

## Influences of soil volume and an elevated CO<sub>2</sub> level on growth and CO<sub>2</sub> exchange for the Crassulacean acid metabolism plant *Opuntia ficus-indica*

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Nobel, P. S., Cui, M., Miller, P. M. and Luo, Y. 1994. Influences of soil volume and an elevated CO<sub>2</sub> level on growth and CO<sub>2</sub> exchange for the Crassulacean acid metabolism plant *Opuntia ficus-indica*. – *Physiol. Plant.* 90: 173–180.

Effects of the current (38 Pa) and an elevated (74 Pa) CO<sub>2</sub> partial pressure on root and shoot areas, biomass accumulation and daily net CO<sub>2</sub> exchange were determined for *Opuntia ficus-indica* (L.) Miller, a highly productive Crassulacean acid metabolism species cultivated worldwide. Plants were grown in environmentally controlled rooms for 18 weeks in pots of three soil volumes (2 600, 6 500 and 26 000 cm<sup>3</sup>), the smallest of which was intended to restrict root growth. For plants in the medium-sized soil volume, basal cladodes tended to be thicker and areas of main and lateral roots tended to be greater as the CO<sub>2</sub> level was doubled. Daughter cladodes tended to be initiated sooner at the current compared with the elevated CO<sub>2</sub> level but total areas were similar by 10 weeks. At 10 weeks, daily net CO<sub>2</sub> uptake for the three soil volumes averaged 24% higher for plants growing under elevated compared with current CO<sub>2</sub> levels, but at 18 weeks only 3% enhancement in uptake occurred. Dry weight gain was enhanced 24% by elevated CO<sub>2</sub> during the first 10 weeks but only 8% over 18 weeks. Increasing the soil volume 10-fold led to a greater stimulation of daily net CO<sub>2</sub> uptake and biomass production than did doubling the CO<sub>2</sub> level. At 18 weeks, root biomass doubled and shoot biomass nearly doubled as the soil volume was increased 10-fold; the effects of soil volume tended to be greater for elevated CO<sub>2</sub>. The amount of cladode nitrogen per unit dry weight decreased as the CO<sub>2</sub> level was raised and increased as soil volume increased, the latter suggesting that the effects of soil volume could be due to nitrogen limitations.

**Key words** – CO<sub>2</sub>, Crassulacean acid metabolism, global climate change, *Opuntia ficus-indica*, productivity, root growth, shoot growth.

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### Introduction

Increasing levels of atmospheric CO<sub>2</sub> have been documented annually at the Mauna Loa Observatory since 1958 (Keeling and Whorf 1990), and the effects of elevated CO<sub>2</sub> levels on photosynthesis and productivity of many C<sub>3</sub> and C<sub>4</sub> crop species have been determined (Cure and Acock 1986, Strain and Cure 1986, Drake and Leadley 1991, Lawlor and Mitchell 1991). However, relatively few studies have examined the effects of elevated CO<sub>2</sub> levels on species with Crassulacean acid metabolism (CAM; Idso et al. 1986, Nobel and Hartsock 1986, Sza-

rek et al. 1987, Huerta and Ting 1988, Nobel and Garcia de Cortázar 1991). Virtually nothing is known about the effects of elevated CO<sub>2</sub> levels on root growth of CAM plants, which in terms of numbers of species outnumber C<sub>4</sub> plants more than 5-fold (Nobel 1991). Moreover, certain CAM plants, such as the widely cultivated *Opuntia ficus-indica* used in the present study, can achieve productivities that exceed those of most C<sub>3</sub> and C<sub>4</sub> species (Nobel 1988, 1991). The potentially high productivity of certain CAM species, their agronomic importance for food and fodder in many arid and semi-arid regions (Russell and Felker 1987), and the high water-use effi-

Received 27 April, 1993; revised 14 September, 1993

ciency of CAM plants in general (Kluge and Ting 1978, Nobel 1988) lend importance to understanding the effects of anticipated increases in atmospheric CO<sub>2</sub> levels for these species.

