Habitat, CO$_2$ Uptake and Growth for the CAM Epiphytic Cactus Epiphyllum phyllanthus in a Panamanian Tropical Forest

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Habitat, CO_2 uptake and growth for the CAM epiphytic cactus *Epiphyllum phyllanthus* in a Panamanian tropical forest

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ABSTRACT. In the tropical forest of Barro Colorado Island, habitat characteristics, diel acidity changes, CO_2 uptake and growth were investigated for the epiphytic cactus *Epiphyllum phyllanthus* (L.) Haw. It occurred most frequently in tree cavities with its roots in canopy soil and was especially abundant on two tree species: *Platypodium elegans* J. Vogel and *Tabebuia guayacan* (Seem.) Hemsl. Its maximum net CO_2 uptake rates were low under natural conditions (1.4 μmol m^{-2} s^{-1}) but were comparable to those of other CAM and C_3 epiphytes under wet conditions in a screenhouse. Under both natural conditions and in the screenhouse, partial shade enhanced growth and CAM activity. When plants grew under a photosynthetic photon flux of *c.* 4 mol m^{-2} d^{-1}, their nocturnal acidity increase and total net CO_2 uptake were twice as much as for plants growing at lower (an average of 2.4 mol m^{-2} d^{-1}) and higher (7.7 mol m^{-2} d^{-1}) photosynthetic photon fluxes. Stem elongation was 27% greater at the intermediate photosynthetic photon flux. Seedlings of *E. phyllanthus* survived three months of drought and responded rapidly to rewetting, recovering fully within three days. Transpiration rates and nocturnal acidity increases also recovered to the values of well-watered plants a few days after rewetting, indicating that this species can take advantage of episodic rainfall during the dry season.

KEY WORDS: Cactaceae, CO_2 uptake, Crassulacean acid metabolism, *Epiphyllum phyllanthus*, epiphyte, habitat, Panama, photosynthetic photon flux, succulence, tissue acidity.

INTRODUCTION

Although most species in the family Cactaceae inhabit arid and semi-arid regions, about 10% of the approximately 1600 species are epiphytes that occur mostly in tropical forests (Gibson & Nobel 1986, Kress 1986). These epiphytic cacti tend to have flat spineless stems that can maximize the absorption of the photosynthetic photon flux (PPF, wavelengths of 400–700 nm) in their shaded habitats. Because epiphytic habitats are characterized by temporary or prolonged water shortage, epiphytic cacti show adaptations to cope with desiccating conditions, including stem succulence, Crassulacean acid metabolism (CAM) and special root features, adaptations similar to those of desert cacti (Lüttge 1989, Nobel 1988, North & Nobel 1994). For plants that grow in the canopy with limited water availability, CAM is beneficial because CO_2 uptake occurs at night when the air temperatures are lower and the atmospheric relative humidity is higher, leading to less water loss. Besides the Cactaceae, the

Bromeliaceae, Orchidaceae and Polypodiaceae have many epiphytic members with CAM (Lüttge 1989). Indeed, CAM epiphytes apparently outnumber terrestrial CAM species (Nobel & Hartsock 1990, Winter *et al.* 1983).

Among epiphytes, CAM species are more abundant than C_3 species in drier forests (Smith *et al.* 1986), where location on the host tree is more important for moisture procurement than in humid forests (Benzing 1990). When there is a vertical stratification of epiphytes on tall trees, CAM species tend to occupy more exposed habitats than C_3 species (Benzing 1990, Winter *et al.* 1983). In addition, the reliance on CAM can be directly related to stem succulence for epiphytic cacti (Nobel & Hartsock 1990), which tend to be less drought tolerant than the generally more massive desert cacti (Medina *et al.* 1989, Nobel 1988). Roots of epiphytic and desert cacti are similar in their responses to drought, although certain epiphytic species recover more rapidly following rainfall (North & Nobel 1994). Therefore, the occurrence of brief rainfall events in a dry season can diminish the effect of drought on epiphytes. Many CAM epiphytes and CAM terrestrial species grow under extreme shade (Benzing 1990, Medina *et al.* 1989, Winter *et al.* 1986). Indeed, CAM plants in the tropics can experience severe photoinhibition when they are exposed to full sunlight (Medina *et al.* 1986, 1989). Also, PPF saturation occurs at *c.* 200 μmol m^{-2} s^{-1} for epiphytic cacti but at *c.* 800 μmol m^{-2} s^{-1} for terrestrial cacti (Nobel 1988, Nobel & Hartstock 1990). Even though PPF and water availability are important environmental factors in the ecology and evolution of epiphytes (Lüttge 1989), there are few studies of their effects on epiphytic plants, particularly under natural conditions.

In general, PPF and water availability are the most important environmental factors limiting epiphytic growth and distribution in tropical forests, although the epiphyte–host relationship is also significant and frequently related to these factors (Benzing 1983, Johansson 1974). The epiphytic cactus *Epiphyllum phyllanthus* (L.) Haw., which occurs in tropical America from Mexico to Paraguay (Bravo-Hollis 1978), was chosen to determine the effects of different PPFs on nocturnal increases in tissue acidity, daily net CO_2 uptake patterns and growth. Certain habitat characteristics were also investigated, including host specificity and location of the epiphyte on the host tree. Responses of water relations parameters, diel tissue acidity and growth under different PPF and water availability were also examined for *E. phyllanthus* maintained in pots in a screenhouse.

MATERIALS AND METHODS

Plant species and study site

Epiphyllum phyllanthus (L.) Haw. (Cactaceae) was studied from September 1992 to September 1993 on Barro Colorado Island (9° 09′ N, 79° 51′ W), a 1500-ha reserve within the Barro Colorado Natural Monument, Republic of Panama. The island is covered by a semi-evergreen moist tropical forest with a canopy height of 35–40 m and has a mean annual rainfall of approximately

2600 mm, with a marked dry season from mid-December to May (Leigh & Wright 1990). Of the two varieties of *E. phyllanthus* on Barro Colorado Island, this study involved the more frequent *E. phyllanthus* (L.) Haw. var. *columbiense* (Weber) Kimn. (Croat 1978). Its flattened pendant stems can be 3 cm wide, about 2 mm thick and up to 100 cm long; flower and fruit production occurred mainly from July to September.

