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GROWTH IRRADIANCE EFFECTS ON PHOTOSYNTHESIS AND GROWTH IN TWO CO-OCCURRING SHADE-TOLERANT NEOTROPICAL PERENNIALS OF CONTRASTING PHOTOSYNTHETIC PATHWAYS[1]

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Dieffenbachia longispatha (C3) and *Aechmea magdalenae* (Crassulacean acid metabolism, CAM) are syntopic, neotropical forest perennials in central Panama that are restricted to shaded habitats. This is of particular interest for *A. magdalenae* because, like other understory CAM bromeliad species, it appears functionally and structurally to be better suited to life in full sun. Growth irradiance (GI) effects on photosynthesis and growth in both species were explored in the context of sun/shade trade-off concepts largely derived from studies of C3 plants. Potted plants were grown outdoors in 1, 55, and 100% full sun for 5 mo under well-watered conditions. While both species grew faster in high compared to low light, maximum relative growth rates (RGR) in full sun were still extremely slow with *A. magdalenae* showing a RGR approximately half that of *D. longispatha*. Photosynthetic capacity increased with GI in *D. longispatha* but not in *A. magdalenae*. *Aechmea magdalenae* responded to GI with shifts in the activity of the different CAM phases. Both species were photoinhibited in full sun, but more so in *A. magdalenae*. Despite possessing many traits considered adaptive in high light, these results suggest that *A. magdalenae* is unlikely to attain sufficient growth rates to thrive in productive, high-light habitats.

Key words: Bromeliaceae; chlorophyll fluorescence; Crassulacean acid metabolism; growth analysis; Panama; photoinhibition; photosynthetic acclimation; tropical forest ecology.

Physiological and morphological contrasts between C3 plants that thrive in open, sunny habitats and those that thrive in shaded habitats provide one of the best documented examples of phenotypic and evolutionary trade-offs in plant ecology (reviewed in Grime, 1977; Bazzaz and Pickett, 1980; Björkman, 1981, Evans et al., 1988, Pearcy and Sims, 1994; Larcher, 1995; Valladares, 2003; Givnish et al., 2004). Shade-grown C3 plants, as compared to those grown in high light, allocate relatively more biomass to photosynthetic tissues, producing thin, horizontally oriented foliage with little intracanopy shading. These shade leaves, in turn, have relatively high chlorophyll concentrations and high coefficients of light absorption. These features all contribute to the efficient interception and absorption of light for use in carbon gain. Shade-grown C3 plants also have relatively little root biomass and relatively low foliar concentrations of nitrogen-rich photosynthetic enzymes, obliging low transpiration rates and low light-saturated rates of photosynthesis. These features render shade-grown C3 plants more susceptible to light, drought, and heat stress in the event of sudden exposure to high light as may happen to understory plants during gap formation or deforestation (Mulkey and Pearcy, 1992; Lovelock et al., 1994). Thus, the physiological and morphological traits that allow shade-grown C3 plants to thrive in the understory are detrimental to their success in high light.

All the aforementioned traits, both at the leaf- and whole-plant level, exhibit a high degree of phenotypic plasticity, allowing individual genotypes or species to perform well over a range of light conditions (e.g., Silvera et al., 2003). But, consistent with evolutionary trade-off models, the range of plasticity in these characters generally differs between fast-growing plants native to productive high-light habitats as compared to plants native to low-light habitats (Seemann et al., 1987; Pearcy and Sims, 1994). For example, the light-saturated photosynthetic rates in light-demanding, early-successional tropical C3 tree species grown in the sun may be ~200% greater than that of the same species when grown in the shade. By contrast, the light-saturated photosynthetic rates in shade-tolerant, late-successional tropical C3 tree species grown in the sun is typically less than 100% greater than that of the same species when grown in the shade (Strauss-Debenedetti and Bazzaz, 1996). Similar differences in plasticity for other plant traits exist between sun-adapted and shade-adapted C3 species (e.g., Kitajima, 1996; Givnish et al., 2004). These differences in light-dependent phenotypic plasticity can, in large part, explain why certain C3 species are limited to either bright or shaded habitats (Bazzaz and Pickett, 1980; Sims and Kelley, 1998). The extent to which this sun/shade trade-off model can explain the local distribution of Crassulacean acid metabolism (CAM) species is not well known.

The present study examined how some of the aforementioned leaf and whole-plant characteristics responded to variation in growth irradiance in two syntopic neotropical understory perennials; the CAM-dependent monocot herb, *Aechmea magdalenae* André ex Baker (Bromeliaceae) and the C3-dependent monocot herb, *Dieffenbachia longispatha* Engler and Krause (Araceae). Previous studies have shown that, when growing in their native understory habitat, *D. longispatha* displays traits typical of shade-adapted species but that *A. mag-*

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TABLE 1. Summary of light and temperature conditions in each of the three light treatments. Microclimate data were collected for a minimum of 10 d per month for the duration of the 5-mo growth experiment ($N = 65$). Growth irradiance treatment is expressed as a percentage of full sun conditions. Reported values are the means or medians (third row; daytime temperature) ± 1.0 SE. Different superscripts within a row indicate a significant difference from an analysis of variance at $P < 0.05$.

Growth irradiance treatment (% full sun)	1	55	100
Total daily photon flux density (mol · m^{-2})	0.17^{A} (± 0.01)	11.66^{B} (± 0.60)	21.01^{C} (± 0.95)
Maximum photon flux density (μmol · m^{-2} · s^{-1})	87^{A} (± 8)	947^{B} (± 37)	1629^{C} (± 58)
Median day time temperature (°C)	27.1^{A} (± 0.1)	29.3^{B} (± 0.2)	28.9^{C} (± 0.2)
Maximum day time temperature (°C)	30.6^{A} (± 0.2)	34.5^{C} (± 0.4)	33.1^{B} (± 0.4)

