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Photosynthesis and Optimal Light Microhabitats for a Rare Cactus, *Mammillaria gaumeri*, in Two Tropical Ecosystems

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ABSTRACT

Mammillaria gaumeri, an endemic cactus from Yucatan, is threatened due to human-mediated habitat fragmentation but knowledge regarding factors that would inform management plans is limited, including information on optimal microhabitats and growth. We studied seasonal patterns of microclimate, net CO₂ uptake and growth of adult individuals during the dry, rainy and northwind (late fall to winter) seasons in separate populations located in a coastal dune and in a dry forest. To provide an assay of primary productivity, we measured the production of new axillary buds (areoles) from the apex. We found that patterns of net CO₂ uptake in the three seasons were consistent with obligate crassulacean acid metabolism. The reduction in soil water potential and the increase in water vapor pressure deficit led to a reduction in 24-h net CO₂ uptake from 18.0 to 1.3 mmol CO₂/m², after 30 d of drought. Dry-weight gain was maximal during the rainy season and there was no growth during the dry season, thus seasonal patterns of net CO₂ uptake and growth for *M. gaumeri* reflected soil and atmospheric water contents. Annual dry-weight gain increased linearly with plant size and with total daily photosynthetic photon flux density (PPFD) up to 80 percent of ambient. Maximal growth was in exposed microhabitats receiving 60–80 percent of total ambient PPFD. We hypothesize that low-magnitude disturbances, resulting in more exposed microhabitats, might be beneficial for growth and conservation of adult individuals of this rare species.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Cactaceae; coastal dune; Crassulacean acid metabolism; photosynthetic photon flux density; relative growth rate; tropical dry forest; Yucatan.

MEXICO IS THE MOST IMPORTANT CENTER FOR DIVERSITY OF THE FAMILY CACTACEAE and of the 850 cactus species native to Mexico, 285 are listed in the National Government Document for the Protection of Flora and Fauna as threatened or in a degree of danger (Diario Oficial de la Federación 2001). *Mammillaria gaumeri* (Britton & Rose) Orcutt is a rare globular cactus endemic to the Yucatan Peninsula, which occurs only in the northern coast and is restricted to the coastal dune scrubland and the tropical dry deciduous forest (Durán *et al.* 1998). Human activities, such as road construction, cattle range management, and agriculture have fragmented *M. gaumeri* populations (Flores & Espejel 1994, Chen *et al.* 1999).

Microclimate influences processes such as photosynthesis and respiration that directly affect plant productivity as well as other processes that affect seedling and adult survival, clonal architecture, and growth habit (Jones 1985, Kephart & Paladino 1997). Microclimatic information is thus vital for field studies and the elaboration of models and management plans for endangered plant species. Unfortunately, species responses to small-scale microclimatic variability or heterogeneity receive little attention (Bell & Lechowics 1994). Consequently, many ecological studies of threatened plants lack the necessary information in order to apply conservation models for effective management (Schemske *et al.* 1994).

Mortality rates of cacti decrease with plant size, while fecundity and growth rates increase (Schmalzel *et al.* 1995, Godínez-Alvarez

et al. 1999), as occur for most plants (Zotz 2000); thus, individual growth rates can be predictive of survival. Time of flowering also depends on individual biomass (García de Cortázar & Nobel 1992, Bowers 1996), and a positive relationship exists between plant size and fruit production (Rae 1995, Bullock & Martijena 1998). Because many cactus species can reproduce vegetatively as well as sexually, the survival and expansion of populations of endangered and endemic species can depend directly on the primary productivity of its members.

We measured microclimatic factors simultaneously with net CO₂ uptake and growth for *M. gaumeri* in the field in two sites: a coastal dune and a dry deciduous forest. We characterized the local microclimate surrounding individuals, quantified primary productivity of these individuals using a nondestructive measurement of growth, and were thus able to predict individual plant growth rates under different conditions to determine particular periods of productivity and stress. Such information will assist in propagation efforts and site selection for the reintroduction of this endangered species. This information will also complement the demographic, population genetics, and pollination studies, which are currently underway for this rare species.

METHODS

FIELD SITES.—The climate of the northern coast of the Yucatan Peninsula is semi-arid with an average mean air temperature of

