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Water relations of epiphytic and terrestrially-rooted strangler figs in a Venezuelan palm savanna

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Abstract Water use patterns of two species of strangler fig, *Ficus pertusa* and *F. trigonata*, growing in a Venezuelan palm savanna were contrasted in terms of growth phase (epiphyte and tree) and season (dry and wet). The study was motivated by the question of how C3 hemiepiphytes accommodate the marked change in rooting environment associated with a life history of epiphytic establishment followed by substantial root development in the soil. During the dry season, stomatal opening in epiphytic plants occurred only during the early morning, maximum stomatal conductances were 5 to 10-fold lower, and midday leaf water potentials were 0.5–0.8 MPa higher (less negative) than in conspecific trees. Watering epiphytes of *F. pertusa* during the dry season led to stomatal conductances comparable to those exhibited by conspecific trees, but midday leaf water potentials were unchanged. During the rainy season, epiphytes had lower stomatal conductances than conspecific trees, but leaf water potentials were similar between the two growth phases. There were no differences in $\partial^{13}C$ between the two growth phases for leaves produced in either season. Substrate water availability differed between growth phases; tree roots extended down to the permanent water table, while roots of epiphytic plants were restricted to material accumulated behind the persistent leaf bases of their host palm tree, *Copernicia tectorum*. Epiphytic substrate moisture contents were variable during both seasons, indicating both the availability of some moisture during the dry season and the possibility of intermittent depletion during the rainy season. Epiphytic strangler figs appear to rely on a combination of strong stomatal control, maintenance of high leaf water potentials, and perhaps some degree of stem water storage to cope with the fluctuating water regime of the epiphytic environment.

Key words Carbon isotope discrimination · *Ficus* · Hemiepiphyte · Plant water relations · Strangler fig

Introduction

The hemiepiphytic growth form includes plants that germinate and grow as epiphytes, but subsequently establish substantial and permanent rooting connections with the soil (primary hemiepiphytes *sensu* Putz and Holbrook 1986). The most conspicuous of these in terms of habitat breadth, number of species, and biomass, are the stranglers. These plants take their name from the anastomosing growth of their roots, which enclose the host tree in a solid sheath, enabling the strangler to go on to become a free-standing tree (Dobzhansky and Murca-Pires 1954; Holbrook and Putz 1996). Such a dramatic shift in growth form is matched by few other life histories, and characteristics that permit a single individual to thrive sequentially in two distinct environments have only recently been addressed (Putz and Holbrook 1986; Ting et al. 1987; Borland et al. 1992). The epiphytic environment is characterized by frequent and severe episodes of low substrate moisture availability and epiphytic plants typically exhibit physiological and morphological traits that enable them to withstand intermittent drought (Benzing 1990). The leaves of most stranglers, however, give little visual indication of being particularly drought tolerant and are outwardly similar to congeneric species of similar habitat and adult growth form but which

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germinate and grow directly in the soil. Nevertheless, stranglers are frequently abundant in seasonally dry regions such as tropical deciduous forests and savannas (Putz and Holbrook 1986; Williams-Linera and Lawton 1995) raising the question of how these plants withstand the moisture regime experienced as an epiphyte without later compromising their ability to make use of the more abundant and stable soil water reserves.

The majority of stranglers are members of two genera: *Ficus* (Moraceae) and *Clusia* (Clusiaceae). Reports of crassulacean acid metabolism (CAM) in *Clusia* (Tinoco Ojanguren and Vazquez-Yanes 1983) have led to extensive field and laboratory studies of the occurrence and deployment of this water-conservative photosynthetic pathway in relation to growth form (tree vs. epiphyte) and environmental conditions (e.g., Popp et al. 1987; Sternberg et al. 1987; Borland et al. 1992; Franco et al. 1992; Zotz and Winter 1993). The ability to switch between CAM and C3 photosynthesis appears to afford these plants the physiological flexibility to adjust to fluctuations in moisture availability. In contrast, less attention has focused on how the more abundant and diverse strangler figs survive the rigors of the epiphytic habit and go on to become large trees (Ting et al. 1987; Putz and Holbrook 1989). This study examines patterns of leaf gas exchange and water potential of epiphytic and terrestrially-rooted members of two species of *Ficus* growing in a Venezuelan palm savanna as part of an effort to understand how C3 hemiepiphytes are able to grow successfully as both epiphyte and tree. In particular, we address the question of whether there are underlying differences in how the two growth forms regulate their water balance and whether any such differences are primarily physiological or developmental in origin. Because we are interested in whether the manner in which these plants respond to changes in moisture availability differs between epiphytic and tree, we contrast the extremes in both growth form (plants lacking any root in contact with the ground and free-standing trees) and season (middle of the dry and wet seasons).

