



Responses of some North American CAM plants to freezing temperatures and doubled CO₂ concentrations: implications of global climate change for extending cultivation

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Environmental influences on the cultivation of Crassulacean acid metabolism (CAM) plants, which are especially well adapted to arid regions with limited rainfall, were evaluated with respect to two aspects of global climate change. Cellular uptake of a vital stain, which occurs in living cells only, was halved at $-6 \pm 1^\circ\text{C}$ for the cultivated CAM species *Agave salmiana*, *Opuntia ficus-indica* and *Stenocereus queretaroensis* growing at day/night air temperatures of $30^\circ\text{C}/20^\circ\text{C}$ compared with -12°C for the wild species *Opuntia humifusa*. When plants were grown at reduced temperatures of $10^\circ\text{C}/0^\circ\text{C}$, stain uptake was halved at about -8°C for the cultivated species but at -24°C for *O. humifusa*. The greater low-temperature sensitivity and the lesser low-temperature acclimation of the cultivated species severely limit the regions where they can presently be grown, but such regions will expand as air temperatures rise accompanying global climate change. When the atmospheric CO₂ concentration was doubled from the current ambient value of $360 \mu\text{mol mol}^{-1}$ to $720 \mu\text{mol mol}^{-1}$, net CO₂ uptake over 24-h periods increased 36% for *A. salmiana* and *S. queretaroensis*; about one-third of the increase resulted from higher net CO₂ uptake rates in the last 4 h of daytime and two-thirds from higher rates during the first 8 h of the night. The doubled atmospheric CO₂ concentration predicted to occur before the end of the twenty-first century will increase CO₂ uptake and hence biomass productivity of such CAM species, further expanding the regions where they may be profitably cultivated.

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Introduction

Crassulacean acid metabolism (CAM) plants take up CO₂ primarily at night, leading to a high water-use efficiency that has important consequences for arid regions with limited rainfall (Walter, 1985; Nobel, 1988; Salisbury & Ross, 1991). For such plants,

most of the CO₂ taken up diffuses in through nocturnally open stomates and is fixed into organic acids using phosphoenolpyruvate carboxylase (PEPCase). Lower temperatures at night decrease the rate of water loss by CAM plants compared with the same degree of stomatal opening during the daytime, when stomates are open in C₃ and C₄ plants (Nobel, 1991*a*; Salisbury & Ross, 1991). Net CO₂ fixed over 24-h periods divided by the accompanying water loss is generally 10 to 15 mmol CO₂ mol⁻¹ H₂O for cultivated CAM plants, which represents a three- to eight-fold higher water-use efficiency than for C₃ or C₄ plants under comparable conditions (Nobel, 1991*b*). Because of their high water-use efficiency, CAM plants are especially well adapted to drier environments, which could change future utilization of the approximately one-third of the earth's land surface that is arid or semi-arid (Walter, 1985). Moreover, when supplied with water, certain cultivated CAM species can have high productivities, exceeding those of nearly all presently important crop species. Specifically, *Agave mapisaga* Trel., *A. salmiana* Otto ex Salm., *Opuntia amyclea* Tenore and *O. ficus-indica* (L.) Miller can all have annual above-ground productivities exceeding 38 tons dry weight ha⁻¹ year⁻¹, with harvests up to 50 tons ha⁻¹ year⁻¹ for *O. ficus-indica* (Nobel, 1991*a*, 1994; Nobel *et al.*, 1992).

