

Tree Physiology

Guillermo Goldstein
Louis S. Santiago *Editors*

Tropical Tree Physiology

Adaptations and Responses in a
Changing Environment

 Springer

Tree Physiology

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Preface

Our World is changing rapidly, yet, how tropical forests will respond to this change and in turn dampen or accelerate its ripple effects is essentially a physiological question. Addressing important questions regarding the impacts of changes in land utilization, such as deforestation, and effects of global climate change will require specific information on tropical tree physiology. Earth system modeling scientists are clamoring for more physiological data from tropical trees. It seems that the scarcity of information on the physiological responses of trees is the greatest source of uncertainty in predicting how the tropical rain forests will respond to increasing greenhouse gases and in particular increasing atmospheric CO₂. For example, tree species can adjust their physiological behavior to increasing global temperatures or decreases in precipitation, or they can be replaced by other species better adapted to the new environmental conditions. It is also true that the physiology of tropical trees has not been as well-studied as the physiology of trees from temperate regions, leading to major gaps in our understanding of how tropical trees interact with the Earth system over a range of scales.

It is known that the physiological behavior of both tropical and temperate trees is regulated by similar mechanisms. The differences, however, are related to the unique selective pressures to which tropical trees have been subjected during the evolutionary process and its adaptive consequences. The idea put forward by Theodosius Dobzhansky in the 1950s that tropics and temperate zones are areas where selection operates differently, generated fruitful lines of thinking and research. His contention was that in temperate areas mortality was essentially climatically determined, with little or no competition pressure, while in the tropics, where the environment is relatively more constant, at least in terms of seasonal changes in temperature, mortality is the result of the effects of population size and competition. This paradigm of evolutionary pressures has changed substantially but some aspects of it still remain as a guide for understanding differences in patterns of adaptation between temperate and tropical plants. Negative density dependence prevents any single tree species from dominating most tropical forest ecosystems. The reasons for this must be sought not only in ecological and demographic

processes but also among the highly diverse physiological characteristics of tropical trees. In the tropics, seasonal temperature variations are relatively small compared to diurnal temperature changes and if soil water is available, growth and metabolic activities can be maintained throughout the entire year. Heavy herbivore pressure is continuous and the adaptive responses of tropical plants to herbivory are impressive. The physiological implications of various types of mutualisms found among tropical trees are also important. Many trees have a relatively short life span of less than 200 years in the wet tropics compared to more than a 1000 years in some temperate-zone trees.

There has been a substantial increase in the number of studies of tropical tree physiology during the last few decades. The reason for this is not only that trees are the dominant growth form in most tropical ecosystems, but also because of increasing availability and refinement of equipment such as portable photosynthesis systems and instruments for studying water relations of plants. Furthermore, a substantially larger number of tropical biologists are now involved in more mechanistic studies. The use of tower cranes during the last 25 years has allowed scientists to reach the canopy of tropical forests, one of the ultimate frontiers for unveiling not only new organisms but also new processes that were unthinkable just a few years ago.

A distinct feature of tropical trees is not only their high species diversity but also the large variety of life history traits and growth forms that are mostly unique to the tropics such as hemiepiphytic trees, stem succulent trees such as baobab trees, mangroves, palms and other arborescent monocots, and unusual arborescent plants near tree line that are not traditional trees. The wide range of shade tolerance from rapidly growing pioneer trees during gap-phase regeneration to species that can survive by growing slowly in deep shade contribute to this diversity.

Tropical trees tend to grow in habitats where soil water availability is high all year round or at least in habitats where it is seasonally available. They grow in arid environments where they access deep soil water such as in the case of phreatophytic trees. They also occur along altitudinal gradients within the tropics up to the upper tree line and in some cases, such as the caulescent giant rosette plants, they can grow above the continuous forest line. They extend to the subtropics, and in many cases they share close phylogenetic relationships with subtropical tree species, and the structure and function of subtropical forests are in many cases similar to tropical forests, in regards to gap-phase regeneration and the high abundance of lianas.

Through 20 chapters authored by 55 people, this book captures the current state of knowledge of the main physiological characteristics of tropical trees. The book was as a way to not only to provide information gathered during the last few years across the world, but also for laying the foundation for discussing controversial paradigms and new hypothesis of physiological process and mechanisms of trees. Thus this book will surely capture the attention not only of tropical biologists but also of biologists working in many different types of environments around the globe. Physiological consequences of global environmental change will permeate most book chapters, as it provides a dynamic arena for tropical trees to respond. The book is organized in six main parts. The first one is on the physiology of unique