Field studies

Field studies were carried out on a 50-ha plot where all free-standing, woody plants $\geqslant$1 cm in diameter at breast height (dbh) have been mapped (Hubbell & Foster 1983). A randomly chosen stratified sample of 2925 trees of 181 species with trunks $\geqslant$20 cm dbh was obtained from the Forest Dynamics Project at the Smithsonian Tropical Research Institute and examined with binoculars for the presence of *E. phyllanthus*. The following parameters were recorded: location of *E. phyllanthus* on host tree, number of plants per tree, number of stems per plant and height of *E. phyllanthus* above the forest floor.

To measure physiological properties, a pair of ascenders was used on a climbing rope hanging from a large branch to reach the plants. The photosynthetic photon flux (PPF) on the more exposed surface was measured every 30 min using an LI-190SA quantum sensor and an LI-189 quantum meter (Li-Cor, Lincoln, NE). CO_2 uptake by the more exposed surface was determined with an ADC portable CO_2 measurement system (Analytical Development, Hoddesdon, UK) on 5–6 March 1993 at the middle of 30–50 cm stems for plants growing at 24–27 m above the ground on *Platypodium elegans* J. Vogel. Integration of the diel curves for PPF and net CO_2 uptake were done using an XLP 1212 digitizing tablet (Kurta, Phoenix, AZ) and Sigma-Scan (Jandel Scientific, Corte Madera, CA). Data are expressed on a projected stem area basis. Tissue acidity was determined at dusk and dawn on 7–8 April 1993 for plants on *Terminalia amazonica* (J. F. Gmel.) Exell at approximately 20 m above the ground; cylindrical cores (13 mm in diameter) through the stems were removed from midstem, wrapped in parafilm and transported to the laboratory in plastic bags. After grinding with a mortar and pestle, 60 cm^3 distilled water were added and the slurry was titrated to pH 7.4 using 1 mM NaOH (Nobel & Hartsock 1983). Data are expressed on a projected stem area basis. Soil and stem water potentials were determined psychrometrically in the early morning with an SC-10 sample chamber (Decagon Devices, Pullman, WA).

Screenhouse studies

Stem cuttings were collected from two mature plants of *E. phyllanthus* growing on a tree in the peninsula of Bohio within the Barro Colorado Natural Monument and from recently fallen plants at Barro Colorado Island. All stem cuttings were placed in 1500-cm^3 pots containing equal parts of a nutrient-rich soil and sand and maintained in a screenhouse with a maximum PPF of 600 $\mu mol\ m^{-2}\ s^{-1}$ (day-time average of 260 $\mu mol\ m^{-2}\ s^{-1}$, leading to

7.3 mol m^{-2} d^{-1}), a mean relative humidity of 85%, a mean air temperature of 27°C and a mean diurnal temperature range of 8°C; light and temperature overlapped values at 20–25 m in the forest canopy (Windsor 1990). All plants were watered twice a week to maintain the water potential in the root zone above −0.2 MPa. Four weeks after rooting, plants received three different light treatments: exposed (7.3 mol m^{-2} d^{-1}), shaded with a plastic screen to approximately 50% of incident PPF (3.6 mol m^{-2} d^{-1}) and shaded to approximately 30% of incident PPF (2.3 mol m^{-2} d^{-1}). Length of the new stems was recorded weekly; after 10 weeks, tissue acidity and CO_2 uptake were measured as described above.

Two hundred seedlings were grown from current-year seeds (germination rate of 96%) and maintained in 200-cm^3 pots in the screenhouse under similar conditions as the cuttings but shaded to approximately 50% of incident PPF. Four weeks after germination, water was withheld from some plants (the water potential in the root zone became −2.0 MPa at 22 days). Stem length was recorded weekly. After four weeks of drought, the soil was rewetted and succulence, tissue acidity and transpiration were determined. Transpiration was determined by weighing the pots, which were covered with plastic and aluminium foil to minimize evaporation from the soil surface (evaporation from covered pots without plants was negligible). Stem area was determined with a Li-Cor LI-3000 area meter. Stem water potential was measured at noon using a pressure chamber (SoilMoisture Equipment, Santa Barbara, CA). To measure succulence (tissue water content per unit stem area), samples 4 mm in diameter were removed from midstem with a cork borer, weighed and then dehydrated at 65°C in an oven until no further weight change occurred (generally 48 h).

Statistical analysis

Chi-squared analysis was used to test the relation between tree species and the presence of *E. phyllanthus* (Zar 1974). Differences in trunk diameter within species for trees with and without the cactus were tested using Student's t-test. An estimation of the abundance of this cactus in the 50-ha plot was obtained by using stratified random sampling, considering only the tree species with the cactus (Scheaffer *et al.* 1986). Differences in tissue acidity, succulence, transpiration and maximum length increase were tested using one-way ANOVA and the Tukey test.

RESULTS

Field studies

Microhabitat. Epiphyllum phyllanthus occurred on 22 of the 181 tree species within the 50-ha plot, although it was not evenly distributed among host trees ($P < 0.01$; Table 1). For instance, 50% of the trees with *E. phyllanthus* belonged to *Ceiba pentandra* (L.) Gaertn., *Platypodium elegans*, *Tabebuia guayacan* and *Terminalia oblonga* Pitt. The number of stems averaged 45 ±6 (mean ±s.e. for N =

Table 1. Occurrence of *Epiphyllum phyllanthus* on tree species for Barro Colorado Island. A total of 2925 trees ≥20 cm in diameter in the 50-ha Forest Dynamics Project plot (Hubbell & Foster 1983) were examined for the presence of *E. phyllanthus*. The average number of plants of *E. phyllanthus* per tree and number of stems per plant (mean ±s.e. if N ≥ 3) were recorded.

