusia* is about as efficient on a wood area basis as that of the other species. However, K_l of *Clusia* was much lower than in the other species, i.e. its stems were less efficient on a unit leaf area basis and *Clusia* supports a large leaf area

Table 2.4. Comparison of hydraulic architecture parameters of hemi-epiphytic *C. uvitana* with other tropical woody species with respect to the parameters of hydraulic conductivity K_s (specific stem conductivity) and K_l (conductive stem per unit of leaf area) as well as xylem pressure at 50 % loss of hydraulic conductivity (Ψ_{xp50}) and evaporation (E). Rounded values from Zotz et al. (1994, 1997) and Patiño et al. (1995)

	<i>C. uvitana</i>	Others
K_s ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$)	0.7 to 2.1	1.3 to 2.5 (4 to 14 ^a)
K_l ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1} \times 10^4$)	0.9 to 2.4	5 to 30
Ψ_{xp50} (MPa)	-1.3	-1.0 to -6.2
E:		
average maximum ($\text{mg s}^{-1} \text{m}^{-2}$)	12	50 to 80
average ($\text{mg s}^{-1} \text{m}^{-2}$)	2.3 ^b	10 to 26
mean daily ($\text{g 24 h}^{-1} \text{m}^{-2}$)	198 ^c	902 to 2227

^a Values for *Ficus*

^b *Clusia minor* showed a value of 1.8

^c *C. minor* showed a value of 153

per unit stem area. This may be explained by both the hemi-epiphytic life form and the performance of CAM of *C. uvitana* as compared to the other species, i.e. this work does not distinguish between variants 1 and 2 and variants 3 and 4 above. It was also shown, however, in the study of Zotz et al. (1994) that the vulnerability to cavitation, i.e. the relative loss of hydraulic conductivity under a pressure applied via a pressure chamber, was rather high in *C. uvitana*. In the other tree species the range of xylem pressure at which 50% loss of the hydraulic conductivity occurred, Ψ_{xp50} , was large extending from -1.0 to -6.2 Pa (Table 2.4), depending on their ecological performance, where the less negative values were characteristic for drought evaders and the more negative values for drought tolerators. The high Ψ_{xp50} -value of *C. uvitana* of -1.3 Pa indicates that it is a drought evader. This performance is most likely based on the use of CAM as an adaptation to limited water supply as discussed in Chaps. 8 and 9. This is corroborated by the comparatively low evaporation rates observed in *C. uvitana* (Table 2.4). Although a systematic comparison with respect to points 1 to 4 above is not available in the literature, this certainly suggests a strong influence of the option to perform CAM on hydraulic architecture. Moreover, in another study, Patiño et al. (1995) compared the hemi-epiphytic C_3 /CAM-intermediate *C. uvitana* with four C_3 hemi-epiphytic and three C_3 terrestrial species of *Ficus*. Ranges of values of K_s , K_1 and H_v are given in Table 2.5. The ranges of K_s values for the hemi-epiphytic and the terrestrial *Ficus* species overlap, but as expected from the generalization given above, the range of values reaches higher levels in the former. However, for the hemi-epiphytic *C. uvitana* the K_s value is much lower and the fact that it can afford much lower specific stem conductivity than the C_3 hemi-epiphytes of *Ficus* must be due to its option to perform CAM. As also expected, K_1 values are lower in hemi-epiphytic *Ficus* species than in the free standing ones, again meeting the expectations from the general pattern given above, but the values for *Clusia* are still much lower. This indicates that in addition to hemi-epiphytism hydraulic architecture is related to performance of CAM.

Table 2.5. Comparison of hydraulic architecture parameters of hemi-epiphytic *C. uvitana* with hemi-epiphytic and free standing trees of *Ficus*. Specific stem conductivity (K_s), cross section per unit leaf area (H_v), conductive stem per unit of leaf area (K_1). Rounded values from Patiño et al. (1995)

	K_s ($\text{kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)	$H_v \times 10^4$	$K_1 \times 10^4$ ($\text{kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)
<i>Ficus</i> free standing	11 to 14	2.0 to 6.1	23 to 52
<i>Ficus</i> hemi-epiphytic	7 to 34	1.0 to 2.2	7 to 23
<i>C. uvitana</i> hemi-epiphytic	1.1	1.4	1.5

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