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## WHOLE-PLANT CONSEQUENCES OF CRASSULACEAN ACID METABOLISM FOR A TROPICAL FOREST UNDERSTORY PLANT

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**Abstract.** We examined leaf and whole-plant characteristics in mature individuals of several herbaceous species growing in the understory of a tropical moist forest in central Panama. Our objective was to see if contrasts in leaf physiology among Crassulacean acid metabolism (CAM) and C<sub>3</sub> plants were associated with differences in whole-plant structure or performance in a habitat that is considered atypical for CAM. Foliage of *Aechmea magdalenae*, an understory CAM bromeliad, has a higher maximum photosynthesis rate, and greater nitrogen, chlorophyll, and water contents on a leaf-area basis compared to three sympatric C<sub>3</sub> species. Leaf characteristics of two other understory CAM bromeliads, *Ananas comosus* and *Bromelia plumieri*, were similar to that of *Aechmea*. *Aechmea*, compared to three sympatric C<sub>3</sub> species, allocates less biomass to roots and more to foliage. The annual aboveground relative growth of *Aechmea* was lower than it was for the C<sub>3</sub> species, despite *Aechmea*'s higher photosynthetic capacity. This is consistent with the hypothesis that the efficient use of transient periods of high light for carbon gain is critical to the success of this CAM species as an understory plant. Maximum growth in *Aechmea* occurred during the dry season, whereas for the C<sub>3</sub> species growth was greatest during the wet season, suggesting that variation in photosynthetic pathway can provide a basis for temporal niche differentiation among tropical forest herbaceous perennials.

**Key words:** *Aechmea magdalenae*; Barro Colorado Island; biomass allocation; bromeliad; C<sub>3</sub>; Crassulacean acid metabolism; niche; Panama; photosynthesis; plant growth; sunflecks; tropical forest.

### INTRODUCTION

Carbon assimilation through Crassulacean acid metabolism (CAM) is regarded as an adaptive trait for plant species native to high-light, water-limited habitats (Taiz and Zeiger 1991). Ecophysiological studies of CAM have focused on desert succulents and upper canopy epiphytes from tropical forests (reviewed in Osmond 1978, Winter 1985, Lüttge 1987, Griffiths 1988, Nobel 1988, Smith 1989, Martin 1994, Winter and Smith 1996a). Nocturnal CO<sub>2</sub> uptake in CAM is coupled to daytime stomatal closure and decarboxylation of stored organic acids. This minimizes water loss and maximizes the CO<sub>2</sub> within the leaf (C<sub>i</sub>) when light is available to drive photosynthesis. These factors would seem to be of little value for carbon gain in plants under low-light, mesic conditions. Moreover, because the daily quantum requirement for carbon gain in air is ~10% greater for CAM compared to C<sub>3</sub> photosynthesis, CAM should be disadvantageous in light-limited habitats (Winter and Smith 1996b). Nevertheless, the occurrence and ecological importance of CAM in terrestrial plants growing in neotropical forest understories is well documented (Brokaw 1983, Medina 1987, Adams

1988, Pfitsch and Smith 1988, Lee et al. 1989, Murawski and Hamrick 1990, Medina et al. 1991, Lerdaun et al. 1992, Medina et al. 1993, Skillman and Winter 1997, Villegas 1997).

*Aechmea magdalenae* is a shade-tolerant, terrestrial bromeliad that expresses CAM constitutively (Pfitsch and Smith 1988) and is widely distributed between Ecuador and Mexico (Croat 1978). In central Panama, where this study was conducted, the distribution of *Aechmea* is largely restricted to mesic understory sites. Local populations of *Aechmea* frequently dominate the understory vegetation, which is otherwise primarily made up of C<sub>3</sub> species (Brokaw 1983). Surprisingly, *Aechmea* plants from the shaded understory have maximum photosynthetic rates greater than that of sympatric C<sub>3</sub> plants (Königer et al. 1995). Although a high photosynthetic capacity in the understory can facilitate high rates of leaf carbon gain during sunflecks, shade plants generally have low photosynthetic capacities. For understory CAM plants, maximum carbon gain can be achieved if the sunflecks coincide with phase III (the daytime decarboxylation portion of the daily CAM cycle) because the photosynthetic apparatus is CO<sub>2</sub>-saturated at this time (Winter 1985). The physiological ecology of *Aechmea* is intriguing both because it expresses CAM constitutively in a mesic, low-light habitat and because it has a high photosynthetic rate for a shade plant. There is little information on the photosynthetic potential for other understory CAM brome-

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PLATE 1. Illustration of similar sized individuals of the four study species. From left, *Aechmea magdalenae* (Bromeliaceae), *Calathea inocephala* (Marantaceae), *Dieffenbachia longispatha* (Araceae), and *Heliconia vaginalis* (Musaceae). Drawing by Francesco Gatesco.



liads. It is also unknown how whole-plant characters such as biomass allocation or plant growth in *Aechmea* compare to that of other understory herbaceous perennials.

Plant growth and biomass allocation are interactive responses that vary by genotype, local environment, and developmental state. Consequently, it is difficult to predict growth or allocation patterns for plants under natural conditions (Körner 1991). Optimal allocation theory predicts that plants will maximize growth under a given set of resource conditions by partitioning biomass so as to maximize the acquisition of limiting resources (Bloom et al. 1985, Bazzaz 1997). Among  $C_3$  species in arid regions,  $\geq 50\%$  of the whole plant is allocated below ground. But in desert CAM plants (e.g., agaves and cacti), as little as 10% of the plant is found below ground (Nobel 1988). Under light limiting conditions of a forest understory, plant biomass would be expected to be preferentially allocated to leaf tissue in CAM and  $C_3$  species alike. However, in the tropical moist forests of central Panama, shallow rooted understory plants may become drought stressed during the dry season (Rundel and Becker 1987, Mulkey et al. 1991, Wright et al. 1992). Even in this shaded forest habitat, contrasts in photosynthetic pathway among understory species may result in different biomass allocation patterns and other whole-plant characteristics.