	Number of trees examined		*E. phyllanthus* characteristics	
Tree species	Total	With *E. phyllanthus*	Number per tree	Stems per plant
Alchornea costaricensis Pax & Hoffm.	8	2	2.0	9± 4
Alseis blackiana Hemsl.	14	1	1	30
Anacardium excelsum (Bertero & Balb.) Skeels	22	3	1.7	17± 4
Aspidosperma cruenta Woods.	8	1	1	9
Beilschmiedia pendula (Sw.) Hemsl.	10	1	1	20
Brosimum alicastrum Sw.	12	2	1.0	34
Casearia arborea (L. C. Rich.) Urban	15	1	1	50
Ceiba pentandra (L.) Gaertn.	16	5	1.4	58±27
Dipteryx oleifera Benth.	19	3	2.0	50± 6
Ficus costaricana (Liebm.) Miq.	7	1	1	15
Guatteria dumetorum Fries	9	1	1	10
Lonchocarpus latifolius DC.	6	1	2	30
Platypodium elegans J. Vogel	15	10	3.0	38± 6
Platymiscium pinnatum (Jacq.) Dug.	12	1	1	5
Pseudobombax septenatum (Jacq.) Dug.	8	1	3	19± 9
Sapium aucuparium Jacq.	11	3	1	38±12
Scheelia zonensis Bailey	20	1	1	3
Simarouba amara Aubl.	10	1	2	35
Tabebuia guayacan (Seem.) Hemsl.	19	7	3.6	32± 7
Terminalia amazonica (J. F. Gmel.) Exell	13	2	1.5	34± 6
Terminalia oblonga Pitt.	16	5	1.0	53±23
Tetragastris panamensis (Engler) O. Kuntze	14	1	1	5

67 plants) for these four species, which was larger than the 29 ±8 stems (N = 39 plants) for the other 18 host species ($P < 0.05$; Table 1). Within the four species, the trunk diameter was greater for the trees with the cactus (106 ±8 cm for N = 27 trees) compared to those without it (66 ±20 cm for N = 39 trees; $P < 0.05$). Of the 106 individual plants of *E. phyllanthus*, 52% occurred on *P. elegans* and *T. guayacan* (Table 1).

Epiphyllum phyllanthus occurred most frequently (69%) in crotches, bark crevices or holes on the upper trunks (Figure 1). The rest of the plants occurred in holes of primary branches (23%) or directly on the trunks of the host trees (8%). For the sample considered, the epiphytic cactus occurred in cavities of the trunk on *P. elegans* and *T. guayacan* and in cavities of the primary branches on *C. pentandra* and *T. oblonga*. The average height above the ground for *E. phyllanthus* was 24.7 ±0.9 m (N = 106 plants). Based on the total number of the 22 host tree species on which *E. phyllanthus* occurred (Table 1), the abundance of this epiphytic cactus in the 50-ha plot was estimated as 340 ±63 plants.

Physiology. Net CO_2 uptake by *E. phyllanthus* occurred primarily at night (Figure 2). The total net CO_2 uptake over a 24-h period was 40 mmol m^{-2} d^{-1}

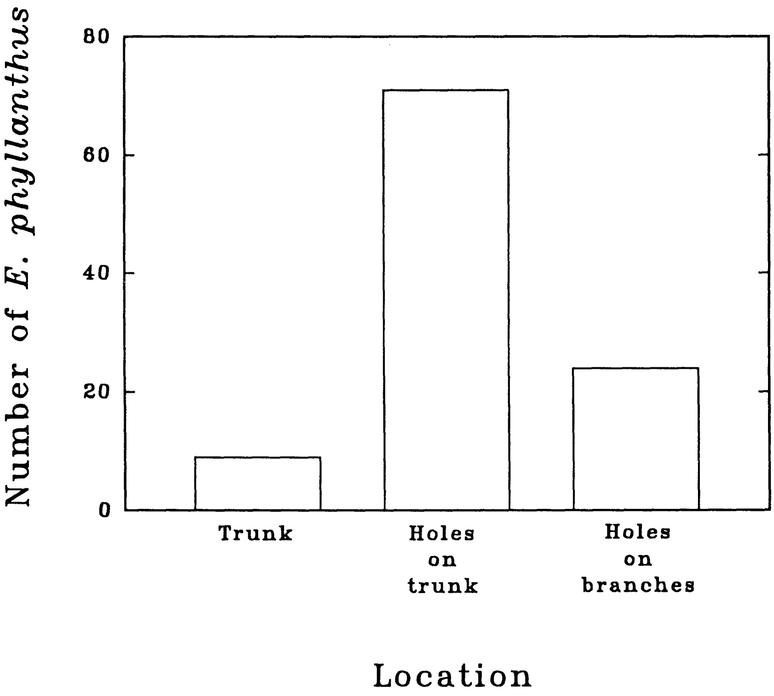

Figure 1. Location of *Epiphyllum phyllanthus* on host trees on Barro Colorado Island. Plants occurred directly on the trunks or in holes, bark crevices and crotches of the trunks or the primary branches.

in the canopy of *P. elegans*, 8% occurring during the day-time. The maximum net CO_2 uptake rate averaged 1.4 μmol m^{-2} s^{-1}, which was maintained for several hours near midnight (Figure 2).

Greater nocturnal increases in titratable acidity occurred for stems exposed to an ambient total daily PPF of 3.9 mol m^{-2} d^{-1} in the canopy of *Terminalia amazonica* compared to lower (2.5 mol m^{-2} d^{-1}) and higher (8.2 mol m^{-2} d^{-1}) ambient PPFs (Figure 3). For 3.9 mol m^{-2} d^{-1}, the nocturnal acidity increase corresponded to 178 mmol H^+ m^{-2}, which was twice as much as that at the other PPFs ($P < 0.01$). The water potential in the root zone for *E. phyllanthus* at the intermediate PPF averaged -0.06 ± 0.01 MPa (mean ±s.e. for $N = 3$ plants) on 6 April 1993 and was -0.10 ±0.02 MPa after four days without rain. The water potential at the middle of the stems (which averaged 32 cm in length) averaged -0.52 ±0.02 MPa ($N = 12$ stems) and was similar for plants growing at the three different ambient PPFs (Figure 3).

