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Light microhabitats, growth and photosynthesis of an epiphytic bromeliad in a tropical dry forest

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Abstract

In the tropical dry forest of Dzibilchaltún, Yucatan, Mexico, light microhabitats, tissue acidity changes, chlorophyll fluorescence and growth were investigated for the epiphytic bromeliad *Tillandsia brachycaulos* Schltdl. Most individuals occurred in sites between 20 and 60% of the height of the tree, and directly on the main trunk or branches closed to the main trunk. During the dry season, individuals received about nine times more photon flux density (PFD) than during the rainy season. Individuals that occurred under 30–59% of the daily ambient PFD showed greater leaf length increase and monthly leaf production, and produced more flowers than individuals in the brighter (>60% of ambient PFD) and the darker (11–29% of ambient PFD) light microhabitats. Well-watered plants acclimated to deep shade (6% of ambient PFD) showed values of tissue acidity similar to plants under higher light treatments. Well-watered plants under 60% of daily ambient PFD showed low values of maximum quantum efficiency at midday during most of the year but showed similar values of tissue acidity than plants under 6 and 30% of ambient PFD. Leaf temperatures of plants in low sites within the canopy and on the forest floor were significantly higher than the air during about 1 h, indicating that those plants could not dissipate the excess of heat. Individuals located in the most shaded microhabitats could also receive less amount of water from rainfall and dew. Therefore, it would be less damaging for this epiphytic bromeliad to occur in the most exposed microhabitats than in the most shaded microhabitats in this tropical dry forest.

Introduction

Epiphytic bromeliads are a conspicuous element in forests of tropical America and their abundance and diversity are related to the amount of rainfall (Gentry and Dodson 1987; Benzing 2000; Nieder et al. 2001). A vertical gradient in light in these forests shows a vertical stratification in epiphytic species, where some species grow at high irradiation and some under extreme shade (Pittendrigh 1948; Medina et al. 1989; Benzing 1990). In seasonally dry forests, however, environmental changes pronounce even more the vertical stratification in epiphytic species within the canopy, because of the seasonal moisture availability and the deciduousness of host trees. To cope with these resulting desiccating conditions, epiphytic bromeliads show several adaptations such as succulence, water-impounding shoots (tanks), crassulacean acid metabolism (CAM) and foliar trichomes (Benzing 1990). Also, for most epiphytic species, location on the host tree is usually related to the degree of one or more of these adaptive characteristics (Winter et al. 1983; Andrade and Nobel 1996, 1997; Hietz and Briones 1998).

Vertical stratification of epiphytic bromeliads has been correlated to the capacity for photoprotection and shade tolerance (Griffiths and Maxwell 1999). Moreover, in some epiphytic bromeliads the ability to acclimate to changes in irradiation is important for growth and survival (Maxwell et al. 1995). In particular, epiphytes reduce gas exchange and growth, and experience photoinhibition, when they are exposed to high photon flux density (PFD) or full sunlight (Winter et al. 1986; Medina et al. 1989; Andrade and Nobel 1996; Martin et al. 1999; Laube and Zotz 2003), although the growth of *Tillandsia usneoides* is apparently not affected for changes in PFD (Martin et al. 1985). However, the response of epiphytes to shade has been less documented. For instance, growth and CAM activity of the epiphytic cactus *Epiphyllum phyllanthus* are enhanced under partial shade and reduced under extreme shade (Andrade and Nobel 1996). In contrast, shading can reduce CO_2 uptake of some CAM epiphytic bromeliads (Griffiths et al. 1986) and some terrestrial CAM plants can also grow under excessive shade, such as the bromeliad *Aechmea magdalenae*. Individuals of this species grow well in the understory of lowland tropical forest and plants closer to gaps show a higher growth rate (Pfitsch and Smith 1988), although a continuous increase in PFD cause them chronic photoinhibition (Skillman and Winter 1997). Similarly, epiphytic bromeliads that show a vertical stratification tend to grow faster when they occur closer to the top of the trees (Hietz et al. 2002), but experience photoinhibition when they occur in the most exposed sites (Graham and Andrade 2004). Therefore, although some epiphytic and terrestrial bromeliads show many characteristics typical of sun-adapted plants (such as CAM), they occur in deep shade. But no reports have been made on the tolerance of these species to different levels of shade in their natural environments.

In tropical dry forests, vertical gradients in humidity and exposure are not as great as in humid forests but a vertical stratification of epiphytic species has been reported (Graham and Andrade 2004). Also, individuals of the epiphytic bromeliad *Tillandsia brachycaulos* show a vertical stratification in a tropical dry forest of Yucatan, where they occur from a few centimeters above the forest floor to the top on the host trees (Mondragón et al. 1999). We hypothesize that growth and reproduction would be limited for those individuals that occur in the darkest and the brightest light microhabitats within the canopy in a tropical dry forest of Yucatan, Mexico. Plants that grow low in the canopy would have a lower photosynthetic rate and plants high in the canopy would experience photoinhibition. A series of long-term field observations and experiments to measure growth and photosynthesis under different light microhabitats were carried out to test this hypothesis. Long-term measurements of growth for epiphytic bromeliads are few (Benzing 1990; Zotz 1995, 1998; Mondragón et al. 1999; Richardson et al. 2000; Hietz et al. 2002; Pett-Ridge and Silver 2002) and none takes into consideration the vertical stratification and light microhabitats. In addition, dislodged individuals of *T. brachycaulos* do not survive for more than a year on the floor of a tropical dry forest (Mondragón 2000), probably because they could not dissipate the excess of temperature during the hottest hours of the day. Thus, air and leaf temperatures of individuals at different heights within the canopy were also measured to determine the amount of heat they could not dissipate.

Methods

Study site and species

Field measurements were made at the archeological reserve Dzibilchaltún (21°05′ N, 89°35′ W, 8 m elevation) on the Yucatan Peninsula, Mexico. The site is a subtropical dry to tropical arid forest in the Holdridge system (Thien et al. 1982). Mean annual rainfall and temperature are 700 mm and 25.8 °C, respectively (Thien et al. 1982). A marked dry season (March–May; when most of the trees are leafless) is separated from the rainy season (June–October) by an early dry season (November–February), known locally as 'nortes' and characterized by up to 3-d events of strong winds (>80 km h^{-1}), little rainfall (20–60 mm) and low temperatures (<20 °C; Orellana 1999).

Tillandsia brachycaulos Schltdl. occurs from southern Mexico to Venezuela (Smith and Downs

1977) and is abundant in the study site. Seedlings are common but 60% of the individuals propagate by sympodial branching (Mondragón et al. 1999). *Tillandsia brachycaulos* exhibits CAM (Martin 1994; Graham and Andrade 2004) and is considered atmospheric (ecophysiological type V, according to Benzing 2000).