In this paper we report the findings from a comparative study of leaf and whole-plant characteristics between mature individuals of several herbaceous species growing in the understory of a tropical moist forest in central Panama. The objectives were (a) to study the structural and functional characteristics of leaves in *Aechmea* compared to other understory CAM bromeliads as well as sympatric  $C_3$  herbaceous species, (b) to study allocation patterns of *Aechmea* compared to sympatric  $C_3$  herbaceous species, and (c) to examine seasonal and annual growth rates in *Aechmea* compared to sympatric  $C_3$  herbaceous species. The results indicate that shade tolerant CAM bromeliads differ at the leaf and whole-plant level from the more typical  $C_3$

herbs of tropical forests and suggest that CAM in these species is critical to their ecological success in this low-light, mesic habitat.

#### MATERIALS AND METHODS

This work was conducted in the Barro Colorado National Monument (BCNM), a forest reserve in central Panama ( $9^{\circ}10' N$ ,  $79^{\circ}51' W$ ) that includes Barro Colorado Island (BCI) and several adjacent mainland peninsulas. The BCNM is classified as a tropical moist forest in the Holdridge life zone system (Croat 1978). Annual precipitation totals  $\sim 2600$  mm, with a distinct wet (May–December) and dry (January–April) season. Long term records (1929–1995) indicate the average monthly precipitation is 236–417 mm and 32–92 mm for the wet and dry seasons, respectively (Environmental Science Program, Smithsonian Tropical Research Institute). The understory light environment on BCI has been well characterized, including analyses of seasonal variation in irradiance (Smith 1987, Smith et al. 1992, Valladares et al. 1997; M. K. R. Würth, K. Winter, and C. Körner, *unpublished data*). Würth et al. (*unpublished data*) report mean understory photosynthetic photon flux densities (PPFDs) of  $\sim 8$  and  $12 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the wet and dry seasons, respectively. Despite these seasonal differences, light in the intact forest understory seldom exceeds 1 or 2% of full sun except during brief sunflecks. Smith et al. (1992) found that most of the increase in understory light associated with the dry season on BCI was due to increased sunfleck frequency. Further information on the vegetation, climate, and ecology of BCI is given in Croat (1978) and Leigh et al. (1996).

Biomass and allocation patterns were characterized for four herbaceous species common in the BCNM (see Plate 1): (1) *Aechmea magdalenae* (André ex Baker (Bromeliaceae), (2) *Calathea inocephala* (O. Kuntze) Kenn. and Nic. (Marantaceae), (3) *Dieffenbachia longispatha* Engler and Krause (Araceae), and (4) *Heliconia vaginalis* Benth, Bot. Voy. (Musaceae). Leaf structure and physiology were also evaluated for

TABLE 1. Characteristics of leaves from each of three CAM and three C<sub>3</sub> herbaceous monocot species growing in the rain forest understory in the Barro Colorado National Monument in central Panama.

Variable	CAM		
	<i>Aechmea magdalenae</i>	<i>Ananas comosus</i>	<i>Bromelia plumieri</i>
Photosynthetic capacity ( $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	13.8 <sup>b</sup> $\pm$ 0.9	18.3 <sup>b</sup> $\pm$ 1.2	24.7 <sup>b</sup> $\pm$ 4.1
Respiration ( $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	0.9 <sup>b</sup> $\pm$ 0.1	1.1 <sup>b,c</sup> $\pm$ 0.2	1.6 <sup>c</sup> $\pm$ 0.1
Photosynthetic capacity ( $\text{nmol O}_2\cdot(\text{g dry mass})^{-1}\cdot\text{s}^{-1}$ )	131 $\pm$ 7	129 $\pm$ 7	124 $\pm$ 19
Photosynthetic capacity ( $\mu\text{mol O}_2\cdot(\text{mmol chl})^{-1}\cdot\text{s}^{-1}$ )	19.6 <sup>b,c</sup> $\pm$ 0.4	22.4 <sup>c</sup> $\pm$ 0.8	63.8 <sup>d</sup> $\pm$ 4.1
Photosynthetic capacity ( $\mu\text{mol O}_2\cdot(\text{mol N})^{-1}\cdot\text{s}^{-1}$ )	133 <sup>b</sup> $\pm$ 6	137 <sup>b</sup> $\pm$ 9	482 <sup>c</sup> $\pm$ 56
Specific leaf mass ( $\text{g dry mass}/\text{m}^2$ )	108.5 <sup>c</sup> $\pm$ 3.9	139.2 <sup>d</sup> $\pm$ 5.1	205.7 <sup>e</sup> $\pm$ 7.0
Leaf thickness (mm)	0.67 <sup>c</sup> $\pm$ 0.02	1.22 <sup>d</sup> $\pm$ 0.06	1.39 <sup>e</sup> $\pm$ 0.03
Leaf toughness (kPa)	>3115	>3115	>3115
Leaf water content ( $\text{g}/\text{m}^2$ )	509.7 <sup>c</sup> $\pm$ 13.1	992.7 <sup>d</sup> $\pm$ 48.7	929.8 <sup>d</sup> $\pm$ 25.6
Total chlorophyll ( $\mu\text{mol}/\text{m}^2$ )	696 <sup>e</sup> $\pm$ 12	560 <sup>a,b,c</sup> $\pm$ 51	622 <sup>b,c</sup> $\pm$ 38
Nitrogen ( $\text{mmol}/\text{m}^2$ )	100 <sup>b</sup> $\pm$ 6	122 <sup>b,c</sup> $\pm$ 14	153 <sup>c</sup> $\pm$ 8
Nitrogen (percentage dry mass)	1.3 <sup>a</sup> $\pm$ 0.1	1.2 <sup>a</sup> $\pm$ 0.1	1.0 <sup>a</sup> $\pm$ 0.0