Although elevated CO<sub>2</sub> levels have little effect on net CO<sub>2</sub> uptake for C<sub>4</sub> plants, most C<sub>3</sub> plants initially respond to elevated atmospheric CO<sub>2</sub> levels by increased net CO<sub>2</sub> exchange and increased biomass accumulation (Arp 1991). However, when some C<sub>3</sub> species are grown at elevated CO<sub>2</sub> levels for periods of a few weeks or months, they acclimate to the elevated levels and the initially higher net CO<sub>2</sub> exchange rates decline to values similar to those measured under current CO<sub>2</sub> levels. Feedback inhibition due to root restriction by small soil volumes can cause the observed decline in net CO<sub>2</sub> exchange after long-term exposure to elevated CO<sub>2</sub> (Arp 1991, Thomas and Strain 1991, Bernston et al. 1993), although nutrient availability can be more important for some species (McConnaughay et al. 1993). For CAM plants, the long-term response to elevated atmospheric CO<sub>2</sub> levels may also be affected by acclimation or by decreased sink strength due to restricted root volumes, such as for those species that have roots occurring in rock crevices or are planted in close proximity in intensive agriculture. The present study therefore measured the net CO<sub>2</sub> uptake and above- and belowground growth under current and elevated CO<sub>2</sub> levels for the most widely cultivated CAM plant, *Opuntia ficus-indica* (Russell and Felker 1987, Nobel 1988), over an 18-week period for three soil volumes, the smallest of which was intended to restrict root growth.

## Materials and methods

Similar-sized terminal cladodes were harvested from *Opuntia ficus-indica* (L.) Miller (Cactaceae) growing at the Agricultural Experiment Station, University of California, Riverside. Fresh weight was measured for each cladode, and the cut surfaces were allowed to heal for 7 days before planting. To estimate initial dry weight from initial fresh weight, 15 cladodes were dried at 80°C in a forced-draft oven until no further weight change occurred (generally 3 days). Their dry weight averaged 85 ± 5 g (mean ± SE), which was 6.06 ± 0.14% of their fresh weight. The cladodes were ranked by fresh weight and grouped into 20 sets of four, each set containing one cladode from each quartile of the ranked fresh weights. Groups of two sets were randomly assigned to three different soil volumes in rectangular pots that were 23 cm deep: 2.6 l (small pots), 6.5 l (medium pots) or 26 l (large pots). Cladodes were placed in a 1:1 (v:v) mixture of sand and soil from the Agricultural Experiment Station, with approximately one-third of the cladode area beneath the media surface. Sets were randomly assigned to the current local CO<sub>2</sub> partial pressure (an average of 38 Pa) or to an elevated CO<sub>2</sub> level (74 ± 1 Pa).

The plants were maintained in two controlled environment rooms at the University of California, Los Ange-

les. Both rooms had day/night air temperatures of 25°C/20°C. Light levels of 310 μmol m<sup>-2</sup> s<sup>-1</sup> photosynthetic photon flux density (PPFD, 400–700 nm; measured with a LI-190S quantum sensor [LI-COR, Lincoln, NE, USA] and provided by warm white fluorescent lamps [General Electric, Schenectady, NY, USA]) and a photoperiod of 14 h led to a total daily PPFD of 16 mol m<sup>-2</sup> day<sup>-1</sup>. The CO<sub>2</sub> partial pressure in one room was maintained at 74 Pa (36 Pa above the current local value) by introducing CO<sub>2</sub> and was continuously monitored with a LI-COR 6200 IRGA portable photosynthesis system calibrated with gases of known composition. Cladodes and CO<sub>2</sub> levels were alternated between the two rooms on a biweekly basis by moving the pots and the CO<sub>2</sub> addition system. All plants were watered twice per week with 0.5-strength Hoagland's solution No. 1 supplemented with micronutrients (Hoagland and Arnon 1950) for the first 2 weeks and with 0.1-strength solution thereafter. The water potential in the root zone was thereby maintained above -0.15 MPa (measured with PCT-55-15 soil thermocouple psychrometers [Wescor, Logan, UT, USA]).

At 10 and 18 weeks, gas exchange was measured using the LI-COR 6200 for plants under the current as well as the elevated CO<sub>2</sub> levels. A 250-cm<sup>3</sup> leaf cuvette with an acrylic cylinder (5 cm in diameter, 2 cm long) having two layers of gasket on the protruding end was placed firmly on the side of an individual cladode to measure net CO<sub>2</sub> uptake. Sets of plants were also periodically harvested. The projected areas of main roots and their lateral roots were separately determined with an area meter (Delta-T Devices, Cambridge, UK) and multiplied by π to obtain surface areas. Areas of basal (planted) cladodes and the daughter cladodes developing on them were also measured. Dry weights were determined for all harvested organs after they were dried at 80°C. Total nitrogen content in shoots and roots was analyzed using a micro-Kjeldahl technique (Bremner 1965) with about 0.1 g of powdered samples. Nitrogen contents were determined using a M/CFA continuous flow analyzer (Orion Scientific Instruments, Pleasantville, NY, USA). Data were statistically analyzed by two-way ANOVA using CoStat (CoHort, Berkeley, CA, USA).