dalenae displays many traits typical of sun-adapted plants (Pfitsch and Smith, 1988; Königer et al., 1995; Skillman and Winter, 1997; Skillman et al., 1999; Valladares et al., 2002). First, the fact that *A. magdalenae* is a constitutive CAM species is unexpected for an understory species because of the greater quantum costs for carbon gain in CAM compared to C3 photosynthesis (Winter and Smith, 1996). Second, shade-grown plants of *A. magdalenae*, compared to co-occurring C3 understory plants, maintain substantially higher rates of light-saturated photosynthetic oxygen evolution (P_{max}) and leaf nitrogen contents (N_L) when expressed on an area basis (Königer et al., 1995; Skillman et al., 1999). Finally, like many bromeliad species, the leaves of this species are thick and are oriented semi-vertically, lowering the efficiency of light interception per unit leaf area compared to typical C3 shade plants (Skillman et al., 1999; Valladares et al., 2002). Moreover, *A. magdalenae* is not an isolated anomaly but rather appears to be representative in most respects of a large number of shade-tolerant, constitutive-CAM bromeliad species (Griffiths and Smith, 1983; Medina, 1987; Fetene et al., 1990; Medina et al., 1991; Martin, 1994; Benzing, 2002; Fernandes et al., 2002; Scarano et al., 2002). The fact that *A. magdalenae*, like other shade-tolerant CAM bromeliads, displays many traits characteristic of sun-adapted species, suggests two questions in the context of classic sun/shade trade-off models: Does *A. magdalenae* exhibit the high degree of light-dependent phenotypic plasticity found in typical sun-adapted species? Does *A. magdalenae* perform better in high light than would otherwise be expected of a shade-tolerant species? We hypothesized that established individuals of this shade-tolerant CAM plant might perform far better than *D. longispatha*, a typical shade-adapted C3 plant, when both species were grown in high light.

The specific objectives of this study were to examine the influence of extreme variation in growth irradiance on photosynthesis, biomass allocation, and plant growth in established individuals of *A. magdalenae* (CAM) and *D. longispatha*. *Dieffenbachia longispatha* was selected for comparative purposes based upon previous work showing that it commonly occurs with *A. magdalenae* in central Panama where this work was conducted and because it exhibits typical shade-adapted traits that potentially limit its performance in bright sun (Königer et al., 1995; Skillman and Winter, 1997; Skillman et al., 1999; Valladares et al., 2002). Both species were grown for 5 months under approximately 1, 55, and 100% of full sun conditions during the wet season in central Panama. Leaf structural and functional attributes were evaluated and patterns of biomass allocation and growth were quantified. Findings from this work may help explain why the representative shade-tolerant CAM bromeliad *A. magdalenae* seldom occurs in open habitats despite having many characteristics typical of sun-adapted plants.

MATERIALS AND METHODS

Study site and study species—This study was conducted in Panama with plants from the Barro Colorado Nature Monument (BCNM), a forest reserve in central Panama (9°10′ N, 79°51′ W) that includes Barro Colorado Island (BCI) and the adjacent mainland peninsulas. The BCNM is classified as a tropical moist forest under the Holdridge life zone system (Croat, 1978). Annual precipitation averages approximately 2600 mm with a distinct wet (May–December) and dry season (January–April). Detailed descriptions of vegetation, climate, and ecology of the island can be found in Croat (1978).

Photosynthetic and growth responses of the terrestrial CAM bromeliad *A. magdalenae* and the C3 perennial herb, *D. longispatha* were assessed when grown under a broad range of light conditions, from ~1 to 100% of full sun. Both of these herbaceous, perennial monocots are abundant and often co-occur in the BCNM (Croat, 1978; Skillman et al., 1999). Furthermore, both species have similar in situ annual growth rates, rooting depths, and biomass allocation patterns (Skillman et al., 1999).

Growing conditions—Small juvenile plants of both species were collected on the Gigante Peninsula of the BCNM and were allowed to establish in 1-L pots for several months under low light (2–5% full sun) in a screened growing house. An initial harvest was made on eight randomly chosen plants of each species at the start of the wet season. At the same time, the remaining potted plants of both species were transplanted into 19-L pots containing a 1 : 2 mixture of washed sand and forest soil. Between six and eight plants of each species were then randomly assigned to each of three light treatments. Using neutral density shade screen, shade house structures were established for growth of plants under full sun (i.e., no shade screen), approximately 50% of full sun, and approximately 1% of full sun. These plants were grown for 5 mo under these conditions. Light and temperature conditions in the three light treatments were frequently monitored (Table 1) with calibrated quantum sensors and shielded thermocouples connected to an electronic datalogger (Li-1000, Li Cor, Lincoln, Nebraska, USA). On average, the low-light treatment received ~1% of the total daily PFD of the full sun treatment, while the medium light treatment received ~55% of the full sun treatment (Table 1). All plants received natural rainfall and additional water as needed. All plants received commercial nutrient fertilizer (Miracle-Gro 15-30-15 All Purpose Plant Food, Marysville, Ohio, USA) at the recommended concentrations once per week during establishment and throughout the course of the experiment.

Foliar characteristics—Near the end of the 5-mo growing period, several aspects of leaf physiology and composition were evaluated on healthy, fully expanded leaves of both species. Sampled leaves had developed on the plants in each of the respective light treatments. The maximum light- and CO_2-saturated rate of photosynthetic oxygen production (P_{max}) was measured at 30°C, 5% CO_2 in air, under ~1500 μmol photons · m^{-2} · s^{-1} in harvested