Field measurements

Individual locations of *T. brachycaulos* (> 5 cm height) were recorded in the canopies of eleven commonly-occurring species of host trees, selected within a 200-m transect. Height above the ground for each individual was measured with a flexible tape and tree height was calculated geometrically with distance and angle measurements. Also, the orientation (using a pocket compass), the distance from the main trunk to the site of the branch where each individual was established, and the vertical inclination of each individual were determined.

Photon flux density (PFD) was measured for approximately 48 h about 20 mm above randomly selected individuals (mean number of individuals per tree = 8.8 ± 0.6) using gallium arsenide phosphide photodiodes (Hamamatsu Corporation, New Jersey, USA). Diodes were calibrated against a quantum sensor LI-190SB (LI-COR, Inc., Lincoln, Nevada, USA) and measurements were collected every 5 s using a data logger (CR21X and CR10X, Campbell Scientific, Utah, USA) in reference to two additional sensors placed above the canopy at approximately 15 m above the ground. Dry season measurements were made from 11 to 29 May 2001, for 131 individuals. Wet season measurements were made from 19 September to 10 October 2001 above the same individuals, however only 110 individuals persisted because of wind displacement or host tree branch senescence.

Size and total number of leaves were measured for each selected individual on July 2001 and then the newest leaf was marked, so leaf growth and leaf production could be recorded each month. Also, flowering events and the number and growth of the ramets produced (which usually appear after each flowering event) were recorded. Individuals were grouped according to the light regime that they received during the dry season: 11–29% (n = 24), 30–59% (n = 81), and ≥60% (n = 13) of the average daily PFD above the canopy.

Light controlled experiments

Plants were collected in the field (about 80% of them from the forest floor), placed on wooden sticks (1.40 m above the ground), maintained under neutral-density shade cloth providing approximately 60, 30 and 6% of the ambient PFD (measured with photodiodes as described above), and watered daily for a week and then 3 times a week. Experiments started on October 2001 with 47 individuals in each light treatment, in the nursery of the Centro de Investigación Científica de Yucatán (CICY). Physiological measurements were performed during the early dry ('nortes'), dry and rainy seasons in January, May and September of 2002, respectively.

Tissue acidity was measured after collecting, from mid-rosette, 3–4 leaves per plant (0.3–0.8 g fresh weight; n = 12 plants) at dusk and before dawn the following day. Titratable acidity was quantified from frozen samples by boiling chopped leaves with 70% ethanol for 5 min and titrating the resulting solution with 0.01 N NaOH to a pH of 7.0 (Zotz and Andrade 1998) as measured with an electronic pH meter (Model 744; Metrohm Ltd., Herisau, Switzerland).

Maximum quantum efficiency (F_v/F_m; variable fluorescence/maximal fluorescence) was measured with a portable chlorophyll fluorescence meter (Plant Efficiency Analyzer, Hansatech Instruments Ltd., Kings Lynn, UK). Measurements were performed on 3 consecutive days (n = 15 plants) every 3 h, from 7:00 h to 19:00 h during the early dry and the rainy seasons, and from 6:30 h to 16:30 h during the dry season. Leaves were maintained dark-adapted by being covered with opaque clips placed an hour before each measurement.

Leaf water potential was also measured on 3 consecutive days using Wescor C-52 sample chambers and an HR-33T Microvoltmeter (Wescor, Logan, Utah, USA). Leaves were collected in the study site (n = 9–10 plants), transported to the laboratory in sealed vials, excised in small pieces, and placed in the previously calibrated chambers during 2 h.

Leaf temperatures and heat conduction rate

Microclimate and plant temperatures were monitored on collected *T. brachycaulos* plants placed on the soil and at different heights on the trunk of an individual *Caesalpinia gaumeri* tree in the Centro de Investigación Científica de Yucatán (CICY) Botanical Garden from November 12 to December 14, 2001. Plants were placed on the northeast, southeast and southwest side of the tree at each height. Leaf temperatures (T_L) were measured on the abaxial surface of one expanded leaf from mid-rosette, with a 0.08-mm-diameter copper–constantant thermocouple, attached with porous, adhesive tape. At the different tree levels, air temperature and humidity were measured with a Vaisala shielded probe (HMP35C-L, Campbell Scientific), wind speed with a three-cup anemometer (Met One Inc., Grants Pass, OR, USA), PFD with a quantum sensor (LI-190SB, LI-COR Inc.). All variables were sampled at 15-s intervals and average values were recorded every 10 min with a datalogger (CR21X, Campbell Scientific) equipped with a 16-channel multiplexer (AM416, Campbell Scientific). Although this methodology to measure leaf temperatures underestimate the true T_L (Tyree and Wilmot 1990), it is unlikely that overestimates the T_L, so high significant values could be detected to prove our hypothesis.

The amount of heat across the leaf boundary layers and convected away from the leaf (J_H) was calculated as (Nobel 1991): $J_H = 2K^{air} (T^{leaf} - T^{air})/\delta^{bl}$, where K^{air} is the thermal conductivity coefficient of air and δ^{bl} is the average boundary layer thickness, which was calculated from the standard formula (Nobel 1991): : $\delta^{bl}_{(mm)} = 4.0(l_{(m)}/\upsilon_{(m\,s^{-1})})^{1/2}$, where $l_{(m)}$ is the average leaf dimension in the downwind direction in m (leaf width for this epiphyte), and $\upsilon_{(m\,s^{-1})}$ is the ambient wind speed in m s^{-1}. The amount of latent heat, due to transpiration, was considered to be zero during the day because plants had the stomata closed when not well watered (Graham and Andrade 2004).

Statistical analysis

Chi-squared analysis was used to test the vertical and horizontal distributions of *T. brachycaulos* in the trees (Zar 1974). Linear correlations were obtained to describe the relationships of both plant height and number of leaves of *T. brachycaulos* and the percentage of daily PFD; values for number of leaves were transformed using the square root transformation and values for percentage of daily PFD were transformed using the arcsine transformation before the analysis (Zar J. 1974). One-way analysis of variance and multiple comparison methods were performed to test differences in leaf elongation and monthly leaf production within seasons, and differences in tissue acidity and maximum quantum efficiency among different light treatments.

