Synergistic Effects of Elevated CO2 and Fertilization on Net CO2 Uptake and Growth of the CAM Plant *Hylocereus undatus*

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**ABSTRACT.** This study examined the response of the crassulacean acid metabolism (CAM) vine-cactus fruit crop species *Hylocereus undatus* to two CO2 regimes [enrichment (1000 μmol mol⁻¹) vs. ambient control (380 μmol mol⁻¹)] and to two fertilization regimes [0.5- vs. 0.1-strength Hoagland’s solution (designated high and low, respectively)]. CO2 enrichment increased total daily net CO2 uptake, nocturnal acid accumulation, shoot elongation, and total dry mass by 39%, 24%, 14%, and 6% (averaging the two fertilization regimes) versus ambient CO2 treatment, respectively. Plants exposed to high fertilization demonstrated 36%, 21%, 198%, and 79% (averaging the two CO2 regimes) increases versus those receiving the low fertilization regime in total daily net CO2 uptake, nocturnal acid accumulation, stem elongation, and total dry mass, respectively. Plants exposed to high fertilization and elevated CO2 demonstrated 108%, 77%, 264%, and 111% increases versus those receiving the low fertilization regime at the ambient CO2 concentration in total daily net CO2 uptake, nocturnal acid accumulation, stem elongation, and total dry mass, respectively. This response was 25% to 71% higher than the summed effects of the separate responses to each factor, indicating a synergistic effect of elevated CO2 and high fertilization. Thus, it is apparent that *H. undatus* crops grown under a high-fertilization agromanagement regime may benefit from elevated CO2 to a greater extent than those grown with low fertilization.

Most studies on the physiological responses of plants to increasing CO2 concentrations have focused on C3 and C4 photosynthetic pathway plants. It has been found that CO2 enrichment enhances net CO2 uptake and growth of C3 plants by 30% to 40% (Kimball, 1983), whereas in C4 photosynthetic pathway plants, the effect is less marked, being about 10% (Newton, 1991). Studies on the response of CAM plants to elevated CO2 are far more limited than those on C3 and C4 plants (Poorter and Navas, 2003). Among the CAM species that have been studied, the findings are not uniform: some reports found no significant change in CO2 uptake and growth in response to elevated CO2 levels (Holtum et al., 1983; Szarek et al., 1987), whereas other studies reported an increase in these parameters (Drennan and Nobel, 2000; Raveh et al., 1995).

In C3 and C4 plants, a sustained positive response to CO2 enrichment may be attenuated by environmental conditions such as irradiance [including ultraviolet (UV)-B], temperature, ambient ozone concentrations, and the availability of water and nutrients. These factors, alone or in combination, could lead to acclimation during long-term exposure to elevated CO2 concentrations (Poorter, 1993). In particular, it has been found that high nutrient concentrations usually amplify the response of plants to CO2 enrichment (Poorter and Perez-Soba, 2001; Reich et al., 2006). Most of the studies on the response of CAM plants to elevated CO2 were conducted under conditions of low fertilization [0.1- to 0.3-strength Hoagland’s solution (Drennan and Nobel, 2000)], but there have been no systematic studies of the effect of high-fertilization regimes on the response of CAM plants to CO2 enrichment.

A small number of studies have investigated the response to CO2 of the CAM species *H. undatus* (commonly known as pitahaya or dragon fruit), a vine cactus that is indigenous to the tropical and subtropical regions of Central America and that is grown as a crop in a number of countries, including Mexico, some countries of Southeast Asia, and currently in Israel (Mizrahi et al., 1997). Raveh et al. (1995) showed that CO2 enrichment of *H. undatus* resulted in a 34% increase in total daily net CO2 uptake, which enabled the plants to overcome various abiotic stresses. Nobel and De la Barrera (2002) reported stimulation of CO2 uptake by *H. undatus* grown at high N concentrations and ambient CO2: maximal nocturnal net CO2 uptake rates were 2.5 and 9.8 μmol·m⁻²·s⁻¹ at 0.16 and 16 μmol·N, respectively.