## Results

### Organ growth

After a lag period of about 2 weeks, main roots rapidly developed on the basal (planted) cladodes (Fig. 1A). The surface area of main roots increased rapidly and after 6 weeks was higher on plants in medium-sized pots under elevated compared with current CO<sub>2</sub> levels ( $P < 0.05$ ). The number of main roots averaged 31 per basal cladode at 2 weeks, increased relatively slowly to an average of 39 at 18 weeks, and was not significantly affected by the CO<sub>2</sub> level or the soil volume ( $P > 0.05$ ). After 6 weeks, the surface area of lateral roots was greater than that of main roots and for plants in medium-sized pots was

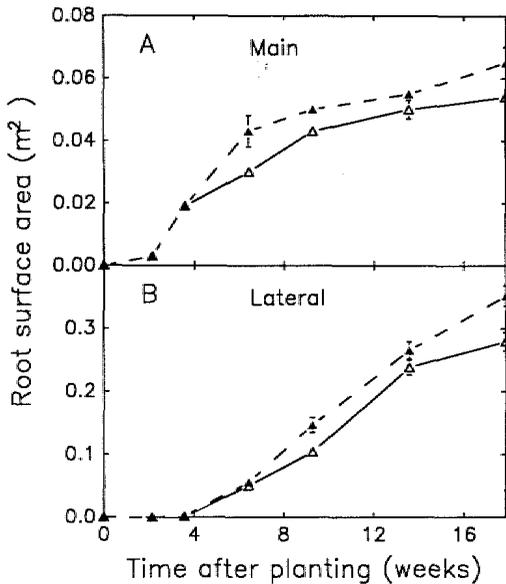


Fig. 1. Influence of CO<sub>2</sub> level on growth of main roots (A) and lateral roots (B) of *Opuntia ficus-indica* over an 18-week period. The CO<sub>2</sub> levels averaged 38 Pa (current;  $\Delta$ ) or 74 Pa (elevated;  $\blacktriangle$ ). Data are means  $\pm$  SE (unless the SE was smaller than the symbol) for  $n=4$  plants in medium-sized pots (soil volume of 6500 cm<sup>3</sup>).

greater under elevated compared with current CO<sub>2</sub> levels (Fig. 1B;  $P < 0.01$ ). At 18 weeks, the surface area of both main and lateral roots increased an average of 105% as soil volume per plant increased 10-fold ( $P < 0.001$ ) but was significantly higher under elevated CO<sub>2</sub> only for plants in the medium-sized pots ( $P < 0.05$ ).

Accompanying the increases in root surface area with CO<sub>2</sub> level and with soil volume were changes in cladode properties for plants in medium-sized pots (Fig. 2). The mean thickness of the basal cladode decreased for just over 6 weeks after planting and then increased. Basal cladode thickness after 2 weeks averaged  $7 \pm 1\%$  (mean  $\pm$  SE,  $n=6$ ) greater under the elevated compared with the current CO<sub>2</sub> level (Fig. 2A;  $P < 0.01$ ).

The decrease in thickness of the basal cladodes (Fig. 2A) was accompanied by the initial growth of first-daughter cladodes (Fig. 2B), while the subsequent increase in thickness of the basal cladodes began soon after the major expansion of these daughter cladodes. Although first-daughter cladodes tended to be initiated sooner on basal cladodes under current compared with elevated CO<sub>2</sub> levels, after 4 weeks their number averaged 2.8 per basal cladode and did not significantly vary with CO<sub>2</sub> level ( $P > 0.05$ ). At 10 weeks and thereafter, the area of such first-daughter cladodes in medium-sized pots tended to be greater under the elevated compared with the current CO<sub>2</sub> level ( $P < 0.05$ ). However, second-daughter cladodes growing on the first-daughter cladodes tended

to be produced earlier and tended to have greater surface areas under current than under elevated CO<sub>2</sub> levels (Fig. 2C).

#### CO<sub>2</sub> uptake

At 10 weeks, the time courses of net CO<sub>2</sub> uptake for basal and daughter cladodes were similar for plants at current and elevated CO<sub>2</sub> levels, and most of the CO<sub>2</sub> uptake occurred at night (Fig. 3). For basal cladodes, the maximal night-time CO<sub>2</sub> uptake rates averaged 22% higher in elevated CO<sub>2</sub>, and their daytime CO<sub>2</sub> efflux rates tended to be higher under the current CO<sub>2</sub> levels. As pot size increased, the nocturnal increase in net CO<sub>2</sub> rate occurred sooner during a daily cycle for basal and for daughter cladodes under the current CO<sub>2</sub> level (Fig. 3A,C). Increasing the soil volume increased the maximal CO<sub>2</sub> uptake rate more for basal cladodes than for daughter cladodes in the current CO<sub>2</sub> level ( $P < 0.05$ ; Fig. 3A,C), but no significant effects on the maximal CO<sub>2</sub> uptake rate occurred for cladodes in elevated CO<sub>2</sub> (Fig. 3B,D).