Materials and methods

Plant material and study sites

Field observations were made in central Venezuela (8°34'N, 67°35'W), approximately 45 km south of the town of Calabozo at an elevation of 70 m above sea level. Natural vegetation in this region consists of dry forest, gallery forest and palm savanna (Troth 1979), but was greatly disturbed in the study area due to cattle grazing and fire exclusion. Precipitation is markedly seasonal, with an annual mean of 1450 mm (Troth 1979). The soil is a vertisol with impeded drainage (Weston et al. 1968). Much of the study area is flooded to a depth of 30–50 cm during the April to October rainy season. Two species of strangler figs, *Ficus pertusa* and *F. trigonata*, are common in this habitat (69 and 37 mature individuals/ha, respectively; Putz and Holbrook 1989). Features of this site that facilitated this study include: open vegetation allowing access to epiphytic and tree leaves receiving similar levels of illumination, a severe dry season, and the existence of a common host species. All of the strangler fig individuals included in this study began their lives as epiphytes growing on the palm *Copernicia tectorum*. Palms are particularly suitable host species for the study of strangler figs because their relatively small crowns cast little shade and because roots of apparently epiphytic individuals cannot access the soil through an internal cavity in the host stem such as often occurs with dicotyledonous hosts (Holbrook and Putz 1995).

Stomatal conductance and leaf water potential

Diurnal courses of stomatal conductance and leaf water potential were recorded for epiphytic and tree-phase individuals during both dry and wet seasons over a 2-year period. Stomatal conductance and leaf water potential were measured using a Li-Cor 1600 porometer and a pressure chamber. Relative humidity was measured with a ventilated psychrometer. Stomatal conductance measurements were restricted to leaves receiving at least 500 $\mu E\ m^{-2}\ s^{-1}$ of photosynthetically active radiation. Pre-dawn water potential measurements were made at first light with subsequent measurements of stomatal conductance and leaf water potential being made at approximately two hour intervals throughout the day. During the rainy season stomatal conductance measurements were not possible before 9 a.m. due to moisture on leaf surfaces. Dry season measurements were made during the beginning of February at which time there had been no measurable precipitation for over 2 months. Wet season data were collected at the end of July, at which point the precipitation had been in excess of 100 mm/month for the May–July period. The wet season data presented were measured on a sunny day immediately following a substantial rainfall. Two to six leaves were measured for each plant. These replicates were averaged for each individual before entering into treatment comparisons. Sample sizes for *F. pertusa* were as follows: dry season stomatal conductance – epiphytes = 8, trees = 8; dry season water potential – epiphytes = 3, trees = 3; wet season stomatal conductance – epiphytes = 3, trees = 3; wet season water potential – epiphytes = 3, trees = 3. For *F. trigonata* the number of individuals studied was: dry season stomatal conductance – epiphytes = 3, trees = 3; dry season water potential – epiphytes = 4, trees = 3; wet season stomatal conductance – epiphytes = 4, trees = 3; wet season water potential – epiphytes = 3, trees = 3. Epiphytes and trees were compared using the statistical package DataDesk^4 (Data Description Inc., Ithaca, N.Y.) to construct a repeated-measures ANOVA which included growth form (epiphyte or tree), individual (nested within growth form) and time (of measurement) as main effects and the interaction between growth form and time. Differences between growth forms were assessed by dividing the mean square due to growth form by the mean square due to individual and comparing these to an *F*-distribution. Interactions between growth form and time (i.e. did the growth forms differ in how the measured parameter changed throughout the day) were compared by dividing the mean square due to the interaction by the error mean square. Missing data points were solely due to equipment failure or logistical problems; no points were omitted from the analysis.

Watering experiment

A short-term watering experiment was conducted during the dry season to determine the degree to which stomatal conductance of epiphytic plants was limited by high vapor pressure deficits versus low substrate moisture content. Six epiphytic individuals of *F. pertusa* (each growing on a different palm) were watered daily for 1 week. The water was applied with a bucket until the rooting medium was saturated (approximately 7 l $plant^{-1}\ day^{-1}$). Diurnal courses of stomatal conductance and leaf water potential were made immediately prior to the first watering and on the day following the last watering. Statistical comparisons were made using repeated-measures ANOVA as described above.