Screenhouse studies

Shading. Greater nocturnal increases in titratable acidity also occurred for plants shaded 50% to an intermediate PPF (3.6 mol m^{-2} d^{-1}) in the screenhouse compared to higher and lower PPFs ($P < 0.01$; Figure 4). In particular, the

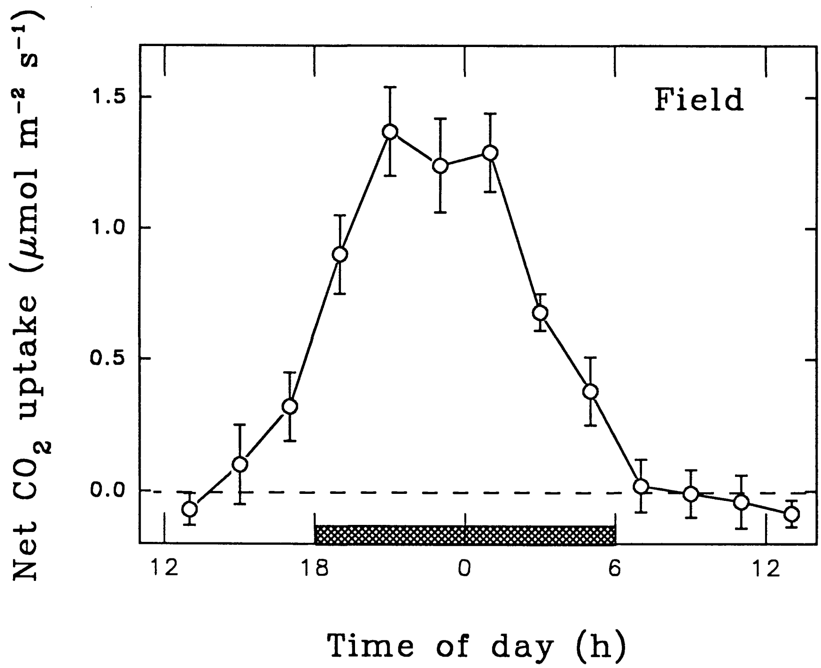

Figure 2. Net CO_2 exchange over a 24-h period by stems of *E. phyllanthus*. Measurements were made for plants growing on *Platypodium elegans* at 24–27 m above the ground on 5–6 March 1993. The PPF averaged 3.7 mol m^{-2} d^{-1}; the hatched bar indicates night. Data are means ±s.e. (N = 3 plants).

nocturnal acidity increase was 204 mmol H^+ m^{-2} for plants shaded 50%. The acidity increase averaged 39% less for unshaded plants at a total daily PPF of 7.3 mol m^{-2} and 48% less for plants shaded *c.* 70% to 2.3 mol m^{-2} d^{-1} (Figure 4). Net CO_2 exchange varied among *E. phyllanthus* exposed to different PPFs in the screenhouse and occurred primarily at night, with maximum values occurring after midnight (Figure 5). The total net CO_2 uptake over a 24-h period was 37 mmol m^{-2} d^{-1} for the plants shaded 70% of the incident PPF in the screenhouse (a net uptake of 47 mmol m^{-2} occurred at night), 83 mmol m^{-2} d^{-1} for plants shaded 50% (90 mmol m^{-2} at night) and 50 mmol m^{-2} d^{-1} for unshaded plants (68 mmol m^{-2} at night). Assuming that plants shaded 70% had a negligible amount of net CO_2 uptake on their darker side of the stems, the $\Delta H^+/CO_2$ ratio was 108/47 or 2.3.

Stem length increased more when the plants were shaded 50% (Figure 6). After six weeks, it averaged 28% greater in plants growing at this intermediate PPF (3.6 mol m^{-2} d^{-1}) than for plants in the other two treatments ($P < 0.05$; Figure 6). After 13 weeks, stem length increased 23.8 cm for plants growing at the intermediate PPF, 20% less for plants shaded 70% ($P < 0.05$) and 33% less for unshaded plants ($P < 0.01$). Stem water potential averaged −0.37±0.03 MPa (N = 12 plants) and was similar for the three PPFs.

Desiccation. Stem length for seedlings of *E. phyllanthus* steadily increased in the screenhouse for plants shaded approximately 50% (to 3.6 mol m^{-2} d^{-1}), the