Notes: Leaves were sampled during the 1995 wet season. Data are means  $\pm$  1 SE; significant differences between species for specific characters are indicated by different superscript letters within a row ( $P < 0.05$  by Scheffé means comparison test). A maximum value of 3115 kPa was assigned for measurements of leaf toughness.

the same four species and two additional terrestrial CAM bromeliads: *Ananas comosus* (L.) Merr. and *Bromelia plumieri* (E. Morr.) L. B. Sm. (= *Bromelia karatas*). All measurements were made on mature plants sampled from populations in the forest. *Ananas* (pineapple) is not native to the BCNM forest but persists from earlier cultivation in maintained clearings and in the adjacent forest. Leaves of *Ananas* were sampled from individuals in low-light microsites and *Ananas* is referred to here as an understory plant.

#### Leaf structure and function

During the wet season of 1995 several leaf characters were quantified in three CAM (*Aechmea*, *Ananas*, and *Bromelia*) and three C<sub>3</sub> species (*Calathea*, *Dieffenbachia*, and *Heliconia*) from the understory. All leaf level measurements were made on healthy, fully expanded leaves. The maximum photosynthesis rate (under light and CO<sub>2</sub> saturation) was assessed on leaf discs of a known area in a Hansatech Leaf Disc Oxygen Electrode (model LD2; Hansatech Instruments, Kings Lynn, UK) as described in Skillman et al. (1996). Dark respiration (in air) was evaluated in the same leaf sample with the O<sub>2</sub> electrode. Measurements of fresh and dry leaf mass were made on the same tissue. For determinations of leaf chlorophyll and nitrogen contents, replicate leaf discs were subsampled from leaves used in photosynthesis measurements. Chlorophyll concentrations were measured spectrophotometrically on 80% acetone extracts using the equations of Porra et al. (1989). Leaf nitrogen concentrations were determined with a CHN Elemental Analyzer (Heraeus, Hanau, Germany) at the University of Würzburg. Leaf lamina thickness was measured with a micrometer on five leaves per species. Leaf lamina toughness was determined after Coley (1983) using a calibrated dynamometer (courtesy of Dr. P. Coley, University of Utah) with a 2 mm diameter

piston assuming a gravitational acceleration constant of 9.78 m/s<sup>2</sup>. Six punches were made per leaf on five leaves per species. The dynamometer piston was not able to penetrate the leaf lamina in any of the three bromeliad species and leaf toughness was listed as >3115 kPa, the maximum value for this particular instrument.

#### Biomass allocation and organ-specific respiration

Mature individuals of *Aechmea*, *Calathea*, *Dieffenbachia*, and *Heliconia* were excavated from natural populations located on the Giganté peninsula in the BCNM. Freshly harvested plants were brought to the laboratory to (a) measure organ specific respiration rates, (b) measure leaf blade length and area, petiole length and diameter, and stem length and diameter, and (c) measure the dry biomass of component organs. A minimum of three individuals per species were sampled during both the wet (1994 or 1995) and dry season (1995). There was no statistically discernible season effect on biomass allocation among excavated plants and data were pooled by species. Seven, six, fourteen, and nine excavated individuals (genets) each of *Aechmea*, *Calathea*, *Dieffenbachia*, and *Heliconia*, respectively, were subdivided for determinations of biomass allocation.

Respiration rates were evaluated on healthy samples of selected, nonleaf organs of each species by the same methods as in *Materials and methods: Leaf structure and function*, above. These data were collected from plants freshly excavated during the wet season to complement the leaf respiration data from the leaf character study. Organ specific respiration rates were measured in 3–5 samples per selected organ per species. Measurements were made in rhizomes and roots of *Aechmea*, petioles and roots of *Calathea*, petioles, stems, and roots of *Dieffenbachia*, and stems and roots of *Heliconia*. Within a species, decisions on which plant

TABLE 1. Extended.

C <sub>3</sub>		
<i>Calathea inocephala</i>	<i>Dieffenbachia longispatha</i>	<i>Heliconia vaginalis</i>
6.1 <sup>a</sup> ± 0.6	4.8 <sup>a</sup> ± 0.4	3.9 <sup>a</sup> ± 0.6
0.5 <sup>a</sup> ± 0.1	0.4 <sup>a</sup> ± 0.1	0.5 <sup>a</sup> ± 0.1
148 ± 15	108 ± 10	96 ± 12
12.8 <sup>abc</sup> ± 2.4	9.8 <sup>ab</sup> ± 0.9	8.5 <sup>a</sup> ± 0.7
40 <sup>a</sup> ± 8	30 <sup>a</sup> ± 2	28 <sup>a</sup> ± 3
40.7 <sup>ab</sup> ± 0.6	44.9 <sup>b</sup> ± 1.4	37.4 <sup>a</sup> ± 1.3
0.21 <sup>a</sup> ± 0.01	0.42 <sup>b</sup> ± 0.01	0.23 <sup>a</sup> ± 0.01
1860 <sup>a</sup> ± 50	2197 <sup>b</sup> ± 73	1708 <sup>a</sup> ± 42
144.1 <sup>a</sup> ± 3.2	272.1 <sup>b</sup> ± 5.9	148.7 <sup>a</sup> ± 2.9
504 <sup>ab</sup> ± 29	432 <sup>a</sup> ± 23	492 <sup>ab</sup> ± 28
66 <sup>a</sup> ± 5	65 <sup>a</sup> ± 4	55 <sup>a</sup> ± 8
2.2 <sup>b</sup> ± 0.1	2.0 <sup>b</sup> ± 0.1	2.1 <sup>b</sup> ± 0.1

organs to evaluate respiration in were based upon predicted importance in terms of biomass allocation.