Perhaps the best measured parameter associated with global climate change is the atmospheric CO₂ concentration. It is currently increasing annually by 2 to 3 μmol CO₂ mol⁻¹ air year⁻¹ (equivalent to 2 to 3 p.p.m. by volume or about 2 to 3 μbar), so atmospheric CO₂ concentrations could double before the end of the twenty-first century (Houghton *et al.*, 1990; Keeling & Whorf, 1990; King *et al.*, 1992; Siegenthaler & Sarmiento, 1993). Because PEPCase is effectively saturated with CO₂ at current atmospheric CO₂ concentrations for C₄ plants, which like CAM plants use mainly this enzyme for the initial fixation of atmospheric CO₂, a doubling of CO₂ will have little effect on the net CO₂ uptake by C₄ plants. This might therefore also be expected for CAM plants as the atmospheric CO₂ concentration is doubled. Indeed, little effect on CO₂ uptake and growth occurs when the CO₂ concentration is doubled under well-watered conditions for the CAM species *Agave vilmoriniana* Berger (Idso *et al.*, 1986; Szarek *et al.*, 1987), *Ananas comosus* (L.) Merr. (Ziska *et al.*, 1991), and *Bryophyllum daigremontanum* (Hamet & Perrier) Berger [syn. *Kalanchoë daigremontanum* Hamet & Perrier] (Osmond & Björkman, 1975). On the other hand, doubling the atmospheric CO₂ concentration increases net CO₂ uptake over 24 h by 30% to 70% for the CAM species *Agave deserti* Engelm., *Ferocactus cylindraceus* (Engelm.) Orc. [syn. *F. acanthodes* (Lemaire) Britton & Rose], and *O. ficus-indica* (Nobel & Hartssock, 1986; Cui *et al.*, 1993).

Another environmental factor associated with global climate change is air temperature. Although predictions of future temperatures vary considerably and projected trends based on measured temperatures are ambiguous, most general circulation models indicate that temperatures should rise by 2°C to 5°C in low and middle latitudes as the atmospheric CO₂ concentration doubles (Adams *et al.*, 1990; Houghton *et al.*, 1990; Sasek & Strain, 1990). CAM plants such as agaves and cacti are extremely tolerant of high temperatures, many species surviving air and tissue temperatures exceeding 55°C (Nobel, 1988). On the other hand, CAM plants in general are not particularly tolerant of freezing temperatures. The northern limit for various species of cacti in the Chihuahuan and Sonoran deserts is where temperatures dip annually below -1°C (Kinraide, 1978; Benson, 1982). Also, seasonal low temperature is the environmental factor that most limits the increased cultivation of *O. ficus-indica*, which is currently utilized in more than 20 countries for fruit, young cladodes (stem segments) used as a vegetable, and mature cladodes used for cattle fodder (Russell & Felker, 1987*a,b*; Nobel, 1994; Pimienta-Barrios, 1994). The influence of freezing temperatures on cell viability and plant survival has not been investigated for many other cultivated CAM species that may become increasingly

important in arid and semi-arid areas as CO₂ concentrations and air temperatures increase accompanying global climate change (Nobel, 1988, 1994).

To see whether the responses to elevated CO₂ concentrations and low temperatures observed for *O. ficus-indica* occur for other cultivated CAM species, two such species native to semi-arid regions of central and western Mexico were examined together with two opuntias. *Agave salmiana* is cultivated as a source of beverages (the sweet-tasting 'agua miel' and the fermented pulque) as well as for the use of its leaves as cattle fodder and its leaf cuticle as a food wrapping (Gentry, 1982; Nobel, 1994). This species, as well as *O. ficus-indica*, is also planted for soil stability and erosion control (Russell & Felker, 1987a; Nobel, 1994; Pimienta-Barrios, 1994). *Stenocereus queretaroensis* (Weber) Buxb. is cultivated for its attractively coloured fruit (commercial varieties are generally deep purple), which is generally eaten fresh but is also utilized in cooking, candy, and as an additive to ice cream (Pimienta-Barrios & Nobel, 1994). To test the hypothesis that ambient CO₂ concentrations can affect net CO₂ uptake and hence biomass productivity, net CO₂ uptake was measured over 24-h periods for both species under the current atmospheric CO₂ concentration and at a doubled CO₂ concentration. To evaluate the influence of low temperature on the survival of cultivated CAM plants, tissue sections from *A. salmiana* and *S. queretaroensis* were subjected to a series of subzero temperatures, and the uptake of a vital stain into living chlorenchyma cells was determined. For comparison, stain accumulation by *O. ficus-indica* and a cold-tolerant cactus in the same genus, *Opuntia humifusa* (Raf.) Raf., was also measured. Implications for future utilization of CAM species could thus be evaluated with respect to the global climate change, which can affect the regions available for cultivation of such species.