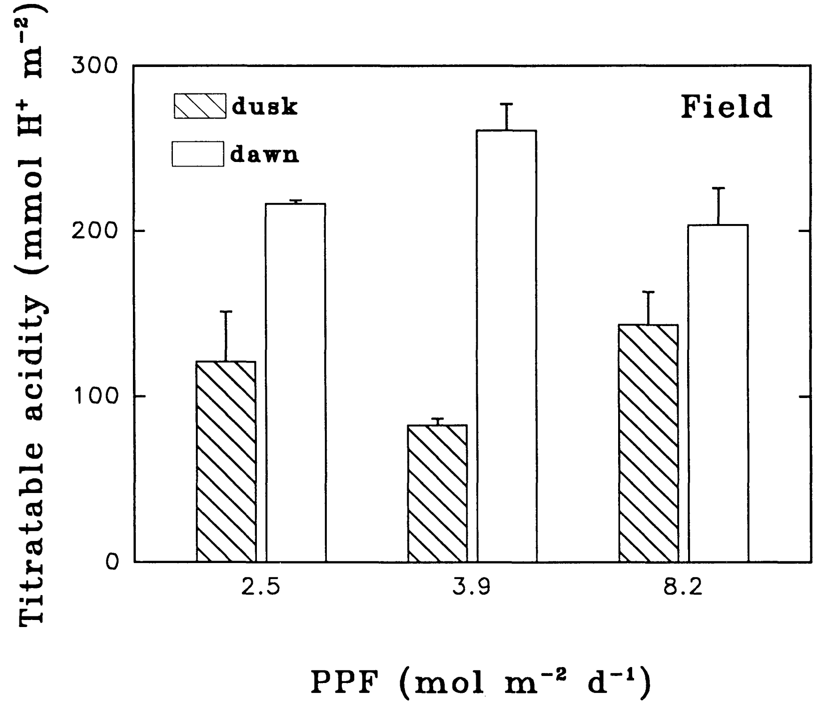

Figure 3. Tissue acidity at dusk and dawn for stems of *E. phyllanthus* growing under different PPFs in the field. Measurements were made for plants growing on *Terminalia amazonica* at 20 m above the ground on 7–8 April 1993. Data are means with s.e. (N = 3 plants).

increase amounting to 73% by 12 weeks (Figure 7a). After one week of drought, stem elongation ceased (Figure 7a), although plants could survive seven months of drought. Stem succulence steadily decreased during drought, the decrease amounting to 73% by 12 weeks (Figure 7b). Succulence recovered an average of 70% by one day after a drought of four, eight or 12 weeks and fully recovered by three days of daily rewetting (Figure 7b).

Droughting seedlings for four weeks essentially eliminated transpiration (Figure 8a) and approximately halved nocturnal acidity increases (Figure 8b). Both processes were restored to initial wet values by three days of daily rewetting (Figure 8). After four weeks of drought, stem water potential was −0.58±0.04 MPa (N = 4 plants), compared with −0.30±0.05 MPa for well-watered plants; it recovered to the values of well-watered plants in less than 24 h after rewetting.

DISCUSSION

Epiphyllum phyllanthus occurred nearly exclusively in cavities in the main trunk or primary branches of large trees, which are sites with a substantial accumulation of organic matter. In particular, *E. phyllanthus* generally becomes established in canopy mat habitats that are composed of nutrient-rich humic soil

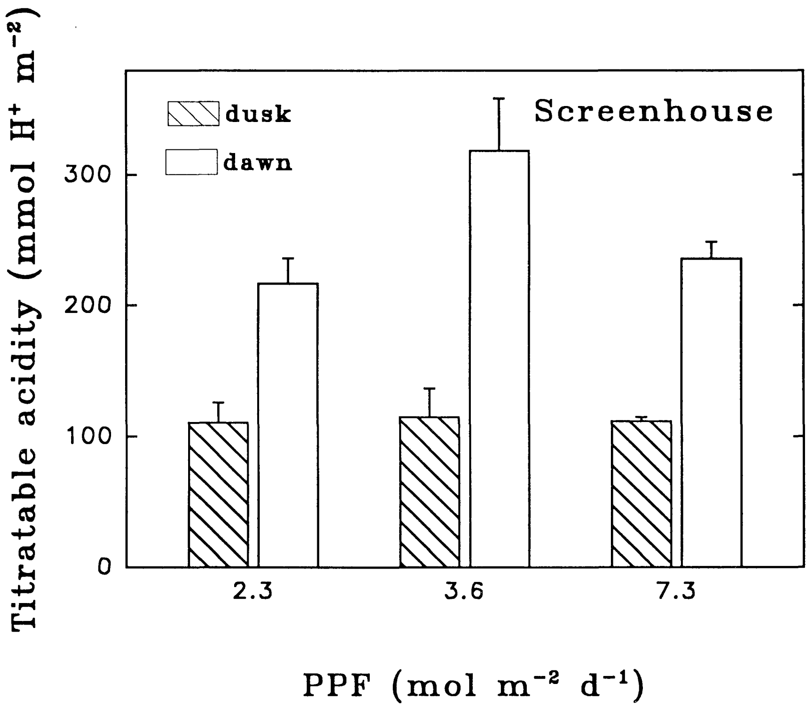

Figure 4. Tissue acidity at dusk and dawn for stems of *E. phyllanthus* growing under different PPFs in a screenhouse. Data are means with s.e. (N = 4 plants).

(Lesica & Antibus 1990) or sometimes in analogous sites in ant nests (Davidson 1988). Strangler figs and other hemiepiphytes also become established in similar pockets of humus on large trees (Putz & Holbrook 1986), where soils can contain more macronutrients than the local terrestrial soils (Lesica & Antibus 1990, Putz & Holbrook 1989). Therefore, nutrient shortages may not be encountered by *E. phyllanthus* inhabiting these microsites.

Even though seeds of *E. phyllanthus* had a high germination rate and seedlings survived prolonged droughts, its abundance was only about seven plants per hectare on Barro Colorado Island. The four species that hosted *E. phyllanthus* most frequently were conspicuous but relatively uncommon trees (Hubbell & Foster 1983). For instance, *Ceiba pentandra* is one of the tallest local trees, has a large trunk and large branches, and hosts many epiphytic species (Croat 1978). Although the bark of *Terminalia oblonga* peels away in large pieces (Croat 1978), apparently preventing the establishment of epiphytic seedlings on the trunk, *E. phyllanthus* became established in holes left by fallen branches. About half of *E. phyllanthus* occurred on *Platypodium elegans* and *Tabebuia guayacan*, the former species having longitudinal invaginations and cavities along its trunk and the latter having a deeply fissured bark (Croat 1978). During the dry season, leaves of *C. pentandra*, *P. elegans* and *T. guayacan* are shed, and resident epiphytes become exposed to more dessicating conditions than during the wet season, so only