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26°C, a maximum of 45°C, and a minimum of 10°C (Thien *et al.* 1982). The region receives < 700 mm average annual precipitation, most of which occurs during the rainy season (June–October). Some precipitation (20–60 mm) occurs in the northwind season from November to February, which is characterized by strong winds (> 80 km/h) and relatively low temperatures (< 22°C). A marked dry season occurs from March to May (Orellana 1999). This study was conducted at San Benito (21°19'10" N, 89°30'40" W), a coastal dune scrubland, and Ría Lagartos (21°34'15" N, 88°06'40" W), a tropical dry deciduous forest. During the last week of April 2003, we mapped and measured all individual *M. gaumeri* using a grid search pattern over 1 ha for each site. The coastal dune vegetation is mostly less than 1 m in height but can reach from 3 to 5 m; common species are *Bravaisia berlandieriana* (Nees) T. F. Daniel (Acanthaceae), *Cordia sebestena* L. (Boraginaceae), *Coccoloba uvifera* (L.) L. (Polygonaceae), and several succulent plant species: *Agave angustifolia* Haw. (Agavaceae), *Acanthocereus tetragonus* (L.) Hummelinck (Cactaceae), *Opuntia dillenii* (Ker Gawl.) Haw. (Cactaceae), and *Myrmecophila christinae* var. *christinae* Carnevali & Gómez-Juárez (Orchidaceae). In the tropical dry deciduous forest, the vegetation height is from 10 to 15 m and most of the trees are leafless during the dry season. Most of the tree species in this community belong to the legume Family; some common tree species are *Acacia gaumeri* S.F. Blake, *Apoplanesia paniculata* C. Presl, *Caesalpinia gaumeri* Greenm., *Diphysa carthagenensis* Jacq., *Leucaena leucocephala* (Lam.) de Wit, *Lysiloma latisiliquum* (L.) Benth. and *Piscidia piscipula* (L.) Sarg.

MICROCLIMATE AND GAS EXCHANGE.—During the rainy season 2003, we measured the photosynthetic photon flux density (PPFD) for 48 h about 20 mm above the center of each of 39 *M. gaumeri* individuals. Twenty gallium arsenide phosphide photodiodes (Hamamatsu Corporation, Bridgewater, NJ, U.S.A.), previously calibrated against a quantum sensor (LI190S, LI-COR, Lincoln, NE, U.S.A.), were connected to a datalogger (CR21X, Campbell Scientific Inc., Logan, UT, U.S.A.) and used to measure PPFD (Pontauiller 1990) simultaneously with a reference quantum sensor placed 5 m above the ground in a nonshaded location. It did not rain during these PPFD measurements. In addition, we measured instantaneous PPFD 20 cm above the ground in 40 randomly selected locations along five 50-m transects using a quantum sensor (LI190s, LI-COR).

In situ gas exchange was measured for four plants simultaneously (mean diameter = 7.0 ± 3.0 cm) with 1.0×10^{-3} m³ cylindrical acrylic chambers placed over the exposed stems and sealed at the bases of the stem with plastic putty. Plants received about 60 percent of ambient PPFD and were within an area of 25 m². The chambers were connected to an infrared gas analyzer (LI-6400, LI-COR) and gas flow was controlled automatically by a set of solenoid valves. Measurements were made automatically every 10 min for 72 h for each season using a datalogger (CR21X, Campbell Scientific), equipped with a 32-channel multiplexer (AM416, Campbell Scientific). Every 5 sec during gas-exchange measurements, we recorded PPFD at 20 mm above each plant and plant temperature, measured with copper–constantan thermocouples 0.2 mm in diameter, inserted 2 mm into the plant. Additionally, we measured

stem temperature for and PPFD above four additional plants in similar microsites. PPFD (Par Lite, Kipp & Zonen, Delft, The Netherlands), air temperature, and relative humidity (HPM45C-L Vaisala shielded probe, Campbell Scientific) were measured at 5 m above the ground for reference. We obtained the stem-to-air water vapor pressure deficit using equations from Jones (1992). At each site, we collected 10 soil samples at a depth of 15 cm (rooting depth is between 1 cm and 15 cm) and determined soil water content gravimetrically (Rundel & Jarrell 1989). We calculated soil water potential from moisture characteristic curves obtained with a WP4 water potential meter (Decagon Devices, Pullman, WA, U.S.A.).

GROWTH.—Because stem height and diameter are not reliable measurements of growth for cacti due to reversible changes in stem water content (Nobel 1988, Mauseth 2004), the production of new axillary buds (areoles) was used as an index. The axillary buds on *M. gaumeri* are distinct, small cushion-like areas from which trichomes, spines, glochids, or flowers may arise. To facilitate identification of newly developed areoles, at the beginning of April 2003 we removed the central spine of three recently developed areoles from the trichome-covered apices (a region *ca* 50 mm in diameter) of 39 plants at each site. At the end of each month, we noted the position of the marked areoles and relative to those, counted the newly developed areoles. We made linear regressions between the diameter of the plant measured at the root–stem junction and total dry weight of the stem to calculate the total dry weight of the stem for any plant diameter. We chose the diameter at the root–stem junction because it changes little compared to the stem diameter. Resulting equations were $y = -0.55 + 1.03x$ ($r^2 = 0.9786$, $P < 0.01$) for plants < 4 cm in diameter at the root–stem junction, and $y = -33.69 + 10.32x$ ($r^2 = 0.9842$, $P < 0.01$) for plants > 4 cm in diameter (Fig. 1A). The sigmoid relationship between the diameter at the root–stem junction and individual areole dry weight was $y = 0.181/(1 + e^{-(x - 6.36)/1.66})$ (Fig. 1, $r^2 = 0.9908$, $P < 0.01$). Stem and areoles samples were dried using a mechanical convection oven (Instrumentos Científicos, México City, México) at 80°C for 3 d. The relative growth rate (RGR) for single individuals was calculated using the equation by Hunt (1982, revised by Hoffmann & Poorter 2002), using the calculated total dry weight of the stem as the initial dry weight.