Results

Plant distribution and light microhabitats

Most of the 751 measured *Tillandsia brachycaulos* individuals (35%) were located on the middle level of the host trees (40–59% of the total height; Figure 1a; $n = 265$ plants; $p < 0.001$) with 16% of the individuals located on the upper part of the trees ($n = 122$) but only 4% on the lower part of the trees ($n = 30$). Also, plants occurred preferentially closer to the main trunk; 32% of the individuals occurred either directly on the trunk, or between the trunk and 20% of the tree cover radius ($p < 0.001$; Figure 1b). Least individuals (17%, $n = 125$) occurred on the northwest side of the trees, compared to the other three orientations (average 27.6%; $p < 0.001$; Figure 1c), and a greater percentage of individuals (32%) were facing to the northeast, compared to the plants that were facing to other three different orientations (average 23%; $p < 0.001$; Figure 1d).

The average daily PFD received by *T. brachycaulos* was 41.8% of the ambient PFD above the canopy during the dry season and 10.8% during the rainy season (Figure 2). Average daily PFD above the canopy for the dates measured during the dry season and rainy season was not so different with the season, 45.4 ± 2.6 mol m^{-2} d^{-1} and 39.3 ± 3.3 mol m^{-2} d^{-1}, respectively ($p = 0.1$). The vertical distribution of *T. brachycaulos* within trees was similar to the distribution with respect to light during the dry season (Figures 1a and 2). Individual plants of *Tillandsia brachycaulos* received an average of 8.7 ± 0.9 times more PFD during the dry season compared to the wet season (Figure 2).

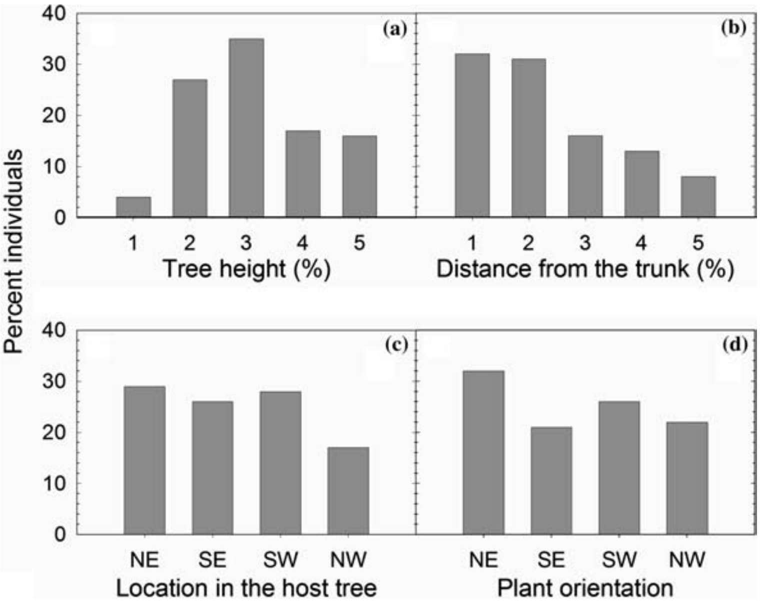

Figure 1. Spatial distribution of *Tillandsia brachycaulos* at the dry forest of Dzibilchaltún, Yucatan. For a and b, numbers represent intervals from 0 to 19.9% (1), 20 to 39.9% (2), 40 to 59.9% (3), 60 to 79.9% (4), and 80 to 100% (5). For c and d, orientations are: northeast (NE), southeast (SE), southwest (SW), and northwest (NW).

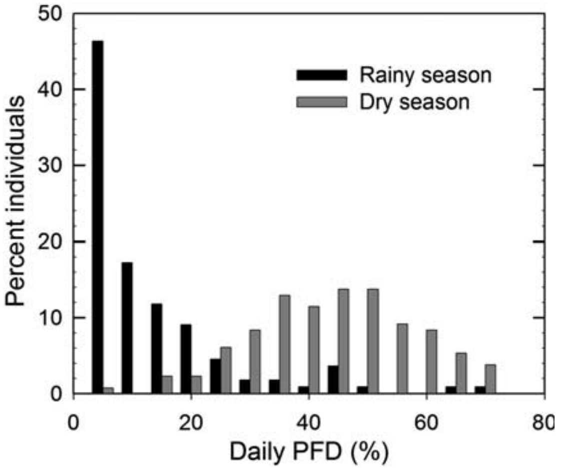

Figure 2. Percent number of sampled individuals of *Tillandsia brachycaulos* with respect to the percent of the total daily photon flux density (PFD) received, relative to the top of the canopy. Measurements were made approximately 20 mm above the same individuals during the rainy (solid bars) and the dry (open bars) season of 2001, in the dry forest of Dzibilchaltún, Yucatan.

Light microhabitats and growth

The average leaf elongation from plants growing in the microhabitat from 30 to 59% of ambient PFD was most of the time higher than the average leaf elongation of plants in the two other light microenvironments (Figure 3a). After 7 months, leaves from plants growing in the intermediate light microhabitat (30–59% of ambient PFD) were the longest and leaves from plants growing in the brightest light microhabitat ($\geq$60% of ambient PFD) were the shortest ($p < 0.01$; Figure 3a). Additionally, plants growing in the brightest microhabitats (>30% of ambient PFD) produced more leaves, especially during the dry season ($p < 0.05$; Figure 3b); most of the time, plants growing in the darkest light microhabitat (11–29% of ambient PFD) produced less leaves than those plants growing in the other two light microenvironments ($p < 0.05$; Figure 3). In fact, at the beginning of the field measurements there was no difference in size in the plants growing at the different light microenvironments ($p > 0.20$; Figure 4a), but there was a slight difference in number of leaves in relation to light ($p < 0.025$; Figure 4b). The range of number of leaves for these plants was from 15 to 49 leaves and individuals growing in less than 20% of the ambient PFD did not have more than 29 leaves (Figure 4b).