Daily net CO<sub>2</sub> uptake integrated over 24 h for basal cladodes was significantly enhanced by elevated CO<sub>2</sub> ( $P < 0.001$ ) and by larger pot sizes ( $P < 0.05$ ) at 10 weeks

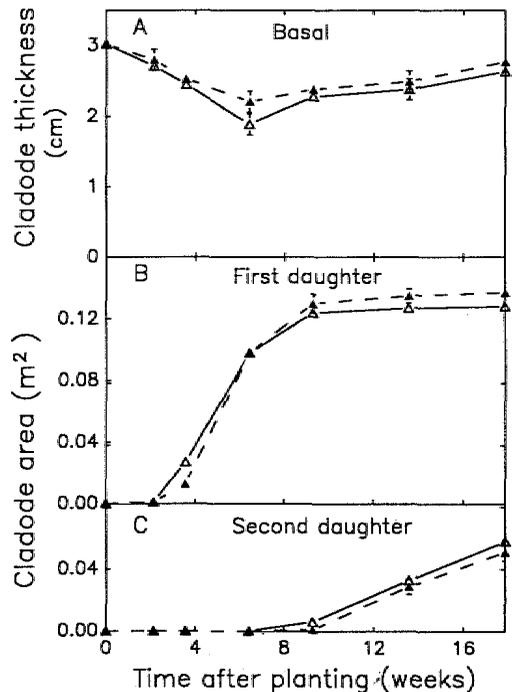


Fig. 2. Influence of CO<sub>2</sub> level on thickness of basal cladodes (A) and growth in area of first-daughter cladodes of *O. ficus-indica* developing on the basal cladodes (B) and second-daughter cladodes developing on the first-daughter cladodes (C) over an 18-week period for current ( $\Delta$ ) or elevated ( $\blacktriangle$ ) CO<sub>2</sub> levels. Data are means  $\pm$  SE for  $n=4$  plants in medium-sized pots.