STATISTICAL ANALYSIS.—The light environment between the two habitats was evaluated with a *t* test. The relationship between growth, plant diameter, and PPFD was evaluated by regression analysis and the slopes of the regression lines were compared to an analysis of covariance (ANCOVA; Zotz *et al.* 2002). Percentages were transformed by the arcsine of the square root before analysis to achieve linearity (Sokal & Rohlf 1995). Normality of distributions was tested using the Kolmogorov-Smirnoff test. To compare net CO₂ uptake rates between site and season, a two-way repeated measures analysis of variance (ANOVA) was used. Means were compared with a Tukey's test and all analyses were performed using Statistica v. 6.0 (StatSoft Inc., Tulsa, OK, U.S.A.).

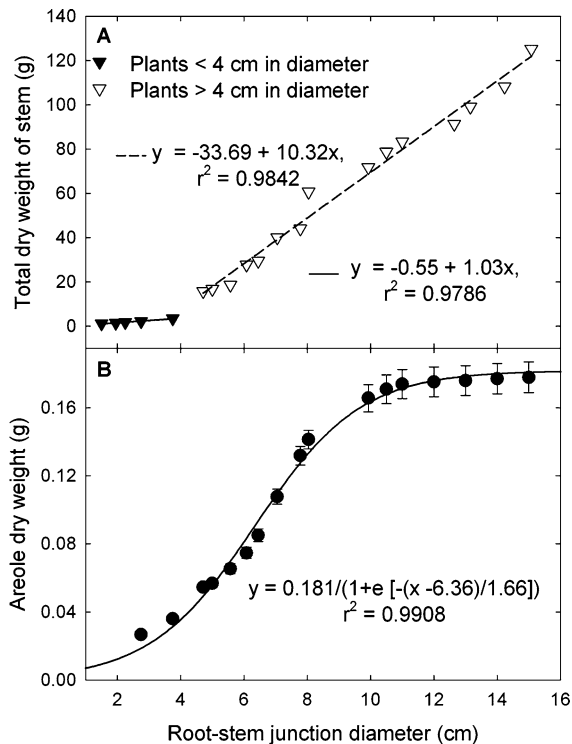


FIGURE 1. (A) Linear regression between plant size (diameter at the junction between the stem and the root in cm) and total stem dry weight (g). (B) Sigmoid regression between plant size and areole dry weight (g). Symbols are mean dry weight \pm SE, $N = 10$.

RESULTS

LIGHT MICROENVIRONMENT.—In both the coastal dune scrubland and the tropical dry deciduous forest, average daily PPFD received by adult plants of *M. gaumeri* was similar ($P > 0.05$). In the coastal dune, the mean (SE) and mode of PPFD received by plants were 55.3 (2.7) percent and 50–60 percent of ambient PPFD, while in the dry forest, the mean and mode were 57.7 (4.0) percent and 40–50 percent of ambient ($P = 0.46$ and $P = 0.50$, respectively). In the coastal dune, the mode occurred under a canopy of shrubs, the most common of which were *Bravaisia berlandieriana* and *C. uvifera* (mean height = 50 cm). In the dry forest, the mode occurred under the canopies of both *D. carthagenensis* and *Enriquebeltrania crenatifolia* (mean height = 1.3 m).

In the coastal dune, about 70 percent of the microsites received a PPFD < 60 percent of the ambient (Fig. 2). Light microsites of 20–40 percent of ambient were common under the canopies of *Bravaisia berlandieriana*, *C. uvifera*, *A. angustifolia*, *Coccothrinax readii*, and unidentified grass species. In contrast, microsites in the dry forest were more exposed, with about 60 percent of the microsites receiving > 60 percent of ambient PPFD. These microsites were common at the edges of tree gaps and vegetation islands within gaps.

A strong correlation between the percentage of ambient PPFD received by an individual and its size occurred in the dry forest

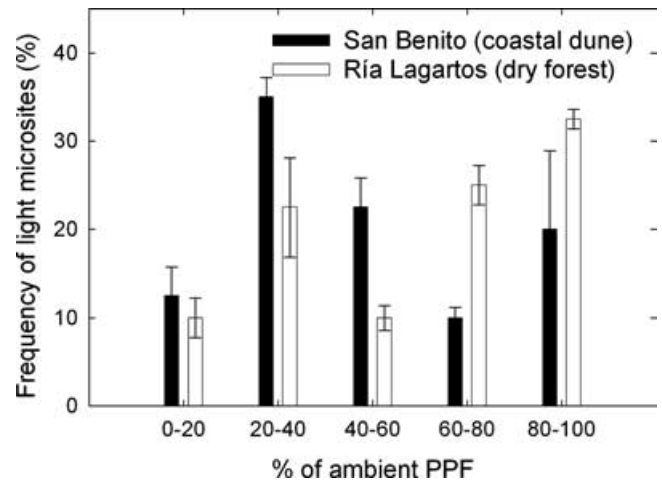


FIGURE 2. Frequency of light microsites with respect to the percentage of total daily photosynthetic photon flux (PPFD) received 20 cm above the ground, relative to the PPFD measured at the top of the canopy. Data are an average of five transects \pm SE, $N = 40$.