Greater flowering percentage was found in plants occurring in the intermediate light microhabitat

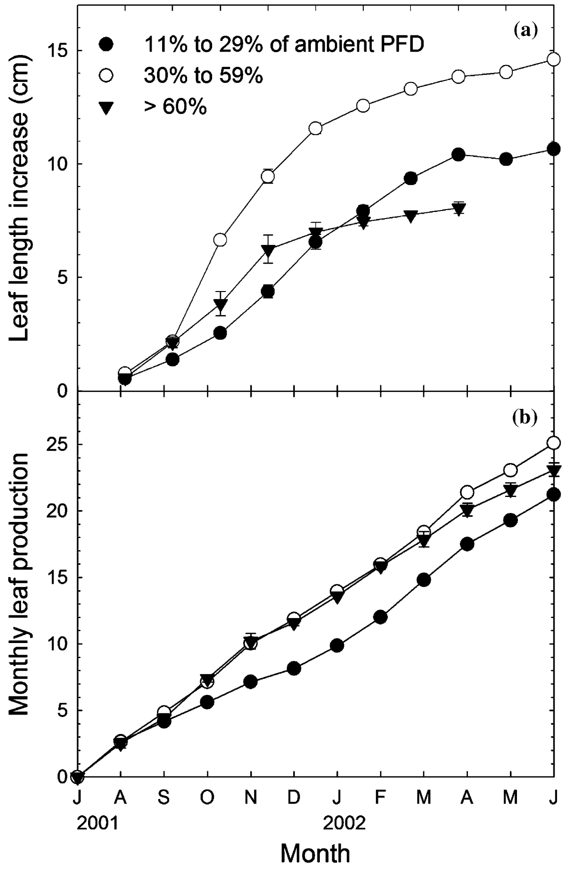

Figure 3. Leaf length increase and monthly leaf production for *Tillandsia brachycaulos* individuals growing in three light microhabitats during eleven months, in the dry forest of Dzibilchaltún, Yucatan. Values are means ± SE, n = from 3 to 81 plants.

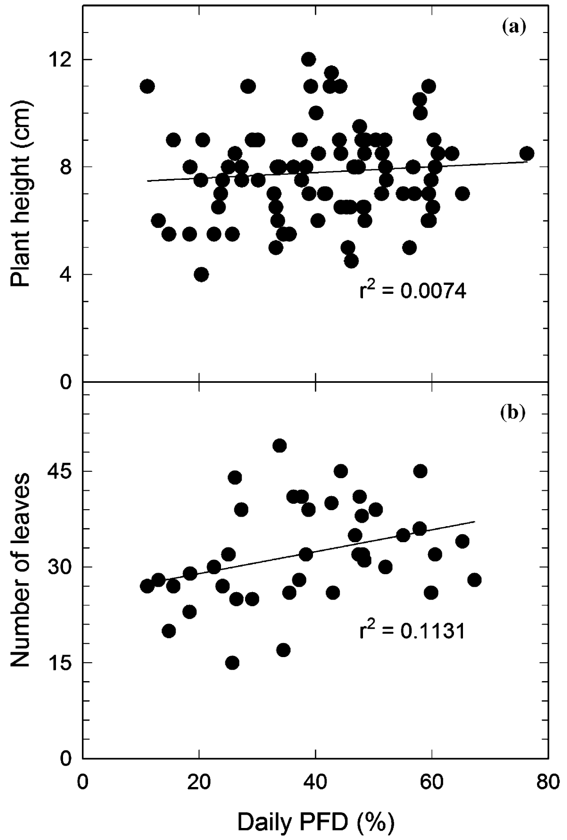

Figure 4. Plant height (a) and number of leaves (b) with respect to the percent of the total daily photon flux density (PFD) relative to the top of the canopy for *Tillandsia brachycaulos* individuals growing at the dry forest of Dzibilchaltún, Yucatan (n = 85 individuals in a, n = 41 in b).

than in the other two light microhabitats ($p < 0.001$; Table 1). Almost 50% of the individuals that were under 30–49% of the ambient PFD produced flowers, compared to 29% of the individuals that produced flowers in the darkest microhabitat and 23% in the brightest microhabitat (Table 1). Similarly, the average production of ramets was greater in plants of the intermediate microhabitat, compared to the two other microhabitats, since most ramets are produced after a flowering event (Table 1). By the end of the field measurements, most individuals (69%) from the brightest microhabitat were lost, compared to the average of individuals lost from the two other light

Table 1. Number of individuals of *Tillandsia brachycaulos* at three light microenvironments at the beginning of July 2001, and number and percentage of individuals that produced flowers and ramets, or were lost during the measurements until June 2002.

Percentage of ambient PFD	Number of individuals	Number of individuals with flowers	Number of individuals with ramets	Number of individuals lost
11–29%	24	7 (29%)	9 (38%)	8 (33%)
30–59%	81	39 (48%)	47 (58%)	30 (37%)
≥60%	13	3 (23%)	3 (23%)	9 (69%)

Table 2. Leaf elongation rate and monthly leaf production for adult plants of *Tillandsia brachycaulos* under three light microenvironments in Dzibilchaltún, Yucatan, Mexico.

Percentage of ambient PFD	Rainy season		Early dry season		Dry season	
	Elongation (cm month^{-1})	Monthly leaf production	Elongation (cm month^{-1})	Monthly leaf production	Elongation (cm month^{-1})	Monthly leaf production
11–29%	$1.28^{a} \pm 0.14$	$1.87^{a} \pm 0.14$	$1.71^{a} \pm 0.20$	$1.91^{a} \pm 0.13$	$0.43^{a} \pm 0.12$	$2.14^{a} \pm 0.13$
30–59%	$2.31^{b} \pm 0.21$	$2.51^{b} \pm 0.07$	$1.67^{ab} \pm 0.23$	$2.07^{a} \pm 0.08$	$0.44^{a} \pm 0.16$	$2.26^{a} \pm 0.10$
≥60%	$1.96^{b} \pm 0.26$	$2.52^{b} \pm 0.20$	$1.06^{b} \pm 0.29$	$1.88^{a} \pm 0.17$	$0.30^{a} \pm 0.25$	$1.88^{a} \pm 0.29$

Data for the rainy season were collected from July to October, for the early dry season from November to February, and for the dry season from March to May. Values are means ± SE (n = from 4 to 81 plants). Values within a column with a different superscript letter are significantly different ($p < 0.05$).

microhabitats (35%; $p > 0.01$; Table 1). Most of the individuals from all the light microhabitats were lost because their supporting branches broke.

The average rate of leaf elongation and monthly leaf production were highest for plants growing in light microhabitats >30% of the ambient PFD during the rainy season than during the other two seasons ($p < 0.05$; Table 2). The lowest values for leaf elongation rate were in the darkest light microhabitat during the rainy season, but, when the host trees started shedding their leaves, the lowest values occurred in all light microhabitats during the dry season ($p < 0.05$; Table 2). Although there was no difference in leaf production among all light microhabitats during both the early dry and the dry seasons ($p > 0.05$), the highest values were always for plants under 30–59% of ambient PFD (Table 2). For ramets, leaf elongation rate was similarly greater during the rainy and early dry season, compared to leaf elongation rate during the dry season (data not shown). However, leaf production was similar in all ramets regardless of the light microhabitat and season. No significant differences were found for both leaf elongation rate and monthly leaf production for ramets in the different light microhabitats within seasons.