leaf discs of a known area using a gas phase oxygen electrode (model LD2, Hansatech Instruments, Kings Lynn, UK) as described in Skillman et al. (1996). Photosynthetic physiology in CAM plants can have four distinct phases (sensu Osmond, 1978), which must be considered in the planning and interpretation of photosynthesis measurements. Phase I refers to the nighttime CO_2 uptake through open stomates wherein carboxylation reactions are mediated by phosphoenolpyruvate carboxylase (PEPCase) leading to the nocturnal accumulation of malic acid in the leaves. Phase III refers to the decarboxylation of the stored malic acid during the day behind closed stomates and the concurrent fixation of this endogenous CO_2 by ribulose bisphosphate carboxylase/oxygenase (RUBISCO). Phase II refers to a transitional period between phase I and phase III early in the morning when both carboxylases (PEPCase and RUBISCO) are potentially active and the open stomata allow uptake of atmospheric CO_2. Phase IV refers to a transitional period between phase III and phase I late in the day when open stomata allow the uptake of atmospheric CO_2, which is fixed predominantly via RUBISCO. Preliminary data confirmed that P_{max} values were independent of the time of day they were measured. Nonetheless, all photosynthetic oxygen flux measurements were made between mid-morning and mid-afternoon, presumably corresponding to the daytime decarboxylation period (CAM phase III). Leaf absorptance was measured on the same leaf pieces using a Li 1800 spectroradiometer (Li Cor). These same leaf samples were oven-dried (70°C) to a constant weight to determine the specific leaf area (SLA; leaf area per unit leaf dry mass). Leaf chlorophyll and nitrogen (N_L) concentrations and carbon isotope ratios were measured for leaf discs of known area subsampled from the same leaves used in the photosynthesis measurements. Chlorophyll concentrations were assessed spectrophotometrically in 80% acetone extractions made from fresh leaf samples after Porra et al. (1989). Foliar N_L was determined with dried, ground leaf samples using a CHN elemental analyzer (Heraeus, Hanau, Germany). Relative differences in carbon isotope ratios ($\delta^{13}C$) were determined for CO_2 derived from 2- to 4-mg samples of dried ground leaf tissue at the Duke University Phytotron. Samples were combusted under oxygen in an elemental analyzer (NA1500 Series 1, Carlo Erba Instruments, Milan, Italy) and analyzed in an isotope ratio mass spectrometer (Siras series II, Micromass, Manchester, UK) in automatic trapping mode. After correcting for other isotopes, the relative abundance of ^{13}C in each sample was referenced against the relative abundance of ^{13}C in a CO_2 standard that had been calibrated against Pee Dee Belemite. Sample sizes for the P_{max}, leaf absorptance, chlorophyll concentration, N_L, and $\delta^{13}C$ data sets were four per species from each of the three light treatments. The maximum photochemical efficiency of photosynthesis was assessed in situ before dawn by measuring the chlorophyll fluorescence parameter, Fv/Fm (PAM 2000 chlorophyll fluorometer, Walz, Effeltrich, Germany) on healthy, fully enlarged intact leaves that had been dark-adapted for 10 min as per standard protocols (Skillman et al., 1996). This was done on six to eight plants per species from each of the three light treatments. To assess nocturnal acidification (CAM phase I activity), dawn-to-dusk fluctuations in titratable leaf sap acidity were measured in four *A. magdalenae* plants from each of the three light treatments.

Biomass allocation and growth—At the end of the 5-mo growing period, plants were removed from the pots, carefully washed free of soil, and divided into leaves, stems/support tissues (includes petioles for *D. longispatha* but not *A. magdalenae*, which is apetiolate), and rhizomes/roots. The total leaf area of each harvested plant was evaluated with an optical leaf area meter (Li-3100, Li Cor). The components of each plant were dried separately to a constant mass and the dry masses were recorded. The relative growth rate (RGR) is the natural log of the change in plant dry mass over the duration of growth. The leaf area ratio (LAR) is the total plant leaf area divided by the total plant dry mass at final harvest. The growth rate per unit leaf area (unit leaf rate; ULR) is estimated from the ratio of RGR over LAR.

Statistics—Effects of growth irradiance on measured variables were inferred using analysis of variance methods and Scheffé means comparisons tests run separately for each species (Steel and Torrie, 1980). Before running statistical models, data sets were checked for homogeneity of variance and, when necessary, appropriate transformations were made.

RESULTS

Foliar characteristics—The maximum rate of photosynthesis (P_{max}), on a leaf area basis, in *A. magdalenae* was relatively high in shade-grown plants but did not acclimate to increases in light (Fig. 1A). *Dieffenbachia longispatha* acclimated to the increasing light with a modest increase in P_{max} per unit leaf area, as is generally observed in shade-adapted C3 plants (Fig. 1A). This same general pattern held when P_{max} was expressed on the basis of leaf dry mass, leaf chlorophyll, and leaf nitrogen (Table 2); P_{max} in *A. magdalenae* was relatively high when grown in deep shade but showed no significant changes with increasing growth irradiance, while P_{max} in *D. longispatha* tended to increase with growth irradiance. *Aechmea magdalenae* had a light-dependent increase in carbon uptake during CAM phase I, as indicated by the nocturnal acidification data (Table 2).

Both species had qualitatively similar changes in leaf morphology and nitrogen concentration in response to the increase in light (Fig. 1B, C). Plants of both species grown in 55% and 100% of full sun produced heavier, thicker leaves than plants grown in deep shade, accounting for the tendency of SLA to decline with light. The SLA of *A. magdalenae*, across all light treatments, was lower than that of *D. longispatha*. Nitrogen concentration per unit leaf area increased with light in both species. Leaf nitrogen concentration per unit area was greater in *A. magdalenae* than in *D. longispatha*, but this pattern was reversed when N_L was expressed per unit leaf mass (cf., Fig. 1B, C).

Pre-dawn measurements of dark-adapted Fv/Fm in leaves of plants in each of the light treatments indicate that both species were chronically photoinhibited when grown in full sun (Fig. 2A). This high-light effect was greater for *A. magdalenae* than it was for the shade-adapted C3 perennial, *D. longispatha*. Similarly, both species tended to have less chlorophyll per unit leaf area in full sun compared to 1% and 55% sun treatments, but this difference was only significant for *A. magdalenae* (Fig. 2B). Likewise, leaf absorptance declined with increasing light for both species, but the effect was greatest for *A. magdalenae* (Fig. 2C). The chlorophyll *a*/*b* ratio was unaffected by growth irradiance treatments in both study species (data not shown).

The $\delta^{13}C$ values for the CAM perennial, *A. magdalenae*, ranged between −13 and −17 per mil and between −28 and −32 per mil for the C3 perennial, *D. longispatha* (Fig. 3). The $\delta^{13}C$ values were observed to become less negative with increasing light in *D. longispatha* and, by contrast, became more negative with increasing light in *A. magdalenae*.