Carbon isotope ratio

Fully expanded leaves from five epiphytes (each growing on a different palm) and five trees of each species were collected during the middle of both dry and rainy seasons for carbon isotope ratio determination. Individuals producing new leaves can be found throughout the year in both species, although peaks in leaf expansion at the population level coincide with the rainy season (Putz et al. 1995). Seasonality in leaf expansion was less pronounced in epiphytic plants and leaf life spans were longer in trees (average lifespan of approximately 5 months) than epiphytes (average lifespan of approximately 2–3 months; Putz et al. 1995). We selected leaves that appeared to have been expanded during the current season. The leaves were dried at 70 °C, finely ground, and the relative abundance of ^{13}C and ^{12}C determined by isotope ratio mass spectrometry at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah. Stable carbon isotope ratio ($\partial^{13}C$) was expressed as the $^{13}C/^{12}C$ ratio relative to PDB (Craig 1957). The data for each species were examined using a two-way analysis of variance with season (wet, dry) and growth form (epiphyte, tree) as factors.

Substrate moisture availability

Moisture release characteristics were determined for material collected from behind the leaf bases of ten *C. tectorum* palms. The epiphytic material was obtained by removing the leaf bases with a machete and extracting the organic material with a small spoon. The samples were sieved, thoroughly mixed, and a moisture release curve was determined using a pressure plate (Klute 1986). For comparison, a similar relationship between water content and applied pressure was made on soil collected at the base of the palm trees.

The moisture content of material collected behind the leaf bases of *C. tectorum* palms was determined during the wet (n = 6) and dry (n = 14) seasons. Each sample was collected from a different palm which were chosen at random from the population of plants supporting either a *F. pertusa* or a *F. trigonata* epiphyte. Samples (50–200 g) were collected at midday, weighed immediately, and dried to a constant weight at 100 °C. Sampling times corresponded with measurements of stomatal conductance and leaf water potential.

Results

Daily course of stomatal conductance and leaf water potential

Dry season

During the dry season stomatal conductance was significantly higher in trees of *F. pertusa* (F = 148.93, P < 0.001) and *F. trigonata* (F = 23.79, P < 0.002) than in conspecific epiphytes (Figs. 1 and 2). Maximum stomatal conductances occurred during the early-to-mid morning in all plants. Trees of *F. trigonata* had conductances up to 400 mmol $m^{-2} s^{-1}$ during the early morning as compared with less than 100 mmol $m^{-2} s^{-1}$ in conspecific epiphytes. Values for *F. pertusa* were lower but the difference between growth phases was similar. Maximum stomatal conductance of *F. pertusa* trees was less than 250 mmol $m^{-2} s^{-1}$, while epiphytes had only a very slight stomatal opening (< 15 mmol $m^{-2} s^{-1}$).

Despite larger stomatal conductance in the trees of both species, midday values of leaf water potential of the tree-phase plants were significantly lower (*F. pertusa*: F = 93.12, P < 0.001; *F. trigonata*: F = 221.61, P < 0.001) than in epiphytes (Figs. 1 and 2). In *F. pertusa* midday water potentials of the trees averaged −1.8 MPa while the epiphytes were always above −1.0 MPa. In *F. trigonata* the trees had midday values of approximately −1.7 MPa while the epiphytes ranged between −0.8 and −1.2 MPa. Pre-dawn leaf water potentials did not differ between epiphytic and tree individuals of *F. trigonata* (t = 0.022, P = 0.37). Epiphytic individuals of *F. pertusa*, however, had significantly more negative pre-dawn values (t = 5.51, P < 0.005).

Wet season

Significant differences in stomatal conductance between epiphytes and trees were also observed during the wet season (Figs. 1 and 2). In *F. pertusa* the trees had stomatal conductance values up to 600 mmol $m^{-2} s^{-1}$, whereas the maximum values for the epiphytes were 200 mmol $m^{-2} s^{-1}$ (F = 26.26, P < 0.01). *F. trigonata* trees had midday values ranging between 400 and 500 mmol $m^{-2} s^{-1}$, while the epiphytes varied between 80 and 170 mmol $m^{-2} s^{-1}$ (F = 51.82, P < 0.001). In contrast to the dry season, stomatal conductance remained high throughout the day. Midday closure in the data exhibited in Fig. 2 for *F. pertusa* was associated with midday clouds.