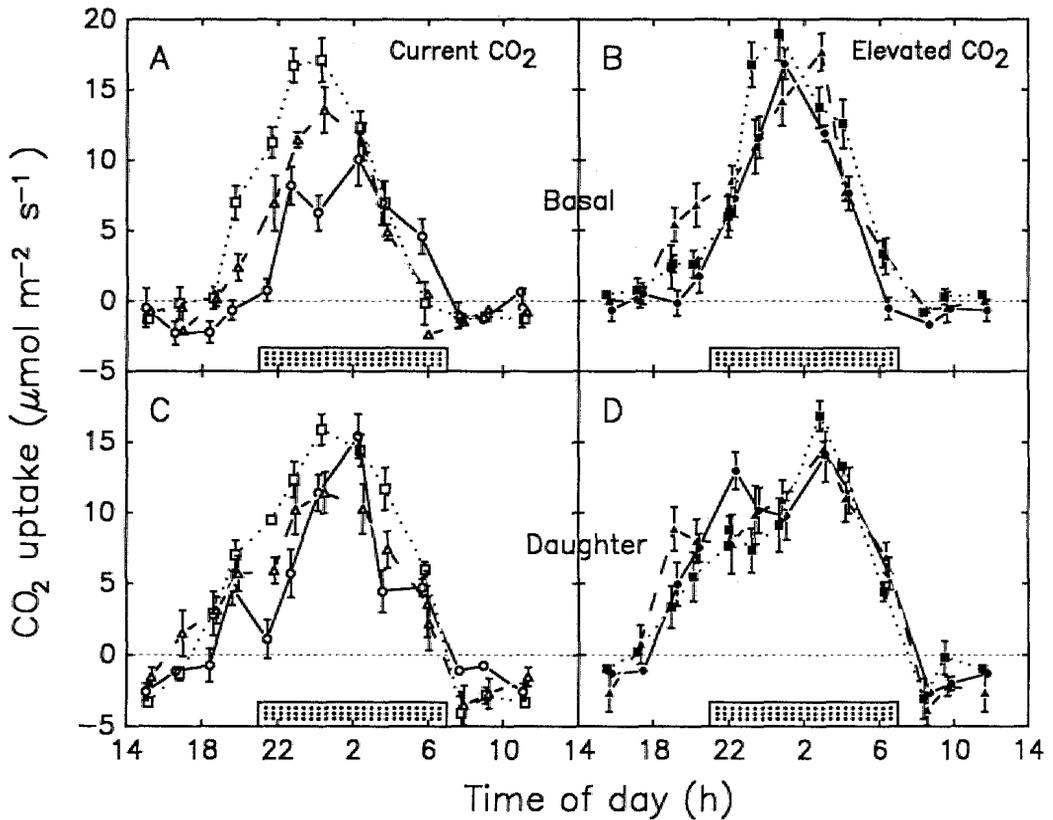


Fig. 3. Daily course of net  $\text{CO}_2$  exchange of *O. ficus-indica* for basal cladodes (A, B) and first-daughter cladodes (C, D) at the current  $\text{CO}_2$  level (A, C;  $\circ$ ,  $\Delta$ ,  $\square$ ) and an elevated  $\text{CO}_2$  level (B, D;  $\bullet$ ,  $\blacktriangle$ ,  $\blacksquare$ ) at 10 weeks. Data are means  $\pm$  SE ( $n=4$  plants) for the three indicated pot sizes (soil volumes of 2600 [ $\circ$ ,  $\bullet$ ]; 6500 [ $\Delta$ ,  $\blacktriangle$ ]; or 26000 [ $\square$ ,  $\blacksquare$ ]).

(Fig. 4A). For daughter cladodes, the effects of  $\text{CO}_2$  were significant ( $P < 0.01$ ), but effects of pot size were not ( $P > 0.05$ ; Fig. 4B). At 18 weeks, only pot size had a significant effect on daily net  $\text{CO}_2$  uptake of basal and daughter cladodes ( $P < 0.01$ ; Fig. 4). Daily net  $\text{CO}_2$  uptake of basal cladodes at 18 weeks for the three pot sizes averaged 25% lower in the current  $\text{CO}_2$  level and 51% lower in elevated  $\text{CO}_2$  than at 10 weeks (Fig. 4A). For daughter cladodes, average daily net  $\text{CO}_2$  uptake was essentially unchanged in the current  $\text{CO}_2$  level and decreased 15% for elevated  $\text{CO}_2$  at 18 weeks compared with 10 weeks (Fig. 4B).

At 10 weeks, the total surface areas of all daughter cladodes were similar for the two  $\text{CO}_2$  treatments (Fig. 2B,C) and the three pot sizes. In contrast, at 18 weeks the surface areas for plants in small, medium and large pots were  $0.171 \pm 0.018$ ,  $0.186 \pm 0.012$  and  $0.323 \pm 0.021$   $\text{m}^2$ , respectively, for the current  $\text{CO}_2$  level (mean  $\pm$  SE for  $n=4$  plants); for the elevated  $\text{CO}_2$  level, the analogous values were  $0.154 \pm 0.013$ ,  $0.188 \pm 0.014$  and  $0.303 \pm 0.020$   $\text{m}^2$ , respectively ( $P > 0.05$  for  $\text{CO}_2$  level;  $P < 0.01$  for pot size). Whole plant daily net  $\text{CO}_2$  uptake averaged

for all three pot sizes was 24% higher at 10 weeks in elevated than in current  $\text{CO}_2$  levels ( $P < 0.01$ ) and was 3% higher at 18 weeks ( $P > 0.05$ ; Fig. 4C). At both 10 and 18 weeks, whole plant  $\text{CO}_2$  uptake increased significantly with pot size ( $P < 0.001$ ). Compared with plants in medium pots, whole plant  $\text{CO}_2$  uptake averaged for the two  $\text{CO}_2$  treatments at 18 weeks was 51% lower for small pots and 90% higher for large pots (Fig. 4C).

#### Biomass accumulation

At 10 weeks,  $\text{CO}_2$  concentration significantly affected biomass accumulation in basal cladodes ( $P < 0.01$ ; Fig. 5A). Dry weight of basal cladodes was then 5% lower than their initial dry weight in the current  $\text{CO}_2$  level but 3% higher at the elevated  $\text{CO}_2$  level (cf. Fig. 2A). The effects of  $\text{CO}_2$  level on the biomass of basal cladodes were inconsistent at 18 weeks (Fig. 5A). Pot size did not significantly affect the dry weight of basal cladodes at 10 or 18 weeks ( $P > 0.5$ ). However, increasing pot size enhanced biomass accumulation in daughter cladodes significantly at 18 weeks ( $P < 0.01$ ; Fig. 5B). Total dry