Allocation and growth—The allocation of plant biomass to foliage, belowground structures (roots and rhizomes), and support tissues (stem and petioles) as a percentage of total plant biomass is depicted for both study species from each of the three light treatments in Fig. 4. Less biomass was allocated to foliage (leaf mass ratio; LMR) and more allocated to support tissues in high light for both species. Absolute biomass belowground increased with growth irradiance in both species (data not shown), but in *D. longispatha* there was a proportionally greater increase in support tissue (thicker stems and petioles) so that the percentage belowground biomass (root mass ratio; RMR) decreased with increasing light. RMR for *A. magdalenae* responded more typically by increasing with increasing light. As expected based upon growth form differences, the

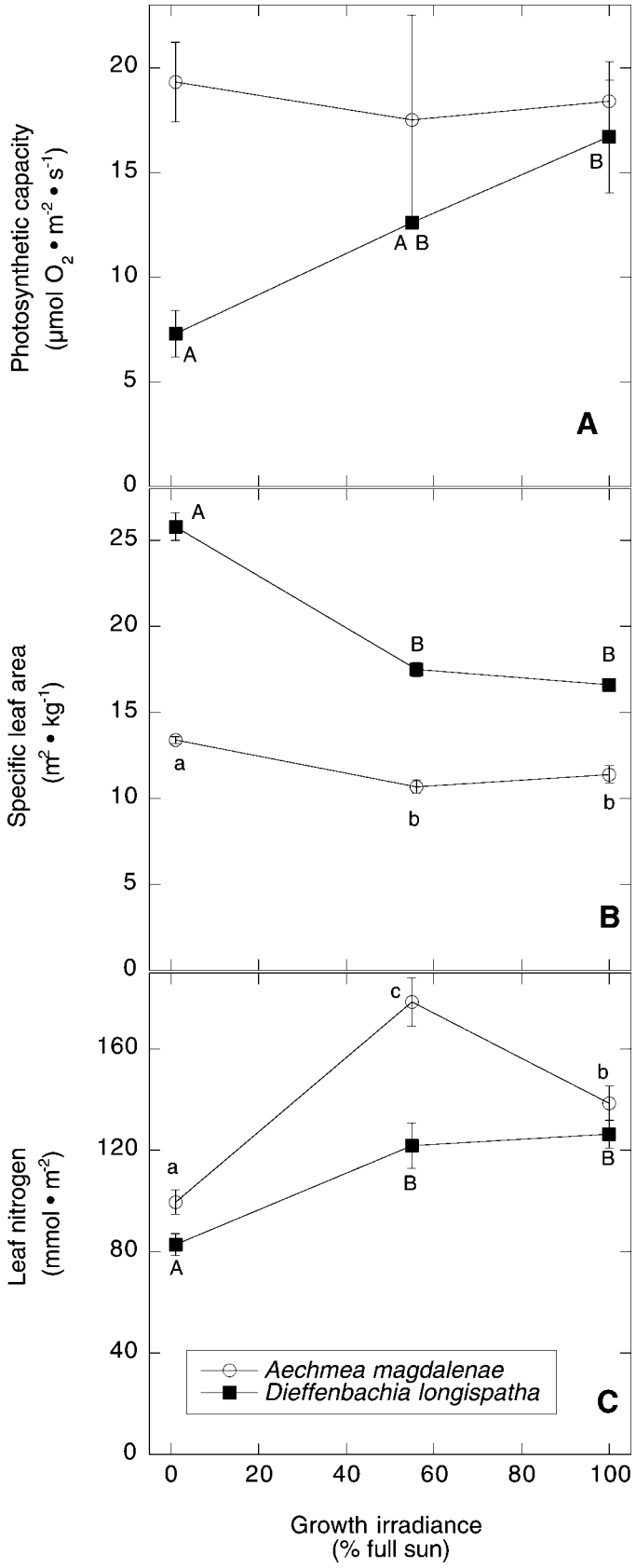

Fig. 1. (A) The light and CO_2 saturated rate of photosynthesis, (B) the specific leaf area, and (C) the nitrogen concentration in leaves sampled from four plants each of *Aechmea magdalenae* and *Dieffenbachia longispatha* from each of the three light treatments. Plotted points are means ± 1 SE. Significant differences between light treatments for each species are indicated by the different letters (lower case = *A. magdalenae*, upper case = *D. longispatha*) next to the data points for that species ($P < 0.05$ by Scheffe means comparison test). An absence of letters indicates that light treatment did not significantly affect that species for that variable.

largest contrast in allocation patterns between the two species is that, across all light levels, *A. magdalenae* has a much greater LMR and a much lower RMR than *D. longispatha*.

Both species had similar relative growth rates and unit leaf rates when grown in deep shade (Fig. 5A, B). Both species grew faster in the higher light treatments, but the strength of this light effect on plant growth was quite different for the two species. *Dieffenbachia longispatha* responded to the higher light treatments with a 10- to 12-fold increase in growth rate, but *A. magdalenae* only showed a 4- to 5-fold increase in growth rate. The analysis of variance indicated that, for each species, growth rates in the 55% and 100% sun treatments were statistically indistinguishable. Leaf area ratio (LAR) generally paralleled the treatment and species differences in LMR (compare Fig. 5C with Fig. 4), but the species differences in LAR were much smaller than they were for LMR, reflecting the low SLA (Fig. 1B) that is characteristic of *A. magdalenae*.

Nocturnal acidification provides an integrated measure of nocturnal carbon uptake which, in turn, is closely associated with overall daily carbon gain patterns in leaves of CAM plants. Consequently, measures of foliar nocturnal acidification may be expected to be more closely linked to whole-plant growth in different light environments than other leaf-level measures of photosynthetic activity such as P_{max} or Fv/Fm. In *A. magdalenae*, the magnitude of the growth irradiance effects upon CAM activity in leaf chlorenchyma cells and upon whole-plant growth was similar as indicated by the strong linear association between nocturnal acidification and ULR (Fig. 6).