Materials and methods

Plant material

Offshoots of *Agave salmiana* var. *salmiana* (Agavaceae) about 22 cm tall were obtained from a commercial plantation in Tequexquinahuac, Mexico. Cladodes of *Opuntia ficus-indica* (Cactaceae) averaging 28 cm in length were obtained from the Agricultural Research Station at the University of California, Riverside, California; these plants had been propagated from material collected in Coahuila, Mexico. Cladodes of *O. humifusa* averaging 8 cm in length were collected at Point Pelee, Ontario, Canada. Stem segments of *Stenocereus queretaroensis* (Cactaceae) averaging 45 cm in length were obtained from a commercial plantation in Techaluta, Jalisco, Mexico. All shoots, which were initially approximately 1-year-old, were placed in a 1:1 mixture of washed quartz sand and soil from the Agricultural Research Station.

The plants were maintained in a glasshouse at the University of California, Los Angeles, for 6 to 10 months before transfer to controlled-environment chambers. The average maximum/minimum day/night air temperatures in the glasshouse were 26°C/17°C, the average photosynthetic photon flux (PPF; wavelengths of 400 to 700 nm) in the planes of the photosynthetic surfaces was about 510 μmol m⁻² s⁻¹ (the total daily PPF averaged 22 mol m⁻² d⁻¹), and the maximum/minimum daily relative humidities averaged 70%/40%. The plants were watered once or twice per week with 0.1-strength Hoagland solution (Hoagland & Arnon, 1950) so that the soil water potential in the root zone was always above -0.4 MPa.

Low-temperature responses

To test for responses to low temperature, eight to ten plants of each species were

transferred to controlled-environment chambers with day/night air temperatures of 30°C/20°C and a 12-h photoperiod, other conditions being essentially the same as in the glasshouse. To induce low-temperature acclimation, a random subset of four or five plants was moved after 4 weeks to a similar controlled-environment chamber with day/night air temperatures of 10°C/0°C.

After an additional 2 weeks, samples approximately 0.5 cm² in area were removed from the shoot of each plant (at 30°C/20°C and 10°C/0°C) with a scalpel and placed in a beaker. A copper-constantan thermocouple was placed in contact with each sample, which was cooled in the dark in a Rheem Manufacturing ULT-80 ultra-low-temperature freezer at 4°C h⁻¹, a cooling rate similar to that observed for cactus stems in the field (Nobel, 1981; Loik & Nobel, 1993). Samples were maintained at a particular subzero treatment temperature for 1 h and then warmed at 5°C h⁻¹ to about 5°C, sliced with a razor blade into sections 0.6 to 0.8 mm thick, and immersed in 5 cm³ of 15 mM of the vital stain neutral red (3-amino-7-dimethylamino-2-methylphenazine (HCl)) at pH 7.4. After storing overnight at 5°C to maximize stain uptake (Onwueme, 1979; Didden-Zopf & Nobel, 1982; Nobel & Loik, 1990), freehand sections approximately three cells thick were examined in distilled water at 100× with an Olympus BH2 phase-contrast microscope. Stain uptake, which occurs only in living cells, was determined for 100 to 150 chlorenchyma cells from each of four sections (about 500 cells total) from each plant at each treatment temperature; data are expressed as a percentage of the stain uptake occurring for samples treated at 0°C, which was generally about 90% of the cells examined. Survival of cactus stems closely parallels the ability of the chlorenchyma cells to accumulate neutral red, so a particular subzero temperature that decreased stain uptake by 50% usually leads to death of about half of the cells (Nobel, 1981; Didden-Zopf & Nobel, 1982).

