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CO_2 Exchange and Growth of the Crassulacean Acid Metabolism Plant *Opuntia ficus-indica* under Elevated CO_2 in Open-Top Chambers[1]

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CO_2 uptake, water vapor conductance, and biomass production of *Opuntia ficus-indica*, a Crassulacean acid metabolism species, were studied at CO_2 concentrations of 370, 520, and 720 $\mu L\ L^{-1}$ in open-top chambers during a 23-week period. Nine weeks after planting, daily net CO_2 uptake for basal cladodes at 520 and 720 $\mu L\ L^{-1}$ of CO_2 was 76 and 98% higher, respectively, than at 370 $\mu L\ L^{-1}$. Eight weeks after daughter cladodes emerged, their daily net CO_2 uptake was 35 and 49% higher at 520 and 720 $\mu L\ L^{-1}$ of CO_2, respectively, than at 370 $\mu L\ L^{-1}$. Daily water-use efficiency was 88% higher under elevated CO_2 for basal cladodes and 57% higher for daughter cladodes. The daily net CO_2 uptake capacity for basal cladodes increased for 4 weeks after planting and then remained fairly constant, whereas for daughter cladodes, it increased with cladode age, became maximal at 8 to 14 weeks, and then declined. The percentage enhancement in daily net CO_2 uptake caused by elevated CO_2 was greatest initially for basal cladodes and at 8 to 14 weeks for daughter cladodes. The chlorophyll content per unit fresh weight of chlorenchyma for daughter cladodes at 8 weeks was 19 and 62% lower in 520 and 720 $\mu L\ L^{-1}$ of CO_2, respectively, compared with 370 $\mu L\ L^{-1}$. Despite the reduced chlorophyll content, plant biomass production during 23 weeks in 520 and 720 $\mu L\ L^{-1}$ of CO_2 was 21 and 55% higher, respectively, than at 370 $\mu L\ L^{-1}$. The root dry weight nearly tripled as the CO_2 concentration was doubled, causing the root/shoot ratio to increase with CO_2 concentration. During the 23-week period, elevated CO_2 significantly increased CO_2 uptake and biomass production of *O. ficus-indica*.

Atmospheric CO_2 concentration could double in the next century if it continues to increase at the present rate (Keeling and Whorf, 1990; Lashof and Tirpak, 1990). Elevated CO_2 concentrations directly and indirectly affect productivity of plant communities (Cure and Acock, 1986; Rogers et al., 1986; Idso et al., 1987). Doubling ambient CO_2 concentration can increase CO_2 uptake and productivity by 50% or more for C_3 crops, but only small effects occur for C_4 crops (Mauney et al., 1979; Kimball, 1983; Lawlor and Mitchell, 1991; Wong and Osmond, 1991). CAM plants are widely distributed in arid and semiarid regions, where they contribute significantly to community biomass production under natural conditions (Nobel, 1988). The few studies of CO_2 uptake by CAM plants under elevated CO_2 concentrations are contradictory. Specifically, a doubling of atmospheric CO_2 concentrations has little effect on net CO_2 uptake for *Kalanchoe daigremontiana* (Osmond and Björkman, 1975), decreases nighttime CO_2 uptake for *Portulacaria afra* (Huerta and Ting, 1988), but enhances CO_2 uptake for *Agave vilmoriniana* under modest soil water stress (Idso et al., 1986; Szarek et al., 1987).

CAM plants and C_4 plants share two major carboxylating enzymes, PEPCase and Rubisco, but carbon reduction catalyzed by these enzymes differs spatially and temporally for these two plant types. PEPCase has a higher affinity for the carbon substrate than does Rubisco (Bowes, 1991), and effects of elevated CO_2 on uptake of CO_2 by CAM plants can be different than for C_4 plants. For instance, under well-watered conditions CAM plants can take up considerable amounts of CO_2 during the daytime by using the C_3 pathway and thereby substantially increasing their daily CO_2 uptake (Nobel, 1988). Responses to elevated CO_2 may also vary with plant age; therefore, a long-term study is needed to understand such effects on net CO_2 uptake and biomass production for CAM plants. *Opuntia ficus-indica*, the species used in the present study, is a widely cultivated CAM plant that can have a high annual above-ground productivity of 47 Mg ha^{-1} $year^{-1}$ (Nobel et al., 1992). Therefore, responses of basal and daughter cladodes of *O. ficus-indica* to elevated CO_2 levels were investigated during a 23-week period. Daily CO_2 uptake, water vapor conductance, Chl content, and biomass production were measured for plants growing at 370 $\mu L\ L^{-1}$ of CO_2 and at two elevated CO_2 concentrations in open-top chambers in the field. Daytime CO_2 uptake was separated from nocturnal CO_2 uptake to assess the possible shift in CO_2 uptake pathway upon exposure to elevated CO_2.