($r^2 = 0.73$, $P < 0.001$; Fig. 3); in the coastal dune the correlation was weaker but also statistically significant ($r^2 = 0.34$, $P < 0.001$). The mean diameter of individuals was similar in both locations (7.0 ± 0.3 cm; $P < 0.01$) and those individuals received about 57 percent of ambient PPFD.

MICROCLIMATE AND CO₂ EXCHANGE.—Average diurnal/nocturnal ambient temperatures were significantly different between seasons but very similar between sites (Fig. 4A and B). During the dry season, the average diurnal/nocturnal ambient air temperature was $34.3 \pm 0.6/26.3 \pm 0.4^\circ\text{C}$ for the dry forest and $34.6 \pm 0.6/26.4 \pm 0.4^\circ\text{C}$ for the coastal dune ($P > 0.05$). For the rainy season, average diurnal/nocturnal ambient air temperature for both sites was 11.8 percent lower than during the dry season ($P < 0.01$). During the

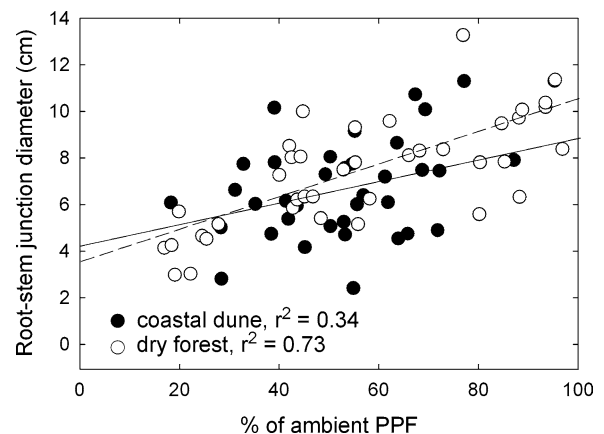


FIGURE 3. Linear regression between plant size and percentage of total daily PPFD received, relative to the PPFD measured at the top of the canopy.

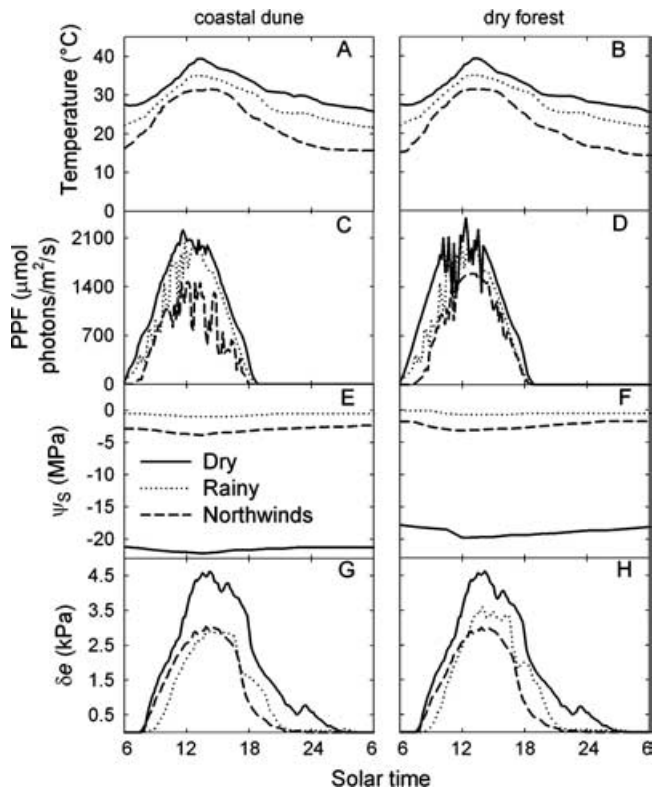


FIGURE 4. Daily time courses of (A) air temperature, (C) photosynthetic photon flux (PPFD), (E) soil water potential (Ψ_s), and (H) water vapor pressure deficit (δe), during clear days in the dry (26–28 April 2003), rainy (26–28 July 2003) and northwind (26–28 November 2003) seasons for San Benito (coastal dune); and daily time courses of (B) air temperature, (D) PPFD, (F) Ψ_s , and (H) δe , during clear days in the dry (3–5 May 2003), rainy (3–5 August 2003) and northwind (3–5 December 2003) seasons for Ría Lagartos (dry forest). Data are the averages for the 3 d measured.

northwind season, diurnal/nocturnal temperatures averaged $27.2 \pm 0.5/18.5 \pm 0.3^\circ\text{C}$ for both sites, a reduction of 25.1 percent compared to the dry season ($P < 0.01$).