tropical growth forms. This group of conspicuous plants is extremely important for understanding the structure, function, and dynamics of tropical forests, as well as understanding why certain species live where they do and not elsewhere. Hemiepiphytic trees with an unusual progression of life stages and obligate epiphytes with a unique photosynthetic pathway, are plants that capture the environmental and demographic wonder of forest ecosystems: Do they start their life cycle (as in the case of hemiepiphytic trees) or spend their entire life cycle (as in the case of obligate epiphytes) in the upper canopy to utilize higher levels of incoming solar radiation or to escape the shady understory with high chances of damage by falling debris and exclusion by competition with other plants? Stem succulent trees, such as the fat-stemmed baobabs, which have captured the imagination and attention of writers, such as in the case of “the little prince” by Antoine de Saint-Exupéry, are fascinating trees occurring mostly in seasonally dry forests. The enlarged stem with photosynthetic surfaces, leaves that drop during the dry season and with little biomass allocation to root systems, appear to have a combination of physiological and anatomical traits that at first sight is difficult to understand. Do their low wood density trunks represent conspicuous water storage? Is stored stem water used for new leaf growth near the end of the dry season or to maintain stem conductance during the rainy season? Does the large size of the stem serve a biomechanical role for providing stability to tall mature trees? Palms are another unique growth form, nearly always associated with tropical environments. The hydraulic architectures of these monocots have long intrigued physiologists working on plant water relations and hydraulic architecture. How can trees that do not have secondary growth, and thus cannot produce new xylem tissue after the plants start growing in height, cope with intensive droughts and the dysfunction of cavitated xylem vessels? Finally lianas, which have solved the problem of reaching the upper canopy without investment in a large diameter stem, can move large amounts of water to transpiring leaves. How did these plants solve this important water economy constraint imposed by a relatively narrow stem?

The second part of the book deals with adaptive responses of trees growing in habitats that are unique to the tropics. Mangrove trees occur in coasts across all tropical regions with roots tapping seawater. Floodplain trees tolerate freshwater inundation for several months in inland tropical regions and in some cases are completely covered by water. At high elevation, tropical giant rosette plants represent one of the most fascinating cases of evolutionary convergence among tropical alpine climates that are characterized as “summer during the day and winter at night.”

The third part of the book discusses emergent paradigms on hydraulic architecture and water relations. The high diversity of tropical tree species allows the use of a wide array of physiological and morphological traits. This provides fertile ground for testing new hypothesis on the adaptive significance of physiological mechanisms for how trees cope with drought, and how they may avoid or repair cavitated xylem vessels, or how close they are to their physiological limits of water availability in the face of extreme climatic events.

The fourth part of the book deals with important responses of trees to a limitation common in tropical soils: low amounts of available nutrients. How valid is the paradigm of widespread phosphorous limitation? What can be inferred from litter manipulation and fertilization experiments in tropical forests? What are the dynamics and the roles of litter accumulation and decomposition? What is the main distinctive characteristic of nutrient cycling in tropical ecosystems dominated by trees? Do nutrients limit the ability of tropical trees to respond to climate change, or can trees adjust and adapt to nutrient limitations to carry on the process of photosynthetic carbon assimilation? Do N and P equally limit the photosynthetic process in tropical trees?

Carbon economy and biomass allocation patterns in tropical trees and forests are the focus of the fifth part of the book. Important issues related to carbon cycling and the strength of carbon sinks across terrestrial ecosystems worldwide are analyzed. In particular, the continuum of physiological traits from high light requiring pioneer trees to slow growing shade-tolerant trees is discussed in terms of primary and secondary succession in tropical forests and gap-phase regeneration. These two groups of trees are considered as the extremes of a gradient of species requiring high light levels for photosynthesis and rapid growth and in species tolerant to diffuse light and the use of light flecks for carbon assimilation. Are there trade-offs in carbon allocation between defense against herbivores and growth? Compared to tropical and temperate forests, subtropical forests have received little attention until now, and the contribution of this region to the global carbon cycle has not been fully assessed. In this part the carbon balance of subtropical forests at different spatial and temporal scales will be analyzed. The reader will be surprised to know that many subtropical forests are strong carbon sinks, and perhaps the strongest when compared to other terrestrial ecosystem.

In the last part, ecophysiological processes at different spatial and temporal scales are analyzed. Until recently the trunks of tropical trees in lowland areas were assumed not to have tree rings. Several studies have found that this is not the case, particularly in seasonally dry environments, which opens a window of opportunities for using tree rings to acquire insights into the ecology and climate sensitivity of tropical trees as well as the possibility of obtaining the age of individual trees. This part also addresses biomechanical characteristics of tree, with special references to the constraints of being a tropical tree. Do tropical trees adhere to the same biomechanical laws as temperate trees?

In the past 20 years since we began working together, we have seen tropical ecophysiology evolve from single species studies to large comparative works that embrace the high diversity of tropical forests. We have seen a transition from descriptive and natural history studies, which provided an important foundation, to advanced quantitative and modeling approaches that reveal broader patterns in space and time. Plant ecophysiology in the tropics has also developed strong linkages to disciplines that focus on larger spatial scales, including community ecology, ecosystem ecology, and landscape ecology, as well as smaller spatial scales such as molecular biology, stable isotope ecology, and genomics. This book represents the work of a community of leading tropical ecophysiologicalists, many of

whom are colleagues and collaborators. We hope that it will provide a useful resource for understanding, conserving, and sustainably managing tropical forests, as well as predicting how these ecosystems will respond to future climate change.