MATERIALS AND METHODS

Open-Top Chambers

Three open-top chambers with transparent side panels (Heagle et al., 1973) were installed at the Agricultural Research Station, University of California, Riverside. The cham-

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Abbreviations: EPI, environmental productivity index; PEPCase, phospho*enol*pyruvate carboxylase.

bers were 2.9 m tall, were 3.0 m in diameter, and had a circular hole 1.8 m in diameter at the top. Local soil was thoroughly mixed and provided to a depth of 50 cm in the chambers. The daily PPFD inside the chambers measured seasonally with a LI-191SB line quantum sensor (Li-Cor, Lincoln, NE) averaged 85% of the daily PPFD outside the chambers. Ambient or CO_2-enriched air entered through ports in the lower panels at a flow rate ensuring an average of three air exchanges per min within the chambers. Temperatures inside the chambers were monitored continuously using thermocouples and were within 3°C of the air surrounding the chambers during the daytime and within 1°C at night.

The three CO_2 concentrations in the chambers were 370, 520, and 720 $\mu L\ L^{-1}$. They were monitored with an AR-5000 IRGA (Anarad, Santa Barbara, CA), which was calibrated twice per week. The flow rate of added CO_2 was adjusted by two mass flow meters controlled within 5 $\mu L\ L^{-1}$ to the CO_2 concentration designed for each chamber.

Plant Material

Cladodes of *Opuntia ficus-indica* averaging 35 cm in length and 18 cm in width, with an initial fresh weight of 1053 ± 33 g, were obtained from a collection maintained at the Agricultural Research Station; their dry weight averaged 6.25% of their fresh weight. They were planted in the open-top chambers on April 4, 1992, with about one-third of each cladode below the soil surface. Eight cladodes facing east to west were placed at 25-cm intervals along each of 12 rows running north to south, and the rows were 17 cm apart. The plants were drip irrigated for 2 h twice weekly at night.

Physiological Measurements

CO_2 uptake and water loss were periodically determined during 24 h with a Li-Cor 6200 portable photosynthesis system. A 0.25-L Li-Cor leaf chamber was modified for use on cladode surfaces. Specifically, the top cover of the chamber was replaced by an acrylic plate with a cylindrical acrylic tube (3.4 cm in diameter, 1.6 cm long). Two layers of foam rubber gasket were attached to the outside end of the cylindrical tube, which was pushed firmly against the surface of cladodes during measurement. For each open-top chamber, measurements, which required about 50 s per cladode, were made on five basal cladodes (April 20, May 4, June 4, July 16, and August 26, 1992) and on five east- to west-facing first-daughter cladodes growing from these basal cladodes (May 4, May 18, June 18, July 29, and September 11, 1992); the same cladodes were used for all measurements. A computer integration program was used to calculate the daytime, nighttime, and daily net CO_2 uptake and water loss based on the instantaneous rates measured hourly (daytime was defined as a PPFD > 10 $\mu mol\ m^{-2}\ s^{-1}$).

For plants at 370 $\mu L\ L^{-1}$ of CO_2, an EPI, which represents the fraction of maximal daily net CO_2 uptake expected based on prevailing environmental conditions, was calculated based on known environmental responses of net CO_2 uptake for *O. ficus-indica* (Nobel and Hartsock, 1984; Nobel, 1988). This EPI was based on the total daily PPFD incident on the cladodes and the average nocturnal temperatures, assuming no limitation on net CO_2 uptake by water. The observed daily net CO_2 uptake was divided by EPI to determine the maximal net CO_2 uptake expected under optimal conditions (the CO_2 uptake capacity) for basal and daughter cladodes at various developmental stages (Nobel, 1988).

Plants were harvested after 23 weeks. Basal cladodes and roots in soil blocks (37 × 25 × 35 cm) were washed in a 26-L container with running water, and root segments were collected with soil sieves (0.1 mm); the loss of approximately 5% of the fine roots was taken into account. Cladode area and thickness as well as chlorenchyma thickness were determined. Cladodes and roots were then dried in a force-draft oven at 80°C until no further weight change occurred.

To determine Chl content, daughter cladodes of approximately 8 weeks of age were sampled using a cork borer (diameter of 20 mm) at about 10:00 h. After the epidermis and water-storage parenchyma were removed, 0.5 to 1.0 g fresh weight of chlorenchyma was macerated, and the Chl was extracted with 80% acetone. To remove cellular debris and mucilage, the extracted solution was centrifuged at 200*g* for 3 min. Absorbance of the supernatant was measured at 646 and 663 nm with a DU 64 spectrophotometer (Beckman, Fullerton, CA) to determine the Chl content (Lichtenthaler and Wellburn, 1983). The Chl content was expressed based on chlorenchyma fresh weight. Data were analyzed with a one-way analysis of variance (CoHort, Berkeley, CA) or a *t* test.