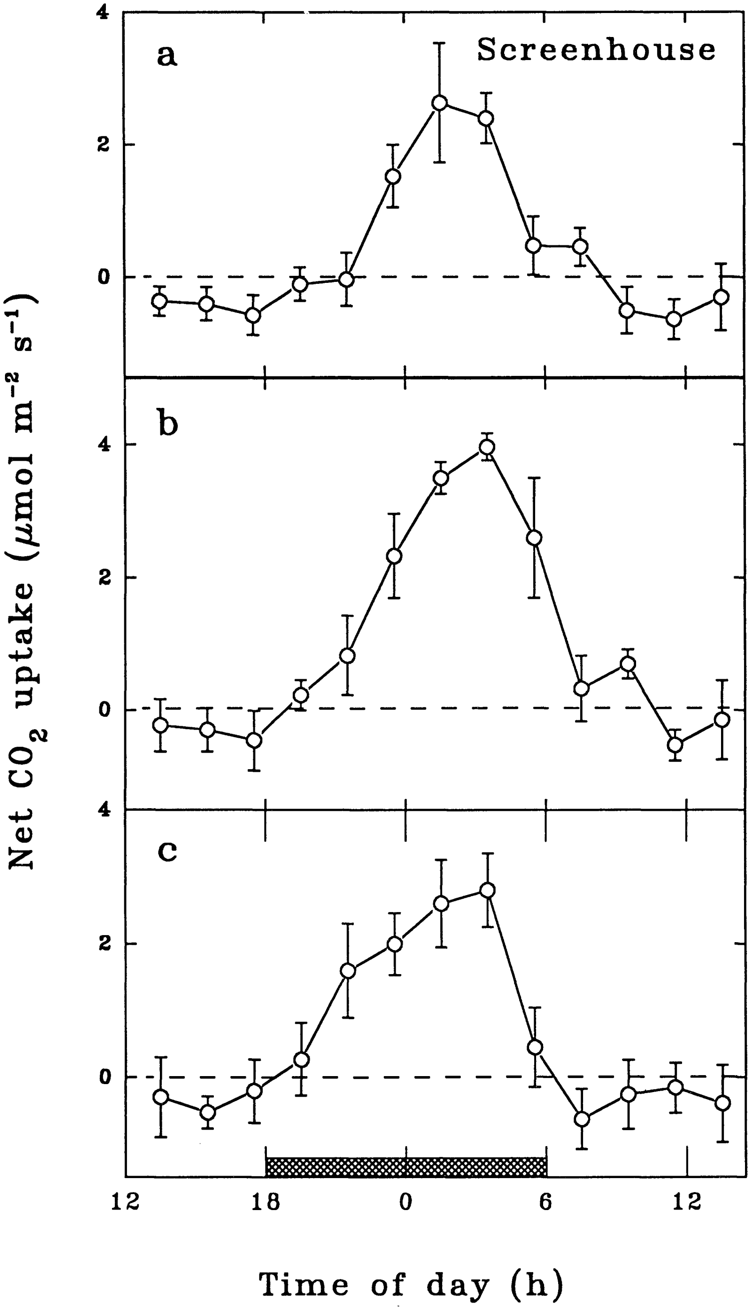

Figure 5. Net CO_2 exchange over 24-h periods by stems of *E. phyllanthus* growing in a screenhouse: (a) a PPF of 2.3 mol m^{-2} d^{-1}; (b) a PPF of 3.6 mol m^{-2} d^{-1}; and (c) a PPF of 7.3 mol m^{-2} d^{-1}. Data are means ±s.e. (N = 4 plants).

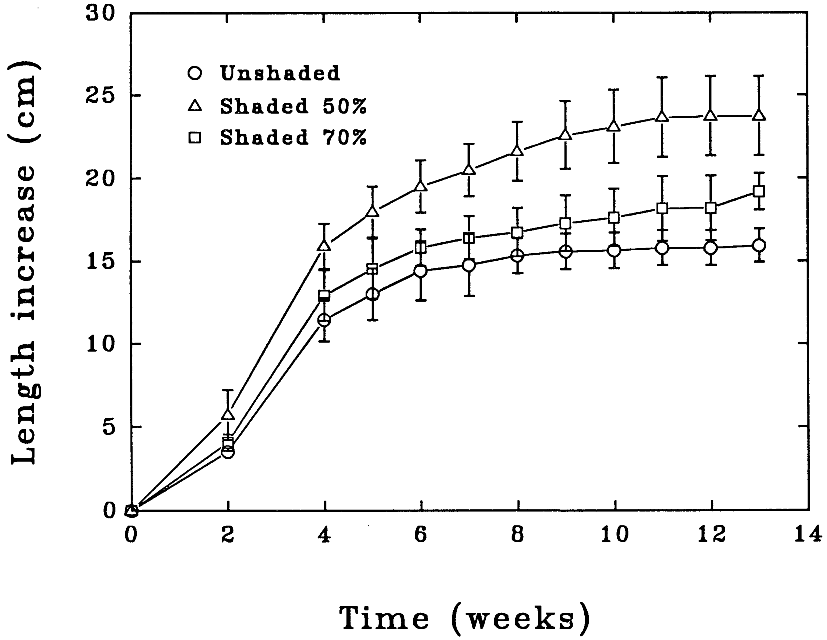

Figure 6. Elongation of stems of *E. phyllanthus* for plants that were unshaded (○), shaded approximately 50% (△) and shaded approximately 70% (□) in a screenhouse. Initial lengths averaged 20.3 cm. Data are means ±s.e. (N = 4 plants).

the more drought-tolerant epiphytic species become established on these host species.