Leaf water potentials were similar between epiphytes and trees of both species during the wet season both during the day (*F. pertusa*: F = 4.00, P = 0.12; *F. trigonata*: F = 0.73, P = 0.44) and before dawn (*F. pertusa*: t = 0.632, P = 0.56; *F. trigonata*: t = 0.879, P = 0.43). Pre-dawn values were similar to those during the dry season for *F. trigonata*, but substantially higher in *F. pertusa* epiphytes. Midday values ranged between −0.4 and −0.8 MPa in both species, markedly higher than during the dry season (Figs. 1 and 2).

Watering experiment

Following one week of daily watering during the dry season, *F. pertusa* epiphytes exhibited a substantial and significant increase in stomatal conductance (F = 81.49, P < 0.001) and pre-dawn leaf water potential (t = 3.147, P < 0.05; Fig. 3). Midday stomatal conductance increased more than ten-fold, while pre-dawn leaf water

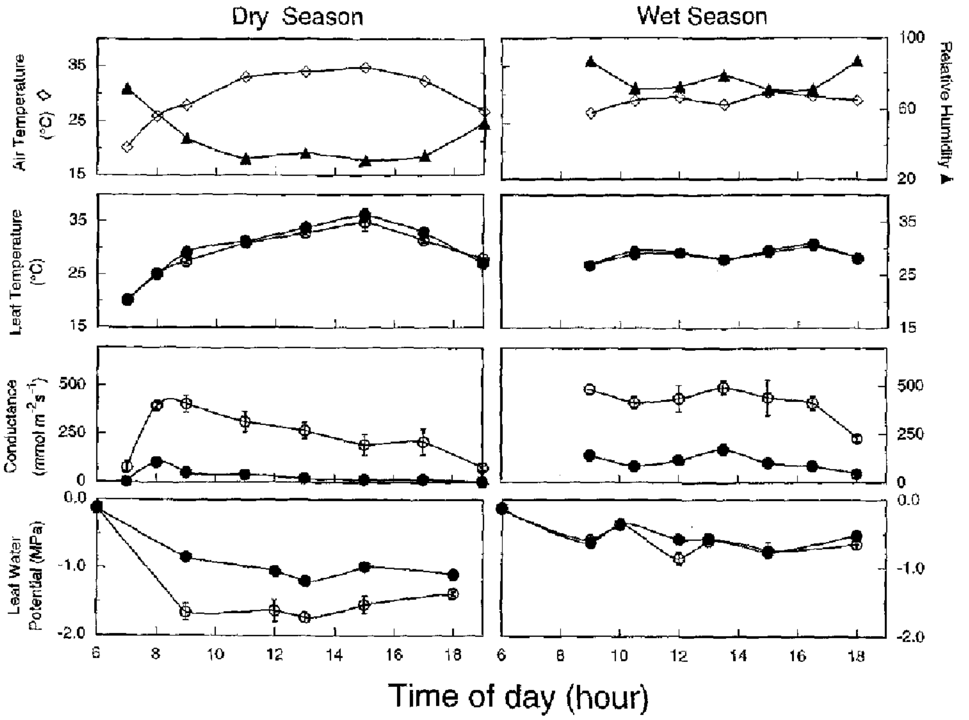

Fig. 1 Representative daily courses of leaf temperature, stomatal conductance, and leaf water potential for epiphytic (●) and terrestrially-rooted (○) individuals of *Ficus trigonata* during dry and wet seasons. Each point represents the mean and standard error of measurements made on three to eight individuals. Air temperature (◇) and relative humidity (▲) are plotted in the *upper panels*