RESULTS

Daily Time Course of Gas Exchange

CO_2 uptake for basal cladodes and first-daughter cladodes occurred chiefly at night (Fig. 1, A and B). Nine weeks after

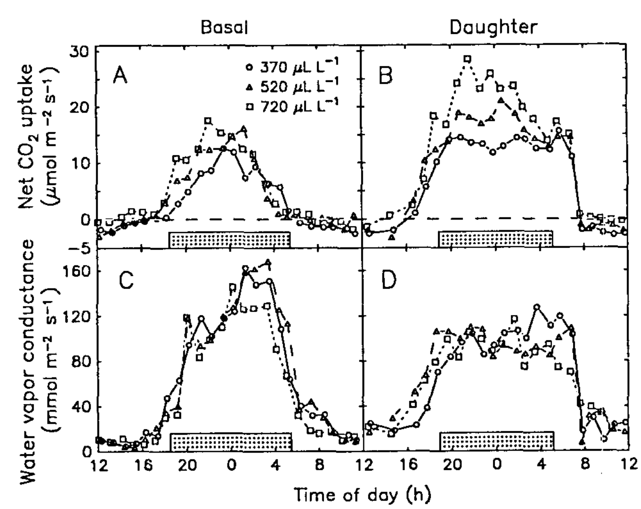

Figure 1. Daily time course of the instantaneous rate of net CO_2 uptake (A and B) and water vapor conductance (C and D) for basal and first-daughter cladodes of *O. ficus-indica*. Measurements were made on basal cladodes 9 weeks after planting (June 4, 1992) and on first-daughter cladodes 8 weeks after emergence (June 18, 1992). Data are means for five plants. SE values averaged 1.1 $\mu mol\ m^{-2}\ s^{-1}$ for CO_2 uptake and 0.19 $mmol\ m^{-2}\ s^{-1}$ for water vapor conductance. Stippled bars indicate night.

planting, the maximal rate of nocturnal CO_2 uptake for basal cladodes was 28% higher in 520 $\mu L\ L^{-1}$ of CO_2 and 41% higher in 720 $\mu L\ L^{-1}$ of CO_2 than at 370 $\mu L\ L^{-1}$ CO_2. No significant difference ($P > 0.05$) occurred in daytime CO_2 uptake among basal cladodes grown in the three CO_2 concentrations for the initial 14 weeks, but daytime CO_2 loss for basal cladodes was smallest for 720 $\mu L\ L^{-1}$ of CO_2 (Fig. 1A). Daily net CO_2 uptake for basal cladodes, obtained by integrating the instantaneous rate during a 24-h period, was 76% higher in 520 $\mu L\ L^{-1}$ of CO_2 and 98% higher in 720 $\mu L\ L^{-1}$ of CO_2 than in 370 $\mu L\ L^{-1}$ of CO_2.

Eight weeks after emergence, the maximal rate of net CO_2 uptake for first-daughter cladodes in 520 and 720 $\mu L\ L^{-1}$ of CO_2 was 43 and 96% higher, respectively, than in 370 $\mu L\ L^{-1}$ of CO_2 (Fig. 1B). From 15 to 20% of daily net CO_2 uptake occurred in the early morning and early evening for all CO_2 treatments, and again, daytime CO_2 loss was lowest in 720 $\mu L\ L^{-1}$ of CO_2. Daily net CO_2 uptake for first-daughter cladodes was 35% higher in 520 $\mu L\ L^{-1}$ of CO_2 and 49% higher in 720 $\mu L\ L^{-1}$ compared with 370 $\mu L\ L^{-1}$.

Maximal water vapor conductance was about 160 mmol $m^{-2}\ s^{-1}$ for basal cladodes and 120 mmol $m^{-2}\ s^{-1}$ for first-daughter cladodes (Fig. 1, C and D). Daily patterns of water vapor conductance were generally similar for both types of cladodes for the three CO_2 treatments. However, water vapor conductance tended to be lower for basal cladodes in 720 $\mu L\ L^{-1}$ of CO_2 during the early morning (Fig. 1C) and for first-daughter cladodes at the 370 $\mu L\ L^{-1}$ of CO_2 during the early evening (Fig. 1D).