Light microhabitats, photosynthesis and leaf temperatures

Tissue acidity was significantly different for plants growing in the three light treatments during the early dry season (Figure 5a). Those plants growing in the light treatment of 30% of the ambient PFD showed the greatest values, followed by plants growing in 60% of the ambient PFD and in 6% of the ambient PFD ($p < 0.05$; Figure 5a). During both the dry and the rainy seasons, no difference in tissue acidity was found for plants in the three light treatments (Figure 5b and c). Tissue water potentials were similar for all treatments during the whole experiment (average = -0.536 ± 0.047 MPa).

Maximum quantum efficiency (F_v/F_m) of plants from the three light treatments varied similarly during the day, but differences among treatments were greatest during the dry season (Figure 6). During the early dry season, F_v/F_m was high at 630 h for plants in all treatments; by midday F_v/F_m was significantly lower (<0.40) for plants under 60% of ambient PFD, compared to F_v/F_m for plants from the other two light treatments ($p < 0.05$), but then it recovered to about 0.7 by late afternoon (Figure 6a). During the dry season, plants growing under 60% of ambient PFD showed a low value for F_v/F_m (about 0.55) in the morning, compared to the two other light treatments (Figure 6b). By midday, F_v/F_m for these plants was the lowest ($=0.38$) and did not recovered in the afternoon. Plants growing under 30% of ambient PFD also showed a decreased in F_v/F_m, but then it recovered to similar values to those for plants growing under 6% of ambient PFD (Figure 6b). During the rainy season, plants growing under 30 and 60% of ambient PFD showed similar F_v/F_mdaily course and their values were different at midday, compared to plants growing at 6% of ambient PFD ($p < 0.05$); the recovery of F_v/F_m was still weak for plants growing under 60% of ambient PFD, because their values were significantly lower than those from plants

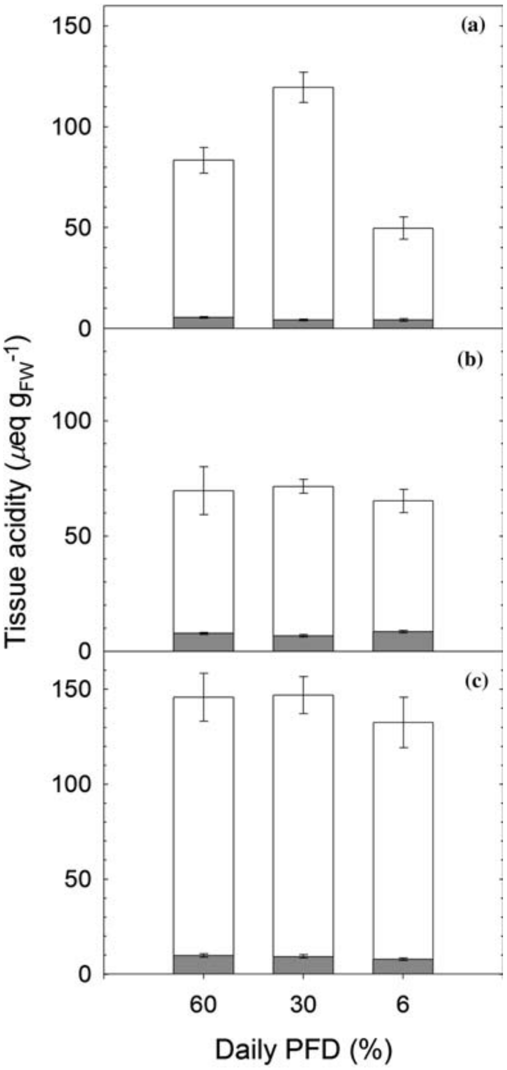

Figure 5. Titratable acidity for *Tillandsia brachycaulos* individuals under three photon flux density (PFD) treatments relative to unshaded conditions, during the early dry (a), dry (b) and rainy (c) seasons. Open bars are from leaves sampled at dawn and solid bars from leaves sampled at dusk the previous day. Values are means ± SE, $n \geq 8$ plants.

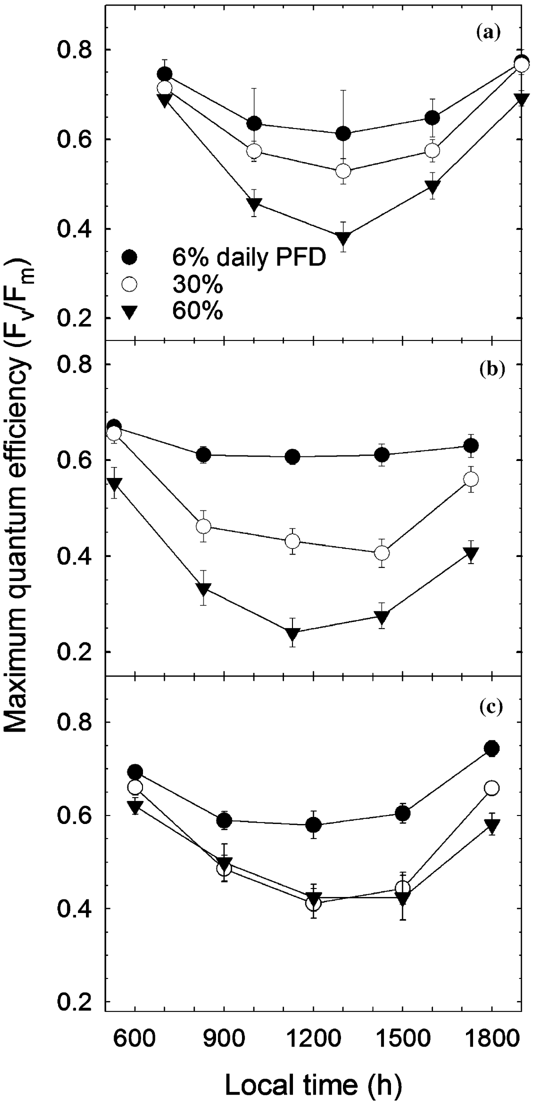

Figure 6. Daily course of maximum quantum efficiency measured as dark adapted chlorophyll fluorescence (F_v/F_m) for *Tillandsia brachycaulos* individuals under three photon flux density (PFD) treatments relative to unshaded conditions during the early dry (a), dry (b) and rainy (c) seasons. Values are means ± SE, $n = 15$ plants.

growing under the other two lights treatments ($p < 0.05$; Figure 6c).