During the dry season, total daily PPFD above the canopy was 46.6 ± 3.4 moles of photons/ m^2 for the dry forest, similar to 46.6 ± 2.8 mol/ m^2 for the coastal dune ($P > 0.05$; Fig. 4C and D), with a photoperiod of 12 h and maximum instant PPFD of *ca* $2250 \mu\text{mol/m}^2/\text{s}$. During the rainy season, the maximum instant PPFD was *ca* $2000 \mu\text{mol/m}^2/\text{s}$, and compared to the dry season, there was an 18 percent decrease in total daily PPFD ($P < 0.01$). During the northwind season, because of a photoperiod of only 11 h and maximum instant PPFD of *ca* $1500 \mu\text{mol/m}^2/\text{s}$, there was a 25 percent reduction in total daily PPFD in comparison to that of the dry season ($P < 0.01$).

After 30 d of drought during the dry season, the lowest soil water potential at a depth of 15 cm (Ψ_s) occurred soon after midday and was -19.8 ± 1.6 MPa for the dry forest and -22.4 ± 2.3 MPa for the coastal dune ($P > 0.05$; Fig. 4E and F). For both sites during the rainy season, average Ψ_s was near field capacity (-0.05 MPa),

due to frequent rain events. During the northwind season, average Ψ_s was -2.32 ± 0.39 MPa for the dry forest and -2.60 ± 0.25 for the coastal dune ($P > 0.05$), representing an 88.3 percent increase from the dry season ($P < 0.01$).

The water vapor pressure deficit (δe) was highest at about 1400 h for both locations during all three seasons (Fig. 4G and H) and was not significantly different between sites. The maximum δe during the dry season was 4.6 ± 0.4 kPa ($P > 0.05$). During the rainy season, the highest δe was 3.57 ± 0.32 kPa for the dry forest and 2.89 ± 0.33 kPa for the coastal dune ($P < 0.05$), about 30 percent less than during the dry season ($P < 0.01$). For the northwind season, highest δe averaged 3.02 ± 0.25 ($P > 0.05$), and was 34.6 percent less than during the dry season ($P < 0.01$).

Gas-exchange patterns during all seasons were consistent with that of obligate crassulacean acid metabolism (CAM) plants (Fig. 5). During the dry season, for adult individuals receiving 70 percent of ambient PPFD and averaging 8.5 cm in diameter at the junction between the stem and the root, stomata were closed almost until midnight and maximum instantaneous net CO_2 uptake rates occurred late in the dark period. Maximum instantaneous net CO_2 uptake rates of *M. gaumeri* for both sites during the dry season averaged $0.51 \pm 0.04 \mu\text{mol/m}^2/\text{s}$ (Fig. 5; $P > 0.05$). Total daily CO_2 uptake averaged 1.35 ± 0.08 mmol/ m^2 ($P > 0.05$); about 13 percent of the carbon gain for both sites was fixed after sunrise during the early morning.

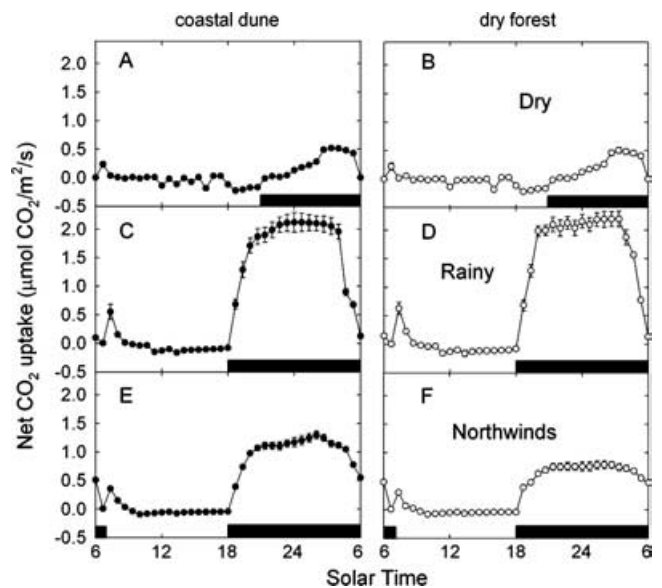


FIGURE 5. Instantaneous net CO_2 uptake in the field for *Mammillaria gaumeri* on clear days in the coastal dune in the (A) dry (26–30 April 2003), (C) rainy (26–30 July 2003) and (E) northwind (26–30 November 2003) seasons and in the dry forest in the (B) dry (3–7 May 2003), (D) rainy (3–7 August 2003) and (F) northwind (3–7 December 2003) seasons. Dark bars indicate the dark period. Values are means \pm SE, $N = 4$ individuals per site, average diameter = 8.5 cm at the stem and the root junction. Measurements were made at an average of 70 percent of the total daily PPFD.

For the rainy season, an average of *ca* 97 percent of the total daily net CO₂ uptake occurred at night. The maximum instantaneous net CO₂ uptake rate was approximately $2.15 \pm 0.14 \mu\text{mol}/\text{m}^2/\text{s}$ for both sites (Fig. 5C and 5D) and total daily net CO₂ uptake was $17.6 \pm 0.27 \text{ mmol}/\text{m}^2$ for the dry forest and $18.8 \pm 0.31 \text{ mmol}/\text{m}^2$ for the coastal dune ($P < 0.05$), which was about nine times the rate during the dry season.