The specific objective of this study was to test the hypothesis that increased levels of fertilization amplifies the effect of CO2 enrichment on net CO2 uptake and growth in *H. undatus*.

**Materials and Methods**

**PLANT MATERIAL.** Rooted shoot cuttings of *H. undatus* were used in this study. Shoots of uniform size (60 ± 2 cm in length) were planted (positioned at random) in 10-L pots, placed 60 cm apart, and filled with volcanic gravel (Tuff Merom Golan, Merom Golan, Israel). These conditions were chosen to ensure that rooting volume did not limit growth (Mizrahi et al., 2007).

**EXPERIMENTAL DESIGN.** The experiments were conducted in Beer-Sheva, northern Negev Desert, Israel (lat. 31°15’N, long.
Plants (n = 10 for each treatment) were grown for 1 year, from Aug. 2006 to Aug. 2007, under conditions of ambient CO₂ [380 ± 10 (SE) μmol·mol⁻¹] or elevated CO₂ [1000 ± 70 (SE) μmol·mol⁻¹]. The plants were grown in a cooled greenhouse in two vented chambers (each 220 cm high, 120 cm wide, and 1000 cm long), one for each CO₂ concentration. Each chamber contained plants receiving two different fertilization regimes, as described below. The locations of the pots and the chambers were changed three times during the experiment to reduce the effect of location. For the chamber with the enriched CO₂ atmosphere, pure CO₂ (cylinders of compressed CO₂; Maxima, Beer-Sheva, Israel) was supplied through a flow meter that controlled the flow rate at about 0.8 L·min⁻¹. Ambient air entered each chamber through a port in the lower panel of the chamber wall opposite to the wall with the vent. The chamber air was changed three times per hour, with the air being vented via a duct to the outside by means of a centrifugal fan. The CO₂ concentration inside each chamber was monitored at 30-min intervals with an automatic four-channel monitoring system (IRGA PTM-48M; PhyTech, Rehovot, Israel). A detailed description of the system is given in Weiss et al. (2009) and references therein.

Plants were fertigated twice a week via a drip irrigation system (8 L·h⁻¹; one dripper per plant) with 2 L of 0.5-strength Hoagland's solution [high (120 mg·L⁻¹ N, 50 mg·L⁻¹ P, and 90 mg·L⁻¹ K)] or 0.1-strength Hoagland's solution [low (24 mg·L⁻¹ N, 10 mg·L⁻¹ P, and 18 mg·L⁻¹ K)]. The N:P:K ratio was the same for high and low nutrient treatments to control for negative physiological responses caused by interaction of the nutrient elements (Zhang et al., 2006). The high nutrient treatment was the same as that giving maximum stimulation of CO₂ uptake observed by Nobel and De la Barrera (2002) under ambient CO₂ conditions. It is also the nutrient treatment recommended in commercial fields. The low values were the same as those used in most of the studies previously performed on CAM plants (Dennnan and Nobel, 2000).

Air temperatures at the midplant height in the chambers were monitored at 30-min intervals with a data logger (MicroLog® EC650; Fourier Systems, New Albany, IN). Average values for monthly maximum and minimum air temperatures were similar for the two chambers and were therefore combined in the graphs shown in Fig. 1A. The monthly average/minimum air temperature averages for the coldest season (December–February) were 19/7 °C, and those for the hottest season (May–September) were 32/19 °C (Fig. 1A). The experiment was conducted under natural photoperiod. The instantaneous photosynthetic photon flux (PPF) inside the chambers was measured at wavelengths of 400 to 700 nm with a TIR-4 quantum sensor (PhyTech) connected to an IRGA PTM-48M system. Monthly average values for total daily PPF were similar for the two chambers and were therefore combined in the graphs shown in Fig. 1B. The monthly average of total daily PPF for the coldest season was 13 mol·m⁻²·d⁻¹, and the average for the hottest season was 20 mol·m⁻²·d⁻¹ (Fig. 1B), the latter value being the optimal total daily net CO₂ uptake for *H. undatus* (Raveh et al., 1995).