Environment and Daily Net CO_2 Uptake

Total daily PPFD per unit surface area was higher for first-daughter cladodes than for basal cladodes (Fig. 2A). The PPFD was greater than 10 mol $m^{-2}\ d^{-1}$, except at 14 weeks for basal cladodes. Average nighttime temperature increased with time after planting for basal cladodes and after emergence for first-daughter cladodes (Fig. 2B). The calculated EPI tended to decrease with time after planting for basal cladodes. After initially lower values, EPI after 4 weeks became higher for first-daughter cladodes than for basal cladodes (Fig. 2C).

Daily net CO_2 uptake for both basal and first-daughter cladodes was higher at higher CO_2 concentrations (Fig. 3). During the 20-week period considered for basal cladodes, daily net CO_2 uptake was 24 to 89% higher in 520 $\mu L\ L^{-1}$ of CO_2 and 41 to 152% higher in 720 $\mu L\ L^{-1}$ than in 370 $\mu L\ L^{-1}$ of CO_2 (Fig. 3A). For first-daughter cladodes throughout the 21 weeks after emergence, daily net CO_2 uptake was 16 to 46% higher in 520 $\mu L\ L^{-1}$ of CO_2 and 41 to 61% higher in 720 $\mu L\ L^{-1}$ compared with 370 $\mu L\ L^{-1}$ of CO_2 (Fig. 3B).

Daily net CO_2 uptake that occurred during the daytime for basal cladodes during 20 weeks averaged −0.01, 0.01, and 0.05 mol $m^{-2}\ d^{-1}$, representing −4, 5, and 17% of total daily net CO_2 uptake at 370, 520, and 720 $\mu L\ L^{-1}$ of CO_2, respectively (Fig. 4A). For first-daughter cladodes throughout the 21 weeks after emergence, CO_2 uptake occurring during the daytime also increased as the CO_2 concentration was increased (Fig. 4B), averaging 0.03, 0.05, and 0.08 mol $m^{-2}\ d^{-1}$, representing 8, 10, and 15% of total daily net CO_2 uptake in 370, 520, and 720 $\mu L\ L^{-1}$ of CO_2, respectively. The percentage of daytime CO_2 uptake decreased with time after planting for basal cladodes in 370 $\mu L\ L^{-1}$ of CO_2 and with time after emergence for first-daughter cladodes for all three CO_2 concentrations (Fig. 4).

Daily water-use efficiency for basal cladodes was higher during the first 9 weeks after planting than later (Fig. 4C) and at 720 $\mu L\ L^{-1}$ of CO_2 was double that at 370 $\mu L\ L^{-1}$. By 20 weeks after planting, no significant difference occurred among treatments ($P > 0.05$). For first-daughter cladodes, daily water-use efficiency initially increased, and 8 weeks after emergence, it was significantly higher in high CO_2 ($P < 0.05$). Twenty weeks after emergence, their water-use efficiency was 43 and 75% higher in 520 and 720 $\mu L\ L^{-1}$ of CO_2, respectively, compared with the 370 $\mu L\ L^{-1}$ of CO_2 (Fig. 4D).

Organ Properties

Twenty-three weeks after planting, basal cladodes and their chlorenchyma were thickest for 720 $\mu L\ L^{-1}$ of CO_2 ($P < 0.05$; Table I). The number of first- and second-daughter cladodes produced per basal cladode was similar among the three CO_2 concentrations. First-daughter cladodes and their chlorenchyma were thickest in 720 $\mu L\ L^{-1}$ of CO_2 (Table I). Total surface area of the daughter cladodes was 14 and 16%

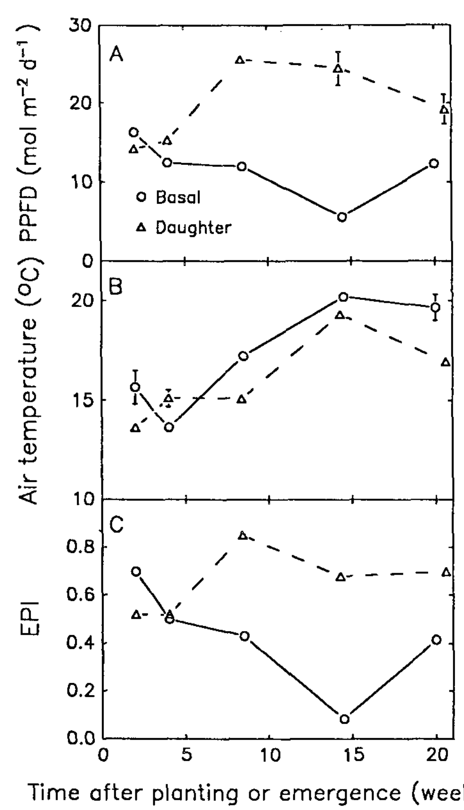

Figure 2. Total daily PPFD on cladode surfaces (A), average nighttime air temperature (B), and calculated EPI (C) versus time after planting for basal cladodes and after emergence for first-daughter cladodes. Data are means ± SE (n = 15), except when the SE was smaller than the symbol.