Buenos Aires
January 2015

Guillermo Goldstein
Louis S. Santiago

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Part I
Physiology and Life History Traits
of Unique Tropical Growth Forms

Hemiepiphytic Trees: *Ficus* as a Model System for Understanding Hemiepiphytism

Guang-You Hao, Kun-Fang Cao and Guillermo Goldstein

Abstract Woody hemiepiphytes that have an epiphytic juvenile growth stage differ crucially in physiology and ecology from common trees. A relatively high degree of ontogenetic plasticity confers these plants stress tolerance during the epiphytic stage and sufficient competitiveness later as independent trees. The genus *Ficus* consists of about 500 hemiepiphytic and about 300 non-hemiepiphytic woody species. Ecophysiological comparative studies between hemiepiphytic (Hs) and non-hemiepiphytic (NHs) *Ficus* tree species reveal that the existence of an epiphytic growth habit even only for a part of their life cycle involves profound changes that persist to a large degree in their terrestrial growth stage. When growing under similar conditions, both as saplings and mature trees, the Hs have physiological traits resulting in conservative water use and drought tolerance contrasting with more prodigal water use and drought sensitivity in NHs. Divergence in water related functional traits between the two groups are centrally associated with a trade-off between xylem water flux capacity and drought tolerance. Two distinct groups of life history traits for Hs and NHs have evolved—epiphytic regeneration with a slow starting growth rate but enhanced ability to tolerate water deficits in the upper canopy environment and regeneration in the forest understory with an initial

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burst of growth to rapidly gain a relatively large seedling size that can better survive risks related to terrestrial regeneration. Evidence shows that the underlying physiology distinguishing these two growth forms mostly involves divergences in adapting to contrasting water regimes but not light conditions, contrary to the conventional hypothesis that hemiepiphytism evolved for gaining access to higher irradiance in the canopy than on the forest floor.

Keywords Drought tolerance · Hydraulic architecture · Plant water relations · Regeneration · Shade tolerance

Introduction

Hemiepiphytes are plants that grow epiphytically for a portion, but not all, of their life cycle. They are customarily subdivided into primary and secondary hemiepiphytes depending on which part of their life cycle has root connections with the ground. Primary hemiepiphytes normally germinate and grow on other plants but later establish substantial and permanent connections with the ground via aerial roots (Kress 1986; Putz and Holbrook 1986). Secondary hemiepiphytes germinate on the ground, climb up their host plants, and then lose stem connections with the soil (Kress 1986; Putz and Holbrook 1986). Primary hemiepiphytes have a true epiphytic stage, during which their ecophysiological traits are very similar to those of the true epiphytes (Zotz and Winter 1994), while secondary hemiepiphytes differ fundamentally from epiphytes, but are rather functionally similar to vines even after the lower part of their stems die back (Holbrook and Putz 1996b; Moffett 2000). For example, many aroid species that are called secondary hemiepiphytes can establish connections with the soil by producing adventitious roots after severing the stem connections with the ground and regaining access to soil resources. The current use of the term hemiepiphyte thus confounds two radically different life cycle characteristics. Zotz (2013a) suggested to entirely discard the term “secondary hemiepiphyte” and instead use Moffett’s (2000) term “nomadic vine” for climbing plants that germinate on the ground and lose the lower part of their stem later during ontogeny. By doing this, the term “hemiepiphyte” is reserved exclusively for species that were formerly called primary hemiepiphytes. We adhere to this definition hereafter in this chapter.

Hemiepiphytes are an important plant component of tropical vegetation. According to a recent census by Zotz (2013b), there are 19 families and 28 genera that contain more than 800 hemiepiphytic species. Among these taxa, *Ficus* (Moraceae) and *Clusia* (Clusiaceae) are the two most important genera that are composed of more than 600 woody hemiepiphytic species combined. In the tropics many of these species are well known as strangers that germinate on tops of other trees and have the potential to strangle their hosts and become structurally independent trees (Fig. 1a–d). In tropical forests of Panama and Zimbabwe 9.8 and



Fig. 1 **a** The epiphytic growth phase of *Ficus altissima* growing in the canopy of a host palm tree showing multiple dangling aerial roots; **b** *Ficus altissima* during its terrestrial growth stage showing multiple “pseudostems” formed by fused aerial roots; **c** a *Ficus concinna* tree strangling a tree; **d** a free-standing stage *Ficus curtipes* tree showing tangled architecture of aerial roots defining the space occupied by a host tree that has been strangled and decomposed. All plants are growing in the Xishuangbanna Tropical Botanical Garden (XTBG), Yunnan, China *Photo credits: GYH*

12.6 % of trees, respectively, were found bearing hemiepiphytic *Ficus* (Guy 1977; Todzia 1986); in Venezuela 13 % of trees >10 cm DBH carried *Ficus* or *Clusia* (Putz 1983). Hemiepiphytic *Ficus* species are also very commonly found on architectural structures especially in tropical and subtropical regions, such as ancient temples in India and old stone walls in urban Hong Kong (Sitaramam et al. 2009; Jim 2014).