Net CO₂ uptake

To examine the effects of atmospheric CO₂ concentrations on net CO₂ uptake, four plants of both *A. salmiana* and *S. queretaroensis* were placed in controlled-environment chambers containing the average current ambient CO₂ concentration of 360 μmol CO₂ mol⁻¹ air, and a second randomly selected set of four plants was placed at an average CO₂ concentration of 720 μmol mol⁻¹. The doubled CO₂ concentration was maintained ± 10 μmol mol⁻¹ using a mass-flow meter and an electronically controlled needle valve through which 100% CO₂ was injected into the controlled-environment chamber while the CO₂ concentration was monitored with a Li-Cor LI-6200 portable photosynthesis system. The plants and the CO₂ injection system were switched weekly between chambers. Before measuring net CO₂ uptake over 24-h periods, plants were maintained in the controlled-environment chambers at day/night air temperatures of 25°C/15°C and a 12-h photoperiod for 4 weeks (other conditions were essentially the same as in the glasshouse).

To measure net CO₂ uptake, a Li-Cor 250 cm³ leaf chamber was modified to fit at mid-organ on the leaves (*A. salmiana*) or stem segments (*S. queretaroensis*) by replacing its top with an acrylic plate from which projected a 3-cm long acrylic tube 5 cm in diameter. Two layers of foam-rubber gasket were attached to the tube's distal end, which in the case of the agave leaves was specially contoured to fit their concave upper surface; the tube was firmly pressed against a photosynthetic surface during measurement on plants while they were in the controlled-environment chambers. To prevent mixing of chamber air with outside air during measurement, the chamber door was covered with a microbiological sterile work station with sleeves to provide access to the Li-Cor LI-6200.

Results

Low-temperature responses

As the subzero treatment temperature was decreased, the percentage of chlorenchyma cells taking up the vital stain neutral red steadily decreased (Fig. 1). For all four species, the decrease occurred at lower temperatures ($p < 0.01$ based on Student's t -test) for plants maintained at day/night air temperatures of $10^{\circ}\text{C}/0^{\circ}\text{C}$ compared with $30^{\circ}\text{C}/20^{\circ}\text{C}$. Specifically, the subzero temperature decreasing the stain uptake by 50% compared with the control, which is defined as LT_{50} , was $-5.1 \pm 0.3^{\circ}\text{C}$ (mean \pm SE, $N = 4$ or 5 plants) for *Agave salmiana* maintained at $30^{\circ}\text{C}/20^{\circ}\text{C}$ and $-7.3 \pm 0.4^{\circ}\text{C}$ for plants at $10^{\circ}\text{C}/0^{\circ}\text{C}$ (Fig. 1(a)). For *Opuntia ficus-indica*, LT_{50} was $-5.6 \pm 0.4^{\circ}\text{C}$ for plants at $30^{\circ}\text{C}/20^{\circ}\text{C}$, decreasing to $-8.1 \pm 0.3^{\circ}\text{C}$ for plants at $10^{\circ}\text{C}/0^{\circ}\text{C}$ (Fig. 1(b)); both LT_{50} s were much lower for *O. humifusa*, $-12.0 \pm 0.4^{\circ}\text{C}$ and $-23.8 \pm 0.8^{\circ}\text{C}$, respectively (Fig. 1(c)). For *Stenocereus queretaroensis*, LT_{50} was at $-7.1 \pm 0.3^{\circ}\text{C}$ for plants at $30^{\circ}\text{C}/20^{\circ}\text{C}$, decreasing to $-8.6 \pm 0.4^{\circ}\text{C}$ for plants at $10^{\circ}\text{C}/0^{\circ}\text{C}$ (Fig. 1(d)).