**GAS EXCHANGE MEASUREMENTS.** Gas exchange was measured, starting from day 212 of the experiment, on third-order shoots (n = eight for each treatment) with an IRGA PTM-48M monitoring system. Measurements were taken over a period of 4 d (15–18 Mar. 2007) and were recorded throughout the day and night at 30-min intervals. To measure net gas exchange of the shoot, the original chamber of the IRGA PTM-48M, which is suitable for measuring flat leaves, was replaced with a chamber enclosing 20 cm² (2 × 10 cm) of shoot surface area. The chamber, which was made of 0.2-cm-thick polyethylene, had a volume of 4 cm³; the airflow through the chamber was 11.6 cm³·s⁻¹. The chamber was attached directly to the shoot with two pieces of cellophane tape. The air, which entered the chamber through two identical openings, one on each side of the chamber, was pumped through the center of the chamber via a 0.4-cm-diameter tube to the IRGA PTM-48M. This set-up created a constant turbulent flow that minimized leaf boundary resistance and permitted a restricted amount of air to be drawn into the chamber. A detailed description of the chamber and the gas exchange calculation is given in Weiss et al. (2009).

**NOCTURNAL ACIDITY ASSAY.** Nocturnal acid accumulation (ΔH⁺), a measure that reflects nighttime CO₂ uptake in CAM plants (Osmond, 1978), was determined 90 d (n = five for each treatment) and 150 d (data not shown) after the beginning of the experiment. Shoot tissue was sampled with a cork borer (0.9 cm in diameter) at dusk [1800 Hr (H₄dusk)] and at dawn [0530 Hr (H₄dawn)].
All tissue samples were frozen immediately in liquid N$_2$ and stored at −20 °C for subsequent analysis. For acid analysis, the shoot tissue was homogenized with 10 mL of double-distilled water with an ice-cold pestle and mortar. The homogenate was titrated against 0.01 N NaOH to pH 7.4. ΔH$^+$ was then estimated as ΔH$^+$ = H$_{\text{dawn}}$ − H$_{\text{dusk}}$ (Nobel and Israel, 1994).

### Shoot nutrient assay

Third-order shoots (n = eight for each treatment) were selected at random at the end of the experiment. Samples were washed with doubly distilled water and were then oven dried at 70 °C to constant mass (48–72 h). The dry mass was ground in a grinder to a fine powder, which was used for further analyses. Samples were acid digested (with concentrated H$_2$SO$_4$) and analyzed for reduced nitrogen content by the Kjeldahl method (Bradstreet, 1965). Phosphorus and potassium concentrations were assayed by coupled plasma atomic emission spectrometry (ICP-AES Optima 3000; Perkin Elmer, Norwalk, CT).

### Measurements of growth and biomass

Total shoot lengths were measured with a measuring tape on 17 Sept. 2006, 27 Nov. 2006, 3 Feb. 2007, and 15 Aug. 2007. At the end of the experiment, the plants were harvested, and shoots and roots were separated. Roots were washed gently to remove soil and were blotted (n = 10 for each treatment). To determine root dry mass, roots were oven dried at 70 °C to constant mass (48–72 h). Shoot dry mass was determined by multiplying total shoot length by the average percentage of dry mass to length ratio of six shoot segments (each 30 cm long) sampled from each of the measured plants.

### Statistical analysis

Statistical analyses were performed with JMP IN 5.0 software (SAS Institute, Cary, NC), using analysis of variance (ANOVA) and Tukey’s honest significant difference (hSD) test, with significance set at $P < 0.05$. Statistical analyses of the effect of CO$_2$ and fertilization and their interaction are summarized in Table 1.

#### Results

### Net CO$_2$ uptake

For *H. undatus*, CO$_2$ uptake occurred mostly at night (Fig. 2). At the high nutrient concentration, net CO$_2$ uptake rate peaked earlier in the night under the elevated CO$_2$ concentration than under the ambient concentration (2200 vs. 0100 HR). For the low nutrient treatment, maximal CO$_2$ uptake rate was recorded earlier in the night (at 2000 HR), regardless of the CO$_2$ treatment. However, for these plants, CO$_2$ uptake rate toward the end of the night (0330–0800 HR) was higher in plants exposed to the ambient CO$_2$ concentration than in those grown with CO$_2$ enrichment (Fig. 2). High nutrient treatment significantly increased the total daily net CO$_2$ uptake by 36% and 49% under the ambient and elevated CO$_2$ treatments, respectively (Fig. 3A, Table 1). CO$_2$ enrichment
There was a significant synergistic effect (CO$_2$) on shoot N and P concentration. There was, however, no significant effect of either factor, alone or in combination, on shoot K concentration (Fig. 5C, Table 1).