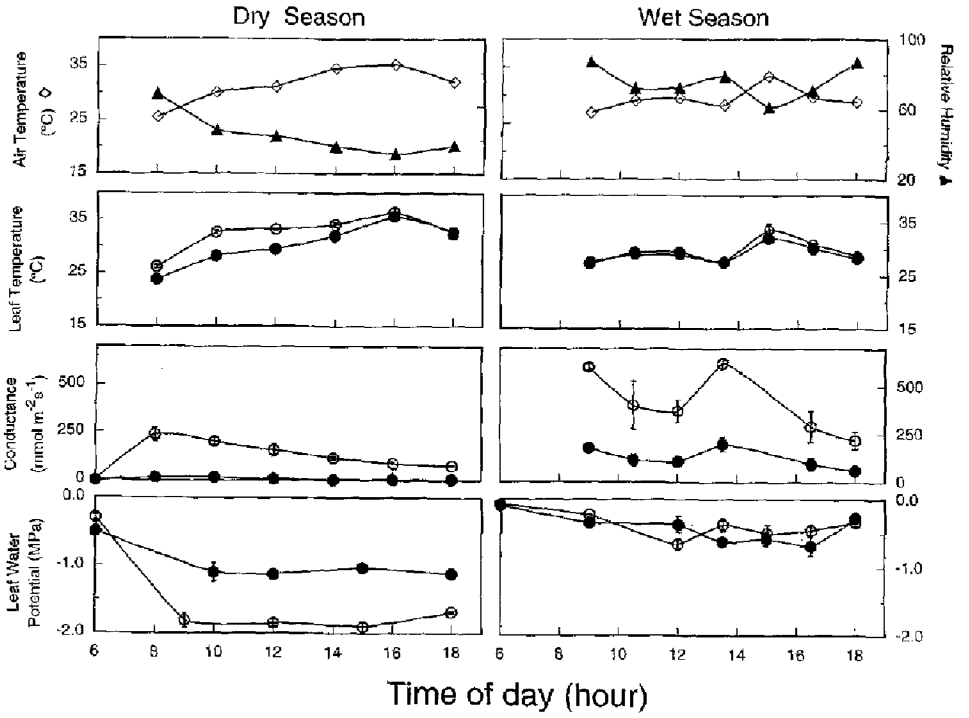

Fig. 2 Representative daily courses of leaf temperature, stomatal conductance, and leaf water potential for epiphytic (●) and terrestrially-rooted (○) individuals of *F. pertusa* during dry and wet seasons. Each point represents the mean and standard error of measurements made on three to eight individuals. Air temperature (◇) and relative humidity (▲) are plotted in the *upper panels*

potentials increased from −0.5 MPa to −0.25 following watering. Midday leaf water potentials, however, were not affected by watering (F = 0.009, P = 0.93) and remained approximately 1.0 MPa higher (less negative) than conspecific trees despite the fact that stomatal conductance of the watered epiphytes was comparable to that measured in the trees (Fig. 3). During the measurements, relative humidity near the leaves was unchanged from conditions existing prior to watering.

∂^{13}C isotope composition

Measured values of foliar ∂^{13}C in *F. pertusa* ranged from −26.42 to −30.66‰ (Table 1). There was a significant effect of season on ∂^{13}C (F = 5.45, $P < 0.05$), but not of growth form (F = 1.34, P = 0.26) or season × growth form interaction (F = 0.06, P = 0.81). ∂^{13}C measurements of *F. trigonata* leaves were also highly variable (−27.08 to −30.34%) and there was no effect

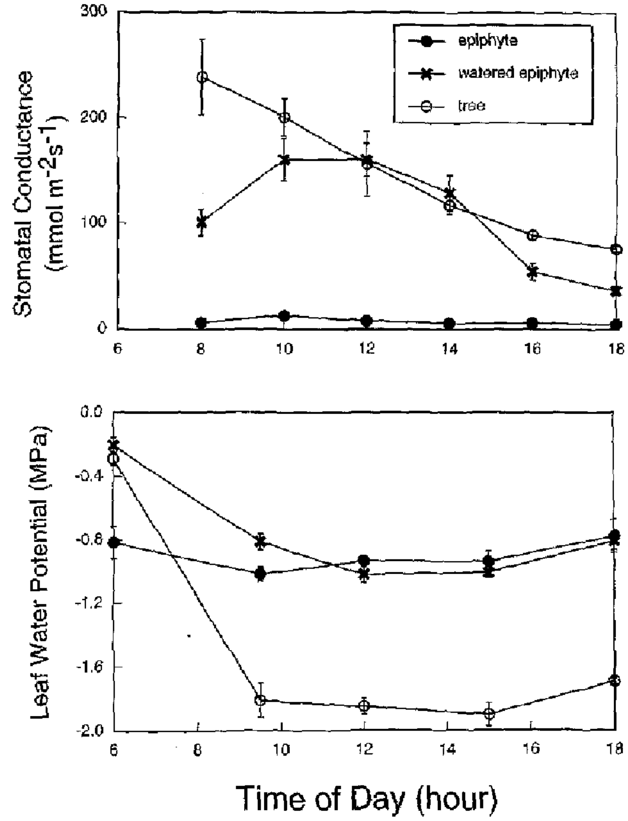

Fig. 3 Diurnal measurements of stomatal conductance and leaf water potential of *F. pertusa* epiphytes during the dry season. *Closed circles* (●) refer to epiphytic individuals; *crosses* (×) represent the same plants following 1 week of watering. Each point represents the mean and standard error of measurements made on six individuals. Data for *F. pertusa* trees (○) from Fig. 2 are included for scale