Net CO₂ uptake

Net CO_2 uptake for both *A. salmiana* and *S. queretaroensis* occurred primarily at night, and the maximal rates were higher under atmospheric CO_2 concentrations of $720 \mu\text{mol mol}^{-1}$ compared with $360 \mu\text{mol mol}^{-1}$ ($p < 0.01$; Fig. 2). Net CO_2 exchange became positive in midafternoon under the doubled CO_2 concentration but not until nighttime under the current ambient CO_2 concentration. For the last one-third of the night and the first two-thirds of the daytime, the rate of net CO_2 uptake was similar for plants under the two atmospheric CO_2 concentrations (Fig. 2). The total daily net CO_2 uptake, obtained by integrating the net CO_2 uptake rates over the 24-h periods, was $481 \text{ mmol m}^{-2} \text{ day}^{-1}$ for *A. salmiana* under the current CO_2 concentration, increasing by 36% ($p < 0.01$) for the doubled CO_2 concentration (Fig. 2(a)). For *S. queretaroensis*, total daily net CO_2 uptake under the current CO_2 concentration was $188 \text{ mmol m}^{-2} \text{ day}^{-1}$, also increasing by 36% ($p < 0.01$) for the doubled CO_2 concentration (Fig. 2(b)). Of the enhancements in daily net CO_2 uptake caused by doubling the CO_2 concentration, 31% occurred during the daytime for *A. salmiana* and 36% for *S. queretaroensis* ($p < 0.01$).

Discussion

Raising the atmospheric CO_2 concentration from 360 to $720 \mu\text{mol mol}^{-1}$ increased the daily net CO_2 uptake for both *Agave salmiana* and *Stenocereus queretaroensis* by 36%. All the increase occurred during the latter one-third of the daytime and the first two-thirds of the night-time, similar to results for *Agave deserti* and *Ferocactus cylindraceus*, whose daily net CO_2 uptake is enhanced 30% by doubling the CO_2 concentration (Nobel & Hartsock, 1986). Net CO_2 uptake can be increased by up to 70% for *Opuntia ficus-indica*, for which the doubling of CO_2 concentration enhances net CO_2 uptake throughout the night and in the early morning as well (Nobel & Israel, 1994). Of the 36% enhancement in daily net CO_2 uptake caused by doubling the atmospheric CO_2 concentration for *A. salmiana* and *S. queretaroensis*, about one-third occurred during the daytime and two-thirds at night. In any case, all five of these CAM species respond advantageously with respect to net CO_2 uptake when the atmospheric CO_2 concentration is increased.

The responses of *A. salmiana*, *O. ficus-indica* and *S. queretaroensis* to low temperatures were quite similar, as judged by the uptake of a vital stain into the