**Shoot length.** Total shoot length was significantly increased by high nutrient treatment at ambient and elevated CO$_2$ concentrations for all the sampling dates (Fig. 6). At the end of the experiment, total shoot length under the high nutrient treatment had increased by 198% at ambient CO$_2$ and by 218% at elevated CO$_2$ (Fig. 6, Table 1) in comparison with the values for low nutrient treatment. Total shoot length was significantly increased (22%) by elevated CO$_2$ only under the high nutrient regime (e.g., in February and Aug. 2007). The elevated CO$_2$/high nutrient combination increased total shoot length by 224% and 264% in Feb. 2007 and Aug. 2007, respectively, in comparison with the ambient CO$_2$/low nutrient combination (Fig. 6, Table 1). These effects were found to be synergistic (Table 1). During January/February, the response of shoot elongation to elevated CO$_2$ was about 3-fold higher for the high nutrient treatment than for low nutrient treatment [increases of 49% vs. 18%, respectively (Fig. 6, Table 1)].

**Biomass.** High nutrient treatment promoted significant increases in total dry mass and shoot dry mass under ambient and elevated CO$_2$ treatments (Fig. 7, A and C). The effect of nutrient treatment on dry mass was more marked than the effect of CO$_2$ treatment. For example, at elevated CO$_2$, the total dry mass increased by 197% at high nutrient versus low nutrient concentrations. However, only under the high nutrient treatment did elevated CO$_2$ significantly increase total dry mass (18% at elevated CO$_2$ vs. ambient CO$_2$) and shoot dry mass (Fig. 7, A and C; Table 1).

Root dry mass was significantly increased (by 56%) under elevated CO$_2$ compared with ambient CO$_2$, but only for the high nutrient treatment (Fig. 7B, Table 1). There was no significant

significantly increased the total daily net CO$_2$ uptake by 39% and 52% under the low and high nutrient treatments, respectively. Under CO$_2$ enrichment, the maximal values of net CO$_2$ uptake rates were 5.2 and 10.2 μmol·m$^{-2}·s^{-1}$ at low and high nutrient treatments, respectively (Fig. 3B). Under the ambient CO$_2$ concentration, maximal net CO$_2$ uptake rate was 3.0 and 4.8 μmol·m$^{-2}·s^{-1}$ at low and high nutrient treatments, respectively. The elevated CO$_2$/high nutrient combination raised the total daily net CO$_2$ uptake by 108% in comparison with the ambient CO$_2$/low nutrient combination (Fig. 3A, Table 1). There was a significant synergistic effect (CO$_2$ × nutrient interaction; Table 1) of the elevated CO$_2$/high nutrient combination on total daily net CO$_2$ uptake. There was no significant effect of the elevated CO$_2$/high nutrient combination on maximal net CO$_2$ uptake rate (Fig. 3B, Table 1).

**Nocturnal acid accumulation.** High nutrient treatment increased the total nocturnal acid accumulation by 21% and 42% under the ambient and the elevated CO$_2$ treatments, respectively (Fig. 4). CO$_2$ enrichment increased the nocturnal acid accumulation by 24% and 46% under the low and high nutrient treatments, respectively. The elevated CO$_2$/high nutrient combination raised the total nocturnal acid accumulation by 77% in comparison with the ambient CO$_2$/low nutrient combination (Fig. 4, Table 1). After 90 d, there was a significant synergistic effect of the elevated CO$_2$/high nutrient combination on nocturnal acid accumulation (Fig. 4, Table 1). Similar results were obtained for the 150-d measurement (data not shown).