Table 1 Stable carbon isotope ratios (∂^{13}C) of recently expanded leaves collected from epiphytic and tree individuals of *Ficus pertusa* and *F. trigonata*. Samples were collected during the middle of each season. Data are mean (SEM) of five individuals

Growth form/	*F. pertusa*		*F. trigonata*	
season	Epiphyte	Tree	Epiphyte	Tree
Dry	−27.80 (0.296)	−27.16 (0.178)	−28.29 (0.638)	−28.97 (0.618)
Wet	−28.75 (0.650)	−28.33 (0.531)	−30.02 (0.364)	−28.27 (0.311)

of either growth form ($F = 1.14$, $P = 0.30$) or season ($F = 1.03$, $P = 0.33$), but the interaction term (season × growth form) was significant ($F = 5.76$, $P < 0.05$). The source of the large variability in ∂^{13}C among individuals of the same species and growth form is unclear.

Substrate moisture content

The water holding capacity of material collected from behind leaf bases of the palm *C. tectorum* greatly exceeded that of soil collected at the base of the palms. At field capacity (0.03 MPa of suction) the water content (% dry weight) of the epiphytic material was approximately 80%, while the equivalent value for the soil was only 38% (Fig. 4). If the available moisture is defined as the total amount of water removed by 1.5 MPa of suction, greater than 90% of the water in the epiphytic material would be mobilized by 0.5 MPa of suction, in contrast to < 70% for the soil.

During the dry season, water contents of the epiphytic rooting material were generally low, but highly variable. The average moisture content during the dry season (22% dry weight) corresponds to a matric potential more negative than the lowest midday leaf water potential measured in the epiphytic plants. Some samples, however, had moisture contents in excess of 40% (estimated matric potentials greater than −0.3 MPa) indicating that the epiphytes may have access to some substrate-held water during the dry season. During the rainy season, moisture levels of epiphytic material were also variable. For example, on a sunny day following several days with rain, the midday moisture content of epiphytic material was 51%, but ranged from 16 to 78%. Moisture contents of epiphytic material declined rapidly between rainfalls during the rainy season, such that after only 2–3 days without substantial precipitation this material became quite dry. This is in accord with our observations that stomatal conductance of epiphytic individuals was relatively high on days following a rainfall event, but declined rapidly over the course of several days if there was no additional precipitation (unpublished work). This suggests that, despite the high water holding capacity of the epiphytic material and the channeling of rainwater into the epiphytic substrate by palm leaf bases, epiphytic individuals may experience periods of low moisture availability even during the rainy season.

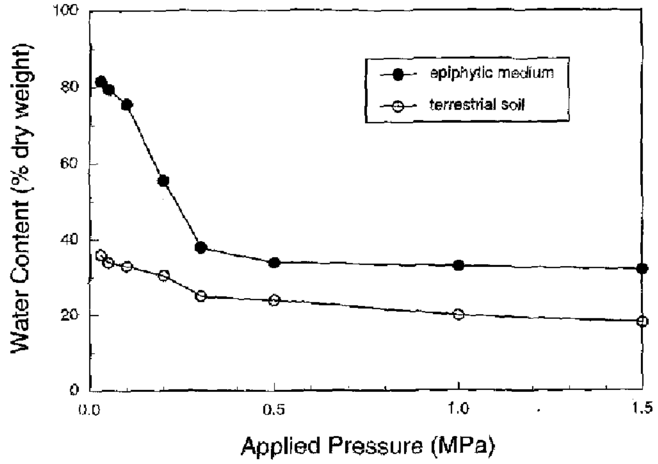

Fig. 4 Moisture release curve for material collected from behind leaf bases of *C. tectorum* (●) and from the top layer (0–10 cm depth) of the soil (○)

Discussion

Epiphytic plants have been well characterized in terms of their ability to thrive in the physiologically dry conditions of forest canopies (Schimper 1903; Madison 1977; Benzing 1990). Because strangler figs must grow as both epiphytes and trees, they may be constrained in the traits they employ to survive in the epiphytic environment or may be restricted to particularly moist microsites within the canopy. Epiphytic-phase strangler figs experience water limitations to a substantially greater degree than conspecific trees. Dry-season stomatal conductances were extremely low in epiphytic individuals and increases in substrate moisture content, either by short-term irrigation or seasonal changes in rainfall, greatly increased stomatal opening (Figs. 1–3). Sensitivity to soil moisture was also observed in the phenology of epiphytic plants. Leaf production in both *F. pertusa* and *F. trigonata* was positively correlated, and leaf loss in *F. pertusa* was negatively correlated, with rainfall during the previous fortnight, whereas phenological behavior of the trees was independent of recent precipitation (Putz et al. 1995).