It is commonly considered that there are several potential advantages to start the life cycle as an epiphyte in tropical forests. One of the most important advantages is that the forest canopy offers higher light availability than the forest understory. It has been suggested that hemiepiphytism evolved in plants that colonized rocky areas as an adaptation to access high light environments in the forest canopy (Dobzhansky and Murea-Pires 1954; Ramirez 1977; Putz and Holbrook 1986; Todzia 1986; Laman 1995; Williams-Linera and Lawton 1995). They may also benefit from minimizing risks of fire, flood, terrestrial herbivores and damage or coverage by falling debris. The advantages of spending the initial part of their life cycle as an epiphyte, however, can be offset by the potential limitations of water and nutrient availability (Benzing 1990; Coxson and Nadkarni 1995; Holbrook and Putz 1996a, b, c; Swagel et al. 1997).

The hemiepiphytic *Ficus* (Moraceae) is the most conspicuous group of species with such life history in terms of habitat breadth, species richness, abundance and dominance in forest ecosystems (Dobzhansky and Murca-Pires 1954; Putz and Holbrook 1986; Holbrook and Putz 1996b). Species in the genus *Ficus* are among the most important components of tropical lowland rainforests throughout the world (Harrison 2005) and are ecologically important due to their interactions with many frugivorous animals and other plant species (Shanahan et al. 2001). This genus consists of about 500 hemiepiphytic species, including stranglers and banyans, and about 300 non-hemiepiphytic woody species (Putz and Holbrook 1986; Harrison 2005). In *Ficus*, the hemiepiphytic habit most likely evolved four times in the subgenera *Urostigma*, *Sycidium*, *Pharmacosycea* and in a closely related group comprised of the subgenera *Conosycea*, *Galoglychia*, *Americana* and *Malvanthera* (Harrison 2005). From the point of view of evolution, it is important to consider the main environmental factors that selected for this specialized growing habit. Comparative studies in ecophysiology between hemiepiphytic and non-hemiepiphytic *Ficus* species provide valuable information about the main differences between these two groups in environmental adaptation of the seedling/sapling and adult stages, which allow us to infer major selective pressures for the evolution of hemiepiphytism.

Because of the radical changes in rooting environment between the two growth phases, developmental and physiological plasticity is important for hemiepiphytes and enables them first to survive the harshness of the epiphytic habitat and then to compete successfully with other trees when they are later rooted in the ground (Holbrook and Putz 1996b). The change from functional epiphyte to tree is accompanied by a shift in rooting volume and characteristics of the rooting zone. Previous studies have found that nutrient availability does not exert a major limitation to the epiphytic phase of hemiepiphytic *Ficus* (Putz and Holbrook 1989),

whereas measurement of stomatal conductance and leaf phenology indicate that water availability is frequently a major constraint as compared to terrestrially rooted trees of the same species (Holbrook and Putz 1996a, b, c). Epiphytes face frequent and severe water deficits even in areas with very humid climate (Benzing 1990). In seasonally dry climates, hemiepiphytes in the epiphytic stage can experience even more severe drought during the dry season.

In hemiepiphytes, the two different growth phases with contrasting environmental conditions make it interesting and convenient for physiological comparative studies. Some hemiepiphytes, such as species of the genus *Clusia*, switch to the more water efficient facultative CAM metabolism when stressed by drought, but all of the species of *Ficus* studied thus far exhibit only C_3 photosynthesis regardless of the life stage (Ting et al. 1987). Strangler *Ficus* in the epiphytic stage avoids water deficit mainly through strong stomatal control to maintain relatively high leaf water potentials (Holbrook and Putz 1996c). During both the rainy season and the dry season, stomatal conductance of epiphytic stage strangler figs is lower than conspecific trees. Throughout the dry season, epiphytic stage strangler figs only open their stomata in the early morning (Holbrook and Putz 1996c). Furthermore, epiphytic phase *Ficus* can better control water loss from leaf surfaces than conspecific tree-phase plants after stomata are closed (Holbrook and Putz 1996a). The smaller guard cell surface area due to lower stomata density enables the epiphytic stage *Ficus* to lose water more slowly compared to tree phase plants of the same species. Due to these water conservation traits, leaf water potentials of epiphytic stage *Ficus* plants are found to be similar or even less negative than conspecific tree-phase individuals (Holbrook and Putz 1996b). Even when both epiphytic phase and tree phase *Ficus* are well supplied with water during manipulative experiments, the leaves of epiphytic plants still exhibit significantly lower stomatal conductance and much lower epidermal conductance, indicating strong developmental changes from the epiphytic to the terrestrial phase (Holbrook and Putz 1996a).

Physiology related to epiphytic-terrestrial phase transition in *Ficus* has been well studied and reviewed by Holbrook and Putz (1996b). This chapter focuses on ecophysiological comparisons between hemiepiphytic (Hs) and non-hemiepiphytic (NHs) *Ficus* tree species grown under similar environmental conditions to better understand intrinsic differences between these two functional groups.