The temperature of fully expanded leaves from plants of *T. brachycaulos* at heights below 0.7 m in a host tree was generally equal to or 0.5 °C cooler than the air temperature before 13:30 h and after 15:20 h (Figure 7); however, these leaf temperatures were significantly higher than the temperatures of the air and leaves from plants at heights from 1.7 to 3.35 m, during approximately 1 h (13:40 h to 14:40 h; Figure 7b). When we took the values for leaf temperatures at 14:00 h, the values of heat conduction rate (J_H) for plants on the soil or at 0.7 m above the floor were too high compared to the values of J_H for plants in other heights in the canopy (Table 3), which indicates a poor dissipation of heat for leaves of the former plants.

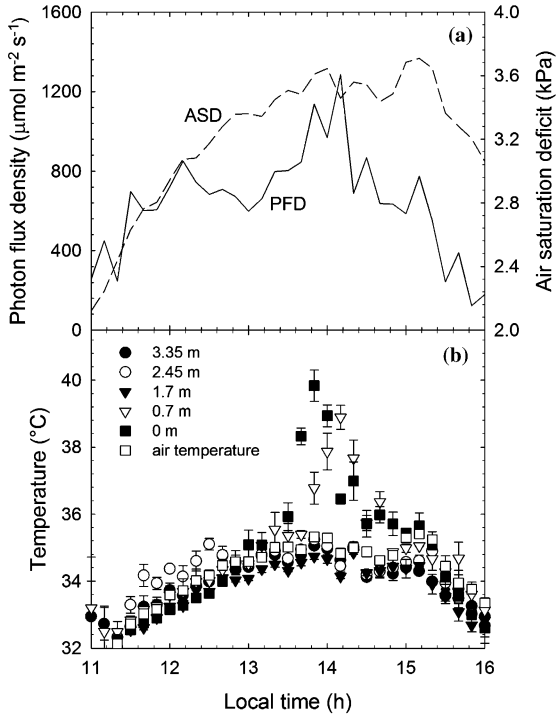

Figure 7. Daily course of (a) photon flux density (PFD), air saturation deficit (ASD) and (b) leaf and air temperatures during a clear day in the early dry season (15 November 2001). Data for leaf temperatures are means ± SE ($n = 3$ plants) for individuals growing at five different tree heights.

Table 3. Heat conduction rate (J_H) for leaves of *Tillandsia brachycaulos* plants placed on the forest floor or at four heights on the trunk and branches of a *Caesalpinia gaumeri* tree; values were calculated from data at 14:00 h.

Height in the tree (m)	Calculated J_H (W m^{-2})
0	352.45 ± 38.73
0.7	276.51 ± 34.59
1.7	− 39.33 ± 31.82
2.5	− 14.25 ± 12.20
3.3	− 67.68 ± 30.31

Values are means ± SE ($n = 3$ similar days).

Discussion

The vertical distribution of *Tillandsia brachycaulos* followed the arrangement that other epiphytic species show in diverse tropical forests (Johansson 1974; ter Steege and Cornelissen 1989; Benzing 1990; Nieder et al. 2000): most individuals occurred in intermediate sites within the canopy of the host trees. However, contrary to the horizontal distribution that occurs in more humid forests, most individuals of *T. brachycaulos* occurred either on the main trunk or in branches near the trunk, similar to the distribution of several species of *Tillandsia* in semi-arid ecosystems (García-Suárez et al. 2003). Trees in Dzibilchaltún dry forest possess a mean basal area of only 0.006 m^2 (González-Iturbe et al. 2002); therefore, main trunk and main branches have more surface area for support than small branches and twigs. Moreover, individuals growing on small and exposed branches experience higher probabilities to fall (Hietz et al. 2002). For instance, in this study, 69% of the individuals of *T. brachycaulos* on the most exposed sites were lost within 11 months. Within the canopy, there were more individuals of *T. brachycaulos* on the south side of the trees and fewer individuals on the northwest side, which correspond to the most shaded microhabitats in this forest. Similarly, more individuals of several species of *Tillandsia* occur on the northeast and the south side and fewer individuals occur in the northwest side of their phorophytes (García-Suárez et al. 2003). The fact that more individuals of *T. brachycaulos* were facing to the northeast could be to avoid overheating during the day, since leaves of these plants (and many other CAM species) cannot move to reduce the radiation load (Nobel 1988; Lambers et al. 1998).

Total daily PFD changed considerably for *T. brachycaulos* between the rainy and the dry seasons, mainly because most of their host trees were deciduous; individuals received about 9 times more PFD during the dry season compared to the rainy season. Plants of *T. brachycaulos* that received from 30 to 59% of the ambient PFD during the dry season showed higher length increase (about 42% in the rainy season and 22% in the dry season) than plants exposed to higher and lower PFDs. Similarly, *Epiphyllum phyllanthus* growing at approximately 50% of the incident PFD shows a stem elongation 27% greater than for plants exposed to higher and lower PFDs (Andrade and Nobel 1996). Also, individuals of *T. brachycaulos* in the intermediate light microhabitats produced significantly higher number of leaves than individuals exposed to higher and lower PFDs. For the monthly leaf production rate, most of the leaves of an individual of *T. brachycaulos* could be replaced within a year. This leaf production rate is higher or similar to the leaf production rate for some bromeliads in more humid forests (Richardson et al. 2000). Plants in the darkest light microhabitat produced fewer leaves and did not show a typical shade–plant response, because shade plants usually show higher leaf area than sun plants (Lambers et al. 1998). In a rosette shape more leaves could indicate more self-shading, thus fewer leaves can be advantageous for individuals in dark microhabitats.

Fewer individuals of *T. brachycaulos* in the darkest and the brightest light microhabitats produced flowers (average 26%) compared to the individuals in the intermediate light microhabitat (> 50% plants produced flowers). The CAM plant *Agave deserti* invests 70% of their carbohydrate reserves to flowering but 30% of the needs are provided from photosynthesis during the process (Tissue and Nobel 1990). Apparently, deep shading reduces the amount of resources needed for the flowering process because reduces CO_2 uptake (Griffiths et al. 1986; Andrade and Nobel 1996). Additionally, individuals of *T. brachycaulos* in the more exposed conditions would experience long-term, photo-oxidative damage (Graham and Andrade 2004), which reduces CO_2 uptake due to damage to the photosynthetic apparatus (Lambers et al. 1998). Population growth of *T. brachycaulos* should then be achieved mainly by individuals in the intermediate light microhabitat; first, because they would produce more seeds and secondly, because genets would continue in the same light microhabitat through the production of ramets after each flowering event. Studies on population demography of CAM plants should take this fact into consideration.