In contrast to the seasonal differences in stomatal conductance of the epiphytic plants, midday leaf water potentials were similar between seasons. Trees exhibited the inverse pattern insofar as they had large seasonal variation in midday leaf water potential, but little change in stomatal conductance. Higher midday leaf water potentials in epiphytic plants compared with conspecific trees during the dry season (Figs. 1 and 2) at first appears in conflict with evidence for limitations in water availability in the epiphytes. Cell sap osmotic potentials estimated from pressure-volume curves of *F. pertusa* and *F. trigonata* epiphytes, however, are on the order of 0.8 MPa higher (less negative) than in conspecific trees (Holbrook and Putz, in press). Estimates of midday leaf turgor pressures based on these values of osmotic potential indicate that epiphytes and trees had similar leaf turgor (between 0.1 and 0.2 MPa). Furthermore, midday leaf water potentials of *F. pertusa* epiphytes were not altered by the increased stomatal conductance induced by watering (Fig. 3). Higher leaf water potentials in epiphytic-phase plants may relate to the moisture holding characteristics of their rooting environment. Although the moisture holding capacity of the material collected from behind *C. tectorum* leaf bases is extremely high at field capacity and substantially higher than the soil at all potentials, the moisture characteristic curve is quite flat at suctions greater than 0.5 MPa (Fig. 4). This, combined with a small total volume of substrate available to the epiphytes, would greatly diminish the amount of marginal gain in water uptake for a further reduction in xylem water potential.

An inherent structural difference between epiphytic and tree growth forms is the greater distance over which water must be transported from soil to leaves in the trees. Nevertheless, the apparent whole-plant hydraulic conductance, estimated by dividing midday transpiration rates by the difference between midday and predawn leaf water potential, was higher in tree individuals than in conspecific epiphytes during both seasons. This eliminates the possibility that the differences in midday leaf water potential observed between the two growth forms during the dry season can be solely attributed to the greater path length for water transport in the trees. Whether the difference in hydraulic conductance between growth forms was due to variation in hydraulic properties, the relationship between leaf area and allocation to structures for water uptake and transport, or both cannot be determined from these data.

Although epiphytic-phase plants appear to experience limitations in water availability during the dry season, they nevertheless retain leaves and may even produce new ones during a period when the majority of the surrounding vegetation is leafless (Troth 1979; Putz et al. 1995). The source(s) of water that the epiphytes utilize for transpiration and leaf expansion during the dry season are not known. Measurements of the water content of material collected from behind the persistent leaf bases of *C. tectorum* indicate that some relatively moist regions do exist. Dewfall represents one avenue of water influx, although whether this represents a significant source relative to the water loss rates of epiphytes is not known. Termite nests are also a potential source of water as their inner walls remain moist due to humidification by metabolic water or active deposition of water by the termites (Noirot 1970). *Nasutitermes ethratae* nests, in which strangler fig roots were observed, occur on more than 90% of the *C. tectorum* trees at this site (Putz and Holbrook 1989).

Epiphytic strangler fig stems are thickened and somewhat fleshy at the base (Putz and Holbrook 1986). These stem "tubers" should allow epiphytic individuals to capitalize on infrequent rainfall events. The presence of a within-plant water storage tissue may also help explain the high pre-dawn water potentials observed in *F. trigonata* during the dry season (Fig. 1). Furthermore, as this water is not subject to losses due to evaporation, deep infiltration, or uptake by roots of neighboring plants, the ability to store water should allow epiphytic individuals to make conservative use of a resource that would be otherwise temporally intermittent in its availability. Effective use of stored water, however, requires a coordination of water use patterns and water potential gradients such that water stored within the plant is not depleted prior to the onset of conditions warranting its storage in the first place (Holbrook 1995). The low stomatal conductances of epiphytic plants (Figs. 1 and 2), high leaf water potentials, and substantially lower epidermal water loss rates of epiphytic leaves compared with conspecific trees (Holbrook and Putz, in press) are consistent with this interpretation.