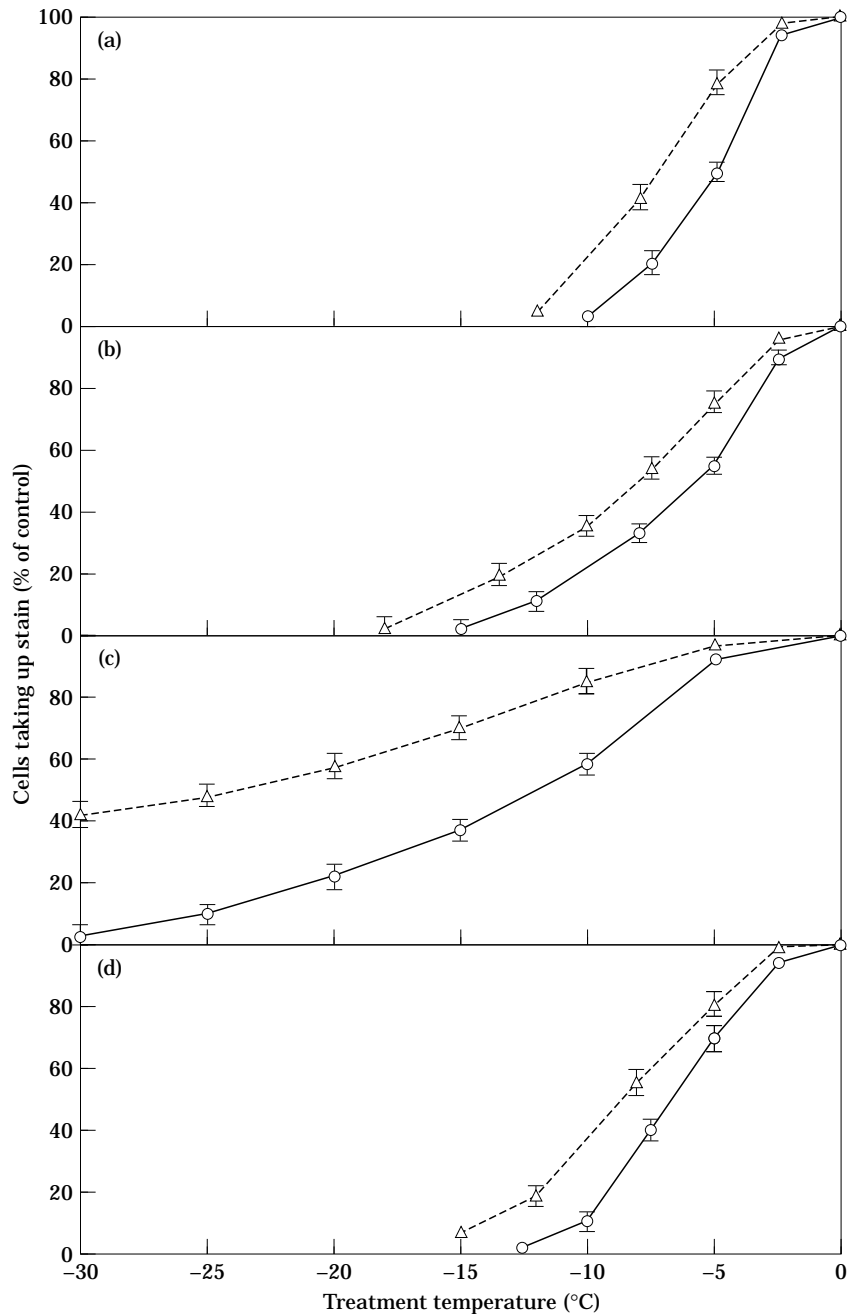


Figure 1. Influence of subzero temperatures on the uptake of the vital stain neutral red by chlorenchyma cells of (a) *Agave salmiana*, (b) *Opuntia ficus-indica*, (c) *O. humifusa*, and (d) *Stenocereus queretaroensis* maintained at day/night air temperatures of 30°C/20°C (○) or 10°C/0°C (△). Approximately 500 cells per plant were examined for samples placed for 1 h at the indicated temperature. Data, which are expressed relative to the control at 0°C, are means \pm SE ($N = 4$ or 5 plants), except when the SE is smaller than the symbol.

chlorenchyma cells, but differed substantially from the response of *Opuntia humifusa*, a cold-tolerant cactus native to northern United States and southern Canada (Benson, 1982; Nobel & Loik, 1990). In particular, for plants growing at day/night air temperatures of 30°C/20°C, the subzero temperature that halved stain uptake (LT_{50}) was $-6 \pm 1^\circ\text{C}$ for the three cultivated species but -12°C for *O. humifusa*. The low-temperature acclimation, defined as the decrease in LT_{50} as the day/night temperatures were decreased by 20°C, averaged 2°C for the three cultivated species but 12°C for *O. humifusa*. Indeed, most chlorenchyma cells are killed at -9°C for *A.*