DISCUSSION

Photosynthesis, photoacclimation, and photooxidative stress—Consistent with previous reports (Skillman et al., 1999), shade-grown *A. magdalenae* had a substantially higher P_{max} than is typically observed in C3 understory herbacaous plants when expressed per unit leaf area, per unit leaf nitrogen, and per unit leaf chlorophyll (Fig. 1A and Table 2). There were no species differences among shade-grown plants when P_{max} was expressed on a leaf mass basis. However, the similarity of P_{max} on a leaf mass basis between shade-grown *A. magdalenae* and *D. longispatha* may be misleading because the structural and functional characteristics of the leaves of these two species are quite different. *Dieffenbachia longispatha* produces classic mesomorphic leaves made of typical photosynthetic chlorenchyma dorsiventrally differentiated into palisade and spongy mesophyll layers (J. Skillman, personal observation). By contrast, a substantial portion of the mass of *A. magdalenae* foliage is nonphotosynthetic, including structural fibers and the prominent water storage parenchyma (Skillman et al., 1999). Nitrogen concentration per unit leaf mass in *A. magdalenae*, ranging from ~2% to 2.5%, was substantially lower than that of *D. longispatha*, ranging from ~3.5% to 4%, across all light levels (cf. Fig. 1B and C). This is consistent with the anatomical distinctions between these species because leaf

TABLE 2. Influence of growth irradiance treatments on different expressions of photosynthetic capacity (P_{max}) in the understory CAM plant *Aechmea magdalenae* and the understory C3 plant *Dieffenbachia longispatha* and nocturnal acidification (ΔH^+), a measure of CAM activity, in *Aechmea magdalenae* only. Growth irradiance treatment is expressed as a percentage of full sun conditions. Values are the means ± 1.0 SE. NA means ''not applicable''. Sample sizes for different measurements are as reported in the Materials and Methods. Different superscripts within a row for each species indicate a significant difference at $P < 0.05$.

	A. magdalenae			*D. longispatha*		
Growth irradiance treatment (% full sun)	1	55	100	1	55	100
P_{max} per unit leaf dry mass (nmol $O_2 \cdot g^{-1} \cdot s^{-1}$)	267 (±32)	216 (±54)	245 (±26)	241 (±34)	264 (±18)	335 (±49)
P_{max} per unit leaf nitrogen (μmol $O_2 \cdot$ mol $N^{-1} \cdot s^{-1}$)	193 (±13)	136 (±40)	135 (±18)	86^A (±10)	106^B (±10)	139^B (±32)
P_{max} per unit leaf chlorophyll (μmol $O_2 \cdot$ mmol $chl^{-1} \cdot s^{-1}$)	27.7 (±3.9)	39.7 (±13.4)	53.8 (±7.0)	11.1^A (±2.3)	18.5^B (±0.8)	31.1^C (±2.2)
Nocturnal ΔH^+ (mmol $H^+ \cdot m^{-2}$)	104^A (±4)	134^{AB} (±26)	148^B (±13)	NA	NA	NA

structural materials and nonphotosynthetic water-storage cells are expected to have lower nitrogen concentrations than green photosynthetic cells.

Dieffenbachia longispatha displayed a modest capacity for photosynthetic acclimation to increased light conditions with an increase in P_{max}, as is typical of shade-adapted species (Strauss-Debenedetti and Bazzaz, 1996). On the other hand, P_{max} did not change in response to increasing light in *A. magdalenae*. This is qualitatively consistent with fluorescence-based analyses of photosynthetic light acclimation in *A. magdalenae* previously reported (Skillman and Winter, 1997) and with findings reported for the shade-tolerant, terrestrial CAM bromeliad *Bromelia humilis* (Fetene et al., 1990). Thus, with respect to photoacclimation of P_{max}, shade-tolerant, terrestrial CAM bromeliads like *A. magdalenae* appear to have extremely limited phenotypic plasticity.

Even though P_{max} in *A. magdalenae* was constant under contrasting growth conditions, the light-dependent increase in nocturnal acidification (Table 2) indicates night-time carbon uptake was greater in high light compared to low (i.e., increased activity of CAM phase I). At the same time, the carbon isotope data (Fig. 3) suggest that there was also a light-dependent decrease in the duration of the day-time decarboxylation period (phase III) with a corresponding increase in daytime C3-like carbon fixation (i.e., increased duration of CAM phases II and/or IV). In principle, light-dependent reductions in the $\delta^{13}C$ in CAM foliage may be caused by (a) increasing diffusion limitations on nocturnal carbon fixation during phase I, and/or (b) an increased reliance on RUBISCO-mediated fixation of external CO_2 during phases II and IV when the stomates are open during the day (Farquhar et al., 1986; Winter and Holtum, 2002). But the observation that nocturnal acidification is higher rather than lower in *A. magdalenae* plants grown in high light largely rules out the first possibility (Table 2). And, consistent with the second possibility, gas-exchange studies by Pfitsch and Smith (1988) demonstrated an increase in the duration of phase IV, and to a lesser extent phase II, in high-light treated *A. magdalenae* plants. In addition, calculations based upon Winter and Holtum's (2002) empirically derived relationship between shoot $\delta^{13}C$ values and the percentage of 24-h carbon gain which occurs during the day also indicate an increase in daytime C3-like carbon fixation with increasing growth irradiance. These calculations, based upon data in Fig. 3, indicate that 24, 38, and 46% of the 24-h carbon gain in the *A. magdalenae* plants grown in low, medium, and high light, respectively, took place during phases II and/or IV. Consequently, we speculate that the absence of an acclimation response of P_{max} in *A. magdalenae* to increases in growth irradiance is functionally compensated for by the apparent flexibility in the relative expression of the different phases of the CAM cycle. This option as a means of greater carbon gain potential when grown in high light would not be available to C3 plants like *D. longispatha*, obscuring simple interpretations of phenotypic plasticity for carbon gain potential in CAM plants based on measurements of variation in P_{max}.