For well-watered plants of *T. brachycaulos*, partial shading also favored nocturnal increase of tissue acidity and photosynthesis. Plants at 30% of the ambient PFD showed the greatest tissue acidity and those plants at 6% of the ambient PFD the lowest tissue acidity, during the early dry season. Other tropical CAM plants showed also an enhancement in their net CO_2 uptake and nocturnal increase of tissue acidity when shaded. For instance, the terrestrial CAM bromeliad *Bromelia humilis* growing at 12% of the ambient PFD exhibits a nocturnal acidity increase twice that of exposed plants (Medina et al. 1986). Also, the epiphytic cactus *Epiphyllum phyllanthus* growing at 50% of the ambient PFD exhibits a 50% greater nocturnal acidity increase than plants exposed to higher and lower PFDs (Andrade and Nobel 1996). In addition, during the early dry season, night temperatures are lower (< 20 °C) than during the rest of the year, resulting in an enhancement of the CAM activity (Nobel 1988; Medina 1989). Maximum quantum efficiency was significantly lower for plants under 60% of the ambient PFD but it later recovered at night as occurs for other tropical CAM plants (Adams and Demming-Adams 1996).

No difference in nocturnal tissue acidity was found among treatments during the dry season and their values were lower than during the early dry and rainy seasons. Maximum quantum efficiency was significantly lower for plants under 60% of the ambient PFD during most of the day and apparently it did not recover in the morning. Nevertheless, the nocturnal acidity increase for plants in the high-light treatment was not lower than the acidity increase for plants in the low-light and intermediate-light treatments. The reduced nocturnal tissue acidity for plants in the dry season could be mediated by higher temperatures during the night than in the early dry season, and by the high water pressure deficits during the day (Andrade 2003). Moreover, to avoid excess transpiration, terrestrial and epiphytic CAM species tend to show maximum stomatal opening later in the night (Nobel 1988; Andrade and Nobel 1997), reducing the amount of nocturnal increase of tissue acidity.

During the rainy season, plants of *T. brachycaulos* in all light treatments showed the highest amount of nocturnal increase of tissue acidity. Well-watered *T. brachycaulos* show CO_2 uptake during all night and even about 12% of its total net carbon uptake is fixed up during the daytime (Graham and Andrade 2004). Furthermore, greater nocturnal acid accumulation for well-watered *T. brachycaulos* occurs under low PFD than under high PFD (Graham and Andrade 2004), suggesting that *T. brachycaulos* is a shade-adapted species. As for *T. usneoides* (Martin et al. 1985), chlorophyll a/b ratios did not change with irradiance (Graham and Andrade 2004) and changes in morphological features other than a fewer number of leaves did not seem to occur, indicating that this species shows a flexibility to adapt physiologically to various microsites within the canopy of the host trees. The limited growth observed in the darkest light microhabitats for *T. brachycaulos* in the field was probably caused for the reduced amount of water intercepted by their leaves rather than the light environment itself; lower in the canopy, rainfall could be intercepted by branches, leaves and other epiphytes (Andrade and Nobel 1997) and individuals received less dew than those in more exposed locations (Andrade 2003).

Leaf temperatures of *T. brachycaulos* plants located on the forest floor or low in the canopy could not dissipate the excess of heat during the hottest hours of the day. Leaves from plants located from 1.7 to 3.35 m above the floor maintain their temperatures very close to the air temperature during the day, except during the rainy season when stomata open also in the day and leaf temperatures are significantly lower than air temperature (Andrade 2003). Leaves of *T. brachycaulos* are relatively small compared to other epiphytic bromeliads (Zotz and Andrade 1998; Graham and Andrade 2004) and most trees in this tropical dry forest show small leaves typical of desert plants. This morphological characteristic allows the plants to reduce transpiration and increase their water use efficiency. Even though *T. brachycaulos* is a drought tolerant plant (Graham and Andrade 2004), individuals lower in the canopy could have fewer number of leaves to reduce transpiration further. Higher leaf temperatures during the day would increase plant respiration rate (Lambers et al. 1998) and reduce its investment for possible reproduction. Even in cooler tropical forests, such as montane forests, bromeliads on the forest floor experience higher rate of leaf area loss, compared to plants on the trees (Pett-Ridge and Silver 2002). However, dislodged epiphytic bromeliads in montane tropical forests can even reproduce on the forest floor (Pett-Ridge and Silver 2002) whereas that dislodged individuals of *T. brachycaulos* die within a year (Mondragón 2000), indicating less microclimate differences between the canopy and the forest floor in montane forests compared to tropical dry forests.

The tolerance to shade and drought of *T. brachycaulos* allows this epiphyte to grow in a vertical stratification within the canopy. However, the more exposed individuals would reduce growth and reproduction for photo-oxidative damage under high PFD conditions. Individuals lower in the canopy would reduce growth and reproduction not only for the low PFD conditions but for the lower amount of water received in these microsites, compared to the higher and more exposed microsites. It would be more costly for the epiphytic bromeliad *T. brachycaulos* to occur low in the canopy in the darkest light microhabitats than high in the canopy in exposed microhabitats, in this tropical dry forest.

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References

Adams W.W. III and Demmig-Adams B. 1996. Energy dissipation and the xanthophyll cycle in CAM plants. In: Winter K. and Smith J.A.C. (eds), Crassulacean Acid Metabolism: Biochemistry, Ecophysiology and Evolution. Springer, Berlin, pp. 97–114.

Andrade J.L. 2003. Dew deposition on epiphytic bromeliad leaves: an important event in a Mexican tropical dry deciduous forest. J. Trop. Ecol. 19: 479–488.

Andrade J.L. and Nobel P.S. 1996. Habitat, CO_2 uptake and growth for the CAM epiphytic cactus *Epiphyllum phyllanthus* in a Panamanian tropical forest. J. Trop. Ecol. 12: 291–306.

Andrade J.L. and Nobel P.S. 1997. Microhabitats and water relations of epiphytic cacti and ferns in a lowland neotropical forest. Biotropica 29: 261–270.

Benzing D.H. 1990. Vascular Epiphytes. General Biology and Related Biota. Cambridge University Press, New York.

Benzing D.H. 2000. Bromeliaceae: Profile of an Adaptive Radiation. Cambridge University Press, Cambridge.

García-Suárez M.D., Rico-Gray V. and Serrano H. 2003. Distribution and abundance of *Tillandsia* spp. (Bromeliaceae) in the Zapotitlán Valley, Puebla, Mexico. Plant Ecol. 166: 207–215.

Gentry A.H. and Dodson C.H. 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Missouri Bot. Garden 74: 205–233.

González-Iturbe J.A., Olmsted I. and Tun-Dzul F. 2002. Tropical dry forest recovery after long-term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. Forest Ecol. Manage. 167: 67–82.