Comparison of Hydraulics and Water Balance

Stem Hydraulic Conductivity

Only few studies have compared hydraulic architecture between woody hemiepiphytic and free-standing tree species (Patiño et al. 1995; Zotz et al. 1997; Hao et al. 2011). These studies demonstrate that hemiepiphytic plants have stems that are less conductive as shown by relatively low leaf-specific hydraulic conductivity (K_1). According to the studies by Patiño et al. (1995) and Zotz et al. (1997), the lower K_1

found in hemiepiphytic *Ficus* and *Clusia* shoots are largely due to their low investment in water conducting tissue, implying a lower wood cross-sectional area per unit leaf area (Huber value; H_v), rather than less conductive sapwood tissues. Their stem hydraulic conductivity values expressed per wood cross-sectional area are even larger than in tropical and temperate angiosperm trees (Zotz et al. 1997). The more recent study by Hao et al. (2011) comparing mature trees of Hs and NHs grown in a common garden, however, found no significant difference in leaf to sapwood area ratio between the two functional groups but substantially lower specific hydraulic conductivity (K_s , i.e. an intrinsic measure of water transport efficiency of the xylem) in Hs than in NHs.

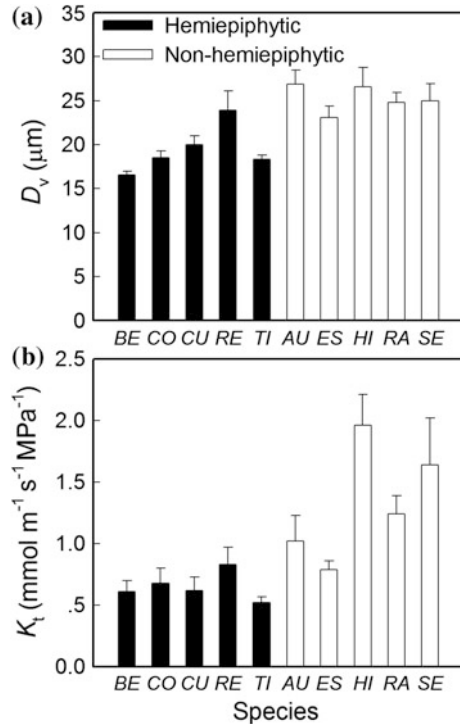
The discrepancies between different studies, however, may largely be due to methodological differences in the way K_s and Huber values are estimated. A close examination of the Patiño et al. (1995) and Zotz et al. (1997) studies reveal that in both studies K_s and H_v were calculated on a whole stem cross sectional area basis rather than the sapwood area basis. This may strongly affect the interpretation of the results of such comparative studies because non-hemiepiphytic *Ficus* species usually have large pith in their stem, but the pith is negligible in the stems of hemiepiphytic species. In the stems of non-hemiepiphytic *Ficus* species, the pith can account for up to 70 % (on average 45 %) of the “wood” cross-sectional area (G.-Y. Hao unpublished). By using only the sapwood area, excluding the pith, for K_s calculation, we find that Hs have sapwoods that are far less efficient in conducting water even when both types of species are growing as independent trees in a common garden (Hao et al. 2011). Consistent with the differences in stem hydraulic conductivity, Hs and NHs show significant differences in leaf properties related to water transport, water conservation and drought tolerance (Hao et al. 2010). These findings can be parsimoniously explained by the hypothesis that Hs are adapted to drought conditions associated with an epiphytic growth stage in the canopy, whereas NHs are selected for strong competitive ability given the higher water availability that they experience during their first growth stages.

Water Flux Through the Leaf

Hemiepiphytic *Ficus* species have low leaf water flux capacity that parallels their relatively low stem-level hydraulic conductivity. Compared with congeneric terrestrial species, Hs have significantly narrower vessels in their leaf petioles and lower theoretical leaf area adjusted hydraulic conductance calculated from petiole xylem vessel dimension measurements (Fig. 2a, b; $P < 0.05$, t-tests). The NHs have vessel lumen diameters that are on average 30 % larger than Hs but the number of vessels per petiole standardized by leaf area does not differ between the two growth forms. The resultant theoretical xylem hydraulic conductance of NHs averages 104 % higher than that of Hs (Hao et al. 2010).

The lower leaf water flux capacity in Hs is consistent with their lower transpirational water requirement per unit leaf area. Compared to NHs grown under similar

Fig. 2 **a** Leaf petiole average vessel diameter (D_v) and; **b** theoretical hydraulic conductance (K_t) of five hemiepiphytic and five non-hemiepiphytic *Ficus* species. Mean values \pm SE for each species are reported ($n = 5-6$). Species name abbreviations: *Ficus benjamina*, BE; *F. concinna*, CO; *F. curtipes*, CU; *F. religiosa*, RE; *F. tinctoria*, TI; *F. auriculata*, AU; *F. esquiroliana*, ES; *F. hispida*, HI; *F. racemosa*, RA; *F. semicordata*, SE (data from Hao et al. 2010)



conditions, Hs have significantly lower stomatal conductance and higher intrinsic water use efficiency measured both on mature trees well rooted in the soil and saplings growing in pots supplied with sufficient water (Hao et al. 2010, 2013). Differences in water use between Hs and NHs are most significant when diurnal courses of leaf gas exchange are compared. Epiphytic stage Hs in their native habitats have been found to open stomata only in the early morning during the dry season (Holbrook and Putz 1996c). When saplings are grown in pots and are well watered, Hs still have lower stomatal conductance and a shorter duration of active CO_2 assimilation on sunny days (Fig. 3a, b). In both groups of species, photosynthetic net assimilation rates reach maximum values around 11:00 h, but rates start to decline in Hs there after until the end of the day, whereas in NHs rates remain at high levels until 14:00 h with an afternoon peak following a slight midday depression (Fig. 3b). The different diurnal patterns of photosynthesis between the two growth forms of *Ficus* are likely associated with the intrinsically low xylem hydraulic conductivity in Hs compared to NHs. Higher water use efficiency in Hs suggests a constitutively conservative water use strategy (Table 1), consistent with adaptations to cope with drought-prone canopy habitats.