At the same time, the increased reliance on C3-like carbon fixation in *A. magdalenae* when grown in bright light may also have contributed to the severe photooxidative stress observed in this species. Indeed, assuming a light-saturated photosynthesis rate of 18 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Fig. 1) and the observed 148 mmol $\cdot m^{-2}$ of titratable acidity in high-light grown *A. magdalenae* (Table 2), it is estimated that under light saturation, the high light *A. magdalenae* plants would only have been able to sustain phase III for 2.2 h, albeit at a high fixation rate during this short interval. This is qualitatively consistent with the prior analysis of the isotope data and it means that, over most of the day, high light *A. magdalenae* plants would have been operating under limiting (i.e., external) CO_2 in phase II and/or IV. Although CO_2 supply limitations under bright light results in photoinhibition in C3 and CAM plants alike, diffusion limitations during the day when the stomates are open are likely to have been greater for *A. magdalenae* than for *D. longispatha* because thick succulent CAM leaves tend to have higher mesophyll resistances than thin C3 leaves (Maxwell et al., 1997). The validity of this latter explanation for severe photoinhibition in *A. magdalenae* would depend upon the internal O_2 concentrations in the leaves during phases II and IV, and the role of internal O_2 in promoting vs. mitigating photoinhibition (Maxwell et al., 1998). Neither factor is well understood at this time. Nonetheless, from the available data, growth in high light conditions appears to increase phase II and IV activities in *A. magdalenae*, which allows for increased carbon uptake capacity during the day, while also raising the quantum requirement of carbon fixation during phase II and IV by promoting photoinhibition.

Growth—Several authors have reported light limitations on growth for *A. magdalenae* plants in the forest (Pfitsch and Smith, 1988; Skillman et al., 1999; Villegas, 2001; Ticktin et al., 2003). Accordingly, these experimental shadehouse plants grew extremely slowly in deep shade and more quickly under brighter light (Fig. 5). What had not been predicted from these

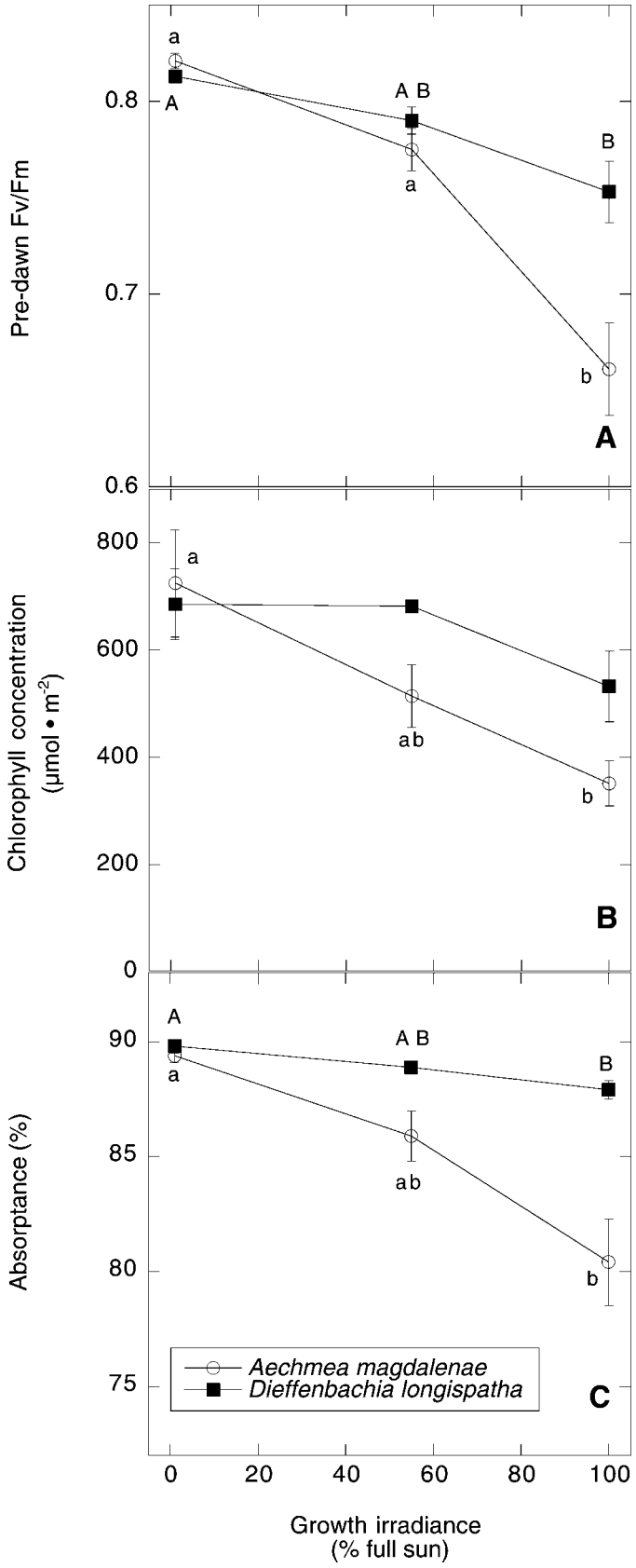

Fig. 2. (A) The pre-dawn chlorophyll fluorescence ratio, Fv/Fm (N = 6–8), (B) leaf chlorophyll concentration (N = 4), and (C) leaf absorptance of 400–700 nm light (N = 4) in leaves sampled from plants of *Aechmea magdalenae* and *Dieffenbachia longispatha* from each of the three light treatments. All other information is described in the caption for Fig. 1.