Graham E.A. and Andrade J.L. 2004. Drought tolerance associated with vertical stratification of two co-occurring epiphytic bromeliads in a tropical dry forest. Am. J. Bot. 91: 699–706.

Griffiths H., Lüttge U., Stimmel K.-H., Crook C.E., Griffths N.M. and Smith J.A.C. 1986. Comparative ecophysiology of CAM and C_3 bromeliads. III. Environmental influences on CO_2 assimilation and transpiration. Plant, Cell Environ. 9: 385–393.

Griffiths H. and Maxwell K. 1999. In memory of C.S. Pittendrigh: does exposure in forest canopy relate to photoprotective strategies in epiphytic bromeliads?. Funct. Ecol. 13: 15–23.

Hietz P. and Briones O. 1998. Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. Oecologia 114: 305–316.

Hietz P., Ausserer J. and Schindler G. 2002. Growth, maturation and survival of epiphytic bromeliads in a Mexican humid montane forest. J. Trop. Ecol. 18: 177–191.

Johansson D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr. Suecica 59: 1–129.

Lambers H., Chapin F.S. III and Pons T.L. 1998. Plant Physiological Ecology. Springer-Verlag, New York.

Laube S. and Zotz G. 2003. Which abiotic factors limit vegetative growth in a vascular epiphyte. Funct. Ecol. 17: 598–604.

Martin C.E. 1994. Physiological ecology of the Bromeliaceae. Bot. Rev. 60: 1–82.

Martin C.E., McLeod K., Eades C. and Pitzer P. 1985. Morphological and physiological responses to irradiance in the CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae). Bot. Gazette 146: 489–494.

Martin C.E., Tüffers A., Herppich W. and von Willert D. 1999. Utilization and dissipation of absorbed light energy in the epiphytic crassulacean acid metabolism bromeliad *Tillandsia ionantha*. Int. J. Plant Sci. 160: 307–313.

Maxwell C., Griffths H., Borland A.M., Young A.J., Broadmeadow M.S.J., and Fordham C.M. 1995. Short-term photosynthetic responses of the C_3-CAM epiphyte *Guzmania monostachya* var. *monostachya* to tropical seasonal transitions under field conditions. Aust. J. Plant Physiol. 22: 771–781.

Medina E., Olivares E. and Díaz M. 1986. Water stress and light intensity effects on growth and nocturnal acid accumulation in a terrestrial CAM bromeliad (*Bromelia humilis* Jacq.) under natural conditions. Oecologia 70: 441–446.

Medina E., Olivares E., Díaz M. and van der Merwe N. 1989. Metabolismo ácido de crasuláceas en bosques húmedos tropicales. Monogr. Syst. Bot. Missouri Bot. Garden 27: 56–67.

Mondragón D. 2000. Dinámica Poblacional de *Tillandsia brachycaulos* en el Parque Nacional de Dzibilchaltún. Centro de Investigación Científica de Yucatán, Mérida, Yucatán, México.

Mondragón D., Durán R., Ramírez I. and Olmsted I. 1999. Population dynamics of *Tillandsia brachycaulos* Schltdl. (Bromeliaceae) in Dzibilchaltun National Park, Yucatán. Selbyana 20: 250–255.

Nieder J., Engwald S., Klauwun M. and Barthlott W. 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni crane plot) of southern Venezuela. Biotropica 32: 385–396.

Nieder J., Prosperi J. and Michaloud G. 2001. Epiphytes and their contribution to canopy diversity. Plant Ecol. 153: 51–63.

Nobel P.S. 1988. Environmental Biology of Agaves and Cacti. Cambridge University Press, Nueva York.

Nobel P.S. 1991. Physicochemical and Environmental Plant Physiology. Academic Press, San Diego.

Orellana R. 1999. Evaluación climática. In: García A. and Córdova J. (eds), Atlas de Procesos Territoriales de Yucatán. Facultad de Arquitectura, Universidad Autónoma de Yucatán, Mérida, Yucatán, Mexico.

Pett-Ridge J. and Silver W.L. 2002. Survival, growth, and ecosystem dynamics of displaced bromeliads in a montane tropical forest. Biotropica 34: 211–224.

Pfitsch W. and Smith A.P. 1988. Growth and photosynthesis of *Aechmea magdalenae*, a terrestrial CAM plant in a tropical moist forest, Panama. J. Trop. Ecol. 4: 199–207.

Pittendrigh C.S. 1948. The bromeliad–Anopheles–malaria complex in Trinidad. I. The bromeliad flora. Evolution 2: 58–89.

Richardson B.A., Richardson M.J., Scatena F.N. and McDowell W.H. 2000. Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. J. Trop. Ecol. 16: 167–188.

Skillman J.B. and Winter K. 1997. High photosynthetic capacity in a shade tolerant Crassulacean acid metabolism plant: implications for sunflecks use, nonphotochemical energy dissipation, and susceptibility to photoinhibition. Plant Physiol. 113: 441–450.

Smith L.B. and Downs R.J. 1977. Flora Neotropica. Monograph No. 14, Part 2: Tillandsioideae (Bromeliaceae). Hafner Press, New York, pp. 663–1492.

ter Steege H. and Cornelissen J.H.C. 1989. Distribution and ecology of vascular epiphytes in Lowland Rain Forest of Guayana. Biotropica 21: 331–339.

Thien L.B., Bradburn A.S. and Welden A.L. 1982. The woody vegetation of Dzibilchaltun, a Maya archeological site in Northwest Yucatan, Mexico. Middle American Research Institute, Tulane University, New Orleans.

Tissue D.T. and Nobel P.S. 1990. Carbon relations of flowering in a semalparous clonal desert perennial. Ecology 71: 273–281.

Tyree M.T. and Wilmot T.R. 1990. Errors in the calculations of evaporation and leaf conductance in steady-state porometry: the importance of accurate measurement of leaf temperature. Can. J. Forest Res. 20: 1031–1035.

Winter K., Wallace B.J., Stocker G.C. and Roksandic Z. 1983. Crassulacean acid metabolism in Australian vascular epiphytes and some related species. Oecologia 57: 129–141.

Winter K., Osmond C.B. and Hubick K.T. 1986. Crassulacean acid metabolism in the shade. Studies on an epiphytic fern, *Pyrrosia longifolia*, and other rainforest species from Australia. Oecologia 68: 224–230.

Zar J. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.

Zotz G. 1995. How fast does an epiphyte grow? Selbyana 16: 150–154.

Zotz G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata*. J. Trop. Ecol. 14: 725–741.

Zotz G. and Andrade J.L. 1998. Water relations of two cooccurring epiphytic bromeliads. J. Plant Physiol. 152: 545–554.