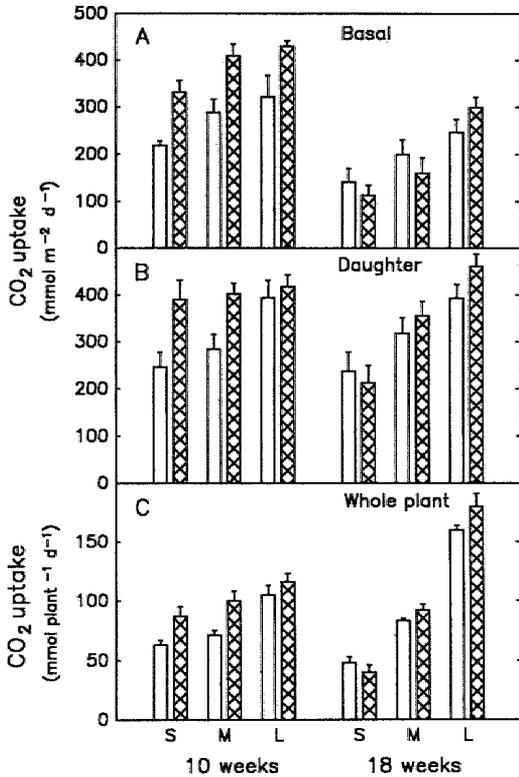


Fig. 4. Daily net CO<sub>2</sub> uptake per unit surface area of basal cladodes (A) and first-daughter cladodes (B) and daily net CO<sub>2</sub> uptake per plant (C) in small (S), medium (M) and large (L) pots at the current CO<sub>2</sub> level (open bars) and an elevated CO<sub>2</sub> level (hatched bars) at 10 and 18 weeks. Data are means  $\pm$  SE ( $n=4$  plants).

weight of daughter cladodes then averaged 16% less in small pots and 107% more in large pots than in medium pots. Dry weight of daughter cladodes at 18 weeks was not significantly affected by the CO<sub>2</sub> level (Fig. 5B).

Doubling the CO<sub>2</sub> level did not significantly affect root biomass except in medium pots ( $P < 0.05$ ), for which root dry weight at 10 and 18 weeks averaged 37% higher for the elevated compared with the current CO<sub>2</sub> level (Fig. 5C). Increasing the pot size increased root biomass significantly at 10 weeks ( $P < 0.05$ ) and at 18 weeks ( $P < 0.001$ ). When averaged for the two CO<sub>2</sub> levels, root dry weight was 31% lower for small pots and 36% higher for large pots than for medium pots at 18 weeks. The root:shoot ratios for the two CO<sub>2</sub> levels then averaged 29% lower for small pots and 10% higher for large pots than for medium pots ( $P < 0.05$ ).

Total plant biomass production by 10 weeks was significantly greater for the elevated CO<sub>2</sub> than for the current CO<sub>2</sub> level ( $P < 0.05$ ; Fig. 3D). When averaged for the three pot sizes, plant dry weight was then 24% greater for the doubled CO<sub>2</sub> level. At 18 weeks, the plant dry weight

gain averaged 8% higher under elevated compared with current CO<sub>2</sub> levels (Fig. 5D). Plant biomass production by 18 weeks increased significantly with pot size ( $P < 0.001$ ). Total plant dry weight gain averaged for the two CO<sub>2</sub> levels was then 20% lower in small pots and 87% higher in large pots than in medium pots (Fig. 3D).

The cladode nitrogen content at 18 weeks tended to increase with pot size and to decrease with CO<sub>2</sub> level