Dimensional measurements of component organs were related to dry mass values for the same organs in order to describe allometric relationships by regression analyses. All such relationships were highly significant with correlation coefficients  $\geq 0.90$  (data not shown). These relationships were used to estimate aboveground biomass and growth in mature individuals of the same species in the forest.

#### *Plant growth and leaf demography*

In November 1994, 12 mature individuals each of *Aechmea* and *Dieffenbachia* were selected for repeated nondestructive measures of aboveground biomass accumulation. Analogous measurements were initiated in February 1995 on 12 individuals each of *Calathea* and *Heliconia*. Plants were censused every two months for all four species through April 1996. Aboveground growth measurements on multiple-stem plants included all stems and are therefore representative of entire genets. Individuals selected for the growth study were large enough to be reproductively mature but not of maximum size since these plants were expected to have a net positive growth rate that was linearly related to time. The final sample size was reduced to 7–10 individuals per species as a result of mortality or cumulative growth that was negative. Measurements included leaf number, midvein length, petiole length and diameter, and stem length and diameter. These data were used with the allometric relationships to estimate whole shoot biomass on each plant at each census date. Standard methods were used to calculate absolute and relative shoot growth rates (Beadle 1993). Measurements of ground area occupied by each plant were used to estimate shoot growth on a land-area basis.

The data set from the growth study was also used to characterize leaf demography for each of the four species. Estimates were made of the number of leaves per plant, the leaf production rate, and the leaf lifespan.

For each species the leaf lifespan was greater than the duration of the observation period precluding a direct measure of leaf longevity. Leaf lifespan was estimated from the number of leaves per plant divided by the leaf production rate.

#### *Statistical analyses*

Species differences in leaf or plant characters were inferred using analysis of variance methods and Scheffé means comparisons tests (Steel and Torrie 1980). The growth study was designed to compare shoot productivity of different species under different seasonal conditions. The different species were not always censused at the same time, which prevented the use of a repeated-measures analysis to look for seasonal differences in growth. A two-way analysis of variance was used to examine species, season, and species  $\times$  season effects on relative shoot growth. For purposes of this analysis, census data collected between January and April were classified as Dry season and data collected between May and December were classified as Wet season. Data sets were checked for homogeneity of variance and, when necessary, appropriate transformations were made prior to running statistical models.

## RESULTS

### *Leaf structure and function*

The maximum photosynthetic rate was higher in the CAM bromeliads than in the C<sub>3</sub> herbaceous species when expressed on a leaf area or nitrogen basis (Table 1). The maximum photosynthetic rate on a chlorophyll basis for the CAM species was, on average, 3 $\times$  greater than that of the C<sub>3</sub> species but differences between species were or were not significant depending upon the species pair under consideration. On a leaf dry mass basis the maximum photosynthetic rate was similar among all species. Leaf respiration rates on a leaf-area basis were two to three times higher for the CAM species than the C<sub>3</sub> species. Chlorophyll per unit leaf area tended to be higher in the CAM species although this difference was or was not statistically significant, depending upon the particular species pair being compared. Nitrogen per unit leaf area was higher in the CAM species compared to the C<sub>3</sub> species. However, on a dry mass basis, foliar nitrogen in the CAM species was only half of that in the C<sub>3</sub> species. Leaves of the CAM bromeliads were thicker, more resistant to penetration, had higher specific leaf masses, and held more water than the foliage of the C<sub>3</sub> perennials (Table 1).

### *Distribution of biomass and organ-specific respiration*

At maturity, *Aechmea* is the largest of the common herbaceous species found on BCI. Among mature plants, total plant mass and total leaf area were  $>5\times$  greater for *Aechmea* compared to the three nonbromeliad species (Table 2). The leaf area ratio was be-

TABLE 2. Whole plant mass and allocation for the CAM bromeliad *Aechmea magdaleneae* and three C<sub>3</sub> herbaceous monocot species growing in the rain forest understory in the Barro Colorado National Monument in central Panama.

Variable	CAM	C <sub>3</sub>		
	<i>Aechmea magdaleneae</i>	<i>Calathea inocephala</i>	<i>Dieffenbachia longispatha</i>	<i>Heliconia vaginalis</i>
Sample size (no. plants)	7	6	14	9
Whole plant dry mass (g)	883.6 <sup>b</sup> ± 148.3	115.7 <sup>a</sup> ± 27.3	159.8 <sup>a</sup> ± 41.9	69.4 <sup>a</sup> ± 11.4
Total plant leaf area (m <sup>2</sup> )	3.30 <sup>b</sup> ± 0.52	0.46 <sup>a</sup> ± 0.07	0.40 <sup>a</sup> ± 0.07	0.37 <sup>a</sup> ± 0.07
Leaf area ratio (m <sup>2</sup> leaf/(kg plant))	3.8 <sup>a,b</sup> ± 0.1	4.6 <sup>a,b</sup> ± 0.8	3.2 <sup>a</sup> ± 0.4	5.3 <sup>b</sup> ± 0.2
Percentage of biomass in leaves	68.0 <sup>b</sup> ± 1.9	29.3 <sup>a</sup> ± 3.3	20.6 <sup>a</sup> ± 2.1	27.3 <sup>a</sup> ± 1.3
in petioles	none	22.4 <sup>c</sup> ± 1.7	13.5 <sup>b</sup> ± 1.3	2.7 <sup>a</sup> ± 0.3
in stems	9.6 <sup>a</sup> ± 1.1	none	38.0 <sup>b</sup> ± 3.3	29.8 <sup>b</sup> ± 2.4
in rhizomes	17.5 <sup>a,b</sup> ± 1.9	11.8 <sup>c</sup> ± 1.3	21.4 <sup>b</sup> ± 1.9	32.8 <sup>c</sup> ± 3.7
in roots	1.9 <sup>a</sup> ± 0.2	36.6 <sup>c</sup> ± 4.5	6.4 <sup>b</sup> ± 0.6	7.3 <sup>b</sup> ± 0.6
Maximum rooting depth (m)	≤0.5	≤2.0	≤0.5	≤2.0