**Shoot nutrient concentration.** High nutrient treatment significantly increased shoot N concentration in comparison with low nutrient treatment (by 171% for the ambient CO$_2$ group and by 105% for the elevated CO$_2$ treatment). At the low nutrient concentration, elevated CO$_2$ did not have any significant effect on shoot N concentration, whereas at the high nutrient concentration, elevated CO$_2$ caused a significant reduction of as much as 41% in shoot N concentration (Fig. 5A). The elevated CO$_2$ treatment in combination with the high nutrient treatment significantly increased shoot P concentration by 50% to 102% in comparison with plants grown under ambient and low nutrient conditions (Fig. 5B). Thus, the nature of the elevated CO$_2$/high nutrient combination had a significant effect on shoot N and P concentration. There was, however, no significant effect on total daily net CO$_2$ uptake. These results were obtained by integrating the instantaneous rates in Fig. 2. Different letters represent significant differences between treatments at $P < 0.05$ (analysis of variance and Tukey’s honestly significant difference test).

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**Fig. 3.** Total daily net CO$_2$ uptake (A) and maximal net CO$_2$ uptake rate (B) in *Hylocereus undatus* plants grown for 212 d at elevated and ambient CO$_2$ (1000 and 380 μmol·mol$^{-1}$, respectively) under high and low nutrient concentrations (0.5- and 0.1-strength Hoagland’s solution, respectively). Values are means ± se ($n =$ eight plants). Total daily net CO$_2$ uptake data were obtained by integrating the instantaneous rates in Fig. 2. Different letters represent significant differences between treatments at $P < 0.05$ (analysis of variance and Tukey’s honestly significant difference test).

**Fig. 4.** Effect of elevated CO$_2$ on the nocturnal acid accumulation of *Hylocereus undatus* plants grown for 90 d at elevated and ambient CO$_2$ (1000 and 380 μmol·mol$^{-1}$, respectively) under high and low nutrient concentrations (0.5- and 0.1-strength Hoagland’s solution, respectively). Values are means ± se ($n =$ five plants). Different letters represent significant differences between treatments at $P < 0.05$ (analysis of variance and Tukey’s honestly significant difference test).
effect of elevated CO$_2$ or high nutrient treatment on root/shoot dry mass ratios (Fig. 7D, Table 1). The elevated CO$_2$/high nutrient combination caused shoot dry mass, root dry mass, and total dry mass to increase by 110%, 100%, and 111%, respectively, in comparison with the ambient CO$_2$/low nutrient combination (Fig. 7, Table 1). These effects were characterized by a synergistic pattern (Table 1).

Discussion

The findings described above support the hypothesis that the response of *H. undatus* to CO$_2$ enrichment increases as nutrient availability increases. The results of this study on a CAM species are consistent with those of earlier studies on C$_3$ and C$_4$ plants (Coleman et al., 1991; Ghannoum et al., 2000; Poorter and Perez-Soba, 2001; Reich et al., 2006). Similar results were found previously for C$_3$ plants (Zhang et al., 2006). The mechanism behind those interactions could be attributed to the fact that elevated CO$_2$ is expected to enhance photosynthesis, which in turn increases growth, resulting in increased nutrient demand. Therefore, increased nutrient availability can support synergistic increases in plant growth and biomass production at elevated CO$_2$, as was previously demonstrated (Poorter and Perez-Soba, 2001; Reich et al., 2006). In our study, the nutrient effect on shoot growth was more than 10 times higher than the effect of elevated CO$_2$, as was found previously for C$_3$ and C$_4$ plants (Coleman et al., 1991; Newman et al., 2006). In contrast, the nutrient effect on root growth (Fig. 7B) was significant only under elevated CO$_2$, as has also been reported for C$_3$ and C$_4$ plants (Carswell et al., 2000; Kim et al., 2000).