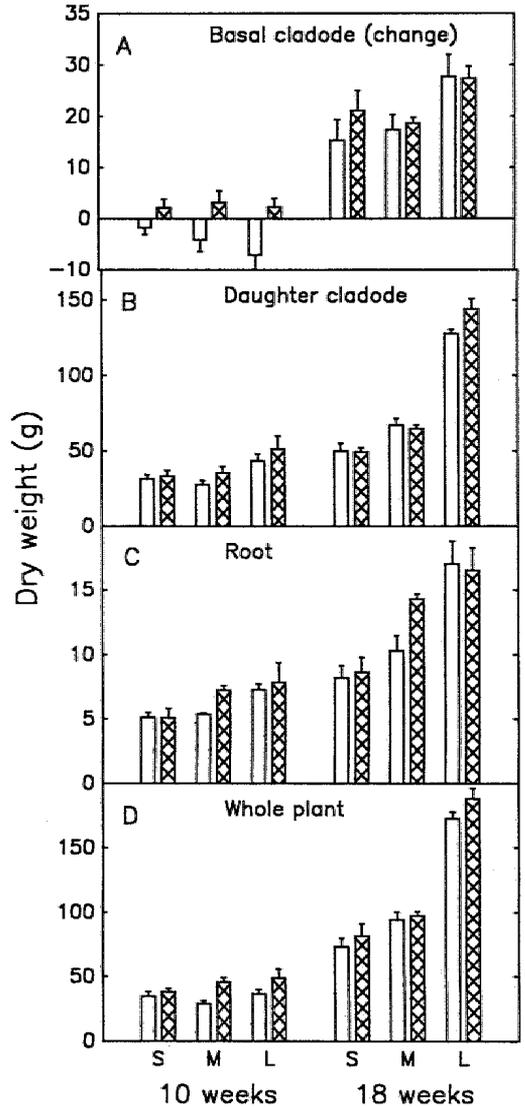


Fig. 5. Dry weight changes of *O. ficus-indica* for basal cladodes (A), dry weight of daughter cladodes (B), dry weight of roots (C), and total plant dry weight production (D) in small (S), medium (M) and large (L) pots at the current CO<sub>2</sub> level (open bars) and an elevated CO<sub>2</sub> level (hatched bars) at 10 and 18 weeks. Data are means  $\pm$  SE ( $n=4$  plants).

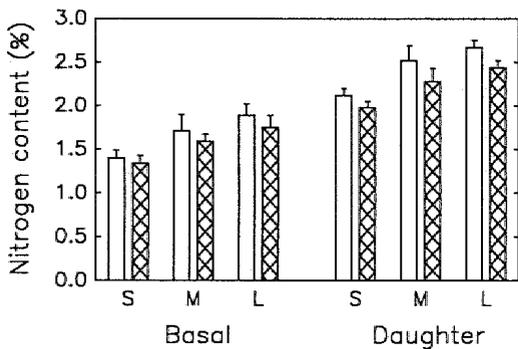


Fig. 6. Amount of nitrogen per unit dry weight in basal and daughter cladodes at the current CO<sub>2</sub> level (open bars) and an elevated CO<sub>2</sub> level (hatched bars) at 18 weeks in small (S), medium (M) and large (L) pots. Data are means  $\pm$  SE (n=4 plants).

(Fig. 6). For basal cladodes, nitrogen increased 33% from small to large pots ( $P < 0.01$ ) and decreased 6% as the CO<sub>2</sub> partial pressure was increased from 38 to 74 Pa ( $P > 0.05$ ; Fig. 6A). For daughter cladodes, nitrogen content increased 25% as pot size increased ( $P < 0.005$ ) and decreased 8% as the CO<sub>2</sub> level was approximately doubled ( $P < 0.05$ ). The nitrogen content for the 6 conditions averaged  $1.61 \pm 0.09\%$  of dry weight for the basal cladodes and  $2.33 \pm 0.11\%$  for the daughter cladodes ( $P < 0.001$ ). The nitrogen content of roots was relatively constant; mean values ranged from 0.79 to 0.84% (n=4 roots) of dry weight for the three pot sizes and the two CO<sub>2</sub> levels.

## Discussion

For *Opuntia ficus-indica* in controlled environment growth rooms, increasing the soil volume 10-fold had greater effects on CO<sub>2</sub> uptake and biomass production than did doubling the CO<sub>2</sub> level. Plant daily net CO<sub>2</sub> uptake at 10 weeks was enhanced 24% by raising the CO<sub>2</sub> partial pressure from 38 to 74 Pa. At 18 weeks such enhancement depended on soil volume and was absent for plants in small pots that restricted root growth. A similar decline in enhanced net CO<sub>2</sub> uptake with time of exposure to elevated CO<sub>2</sub> has been measured for annual crops (DeLucia et al. 1985, Ehret and Jolliffe 1985) and a perennial grass (Tissue and Oechel 1987). This decline has been attributed to chloroplast damage due to excessive carbohydrate accumulation in the shoots (Farrar and Williams 1991) and to changes in ribulose-1,5-bisphosphate carboxylase-oxygenase activity (Sage et al. 1989) as well as to limitations on water or nutrient uptake by roots (Bertson et al. 1993, McConaughay et al. 1993). A 10-fold increase in soil volume increased plant daily net CO<sub>2</sub> uptake by *O. ficus-indica* over 50% at 10 and 18 weeks. When the soil volume is increased 10-fold for C<sub>3</sub> species, the rate of net CO<sub>2</sub> uptake also increases, especially for crop plants (Arp 1991). Larger soil volumes can

enhance photosynthetic capacity by providing more water and nutrients and by increasing the sink strength represented by growing roots (Thomas and Strain 1991, Wong and Osmond 1991, Bertson et al. 1993). Thus, the greater sink strength of roots at the doubled CO<sub>2</sub> level, as evidenced by the greater area for main and lateral roots of *O. ficus-indica*, probably is related to its greater net CO<sub>2</sub> uptake at the higher CO<sub>2</sub> level.