The maximum instantaneous net CO₂ uptake rate during the northwind season was $1.29 \pm 0.07 \mu\text{mol}/\text{m}^2/\text{s}$ for the dry forest and $0.79 \pm 0.08 \mu\text{mol}/\text{m}^2/\text{s}$ for the coastal dune, about 2.5 and 1.5 times that of the dry season for each site ($P < 0.01$). Total daily net CO₂ uptake for *M. gaumeri* was $11.21 \pm 0.17 \text{ mmol}/\text{m}^2$ for the dry forest and $7.47 \pm 0.11 \text{ mmol}/\text{m}^2$ for the coastal dune ($P < 0.01$), almost twelve times greater than during the dry season ($P < 0.01$) and 48.7 percent less than during the rainy season ($P < 0.01$). Similar to the rainy season, an average of 3.05 percent of the total daily net CO₂ uptake occurred during the early morning.

GROWTH.—*Mammillaria gaumeri* individuals grew during both the rainy and northwind seasons but not during the dry season, when

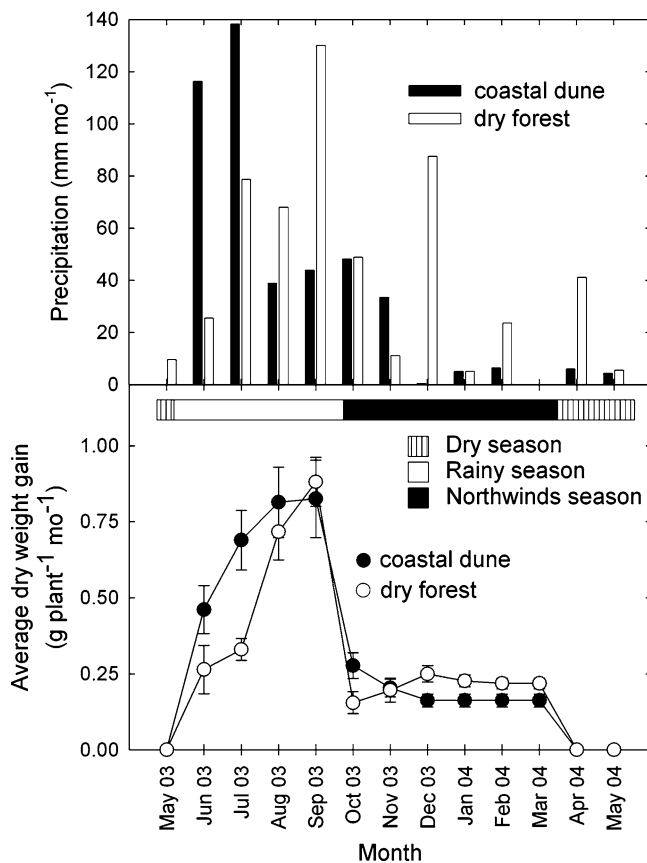


FIGURE 6. A. Monthly precipitation in the dry forest (open bars) and the coastal dune (closed bars). B. Average monthly growth for *Mammillaria gaumeri* in the dry forest and coastal dune from May 2003 to May 2004. Values are means \pm SE, $N = 39$ individuals per site.

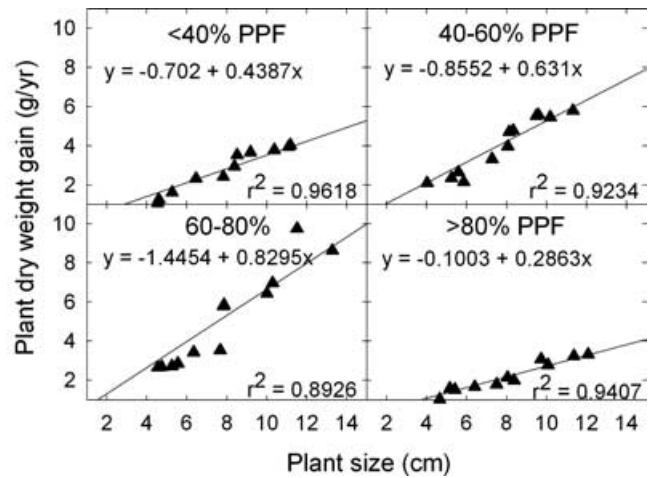


FIGURE 7. Annual dry-weight gain for *Mammillaria gaumeri* individuals of different sizes receiving four different percentages of total daily PPFD.

no new areoles were produced (Fig. 6). The average monthly growth was maximal during August and September 2003 at the end of the rainy season with individuals in both sites gaining an average of $0.8 \pm 0.1 \text{ g}/\text{plant}/\text{mo}$ ($P > 0.05$). During the northwind season, the two sites differed in dry-weight production. In the dry forest, the average dry-weight gain was $0.2 \pm 0.02 \text{ g}/\text{plant}/\text{mo}$, while in the coastal dune, it was 27.3 percent less ($P < 0.01$). However, individual mean diameter between sites was not different ($P > 0.01$).