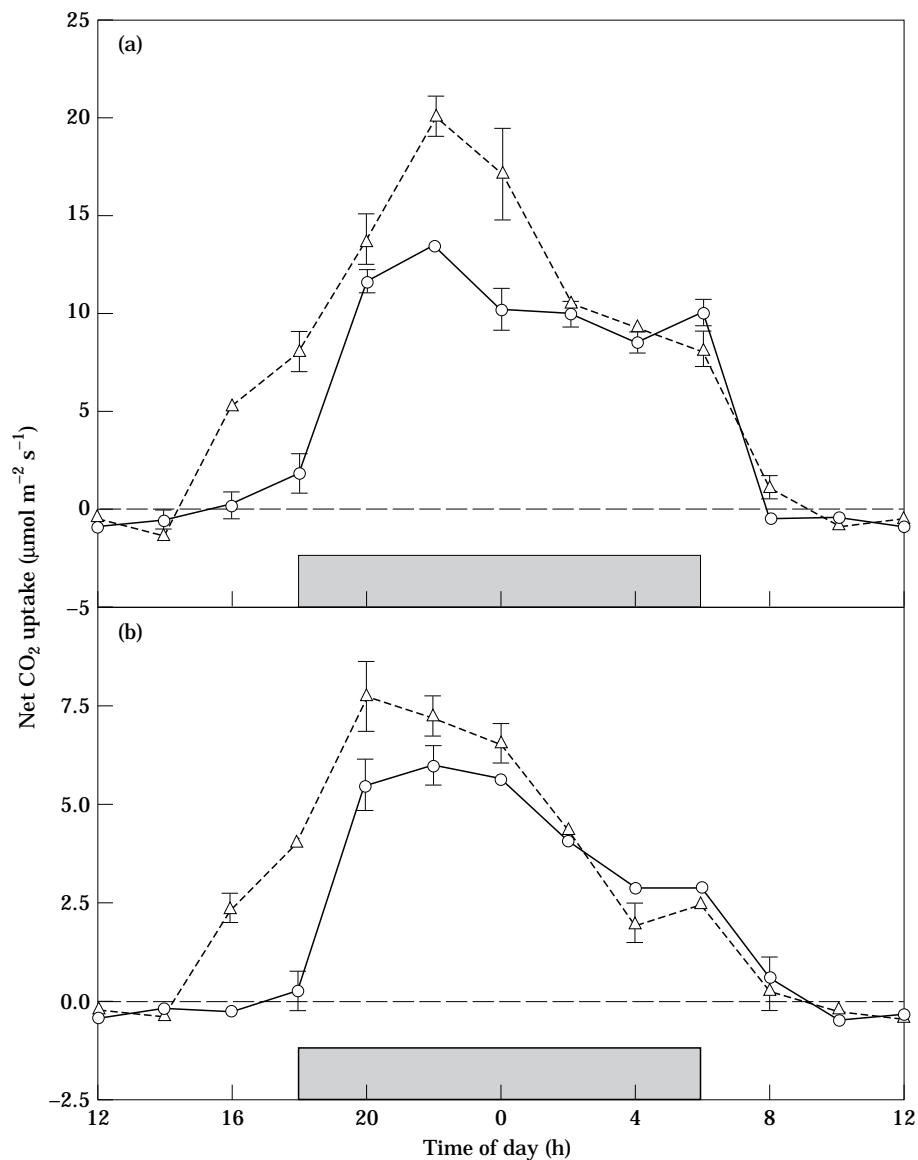


Figure 2. Daily course of the rates of net CO₂ uptake for (a) *A. salmiana* and (b) *S. queretaroensis* under current (○; $360 \mu\text{mol mol}^{-1}$) and doubled (△; $720 \mu\text{mol mol}^{-1}$) atmospheric CO₂ concentrations. Day/night air temperatures were 25°C/15°C, the PPF in the planes of the photosynthetic organs averaged $510 \mu\text{mol m}^{-2} \text{s}^{-1}$ for a 12-h photoperiod, and the plants were well watered. Data are means \pm SE ($N = 4$ plants). The stippled bars indicate night-time.