Initially, basal cladodes of *O. ficus-indica* decreased in thickness, as their biomass was utilized for the growth of roots and daughter cladodes. At 10 weeks, basal cladodes at the current CO<sub>2</sub> level had a net loss of dry weight, whereas a modest increase in dry weight occurred for basal cladodes exposed to the elevated CO<sub>2</sub> level. The latter biomass increase for basal cladodes in part reflected their greater net CO<sub>2</sub> uptake at the doubled CO<sub>2</sub> level. At 10 weeks, daughter cladodes also had greater daily net CO<sub>2</sub> uptake for the elevated compared with the current CO<sub>2</sub> level. Greater daily CO<sub>2</sub> uptake by the basal and daughter cladodes helped to account for the 24% greater dry weight gain at 10 weeks when the CO<sub>2</sub> level was doubled. By 18 weeks, the enhancement in daily CO<sub>2</sub> uptake caused by doubling the CO<sub>2</sub> level was absent for basal cladodes in small and medium pots and for daughter cladodes in small pots, as root properties apparently then became limiting. This caused the enhanced dry weight gain due to the elevated CO<sub>2</sub> level to average only 8% at 18 weeks.

Increasing soil volume increased the shoot dry weight of *O. ficus-indica* more at elevated than at the current CO<sub>2</sub> levels, similar to results for cotton (Thomas and Strain 1991). The average root:shoot dry-weight ratio for *O. ficus-indica* was slightly higher under elevated compared with the current CO<sub>2</sub> level, consistent with the average 2% increase in root:shoot ratio found for C<sub>3</sub> species as the CO<sub>2</sub> level doubles (Arp 1991, Chu et al. 1992, Rogers et al. 1992). The surface area of both main and lateral roots of *O. ficus-indica* was substantially greater at the doubled CO<sub>2</sub> level for plants in medium-sized pots. Because increasing the pot size 10-fold approximately doubled root growth for *O. ficus-indica* in both current and elevated CO<sub>2</sub> levels, its root:shoot ratio substantially increased with increases in soil volume.

Increases in soil volume, which led to increases in root surface area, could lead to greater uptake of water, nitrogen and other nutrients. Because the soil was kept wet ( $\psi_{\text{soil}} > -0.15$  MPa) under all conditions, nutrients may have been the limiting factor. Indeed, the amount of nitrogen per unit dry weight in both basal and daughter cladodes of *O. ficus-indica* increased as pot size increased. Coupled with the increase in dry weight with pot size, the total amount of nitrogen in the cladodes at 18 weeks approximately doubled as the soil volume was increased 10-fold. The amount of nitrogen per unit dry weight in the cladodes also tended to decrease as the CO<sub>2</sub> level was doubled, in agreement with results on other species (Coleman et al. 1991, Chu et al. 1992, Silvola and Ahlholm 1992).

Biomass production in response to elevated CO<sub>2</sub> levels varies with CAM species. The dry weight of well-watered *Agave vilmoriniana* is unaffected when the CO<sub>2</sub> level is doubled, but as watering is decreased the fractional increase is substantial under elevated CO<sub>2</sub> levels (Idso et al. 1986). The dry weight of well-watered *Agave deserti* and *Ferocactus acanthodes* is about 30% greater over a 1-year period when the CO<sub>2</sub> level is doubled (Nobel and Hartssock 1986). Dry mass of new cladodes of *O. ficus-indica* growing for 26 weeks in a 1.5:1 (v:v) gravel:vermiculite mixture in relatively small pots (2 300 cm<sup>3</sup>) but watered three times per week with 0.5-strength Hoagland's solution is 23% greater when the CO<sub>2</sub> level is doubled (Nobel and Garcia de Cortazar 1991). The 1.5-fold greater frequency of watering with a 5-fold higher concentration of nutrients may account for the greater enhancement by elevated CO<sub>2</sub> at the same total daily PPFD compared with the present study.

As the atmospheric CO<sub>2</sub> level rises, increases in the biomass productivity of the agronomically important CAM species *O. ficus-indica* may be minimal for closely spaced plants growing at low light levels. The present study involving doubling of the CO<sub>2</sub> level was also conducted under well-watered conditions. Under conditions of higher PPFD and limited soil moisture, which characterize the habitats of most CAM species, the responses of *O. ficus-indica* to elevated CO<sub>2</sub> may be different. Nevertheless, restricted soil volume can still be expected to diminish the responses of this CAM plant to elevated atmospheric levels of CO<sub>2</sub>.

**Acknowledgements** – This research was supported by the Environmental Sciences Division, Office of Health and Environmental Research, U.S. Department of Energy Carbon Dioxide Research Program grant DE-FG03-91-ER61252 and contract DE-FC03-87-ER60615.

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