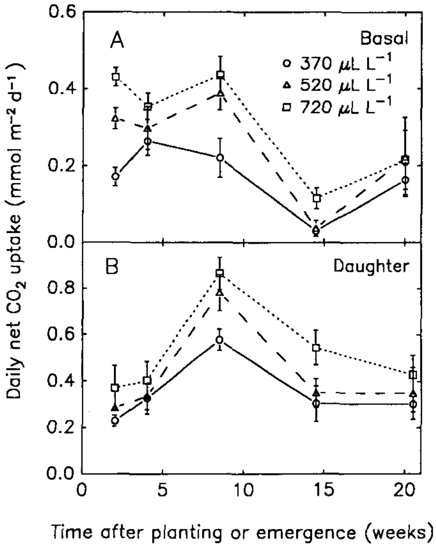

Figure 3. Daily net CO_2 uptake versus time after planting for basal cladodes (A) and versus time after emergence for first-daughter cladodes (B). Data are means ± SE (n = five plants).

higher for 520 and 720 μL L^{-1} of CO_2, compared with 370 μL L^{-1} of CO_2. The dry weights of basal cladodes and first-daughter cladodes were highest at 720 μL L^{-1} of CO_2 ($P < 0.05$; Table I).

Chl *a* and *b* levels in the chlorenchyma of first-daughter cladodes were significantly lower at 720 μL L^{-1} of CO_2 ($P < 0.05$). The total Chl ($a + b$) of first-daughter cladodes was 166 μg g^{-1} fresh weight for 370 μL L^{-1} of CO_2, 135 μg g^{-1} for 520 μL L^{-1}, and 64 μg g^{-1} for 720 μL L^{-1}, but the Chl *a*:Chl *b* ratio remained similar at 3.1 for 370 μL L^{-1} and 3.3 for the elevated CO_2 concentrations. Total Chl per unit cladode surface area was 51 μg cm^{-2} at 370 μL L^{-1} of CO_2, 46 at 520 μL L^{-1}, and 24 at 720 μL L^{-1}.

The dry weight of second-daughter cladodes growing on first-daughter cladodes tended to increase at high CO_2 concentrations (Table I). Root dry weight was significantly higher ($P < 0.05$) in 720 μL L^{-1} of CO_2; it increased 60% from 370 μL L^{-1} to 520 μL L^{-1} and 69% from 520 μL L^{-1} to 720 μL L^{-1} (Table I). Plant dry weight over the 23-week period increased 105, 127, and 163 g for 370, 520, and 720 μL L^{-1} of CO_2, respectively. The root:shoot ratio was also higher at higher CO_2 concentration, varying from 0.036 at 370 μL L^{-1} of CO_2 to 0.053 at 520 μL L^{-1} to 0.076 at 720 μL L^{-1} ($P < 0.05$; Table I).

DISCUSSION

Net CO_2 uptake rates of both basal and first-daughter cladodes of *O. ficus-indica* were substantially higher in elevated CO_2, despite the significantly less Chl. Reductions in Chl content at doubled atmospheric CO_2 also occur for two tropical tree species in 2 to 4 months (Oberbauer et al., 1985), for *Pinus ponderosa* after 2.5 years (Houpis et al., 1988), and for *Liriodendron tulipifera* and *Quercus alba* after 6 months (Wullschleger et al., 1992). A 12% decrease in total Chl occurred for the CAM species *A. vilmoriniana* after exposure to doubled CO_2 for 2 weeks (Szarek et al., 1987). Elevated CO_2 could lead to a decrease in the size of photosynthetic units, leading to reductions in Chl content (Wulff and Strain, 1982). Decreases in Chl content apparently reflect a reduced need for Chl molecules at high atmospheric CO_2 concentrations.

CO_2 uptake capacity under the current CO_2 concentration of 370 μL L^{-1} was calculated using EPI to quantify effects of PPFD and temperature on net CO_2 uptake. For basal cladodes, this capacity increased during the first 4 weeks and was associated with the development of root systems. Thereafter, the CO_2 uptake capacity remained relatively constant at 0.37 mol m^{-2} d^{-1}. For first-daughter cladodes, the CO_2 uptake capacity increased for a few weeks, possibly because of increases in enzymic activity, and decreased after 14 weeks. At 21 weeks after emergence, the CO_2 uptake capacity of first-daughter cladodes was 0.43 mol m^{-2} d^{-1}, slightly higher than the steady value for basal cladodes.