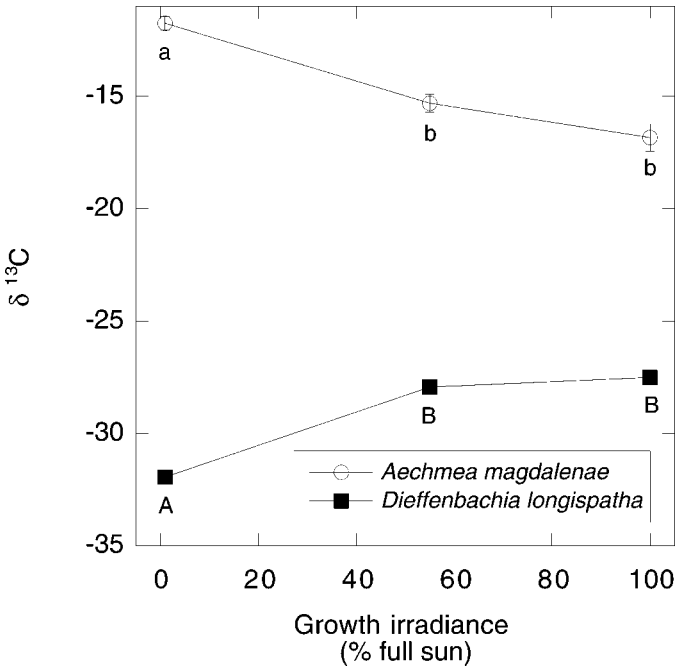

Fig. 3. Effect of growth irradiance on carbon isotope discrimination in leaves (N = 4) from *Aechmea magdalenae*, a constitutive CAM plant, and *Dieffenbachia longispatha*, a C3 plant, sampled from plants in each of the three light treatments. All other information as described in the legend to Fig. 1.

earlier in situ studies was that, in intermediate and high light, growth of *A. magdalenae* was still extremely slow when compared to a shade-adapted C3 species like *D. longispatha*. We interpret the growth rates for each of these species in the medium- and high-light treatments as being their maximal possible growth rates because they started out as small, juvenile plants and were grown under presumably non-limiting conditions of light, temperature, and soil resources. Thus, *A. magdalenae* exhibited a narrower range of light-dependent phenotypic adjustments in growth than *D. longispatha*, a result that contradicts our hypothesis.

The remarkably slow growth of *A. magdalenae* in full sun runs counter to our initial expectation. This is of interest because this species displays many morphological and physiological characters typical of sun-adapted plants. In terms of leaf morphology, leaf orientation, and biomass allocation, *A. magdalenae* has much in common with sun-adapted, leaf-succulent, desert CAM species like *Agaves* and *Yuccas* (Nobel, 1988), some of which can sustain remarkably high rates of growth in full sun given adequate water and nutrients (Nobel, 1996). Thus, plant morphological characters assessed here do not explain the poor growth performance of *A. magdalenae* in full sun. Although the mechanistic basis for the restricted growth in full sun is poorly understood, the data presented here suggest that photosynthetic physiology, more so than whole-plant morphology, places a strong constraint on greater growth of *A. magdalenae* in high light. The inability to increase photosynthetic capacity (P_{max}) with increasing light

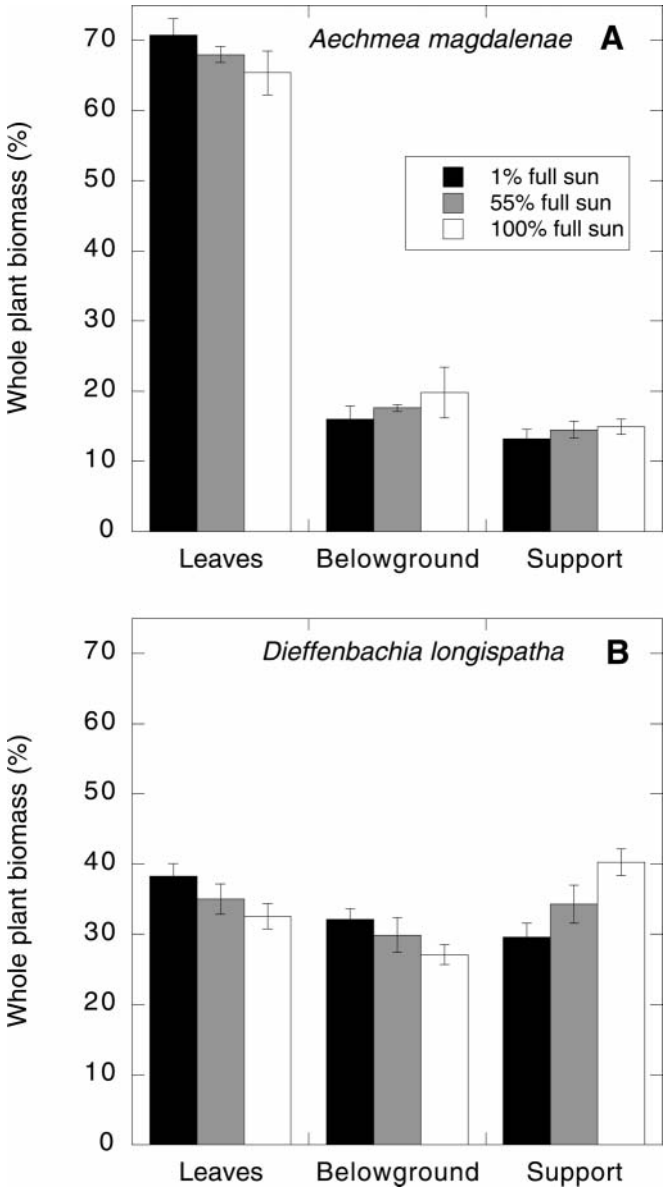

Fig. 4. Biomass allocation patterns in (A) *Aechmea magdalenae* and (B) *Dieffenbachia longispatha* in plants from each of the three light treatments (N = 6–8).

(Fig. 1), the high susceptibility to chronic photoinhibition (Fig. 2), and the close association between nocturnal acidification of individual leaves and whole-plant growth per unit leaf area (Fig. 6), are each consistent with this suggestion. A more complete understanding of the proximal reasons for this limited growth potential awaits further study.