Annual dry-weight gain increased linearly with plant size regardless of light environment (Fig. 7). An increase in ambient PPFD from < 40 to 80 percent resulted in increases in dry-weight gain; however, plants receiving an ambient PPFD higher than 80 percent had significantly less dry-weight gain. (Fig. 7; $P < 0.01$, Tukey's test following ANCOVA). RGR decreased with plant size, but also increased linearly with percent of ambient PPFD, except for the most exposed plants, which had the lowest RGR (Fig. 8).

DISCUSSION

SEASONAL PATTERNS OF CO₂ UPTAKE AND GROWTH.—As for most plants from arid environments, the rainy season coincided with the maximum growth for *M. gaumeri* (Pfutsch & Smith 1988, Larcher 1995, Cervantes *et al.* 2005) and CO₂ uptake patterns were consistent with obligate CAM during all three seasons. During the transition from the rainy season to the dry season, the reduction in soil water potential led to a reduction in daily net CO₂ uptake from $18 \text{ mmol}/\text{m}^2$ to $1.3 \text{ mmol}/\text{m}^2$. Gas exchange, however, still occurred for adult individuals after 30 d drought in both the coastal dune and the dry forest locations. Net CO₂ uptake for *M. gaumeri* began at the end of the light period, when air relative humidity was high and vapor pressure deficit was at its minimum value, similar to other CAM plants (Nobel 1988). As soil water content decreased, the percentage of net CO₂ uptake during the night increased, a

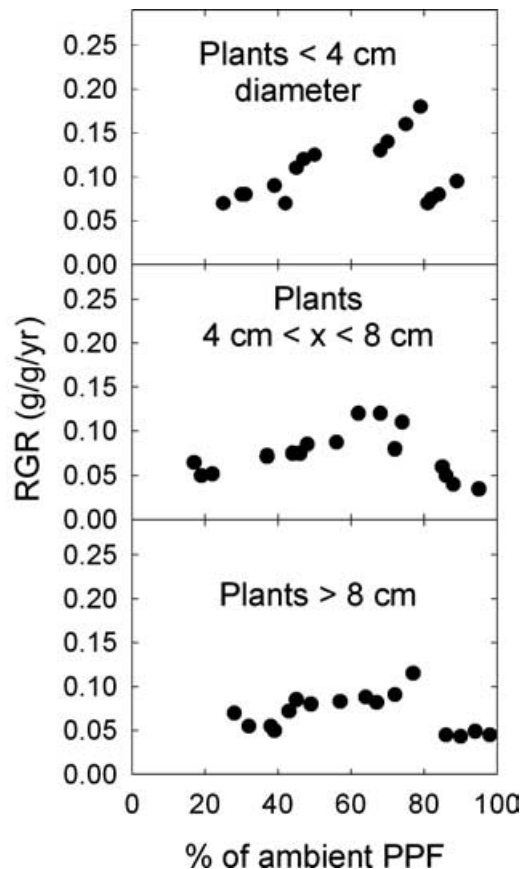


FIGURE 8. Relative growth rate (RGR, g/g/mo) for *Mammillaria gaumeri* individuals of different sizes receiving four different percentages of total daily PPFD.

mechanism leading to significantly reduced water loss during gas exchange and the maintenance of a positive carbon balance during drought (Ting 1985, Lüttge 2004). Thus, the response of *M. gaumeri* is similar to other species adapted to regions with seasonal drought (Andrade & Nobel 1996, Schmidt & Zotz 2001, Pierce *et al.* 2002, Cervantes *et al.* 2005).

Adaptations to unproductive and adverse habitats often include an inherently low RGR (Grime & Hunt 1975, Grime 1979, Chapin 1991, Ball & Pidsley 1995), as exhibited by adult individuals of *M. gaumeri*. For *M. gaumeri*, the annual rate of stem growth decreased with increasing stem size, as occurs for most vascular plants (Zotz 2000), and was similar to the cactus species *Stenocereus thurberi* and *Lophocereus schottii* (Parker 1988).

The optimal diurnal/nocturnal temperatures for net CO₂ uptake by a desert cactus, such as *Ferocactus acanthodes* are 25/13°C (Nobel 1988). However, for tropical cacti, ideal temperatures tend to be similar to the mean temperature of the region (Nobel 1988, Ravetta & McLaughlin 1996, Nobel & De la Barrera 2002). The maximal net CO₂ uptake for *M. gaumeri* was near the diurnal/nocturnal temperatures of 30/20°C, similar to *Agave fourcroydes* (Nobel 1988) and *Hylocereus undatus* (Nobel & De la Barrera 2002).

The effect of lower than optimal temperatures on net CO₂ uptake most likely occurred for *M. gaumeri* during the northwind season at day/night temperatures of 27/18°C, resulting in only 50 percent of the maximum achieved during the rainy season, even though soil water content was moderate. Similarly, the high night temperatures during the dry season, in addition to water deficits, resulted in the delay of net CO₂ uptake for *M. gaumeri* from 1–4 h after the beginning of the dark period, as in other tropical CAM species (Andrade & Nobel 1996, 1997).