Notes: Plants were excavated between July 1994 and November 1995. Data are means ± 1 SE; significant differences between species are indicated by different superscript letters within a row ( $P < 0.05$  by Scheffé means comparison test).

tween 3 and 5 m<sup>2</sup>/kg plant mass across the four understory perennial species and was only found to differ significantly between *Dieffenbachia* and *Heliconia*. Foliage represented nearly 70% of the plant mass in *Aechmea* but only 20–30% of the biomass in the C<sub>3</sub> species. Roots represented only 2% of the plant mass in *Aechmea* and 6–36% of the biomass in the C<sub>3</sub> species. When roots and rhizomes were pooled, the biomass allocated below ground was significantly lower in *Aechmea* and *Dieffenbachia* than it was for *Calathea* or *Heliconia* (Fig. 1). This finding paralleled our observations of maximum rooting depths for these species where the entire root system of *Aechmea* and *Dieffenbachia* individuals were found to be near the surface of the soil but individual roots of *Calathea* and *Heliconia* went down in the soil as much as 2 m (Table 2).

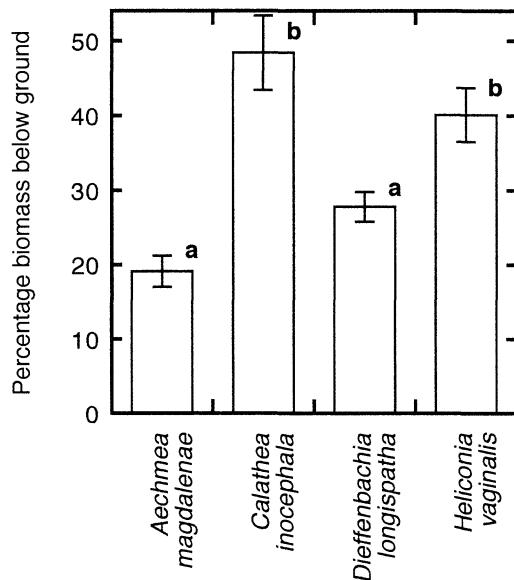


FIG. 1. Percentage belowground biomass from mature plants of each of the four study species excavated from the forest in the Barro Colorado National Monument.

The overall average respiration rate for all species and organ types was  $11.4 \pm 0.8$  nmol·g<sup>-1</sup>·s<sup>-1</sup> (mean ± 1 SE; Table 3). Respiration rates were not different among species and different plant organs except for *Dieffenbachia* and *Heliconia*, where respiration of roots was higher than that of other sampled organs.

#### Leaf demography and growth

The number of leaves per plant and the average leaf production rate was significantly higher for *Aechmea* compared to the C<sub>3</sub> perennials (Fig. 2). Among the C<sub>3</sub> species, *Heliconia* had the most leaves per plant and the highest leaf production rate. Average leaf lifespan for *Aechmea* in the understory exceeded 3 yr and was <3 yr for each of the C<sub>3</sub> species but this difference was not significant.

There was less rain and more available light during the dry season than during the wet season (Fig. 3). The timing of maximum shoot growth in each of the C<sub>3</sub> species occurred during the wet season in 1995. In contrast, maximum shoot growth in *Aechmea* was observed during the dry season of 1995 and again in February 1996 during what was a comparatively late and mild dry season. A two-way analysis of variance indicated that this species × season interaction was significant (Table 4).

The annual absolute shoot growth rate in *Aechmea* was significantly faster than in the other three species (Table 5) as would be expected based on species differences in plant size (cf. Table 2). *Aechmea*, on average, had the lowest annual relative shoot growth rate of the four species studied but was not significantly different in this respect from the other shallow-rooted species, *Dieffenbachia*. *Aechmea*, on average, also had the lowest shoot growth rate on a leaf-area basis but was not significantly different in this respect from *Calathea* or *Dieffenbachia*.

#### DISCUSSION

##### Leaf structure, function, and longevity

The maximum photosynthesis rate was higher for each of the three CAM bromeliads compared to the C<sub>3</sub>

TABLE 3. Organ specific respiration rates sampled for four species growing in the rain forest understory in the Barro Colorado National Monument in central Panama.

Organ specific respiration rates (nmol O <sub>2</sub> ·(g dry mass) <sup>-1</sup> ·s <sup>-1</sup> )	CAM	C <sub>3</sub>		
	<i>Aechmea magdalanae</i>	<i>Calathea inocephala</i>	<i>Dieffenbachia longispatha</i>	<i>Heliconia vaginalis</i>
Leaf	8.9 ± 1.2	11.6 ± 2.3	8.6 <sup>a</sup> ± 1.1	14.0 <sup>a</sup> ± 1.9
Petiole	NA	8.5 ± 0.9	4.0 <sup>a</sup> ± 1.0	ND
Stem	ND	NA	2.1 <sup>a</sup> ± 0.5	12.0 <sup>a</sup> ± 1.6
Rhizome	12.5 ± 2.0	ND	ND	ND
Root	13.6 ± 5.7	12.9 ± 4.5	17.4 <sup>b</sup> ± 3.5	24.4 <sup>b</sup> ± 3.2

Notes: Leaf respiration was measured on leaves sampled during the 1995 wet season ( $n = 6-9$  leaves). All other measurements were made on organs sampled from plants excavated during the wet seasons of 1994 or 1995 ( $n = 3-5$  samples per organ). Data are means ± 1 SE. A one-way ANOVA for species effects on respiration was not significant. Within a species, significant differences between organ respiration rates ( $P < 0.05$  by Scheffé means comparison test) are indicated by different superscript letters within a column.