![Fig. 5. Mean shoot N (A), P (B), and K (C) concentrations (% of dry mass) of *Hylocereus undatus* plants grown for 1 year at elevated and ambient CO$_2$ (1000 and 380 µmol- mol$^{-1}$, respectively) under high and low nutrient concentrations (0.5- and 0.1-strength Hoagland’s solution, respectively). Values are means ± s.e. (n = five plants). Different letters represent significant differences between treatments at *P* < 0.05 (analysis of variance and Tukey’s honestly significant difference test).](image1)

![Fig. 6. Effect of elevated CO$_2$ on total shoot length of *Hylocereus undatus* plants grown for 1 year at elevated CO$_2$ [1000 µmol- mol$^{-1}$ (solid symbols)] and ambient CO$_2$ [380 µmol- mol$^{-1}$ (open symbols)] CO$_2$ and under high [0.5-strength Hoagland’s solution (circles)] and low [0.1-strength Hoagland’s solution (triangles)] nutrient concentrations. Values are means ± s.e. (n = 10 plants). Different letters represent significant differences between treatments within a specific sampling date at *P* < 0.05 (analysis of variance and Tukey’s honestly significant difference test).](image2)
Poorter and Navas (2003). These findings demonstrate a CO2-same range as that found in nine species of CAM plants by biomass due to elevated CO2 for within-treatment variation. The magnitude of the increase in the current study (Fig. 7D, Table 1), probably due to high acclimation of photosynthesis was not evident in our net CO2 nutrient deficiency (Reich et al., 2006). Yet this downward response to elevated CO2 was explained by the limited level of sink strength in the low nutrient treatment, as was also found by Mandre et al. (1995).

For the low nutrient treatment groups, the lack or attenuation of the stimulation of biomass production and total shoot length in response to elevated CO2, as previously found in C3 plants (Carswell et al., 2000), and a similar (P > 0.05) trend was also demonstrated in the current study (Fig. 7D, Table 1), probably due to high within-treatment variation. The magnitude of the increase in biomass due to elevated CO2 for H. undatus was in the same range as that found in nine species of CAM plants by Poorter and Navas (2003). These findings demonstrate a CO2-un saturated photosynthetic process in CAM plants exposed to ambient CO2.

In conclusion, highly fertilized CAM crops may benefit from elevated atmospheric CO2 to a greater extent than CAM plants grown under low fertilization regimes due to the synergistic effect of high nutrition and elevated CO2. These results pave the way for further research into the potential benefits of elevated CO2 for CAM crops under different nutrient conditions.

Fig. 7. Effect of elevated CO2 on the shoot dry mass (A), root dry mass (B), total dry mass (C) and root/ stem dry mass ratio (D) of Hylocereus undatus plants grown for 1 year at elevated and ambient CO2 (1000 and 380 μmol mol−1, respectively) under high and low nutrient concentrations (0.5- and 0.1-strength Hoagland’s solution, respectively). Values are means ± se (n = 10 plants). Different letters represent significant differences between treatments at P < 0.05 (analysis of variance and Tukey’s honestly significant difference test).
way for testing the effect of CO2 enrichment and high fertilization regimes for optimal fruit production. Our findings may be of particular importance in subtropical areas such as Israel, where pitahayas are grown under netting to prevent photoinhibition damage (Raveh et al., 1996; 1998). In this context, it should be noted that stretching a plastic film over the supporting structure during the night to enable enrichment with CO2 should involve only a minimum extra cost, while making a substantial contribution to increasing fruit yield.

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Fig. 8. Observed and predicted relative effects of the interaction between CO2 and nutrient treatments on total daily net CO2 uptake (A), maximal net CO2 uptake rate (B), nocturnal acid accumulation (C), total shoot length (D, E, F, and G measured in Sept. 2006, Nov. 2006, Feb. 2007, and Aug. 2007, respectively), total dry mass (H), root dry mass (I), and shoot dry mass (J) of Hylocereus undatus plants grown for 1 year at elevated and ambient CO2 (1000 and 380 µmol-mol–1, respectively) under high and low nutrient concentrations (0.5- and 0.1-strength Hoagland’s solution, respectively). Predicted values are the summed effects of the separate responses to each factor (CO2 and nutrient treatments). Points above the 1:1 line demonstrate a positive synergistic effect of CO2 and nutrient treatments. Asterisks represent significant interaction between treatments at P < 0.05 (analysis of variance and Tukey’s honestly significant difference test; Table 1).
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