An approximate doubling in net CO_2 uptake was evident 2 weeks after exposing *O. ficus-indica* to an approximately doubled CO_2 concentration. Daytime CO_2 uptake averaged 2% of the total CO_2 uptake at 370 μL L^{-1} of CO_2 and 16% at 720 μL L^{-1}, suggesting a larger role for Rubisco in direct fixation of atmospheric CO_2 under the elevated CO_2 condition. However, most CO_2 was initially fixed by PEPCase for basal and daughter cladodes under all conditions. Because of the high affinity of PEPCase for the carbon substrate, the substantial enhancement of net CO_2 uptake by doubling the CO_2 concentration is unexpected.

Stronger carbohydrate sinks associated with the development of roots and new daughter cladodes may play a role in the large initial response of basal cladodes of *O. ficus-indica* to elevated CO_2. Indeed, the root dry weight was nearly 3-fold greater after 23 weeks when the CO_2 concentration was doubled. The enhancement of net CO_2 uptake by elevated

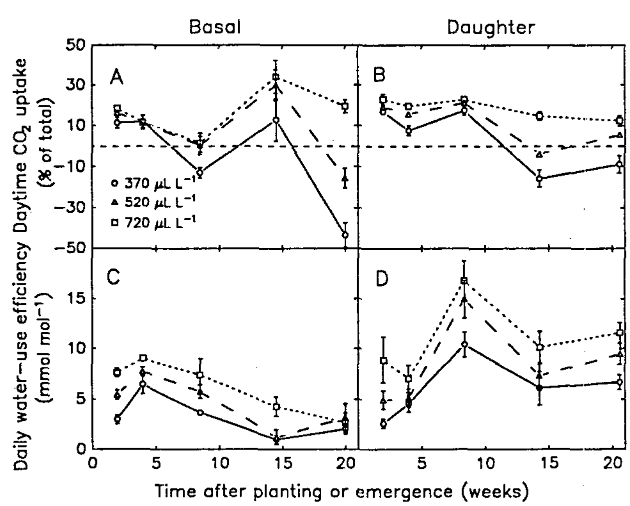

Figure 4. Daytime net CO_2 uptake as a percentage of total daily net CO_2 uptake (A and B) and daily water-use efficiency (C and D) versus time for basal cladodes (A and C) and first-daughter cladodes (B and D). Data are means ± SE (n = five plants).

Table I. *Organ properties of O. ficus-indica at three CO_2 concentrations*

Data were obtained on September 11, 1992, 23 weeks after planting, except for cholorenchyma Chl content, which was measured on June 18, 1992, at 8 weeks after emergence of first-daughter cladodes. Data are means ± SE (*n* = five plants).

Property	CO_2 Concentration (μL L^{-1})		
	370	520	720
Basal cladodes			
Thickness (mm)	31.8 ± 0.4	35.0 ± 1.6	38.9 ± 1.7
Chlorenchyma thickness (mm)	5.2 ± 0.2	5.4 ± 0.2	5.8 ± 0.3
Increase in dry wt over initial value (g/plant)	2.0 ± 2.7	6.6 ± 4.5	19.6 ± 5.5
First-daughter cladodes			
Thickness (mm)	17.9 ± 0.6	19.1 ± 0.6	20.4 ± 0.7
Chlorenchyma thickness (mm)	3.3 ± 0.1	3.7 ± 0.1	3.9 ± 0.1
No./plant	2.8 ± 0.4	2.8 ± 0.4	3.0 ± 0.5
Area (cm^2/plant)	1371 ± 103	1570 ± 132	1596 ± 76
Chl *a* (μg g^{-1} fresh wt)	125 ± 13	104 ± 20	49 ± 5
Chl *b* (μg g^{-1} fresh wt)	41 ± 4	31 ± 9	15 ± 2
Dry weight (g/plant)	51.8 ± 3.9	64.2 ± 5.4	73.6 ± 3.5
Second-daughter cladodes			
Thickness (mm)	12.4 ± 1.4	13.1 ± 0.8	13.9 ± 0.5
Chlorenchyma thickness (mm)	2.7 ± 0.1	2.9 ± 0.1	3.2 ± 0.2
No./plant	4.0 ± 0.9	4.0 ± 1.3	4.0 ± 0.7
Area (cm^2/plant)	1974 ± 396	1957 ± 118	2173 ± 98
Dry weight (g/plant)	44.6 ± 11.1	45.6 ± 3.6	51.3 ± 3.2
Roots			
Dry weight (g/plant)	6.8 ± 0.2	10.9 ± 0.6	18.5 ± 2.1

CO_2 decreased after 10 weeks for both basal and daughter cladodes. A similar decline in enhanced CO_2 uptake with time of exposure to elevated CO_2 occurs for annual crops (DeLucia et al., 1985; Ehret and Jolliffe, 1985) and a perennial grass (Tissue and Oechel, 1987). The decline has been attributed to chloroplast damage due to excessive carbohydrate accumulation in the shoots (Farrar and Williams, 1991) and to limitations by roots (Robbins and Pharr, 1988). Decreases in Rubisco activity occur for certain C_3 and C_4 species under elevated CO_2 (Sage et al., 1989; Bowes, 1991). Elevated CO_2 can also lead to a lower water vapor conductance (Lawlor and Mitchell, 1991), although little effect occurs for the CAM plant *A. vilmoriniana* (Szarek et al., 1987).