† NA (not applicable) indicates that this organ was not present on the indicated species.

‡ ND (not determined) indicates that no measurements were made.

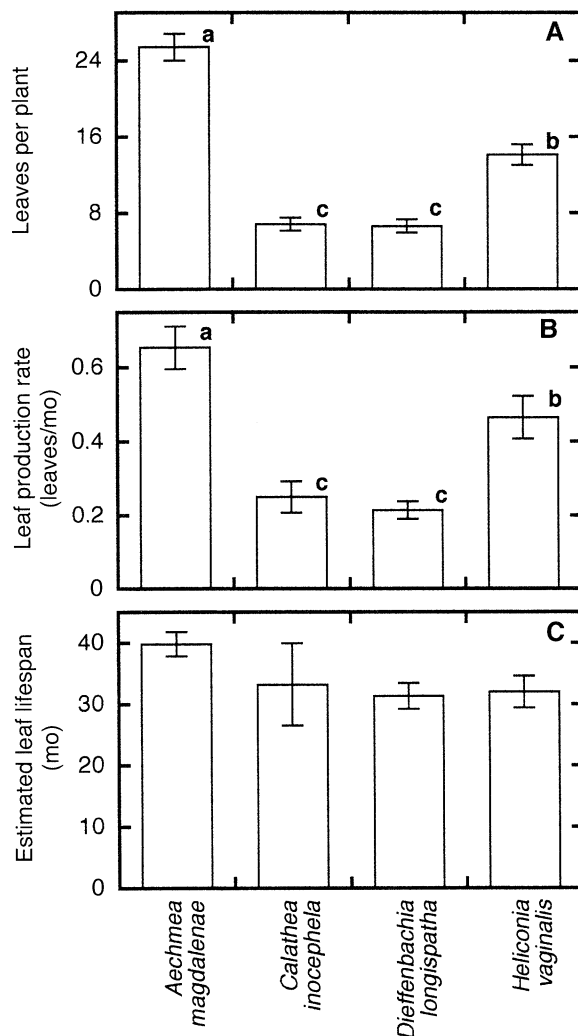


FIG. 2. Leaves per plant (A), the leaf production rate (B), and the estimated leaf lifespan (C) for plants from natural populations of the four study species in the Barro Colorado National Monument forest.

species on the basis of leaf area, chlorophyll, and nitrogen but not on a dry mass basis (Table 1). Differences in leaf photosynthetic capacity between the CAM and C<sub>3</sub> species appear to be biochemically rather than morphologically based. The relatively low photosynthetic capacity per unit leaf mass in the CAM bromeliads reflects the presence of foliar tissues that are nonphotosynthetic in function and low in nitrogen content. This is consistent with the leaf anatomy of most bromeliads (Benzing 1980) and is supported by other leaf structural characteristics assessed here. In the present study, bromeliad leaves were consistently thicker and had a greater water content than leaves of the non-bromeliad species. This agrees with the general observation that a substantial fraction of bromeliad leaf biomass functions as nonphotosynthetic, water-storage parenchyma (Benzing 1980). In addition, much of the nonphotosynthetic material in bromeliad foliage functions for mechanical support and provides resistance to physical damage and herbivory (but see Aiello and Silberglied [1978], Lowman et al. [1996]).

A high photosynthetic capacity is a common, but by no means universal, feature of CAM species grown in the shade (Winter et al. 1986, Adams 1988, Lüttge et al. 1991). In earlier reports for shade-grown CAM bromeliads, *Bromelia humilis* (Fetene et al. 1990) and *Aechmea magdalanae* (Königer et al. 1995) were each shown to have photosynthetic capacities of ~17  $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  while *Ananas cosmosus* (Borland and Griffiths 1989) had a photosynthetic capacity of only 5  $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . It is unclear why maximum photosynthetic rates reported for shade pineapple vary between 5 and 18  $\mu\text{mol O}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (cf. Table 1 and Borland and Griffiths 1989) but the present study suggests that a high photosynthetic capacity is common to many, if not all, shade-grown CAM bromeliads (Table 1).

Maximum photosynthetic rates in CAM tissues evaluated under saturating CO<sub>2</sub> concentrations are thought to reflect achievable carbon assimilation rates during phase III when C<sub>i</sub> is saturating behind closed stomates