Net CO_2 uptake by the stems of *E. phyllanthus* followed a pattern typical for CAM plants. In particular, 92% of the net CO_2 uptake occurred at night, similar to that for terrestrial cacti from the same subfamily (Nobel 1988) but in contrast to the rates of other epiphytic cacti, where sustantial CO_2 uptake occurs during the day-time (Medina *et al.* 1989, Nobel & Hartsock 1990). Maximum net CO_2 uptake rates under natural conditions were low (*c.* 1.4 μmol m^{-2} s^{-1}) and were comparable to the rates of several epiphytic bromeliads in Trinidad (Griffiths *et al.* 1986). Under wet conditions for young plants in the shade house, maximum net CO_2 by *E. phyllanthus* was comparable to that of slow-growing desert cacti such as *Coryphantha vivipara* and *Mammillaria dioica* (Nobel 1988, Nobel & Hartsock 1986). However, the maximum net CO_2 by *E. phyllanthus* occurred later in the night than for other cacti (Nobel 1988, Nobel & Hartsock 1990), presumably because of higher nocturnal temperatures on Barro Colorado Island than in a desert. Total CO_2 uptake over 24-h periods for *E. phyllanthus* under natural conditions was *c.* 40 mmol m^{-2}, similar to the average of 38 mmol m^{-2} d^{-1} for CAM bromeliads under a broad range of environmental conditions (Griffiths *et al.* 1986) and 58 mmol m^{-2} d^{-1} for CAM epiphytic cacti under laboratory conditions (Nobel & Hartsock 1990). Under wet conditions for young plants in the shade house, total daily CO_2 uptake by *E.*

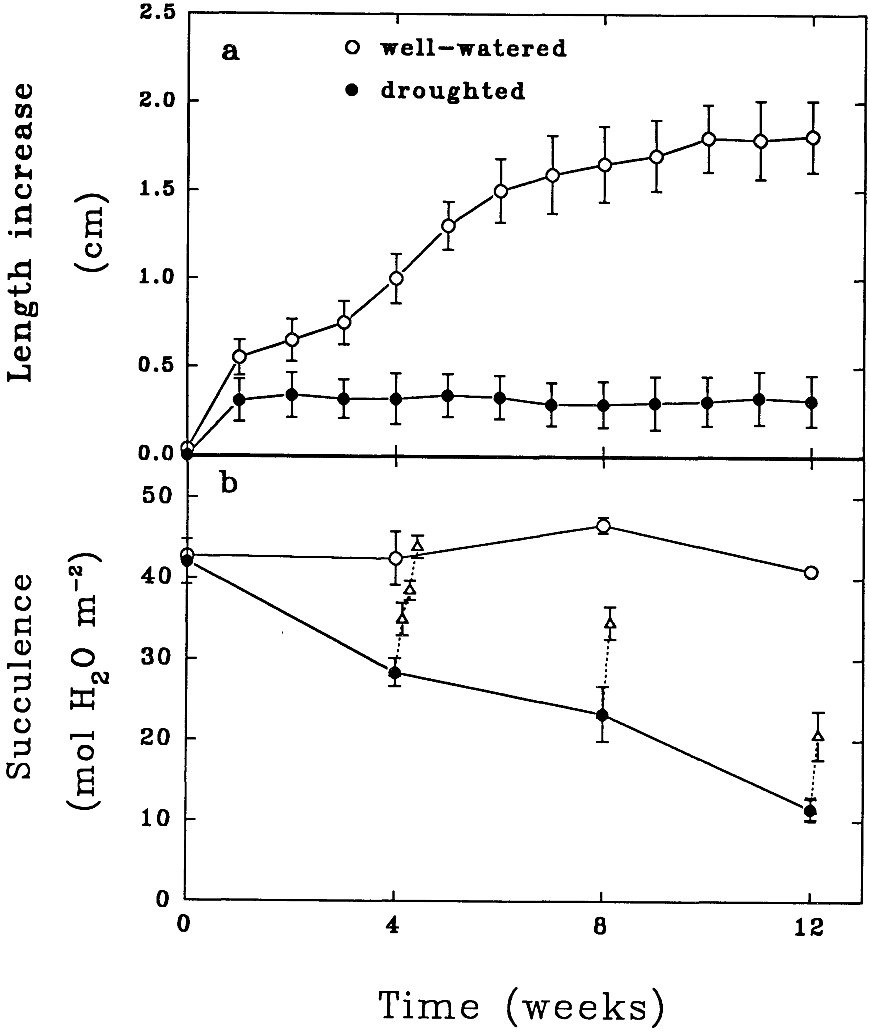

Figure 7. Elongation (a) and succulence (b) for seedlings of *E. phyllanthus* that were well-watered (○) or droughted (●). Measurements of succulence were also made for rewetted seedlings (△). Initial lengths averaged 2.6 cm. All plants were growing in a screenhouse and shaded approximately 50%. Data are means ±s.e. (N = 10 plants).

phyllanthus was 83 mmol m^{-2} d^{-1}. Similarly, total CO_2 uptake is 80 mmol m^{-2} d^{-1} for the intermediate C_3–CAM epiphyte *Clusia uvitana* and 95 mmol m^{-2} d^{-1} for C_3 epiphytes during the wet season in the canopy of Barro Colorada Island (Zotz & Winter 1994). Recycling of respiratory CO_2 for plants shaded 70% accounted for only *c.* 13% of the CO_2 fixed during the night, similar to values for other epiphytic CAM plants (Griffiths 1988, Loeschen *et al.* 1993).

Shading favoured nocturnal increase of tissue acidity, net CO_2 uptake and growth for *E. phyllanthus* in the canopy and in the shade house. Although shading