In juvenile plants of Hs, more conservative water use may contribute to the protection of their xylem vascular systems from catastrophic cavitation when facing unpredictable drought conditions associated with canopy growth in their natural

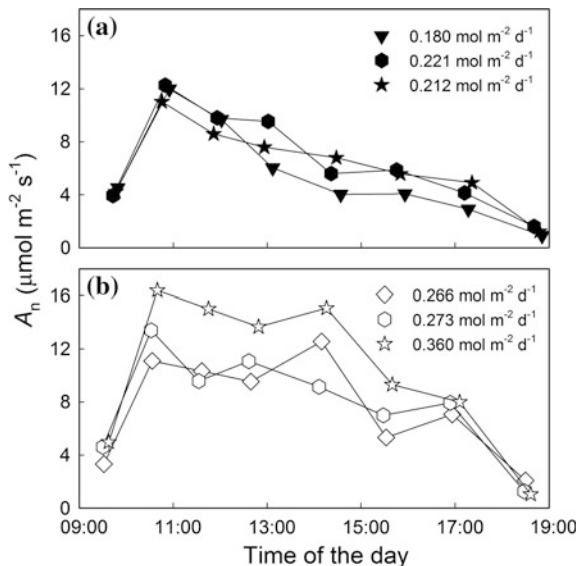


Fig. 3 Leaf net CO₂ assimilation rate (A_n) of (a) hemiepiphytic and (b) non-hemiepiphytic *Ficus* saplings grown under full sunlight. Numbers in panel a and b indicate daily cumulative net assimilation. *Ficus concinna* (▼), *F. tinctoria* (●), *F. virens* (★), *F. hispida* (◇), *F. racemosa* (○), *F. semicordata* (☆). Filled and open symbols indicate hemiepiphytic and non-hemiepiphytic species, respectively (Hao et al. 2013)

habitats. Higher leaf xylem hydraulic conductance as found in NHs indicates adaptation of the leaf vascular system to a more prodigal water use, which is only advantageous under conditions of reliable water sources. Considering the frequently occurring drought stress related to a canopy growth during their early ontogeny, high water flux capacity does not appear to be a beneficial trait for Hs.

Traits Conferring Drought Tolerance

Hemiepiphytic *Ficus* species exhibit traits related to greater drought tolerance compared to NHs (Table 1). They have higher leaf mass per area and lower leaf osmotic potential at turgor loss point (π^0), typical adaptations to drought-prone environments (Hao et al. 2010). The Hs almost completely close their stomata at turgor loss point but all of the NHs maintain relatively high stomatal conductance, resulting in a much larger “safety margin” between stomatal closure and turgor loss point in Hs compared to NHs (Fig. 4). Narrow safety margins can benefit some plants by allowing the maintenance of gas exchange and thus optimizing returns on xylem investment (Brodribb and Holbrook 2004). A prerequisite for this set of functional traits is a relatively reliable water supply to the leaves that may not be

Table 1 Ecophysiological traits of seven hemiepiphytic (H) and seven non-hemiepiphytic (NH) *Ficus* species (values are means \pm 1 SE). Means of the two growth forms were compared using one-way ANOVAs

Functional traits	Prediction	H mean	NH mean	P-value (ANOVA)
Specific hydraulic conductivity (kg m ⁻¹ s ⁻¹ MPa ⁻¹)	H < NH	2.00 \pm 0.22	7.06 \pm 1.28	0.001
Leaf-specific hydraulic conductivity ($\times 10^{-4}$ kg m ⁻¹ s ⁻¹ MPa ⁻¹)	H < NH	2.28 \pm 0.45	9.55 \pm 2.71	0.007
Sapwood density (g cm ⁻³)	H > NH	0.50 \pm 0.03	0.45 \pm 0.03	0.100
Leaf to sapwood area ratio (cm ² mm ⁻²)	H < NH	128.7 \pm 18.0	115.2 \pm 18.5	0.291
Leaf size (cm ²)	H < NH	84.8 \pm 26.2	296.7 \pm 106.6	0.030
Leaf mass per area (g m ⁻²)	H > NH	107.0 \pm 12.5	69.1 \pm 6.5	0.007
Leaf saturated water content (g g ⁻¹)	H < NH	1.88 \pm 0.14	2.30 \pm 0.15	0.025
Maximum net CO ₂ assimilation rate on leaf area basis (μ mol m ⁻² s ⁻¹)	H < NH	13.0 \pm 0.8	13.7 \pm 0.8	0.274
Maximum net CO ₂ assimilation rate on leaf mass basis (μ mol g ⁻¹ s ⁻¹)	H < NH	0.126 \pm 0.016	0.210 \pm 0.028	0.008
Maximum stomatal conductance (mol m ⁻² s ⁻¹)	H < NH	0.301 \pm 0.028	0.408 \pm 0.021	0.003
Intercellular CO ₂ concentration (μ mol mol ⁻¹)	H < NH	290.1 \pm 3.5	305.2 \pm 2.2	0.001
Intrinsic water-use efficiency (μ mol mol ⁻¹)	H > NH	44.6 \pm 2.2	34.3 \pm 1.2	0.001
Leaf nitrogen content (%)	H > NH	2.11 \pm 0.18	1.69 \pm 0.12	0.033
Photosynthetic nitrogen use efficiency (μ mol CO ₂ s ⁻¹ mol ⁻¹ N)	H < NH	83.0 \pm 5.9	181.6 \pm 31.1	0.003