Elevated CO_2 leads to a higher water-use efficiency for most C_3 species (Wong, 1979; Eamus, 1991; Ryle et al., 1992). The daily water-use efficiency was also consistently higher for *O. ficus-indica* grown under elevated CO_2 compared with 370 μL L^{-1}. This was primarily because of increased daily net CO_2 uptake at higher CO_2 concentrations. The enhancement at high CO_2 occurred despite a higher fraction of the daily net CO_2 uptake occurring during the daytime, which generally leads to a lower water-use efficiency. The increased water-use efficiency was associated with higher biomass productivity of *O. ficus-indica,* underscoring its potential in arid and semiarid regions, where it is extensively cultivated for fodder and for fruit (Nobel, 1988).

Doubling the CO_2 concentration increased the net CO_2 uptake for *O. ficus-indica* planted in open-top chambers, which enhanced the dry weight production by 55% in 23 weeks. In a previous phytotron study with *O. ficus-indica* at a PPFD of 400 μmol m^{-2} s^{-1}, doubling the CO_2 concentration increased the dry weight of its daughter cladodes by 23% in 26 weeks (Nobel and Garcia de Cortázar, 1991). Doubling the CO_2 concentration did not significantly increase the dry weight of *A. vilmoriniana* under wet conditions (Idso et al., 1986), although its nocturnal CO_2 uptake was increased by 10% (Szarek et al., 1987). Doubling the CO_2 concentration increases daily net CO_2 uptake the next day by 30% for the CAM species *Agave deserti* and *Ferocactus acanthodes* (Nobel and Hartsock, 1986). In addition to effects on net CO_2 uptake per unit of stem surface area, elevated CO_2 can have morphological effects that can influence plant productivity (Reekie and Bazzaz, 1991). For instance, cladodes were thicker in elevated CO_2 in the present study.

In summary, increasing the CO_2 concentration from 370 μL L^{-1} to 520 or 720 μL L^{-1} of CO_2 greatly increased daily net CO_2 uptake, root growth, and biomass production for *O. ficus-indica* in open-top chambers during a 23-week period. The effects on net CO_2 uptake decreased for basal and daughter cladodes during the second half of the period. The biomass increases were about twice as great as occur for this species under restricted soil volumes at a much lower PPFD during 26 weeks (Nobel and Garcia de Cortázar, 1991). Thus, the responses to CO_2 greater than 370 μL L^{-1} of CO_2 become more apparent when light and soil volume become less limiting for daily net CO_2 uptake. Increasing the CO_2 concentration also increased the water-use efficiency of *O. ficus-indica.* A higher water-use efficiency together with the increased CO_2 uptake capacity under field conditions should enhance the productivity and economic usefulness of this species as atmospheric CO_2 concentrations increase in the future.

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LITERATURE CITED

Bowes G (1991) Growth at elevated CO_2: photosynthetic responses mediated through Rubisco. Plant Cell Environ **14:** 795–806

Cure JD, Acock B (1986) Crop responses to carbon dioxide doubling: a literature survey. Agric For Meteorol **38:** 127–145

DeLucia EH, Sasek TW, Strain BR (1985) Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. Photosyn Res **7:** 175–184

Eamus D (1991) The interaction of rising CO_2 and temperatures with water use efficiency. Plant Cell Environ **14:** 843–852

Ehret DL, Jolliffe PA (1985) Photosynthetic carbon dioxide exchange of bean plants grown at elevated carbon dioxide concentrations. Can J Bot **63:** 2026–2030

Farrar JF, Williams ML (1991) The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant Cell Environ **14:** 819–830

Heagle AS, Body DE, Heck WW (1973) An open-top field chamber to assess the impact of air pollution on plants. J Environ Qual **2:** 365–368

Houpis JLJ, Surano KA, Cowles S, Shinn JH (1988) Chlorophyll and carotenoid concentrations in two varieties of *Pinus ponderosa* seedlings subjected to long-term elevated carbon dioxide. Tree Physiol **4:** 187–193

Huerta AJ, Ting IP (1988) Effects of various levels of CO_2 on the induction of Crassulacean acid metabolism in *Portulacaria afra* (L.) Jacq. Plant Physiol **88:** 183–188