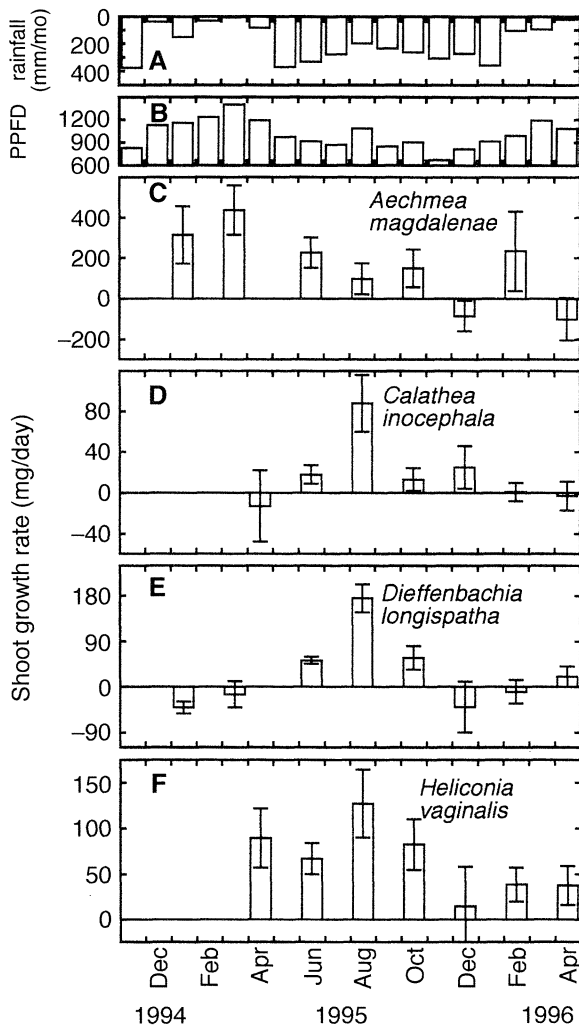


FIG. 3. Seasonal rainfall (A), above-canopy photosynthetic photon flux density, PPF (mol·m<sup>-2</sup>·mo) (B), and shoot growth rates for the four study species (C-F) in the Barro Colorado National Monument forest. Note the different scales on the y axis for C-F. Rainfall and PPF data were provided by the Smithsonian Tropical Research Institute Environmental Sciences Program.

(Osmond et al. 1989). However, for C<sub>3</sub> species in air, as much as half of the carbon fixation potential associated with photosynthesis is diverted to photorespiratory reactions. Consequently, for plants in air, the CAM (phase III) vs. C<sub>3</sub> differences in light-saturated carbon assimilation are expected to be even greater than the observed CAM vs. C<sub>3</sub> differences in light- and CO<sub>2</sub>-saturated oxygen evolution reported in Table 1. We have evidence indicating that the high photosynthetic rates of CAM phase III facilitate higher rates of carbon gain during sunflecks in *Aechmea* growing in the forest compared to co-occurring C<sub>3</sub> plants (Skillman and Winter 1997). In the shade, CAM plants operate in phase III over much of the day (Borland and Griffiths 1996, Skillman and Winter 1997). Our observations that

shade-grown *Bromelia plumieri* and *Ananas comosus* have high photosynthetic capacities (Table 1) similar to that of shade-grown *Bromelia humilis* (Fetene et al. 1990) and *Aechmea magdalenae* (Königer et al. 1995; Table 1) suggests that efficient sunfleck use resulting from a high photosynthetic capacity and saturating C<sub>i</sub> during the day may be common to many shade-tolerant CAM bromeliads.

Any analysis of the foliar characteristics that may affect differential growth and survival among species in a light-limited habitat must include a consideration of leaf longevity (Chabot and Hicks 1982, Reich et al. 1992). Estimates of leaf lifespan for the species studied here were within the range reported for other shade-tolerant species from tropical forests (Coley 1988, Mulkey et al. 1991, Reich et al. 1992, King 1995, Lovelock et al. 1998). Given the tough, resistant foliage of *Aechmea*, we expected this species would exhibit a greater leaf longevity than the C<sub>3</sub> species. Although the estimated leaf lifetime in *Aechmea* was, on average, several months longer than that estimated for the C<sub>3</sub> species (Fig. 2), this difference was not significant. This unexpected result may reflect a comparatively high incidence of leaf death in *Aechmea* due to trampling or bending of the long, thin, heavy, apetiolate leaves that are characteristic of this species and bromeliads in general (Hallwachs 1983). Leaf-level characteristics that should prove advantageous for growth and survival of this CAM bromeliad in the understory include the low nitrogen concentration and high CO<sub>2</sub>-saturated photosynthetic rate but apparently not an extended leaf lifetime.

#### Biomass allocation and aboveground growth

Differences in root/shoot allocation patterns among co-occurring plants of the same growth form are thought to reflect differences in the relative requirements for above- and belowground resources (Bloom et al. 1985, Bazzaz 1997). Compared to the C<sub>3</sub> species, *Aechmea* allocated relatively little biomass below ground (Table 2, Fig. 1) and these differences were not associated with variation among species in root respiration (Table 3). This contrast between understory CAM and C<sub>3</sub> plants in root/shoot allocation is surprising until we recall that light is not the only limiting resource for understory plants in tropical moist forests.

TABLE 4. Species, season, and species × season effects on relative shoot growth rates (ANOVA results).

Source of variation	df	Relative shoot growth rate (mg·g <sup>-1</sup> ·d <sup>-1</sup> )		
		ss	F ratio	P
Species	3	14.2431	2.0937	0.1023
Season	1	48.5194	21.397	0.0000
Species × season	3	28.7604	4.2278	0.0064

Notes: Data from March/April 1995 and from February and April 1996 were classified as dry season. Data from June, August, and October 1995 were classified as wet season.



TABLE 5. Annual above ground growth rates for mature individuals of the CAM bromeliad *Aechmea magdalenae* and three  $C_3$  herbaceous monocot species growing in the rain forest understory in the Barro Colorado National Monument in central Panama.