We specified the predictions in comparison between growth forms to allow one-tailed significance testing. *P*-values smaller than 0.05 are shown in bold face (Modified from Hao et al. 2011)

met by Hs with intrinsically low xylem water transport efficiency. Effective stomatal closure in Hs may thus be important in avoiding too large of a water potential gradient across the plant and hence catastrophic hydraulic failure.

The Hs do not only have earlier stomatal closure in response to leaf desiccation but also exhibit more effective water retaining ability after stomata closure (Fig. 5a, b). Average cuticle conductances are 2.1 and 10.7 mmol m⁻² s⁻¹ in Hs and NHs (*P* < 0.05, *t*-test), respectively. Consequently, after excision Hs can keep their relative water content above 70 %, a threshold for physiological damage to occur in many higher plants, for a period on average 10 times that of the NHs. This may confer Hs a greater ability to persist under severe drought. Leaf desiccation

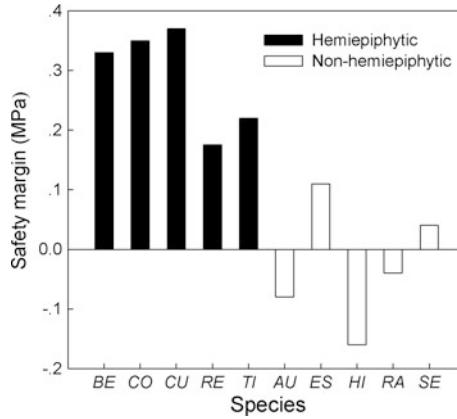


Fig. 4 Safety margin measured as the difference between leaf water potential at 50 % of maximum stomatal conductance ($\Psi_{g_{s50}}$) and leaf osmotic potential at turgor loss (π^0) in five hemiepiphytic and five non-hemiepiphytic *Ficus* species. Species name abbreviations are as in Fig. 2

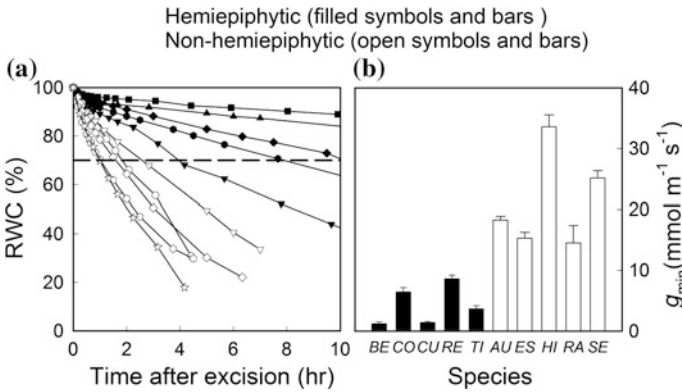
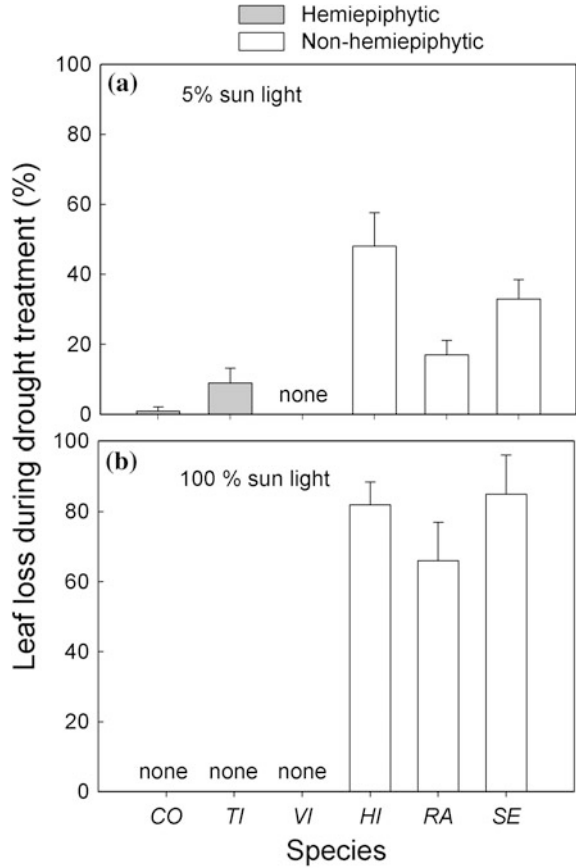