Idso SB, Kimball BA, Anderson MG, Szarek SR (1986) Growth response of a succulent plant, *Agave vilmoriniana*, to elevated CO_2. Plant Physiol **80:** 796–797

Idso SB, Kimball BA, Mauney JR (1987) Atmospheric carbon dioxide enrichment effects on cotton midday foliage temperature: implications for plants water use and crop yield. Agron J **79:** 667–672

Keeling CD, Whorf TP (1990) Atmospheric CO_2 concentrations, Mauna Loa. *In* TA Boden, P Kanciruk, MP Farrell, eds, Trends '90: A Compendium of Data on Global Change. Oak Ridge National Laboratory, Oak Ridge, TN, pp 8–9

Kimball BA (1983) Carbon dioxide and agricultural yield: assemblage and analysis of 430 prior observations. Agron J **75:** 779–782

Lashof DA, Tirpak DA (1990) Policy Options for Stabilizing Global Climate. Hemisphere Publishing, New York

Lawlor DW, Mitchell RAC (1991) The effects of increasing CO_2 on crop photosynthesis and productivity: a review of field studies. Plant Cell Environ **14:** 807–818

Lichtenthaler HK, Wellburn AR (1983) Determinations of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. Biochem Soc Trans **11:** 591–592

Mauney JR, Guinn G, Fry KE, Hesketh JD (1979) Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. Photosynthetica **13:** 260–266

Nobel PS (1988) Environmental Biology of Agaves and Cacti. Cambridge University Press, New York

Nobel PS, Garcia de Cortázar V (1991) Growth and predicted productivity of *Opuntia ficus-indica* for current and elevated carbon dioxide. Agron J **83:** 224–230

Nobel PS, García-Moya E, Quero E (1992) High annual productivity of certain agaves and cacti under cultivation. Plant Cell Environ **15:** 329–335

Nobel PS, Hartsock TL (1984) Physiological responses of *Opuntia ficus-indica* to growth temperature. Physiol Plant **60:** 98–105

Nobel PS, Hartsock TL (1986) Short-term and long-term responses of Crassulacean acid metabolism plants to elevated CO_2. Plant Physiol **82:** 604–606

Oberbauer SF, Strain BR, Fetcher N (1985) Effect of CO_2-enrichment on seedling physiology and growth of two tropical tree species. Physiol Plant **65:** 352–356

Osmond CB, Björkman O (1975) Pathways of CO_2 fixation in the CAM plant *Kalanchoe daigremontiana*. II. Effects of O_2 and CO_2 concentration on light and dark CO_2 fixation. Aust J Plant Physiol **2:** 155–162

Reekie EG, Bazzaz FA (1991) Phenology and growth in four annual species grown in ambient and elevated CO_2. Can J Bot **69:** 2475–2481

Robbins NS, Pharr DM (1988) Effect of restricted root growth on carbohydrate metabolism and whole plant growth of *Cucumus sativus* L. Plant Physiol **87:** 409–413

Rogers HH, Cure JD, Smith JM (1986) Soybean growth and yield response to elevated carbon dioxide. Agric Ecosyst Environ **16:** 113–128

Ryle GJA, Woledge J, Tewson V, Powell CE (1992) Influences of elevated CO_2 and temperature on the photosynthesis and respiration of white clover dependent on N_2 fixation. Ann Bot **70:** 213–220

Sage RF, Sharkey TD, Seemann JR (1989) Acclimation of photosynthesis to elevated CO_2 in five C_3 species. Plant Physiol **89:** 590–596

Szarek SR, Holthe PA, Ting IP (1987) Minor physiological response to elevated CO_2 by the CAM plant *Agave vilmoriniana*. Plant Physiol **83:** 938–940

Tissue DT, Oechel WC (1987) Response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology **68:** 401–410

Wong SC (1979) Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia **44:** 68–74

Wong SC, Osmond CB (1991) Elevated atmospheric partial pressure of CO_2 and plant growth. III. Interactions between *Triticum aestivum* (C_3) and *Echinochloa frumentacea* (C_4) during growth in mixed culture under different CO_2, N-nutrition and irradiance treatments, with emphasis on below-ground responses estimated using the $\delta^{13}C$ value of root biomass. Aust J Plant Physiol **18:** 137–152

Wulff RD, Strain BR (1982) Effects of CO_2 enrichment on growth and photosynthesis in *Desmodium paniculatum*. Can J Bot **60:** 1084–1091

Wullschleger SD, Norby RJ, Hendrix DL (1992) Carbon exchange rate, chlorophyll content, and carbohydrate status of two forest tree species exposed to carbon dioxide enrichment. Tree Physiol **10:** 21–31