Conclusions—*Dieffenbachia longispatha* and *A. magdalenae* alike can *survive* in bright light, but inherent limitations on photosynthetic physiology and growth make it unlikely that either species could attain sufficient growth rates to *thrive* in productive, high-light habitats. More specifically, we have shown that this representative understory CAM bromeliad, *A. magdalenae*, has a limited ability to acclimate to high light and performs quite poorly in high light, even when compared to the more typical shade-adapted tropical forest understory

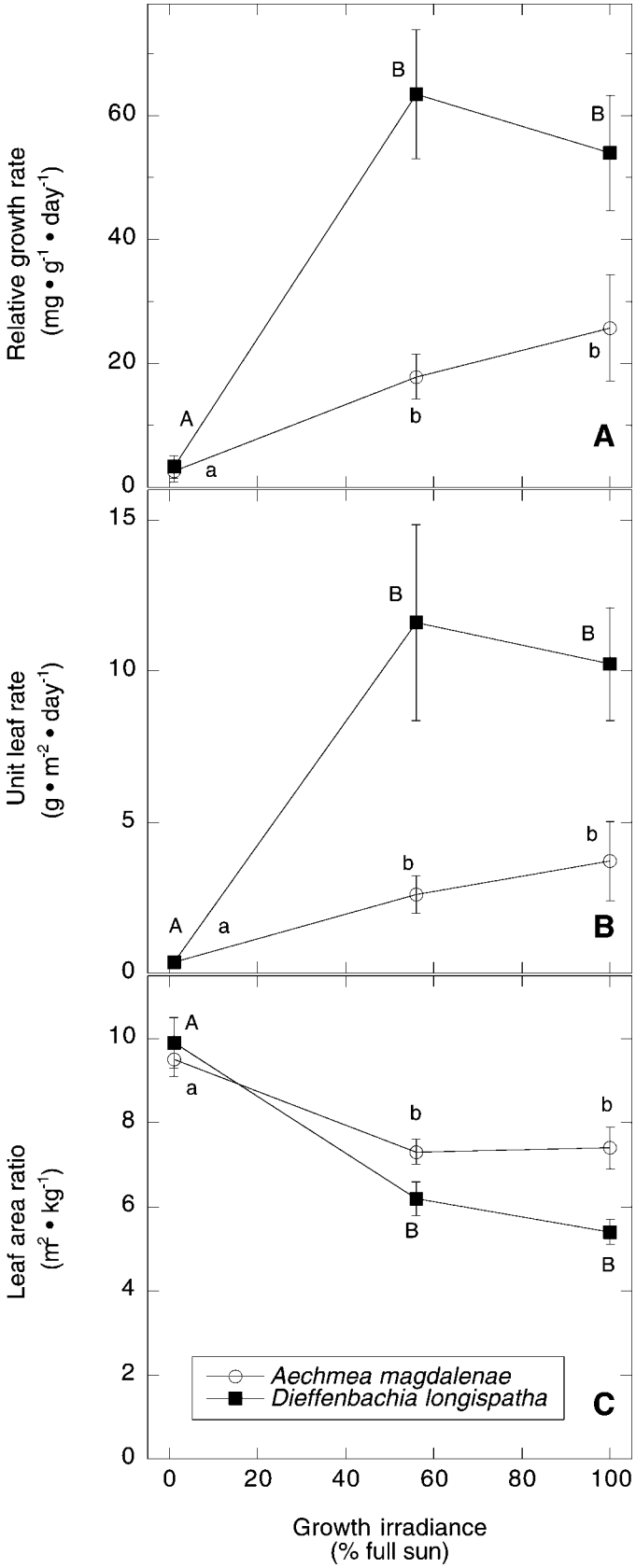

Fig. 5. (A) The relative growth rate (RGR), (B) the unit leaf rate (ULR), and (C) the leaf area ratio (LAR) in 6–8 plants of both study species from each of the three light treatments. All other information is described in the caption for Fig. 1.

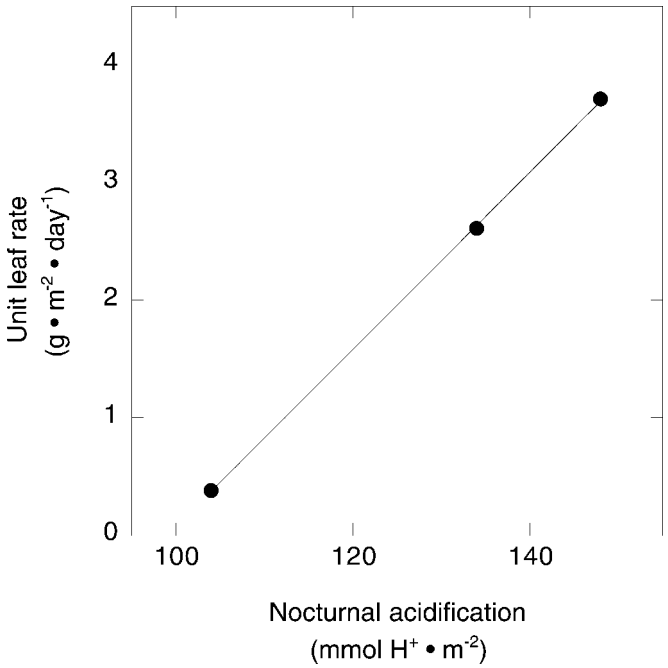

Fig. 6. Relationship between the whole-plant growth rate per unit leaf area (ULR) and nocturnal acidification in leaves of *Aechmea magdalenae* grown under 1, 55, and 100% of full sun. Plotted data are from Table 2 and Fig. 5. The equation for the line of best fit is ULR $= -7.5 + 0.0755 \times \Delta H^+$, $r = 0.9999$.

C3 plant, *D. longispatha*. This argues for the interpretation that *A. magdalenae* is actually highly specialized for life in the understory, despite having many characteristics in common with more productive sun-adapted species. It will be interesting to see if these results can be generalized to various other shade-tolerant, terrestrial CAM bromeliads. The demonstration of strong shade-adaptation in this terrestrial understory bromeliad is also of interest for understanding the evolution of epiphytism in this genus because many related *Aechmea* species are epiphytic, potentially living in bright light in the upper canopy of neotropical forests (Crayn et al., 2004). Viewed more broadly, these findings challenge classic tradeoff models of sun- vs. shade-adapted species. This work demonstrates that the suite of traits in the archetypal shade-adapted species *D. longispatha* (i.e., thin, horizontally positioned, C3 leaves with low photosynthetic capacities) is not necessary for shade adaptation. Simultaneously, we have demonstrated that the reciprocal suite of traits exhibited by *A. magdalenae* (i.e., thick, vertically positioned CAM leaves with a high photosynthetic capacity), does not guarantee ecological success in high light.

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