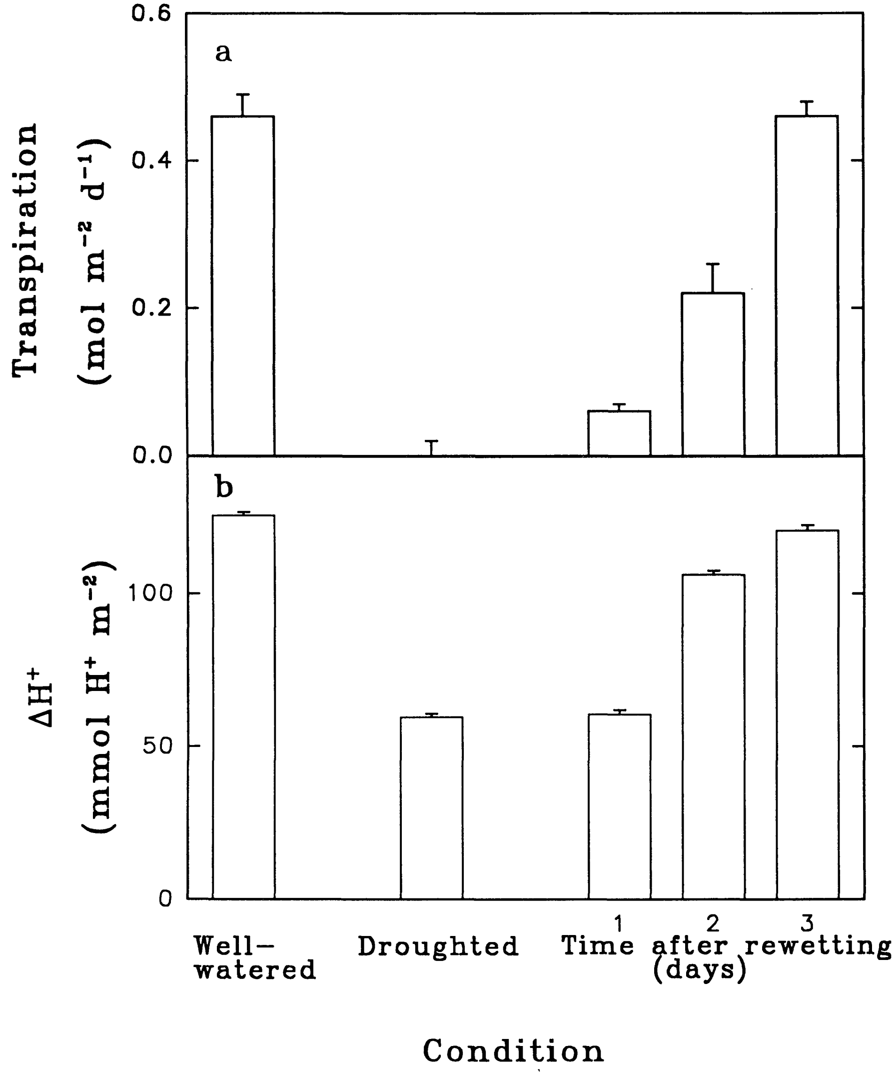

Figure 8. Transpiration (a) and nocturnal increases in tissue acidity (ΔH^+; b) for seedlings of *E. phyllanthus* that were well watered, droughted, or droughted for four weeks and then rewetted. All plants were growing in a screenhouse and were shaded approximately 50%. Data are means with s.e. (N = 5 plants).

reduces CO_2 uptake of some tropical CAM epiphytes (Griffiths *et al.* 1986), other tropical CAM species show an enhancement in their net CO_2 uptake and nocturnal increase of tissue acidity. For instance, the terrestrial CAM bromeliad *Bromelia humilis* growing at a daily PPF of 6 mol m^{-2} d^{-1} (*c.* 12% of the incident PPF) exhibits a nocturnal acidity increase twice that of exposed plants (Medina *et al.* 1986). Similarly, *E. phyllanthus* growing at a daily PPF of 3.6 mol m^{-2} d^{-1} (shaded approximately 50% in the screenhouse) exhibited a 50% greater nocturnal acidity increase than plants exposed to higher and lower daily PPFs (7.3

and 2.3 mol m^{-2} d^{-1}, respectively). Also, stem elongation for *E. phyllanthus* at the intermediate PPF was 27% greater than for plants exposed to the higher and the lower daily PPFs. Although CAM may provide some protection against photoinhibition (Osmond *et al.* 1980), CAM plants under natural conditions can experience photoinhibition when exposed to high PPFs (Adams & Osmond 1988). For instance, the CAM fern *Pyrrosia longifolia* growing in a shady site has a 73% lower photosynthetic O_2 exchange rate after being exposed to full sunlight for 6 h (Winter *et al.* 1986).

After a drought of four weeks, nocturnal increases in tissue acidity were halved and transpiration was essentially eliminated for seedlings of *E. phyllanthus*, indicating that stomata remained closed. Although transpiration was still 50% less than for well-watered plants by the second day of rewetting, nocturnal acidity increase was only 20% less than for well-watered plants. The nocturnal acidity increase also is low for the terrestrial CAM species *Bromelia humilis* 24 h after rewetting plants during the dry season, although tissue water content then reaches values similar to those for plants during the rainy season (Medina *et al.* 1986). Both nocturnal acidity increases and transpiration returned to the values of well-watered plants within three days of daily rewetting for *E. phyllanthus*.

Succulence (water content per unit area) for seedlings of *E. phyllanthus* was reduced 73% during a three-month drought but recovered within a few days after rewetting. Similarly, seven-month-old seedlings of the desert cactus *Ferocactus acanthodes* can survive a loss of up to 84% of their tissue water over a four-month period (Jordan & Nobel 1981). Periods without rain on Barro Colorado Island tend to be shorter than those for deserts, and rainfall within a dry season is rare in many deserts. Thus, although the drought tolerance of *E. phyllanthus* is similar to that of desert cacti, its response to rewetting is apparently more rapid. For instance, roots of *Ferocactus acanthodes* show full recovery only after seven days of rewetting (North & Nobel 1992). Some epiphytic ferns recover to pre-drought values of water potential and stomatal conductance within three days of rewetting (Sinclair 1983), and some orchids can increase their fresh weight to nearly pre-drought levels within 1 h of rewetting their roots (Winter *et al.* 1983). Roots of *E. phyllanthus* respond quickly to rewetting; radial breaks in the periderm of older roots and growth of new roots increase root hydraulic conductivity to pre-drought values, and maximum transpiration occurs four days after rewetting (North & Nobel 1994). Thus, *E. phyllanthus* can take advantage of episodic rainfall during the dry season.

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