Fig. 5 **a** Relative water content (RWC) changes of water-saturated leaves during bench drying after excision ($n = 6$). The horizontal dashed line marks 70 % RWC. *Ficus benjamina* (\blacktriangle), *F. concinna* (\blacktriangledown), *F. curtipes* (\blacksquare), *F. religosa* (\blacklozenge), *F. tinctoria* (\blacklozenge), *F. auriculata* (\circ), *F. esquiroliana* (∇), *F. hispida* (\diamond), *F. racemosa* (\bullet), *F. semicordata* (\star); **b** leaf epidermal conductance. Species name abbreviations are as in Fig. 2 (data from Hao et al. 2010)

avoidance is determined by both the stomatal closure in response to water deficits and water retention after stomata closure, which relates to the resistance to water loss through the epidermal cuticle (Muchow and Sinclair 1989; Holbrook and Putz 1996c). Differences in stomatal control and cuticle conductance may explain the commonly observed leaf wilting and plant dieback in NHs but not in Hs under drought stress both in the field and during drought treatments in pots. The NHs on

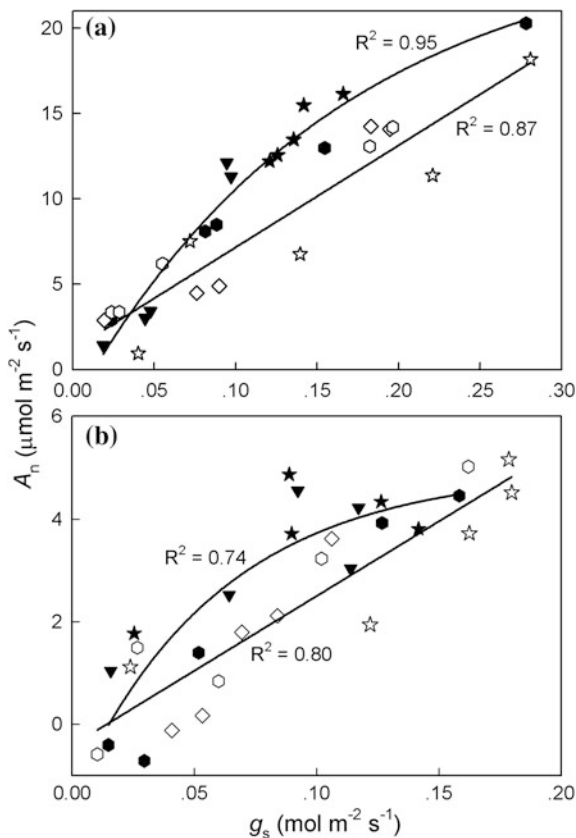
Fig. 6 Percentage of leaf loss due to simultaneous drought treatments of the same degrees to seedlings of hemiepiphytic and non-hemiepiphytic *Ficus* species grown under (a) full sunlight and (b) 5 % sunlight (Hao et al. 2013)



average lost 30 and 70 % of their leaves during a water withholding experiment, whereas Hs did not shed a substantial amount of leaves for a similar degree of drought except in *F. tinctoria* under full daylight (Fig. 6a, b).

When photosynthetic net assimilation rates are plotted against stomatal conductance following a drought treatment in potted plants, contrastingly different patterns are seen between Hs and NHs. The Hs appear to have higher net assimilation rate for a given stomatal conductance (Fig. 7a, b). Furthermore, the Hs show a substantial increase in water use efficiency in response to the drought stress, as shown by the increase in the slopes of the fitted curves, indicating physiological adjustments towards a more efficient water use under drought, whereas this adjustment is lacking in NHs (Fig. 7a, b).

Fig. 7 Leaf net assimilation rate (A_n) vs. stomatal conductance (g_s) following a drought treatment in plants grown under (a) full sunlight and (b) 5 % sunlight. Symbols for each species are as in Fig. 3



Contrasting Water Use Strategies in Hs and NHs

Although conservative water use in Hs contributes to their ability to survive drought-stressed environments typical of epiphytic habitats during their early ontogeny, it negatively affects their photosynthetic carbon assimilation. While light-saturated net CO_2 assimilation rates per unit leaf area do not differ between the two growth forms, assimilation rates per dry mass are significantly lower in Hs (Table 1). The Hs also have lower photosynthetic nitrogen and phosphorous use efficiencies than NHs (Hao et al. 2011). Differences between Hs and NHs extend the finding that species adapted to different environments tend to differ in a cluster of water flux-related traits, including stem hydraulic conductivity, leaf hydraulic conductance and stomatal conductance (Sack et al. 2003, 2005; Dunbar-Co et al. 2009). These traits probably contribute to NHs having a higher photosynthetic capacity per investment in leaf dry mass and a higher growth capacity.

The contrasts between Hs and NHs in maximum flux-related traits and drought tolerance traits are consistent with the hypothesized trade-off between high