Variable	CAM	$C_3$		
	<i>Aechmea magdalenae</i>	<i>Calathea inocephala</i>	<i>Dieffenbachia longispatha</i>	<i>Heliconia vaginalis</i>
Sample size (no. plants)	7	10	7	10
Absolute shoot growth rate (g/yr)	78.3 <sup>a</sup> ± 15.4	7.1 <sup>c</sup> ± 1.5	11.7 <sup>b,c</sup> ± 2.5	23.2 <sup>b</sup> ± 7.2
Relative shoot growth rate (mg·g <sup>-1</sup> ·yr <sup>-1</sup> )	162 <sup>a</sup> ± 20	618 <sup>c</sup> ± 109	178 <sup>a,b</sup> ± 33	402 <sup>b,c</sup> ± 71
Aboveground biomass increment (g·(m <sup>2</sup> land) <sup>-1</sup> ·yr <sup>-1</sup> )	7.4 <sup>a</sup> ± 1.3	8.7 <sup>a</sup> ± 2.0	11.7 <sup>a,b</sup> ± 2.0	17.9 <sup>b</sup> ± 2.8

Notes: Values are for plant dry mass (means ± 1 SE). Significant differences between species ( $P < 0.05$  by Scheffé means comparison test) are indicated by different superscript letters within a row.

It appears that the conservative water use of CAM is coupled to minimal root biomass allocation and is functionally important for growth of *Aechmea* in the forest during the dry season. Comparing the two shallow rooted perennials during the dry season, when water can be limiting in the upper soil, the  $C_3$  species (*Dieffenbachia*) had a negative shoot growth while the CAM species (*Aechmea*) was at its most productive (Table 2, Fig. 3). Thus, as in desert systems, variation in plant water requirements among tropical forest perennials due to differences in photosynthetic pathway is associated with differences in whole-plant allocation patterns. Contrasts among species in mineral nutrient requirements are also important in considering root/shoot allocation patterns. *Aechmea*, compared to the  $C_3$  species, had lower foliar nitrogen concentrations and had the smallest biomass fraction allocated to mineral nutrient acquisition (i.e., roots).

This is the first report of a seasonal separation of growth between understory CAM and  $C_3$  plants. Maximum vegetative growth in the  $C_3$  species took place during the wet season (Fig. 3), which is consistent with growth phenologies reported for other understory  $C_3$  species in the BCNM (Rundel and Becker 1987, Wright et al. 1992). This phenology suggests that these species are able to thrive in deep shade but are relatively intolerant of water limitations during the dry season. Maximum vegetative growth in *Aechmea* occurred during the dry season, which is sharp contrast to that of the  $C_3$  species (Fig. 3) and growth phenologies reported for other understory  $C_3$  species in the BCNM (Rundel and Becker 1987, Wright et al. 1992). The phenology of *Aechmea* conforms to the idea that, compared to the  $C_3$  species, this CAM plant is more drought tolerant and is able to make greater use of transient increases in light for carbon gain (Fig. 3, Table 4). We note that our findings differ from those of Pfitsch and Smith (1988) who reported there was no significant difference between wet and dry season growth in *Aechmea* on BCI during 1983, a strong El Niño year with a long and severe dry season (Leigh et al. 1996). The forest was unusually open following the 1983 dry season as a result of extensive canopy die-back (Smith et al. 1992). It may be that there was no difference in seasonal growth in *Aechmea* over the period observed by

Pfitsch and Smith (1988) due to severe water limitations on growth during the dry season and/or release from light limitations in the forest during the following wet season. The seasonal separation of growth between *Aechmea* and the  $C_3$  species reported here (Fig. 3) suggests that photosynthetic pathway variation can provide a basis for niche differentiation among tropical forest herbaceous perennials.

Before discussing the observed species differences in annual growth, it is worth considering what we might expect based upon known contrasts in the physiology and morphology of these species. On one hand, *Aechmea* has a number of characteristics that should be advantageous for survival and growth in a light-limited habitat including: (a) a high photosynthetic capacity (Table 1) which, when coupled with the saturating  $C_i$  during phase III, will allow greater rates of carbon fixation during sunflecks, (b) the low requirements for leaf nitrogen (Table 1), and (c) a high allocation to leaf biomass (Table 2). On the other hand, *Aechmea* also displays a number of features thought to be detrimental to survival and growth in a light-limited habitat including: (a) the bioenergetic costs of CAM, resulting in a higher quantum requirement per 24-h carbon gain (Winter and Smith 1996b), (b) the vertically oriented leaves characteristic of bromeliads, resulting in reduced light interception compared to horizontal foliage typical of understory vegetation, and (c) the thick leaves (Table 1), which entail greater construction and maintenance costs (on a leaf-area basis) compared to thin leaves typical of most shade plants. Physiological and morphological characteristics of *Aechmea* that are relatively beneficial for growth in the shade must, in part, compensate for those that are relatively detrimental to growth in the shade.

With this perspective, our observation that *Aechmea* had the lowest annual relative shoot growth rate (Table 5) suggests its high photosynthetic capacity, which is rare for a shade plant, is critical to its ecological success in the understory. Whereas the leaf photosynthetic data (Table 1) indicate that *Aechmea* can make greater use of sunflecks for carbon assimilation, the annual growth data (Table 5) suggest that to maintain a net positive carbon balance in the understory this species must make greater use of sunflecks for carbon assimilation.

Findings for *Ananas comosus* and *Bromelia plumieri* indicate that this relationship may apply to other understory CAM bromeliad species as well.

In conclusion, our findings indicate that contrasts in photosynthetic pathway among tropical forest perennial herbs are associated with differences in whole-plant structure and performance. Active dry season growth among the species studied was largely limited to *Aechmea*, apparently reflecting the water-conserving aspect of CAM. Likewise, minimal allocation of resources to belowground tissues appears for *Aechmea* to be a reflection of CAM. This is associated with the high allocation of biomass to foliage in *Aechmea*, which may partially compensate for other characteristics normally not found in shade tolerant species. The low annual growth rate in *Aechmea*, despite a high photosynthetic capacity, suggests that the efficient use of transient periods of high light in the forest is necessary for the persistence of this species in the understory. Results reported here improve our understanding of the role of photosynthetic pathway variation for niche differentiation among tropical forest plants.

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