OPTIMAL LIGHT MICROHABITATS FOR NET CO₂ UPTAKE AND GROWTH.—Although seasonal patterns of net CO₂ uptake and growth for *M. gaumeri* reflected soil and atmospheric water deficits, our results suggest that net CO₂ uptake and growth also depend on incident PPFD. For cacti in arid environments, net CO₂ uptake tends to increase linearly with PPFD, and saturation occurs around 30 mol photons/m²/d (Nobel 1988). In our study during the rainy season, maximum net CO₂ uptake occurred for individuals receiving *ca* 26.5 mol/m²/d (70% of ambient PPFD). A higher PPFD during the dry season (34.7 mol/m²/d) led to a reduction in CO₂ uptake in both locations, possibly due to photoinhibition and a higher water vapor pressure deficit (Cervantes *et al.* 2005). Indeed, for *H. undatus*, a hemiepiphytic cactus that co-occurs with some populations of *M. gaumeri* in tropical low deciduous dry forests, photoinhibition occurs at the low total daily PPFD of 20 mol/m² (Nobel & De la Barrera 2004).

Thus, because growth increased linearly with ambient PPFD only up to 80 percent PPFD, the optimal light microhabitats for growth of adult individuals were those that were moderately exposed. Differences in overstory plant composition between the two sites resulted in differences in the availability of light microsites; however, at both sites *M. gaumeri* individuals occurred in these moderately exposed areas and there was no difference between sites for the highest growth rates observed. Also, the difference in dry-weight gain in individuals growing in the two sites is not due to size or light microenvironment; so, other factors should be involved and this deserves further study with plants growing in common gardens.

CONSERVATION IMPLICATIONS AND RECOMMENDATIONS.—A recent phytogeographic analysis of taxa endemic to the Yucatan Peninsula suggests that the dry, warm conditions of the northern coast of the Yucatan peninsula, along with its relative climatic stability during the last 8000 years and its geologically young soils, have resulted in a narrow area of endemism, the Yucatan dry zone. In this restricted area, there has occurred a speciation of plants adapted to arid environments (Adams & Faure 1997, Espadas *et al.* 2003).

Small areas of endemism are particularly threatened by human disturbances that change the vegetation structure of an ecosystem (Chen *et al.* 1999), modifying species microhabitats. For example, for the coastal dune scrubland of the Yucatan, changes in shrub composition and density due to human activity have affected the population structure and seedling survival for the orchid *M. christinae* var. *christinae* (Rico-Gray & Thien 1987). Thus, the creation of protected natural areas will help preserve species like *M. gaumeri*.

as well as other local endemic and endangered cacti, such as *Pterocereus gaumeri*, *Nopalea gaumeri*, *Nopalea inaperta* and *Pereskopsis scandens* (Durán *et al.* 1998, Méndez *et al.* 2004). However, the mere creation of protected areas may not be sufficient for managing some endangered species.

Because increases in fecundity and seedling survival for two other *Mammillaria* species result in population growth (Contreras & Valverde 2002, Valverde & Zavala-Hurtado 2006), it is critical to avoid disturbances of great magnitude to preserve the perennial shrubs that serve as nurse plants for *M. gaumeri*. However, because survival of cacti is positively correlated with age and size (Schmalzel *et al.* 1995, Godínez-Álvarez *et al.* 1999), low-magnitude disturbances, such as aboveground clearing of small areas that result in more exposed microhabitats, may be beneficial for adult growth. For example, for populations of *M. pectinifera*, the absence of disturbance resulted in a decrease in optimal microhabitat availability and Martorell and Peters (2005) recommend the creation of colonization of patches using appropriate levels of disturbance in management plans for this species.

The conservation of *M. gaumeri* may require a similar strategy, primarily because population maintenance is based largely on individual longevity rather than high recruitment. Earlier work on factors affecting the distribution, abundance, and seedling survival for *M. gaumeri* suggest that optimal microhabitats for seed germination and seedling establishment were different from those suitable for optimal growth (Leirana-Alcocer & Parra-Tabla 1999). Our results indicate that optimal growth for adult individuals of *M. gaumeri* occurred in partially exposed microhabitats, receiving more than 20 percent but less than 80 percent of ambient PPFD. Cervera *et al.* (2006) found, however, that the optimal microhabitats for seed germination and seedling survival of *M. gaumeri* are those receiving 20 percent of ambient PPFD. Thus, although adult individuals growing in optimal microsites would produce more flowers, which will receive more pollinator visits (M. Giovanetti, pers. comm.), optimal microsites for recruitment are also needed.

Physiologically based tools have accurately predicted the productivity of *F. acanthodes*, a desert cactus, and of cultivated CAM plants such as *A. fourcroydes* and *Opuntia ficus-indica* (Acevedo *et al.* 1983, Nobel 1988) and helped determine locations suitable for cultivation of edible cacti in California (Nobel *et al.* 2002). Conservation efforts, therefore, should include the use of physiologically based tools to determine favorable sites for the reintroduction of threatened species after *ex situ* propagation. Because the effects of light and temperature on net CO₂ uptake are masked by water availability for many species, we are currently refining our understanding of the physiology of *M. gaumeri* under controlled laboratory conditions to help us further predict the optimal areas for the reintroduction for this endemic and threatened species (De la Barrera & Andrade 2005).

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