The frequent occurrence of drought in the epiphytic environment leads to the prediction that epiphytic strangler figs should be more efficient in their water use than conspecific individuals rooted in the ground. Because $\partial^{13}C$ largely reflects the ratio of assimilation to stomatal conductance, it can be interpreted as an integrated measure of water-use efficiency provided that leaves experience similar evaporative conditions (Farquhar et al. 1982, 1989). An earlier study of gas exchange in strangler figs reported a higher (more water-use-efficient) dry season $\partial^{13}C$ value in epiphytic individuals compared with conspecific trees of one of two species examined, with similar $\partial^{13}C$ values during the wet season (Ting et al. 1987). In this study there were no differences in $\partial^{13}C$ between growth forms in either season (Table 1). As stomatal conductance was lower for epiphytes in both seasons, these data suggest that the epiphytes also have lower assimilation rates. In both species, however, nitrogen content on a dry weight basis was higher in the epiphytic leaves, while nitrogen contents on a leaf area basis were similar (Putz and Holbrook 1989). It is possible that the capacity for carbon uptake in epiphytic plants might be constrained by external factors (e.g., light, a direct effect of leaf water status on photosynthesis) to a greater degree than in conspecific trees. Although we controlled for illumination during the times when stomatal conductance was actually measured, epiphytic plants, by virtue of their location near the palm's stem, may receive less overall radiation than the foliage of conspecific trees. It is also possible that the degree of fractionation associated with respiration and translocation may differ between the two growth forms, complicating interpretation of the $\partial^{13}C$ data (Farquhar et al. 1989). Finally, interpretation of the carbon isotope data may be complicated by substantial differences in internal leaf structure and stomatal density between the two growth forms (Holbrook and Putz, in press) which could influence $\partial^{13}C$ values through an effect on mesophyll resistance.

An important question concerning how strangler figs thrive as both epiphyte and tree is whether there are underlying differences between growth forms in terms of stomatal response to humidity, leaf water status, or soil moisture content. Although the data collected in this study are not in themselves sufficient to resolve this issue, several observations appear relevant. Epiphytic plants had approximately three-fold lower midday stomatal conductances than conspecific trees during the rainy season when the rooting environment of both growth forms was fully saturated (Figs. 1 and 2). This suggests that the two growth forms may differ in their maximum stomatal conductance. Epiphytic strangler figs (including these two species) have several-fold lower stomatal densities than conspecific trees (Holbrook and Putz, in press) which could account for the lower stomatal conductances observed during the rainy season.

The epiphyte-to-tree transformation is paralleled by changes in size and reproductive status. Epiphytic individuals of *F. trigonata* and *F. pertusa* with syconia were never observed, indicating that the transition from epiphyte to terrestrially-rooted growth form is necessary to attain reproductive maturity (Putz et al. 1995). Juvenile plants are reported to differ from reproductive individuals in a number of physiological parameters (Donovan and Ehleringer 1991; Sandquist et al. 1993). For example, juveniles of *Chrysothamus nauseosus*, a semi-arid shrub, have higher rates of water use and lower water-use efficiency compared with larger, reproductively mature individuals (Donovan and Ehleringer 1992). In contrast, epiphytic strangler figs are more conservative in terms of water use than conspecific trees. Whether this difference between strangler figs and non-hemiepiphytic plants can be solely attributed to external constraints in resource availability imposed by the epiphytic habit is not known. Preliminary studies suggest that the morphological and physiological shifts that accompany the transition from epiphyte to tree are influenced by developmental factors as well as changes in resource availability (Holbrook and Putz, in press).

Potential benefits associated with the epiphytic regeneration niche include increased light levels, and protection from fire, floods, and damage by terrestrial herbivores. Mortality rates of epiphytic individuals, however, were high (Putz et al. 1995) indicating that the epiphytic habit may place exceptional physiological demands on their successful establishment. Hemiepiphytic *Clusia* species survive the frequent limitations in substrate water availability that characterize the epiphytic environment by switching between C_3 and CAM photosynthesis (e.g., Popp et al. 1987; Ting et al. 1987; Borland et al. 1992). Epiphytic strangler figs appear to rely on a combination of strong stomatal control, maintenance of high leaf water potentials, and perhaps some degree of stem water storage to cope with the fluctuating water regime of the epiphytic environment.

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