salmiana, *O. ficus-indica* and *S. queretaroensis* maintained at day/night air temperatures of 10°C/0°C, whereas -25°C is required for such damage to *O. humifusa*. *Opuntia fragilis* (Nuttall) Haw., which is native to extremely cold habitats in western Canada, is even more cold-tolerant than *O. humifusa* (Nobel & Loik, 1990; Loik & Nobel, 1993), and perhaps the most cold-tolerant agave is *Agave utahensis* Engelm., whose LT₅₀ for plants at day/night temperatures of 10°C/0°C is -18°C (Nobel, 1988). These cold-tolerant species are all small in stature and not commercially important but illustrate the genetic diversity available within the two genera with respect to low-temperature sensitivity. Thus, breeding efforts are warranted using other species in the same genera to increase the low-temperature tolerance of cultivated species and hence expand the region for the cultivation of economically important agaves and cacti (Russell & Felker, 1987*b*; Nobel, 1994).

Although general circulation models and other predictors of global climate change are constantly being challenged and improved, certain predicted environmental changes are usually agreed upon. For instance, atmospheric CO₂ concentrations will probably increase by 150 to 350 μmol mol⁻¹ and air temperatures will rise by 2 to 5°C within 100 years (Adams *et al.*, 1990; Houghton *et al.*, 1990; Keeling & Whorf, 1990; Sasek & Strain, 1990; King *et al.*, 1992; Siegenthaler & Sarmiento, 1993). The former will increase the net CO₂ uptake and biomass productivity of cultivated CAM plants and the latter will increase the regions in which they can avoid freezing damage. Changes in rainfall patterns and slight increases in average annual rainfall are predicted to accompany global climate change (Adams *et al.*, 1990; Houghton *et al.*, 1990). Because of their high water-use efficiency, CAM plants have an advantage over C₃ and C₄ plants if rainfall decreases or becomes seasonally less reliable (Nobel, 1988; Salisbury & Ross, 1991), and in addition *O. ficus-indica* shows an increased tolerance of drought under a doubled atmospheric CO₂ concentration (Nobel & Israel, 1994); as for plants in general, productivity of CAM plants will increase with increasing water availability (Nobel, 1991*a*). Extrapolating from the present results with *A. salmiana* and *S. queretaroensis*, which show slightly greater effects of elevated CO₂ on net CO₂ uptake than do *A. deserti* and *F. cylindraceus* but less than *O. ficus-indica* (Nobel & Hartsock, 1986; Cui *et al.*, 1993; Nobel & Israel, 1994), net CO₂ uptake and biomass productivity should increase about 1% for each 10 μmol mol⁻¹ increase in atmospheric CO₂ concentration. For each 1°C increase in ambient air temperatures, cultivation without freezing damage at a particular elevation should be possible 160 to 170 km (100 to 106 miles) further from the equator (Nobel, 1980; Woodward & Sheehy, 1983).

Assuming that *O. ficus-indica* can be raised in regions with annual minimum temperatures above -10°C and using general circulation models to predict temperatures that can accompany a doubling of the atmospheric CO₂ concentration, about 46% more land will be suitable for cultivation of this species in the United States under doubled atmospheric CO₂ concentrations (Nobel, 1991*c*). The increased temperatures accompanying such global climate change tend to decrease the productivity of *O. ficus-indica* per unit ground area within about 30° latitude of the equator (Nobel, 1991*c*; Nobel & Garcia de Cortázar, 1991). In most such regions this decrease would be overridden by the positive effects of doubled CO₂ on net CO₂ uptake and productivity (Cui *et al.*, 1993), including the effects of temperature on net CO₂ uptake under the doubled CO₂ concentration (Nobel & Israel, 1994). For regions at least 30° from the equator, a doubled atmospheric CO₂ concentration and the accompanying climatic changes, including variable effects on precipitation, are predicted to increase the overall productivity of *O. ficus-indica* by an average of 35% (Nobel, 1991*c*).

Breeding programmes to select cultivars of *O. ficus-indica* and other platyopuntias with increased low-temperature tolerance are important for the expansion of the cultivation of such species (Russell & Felker, 1987*a,b*; Nobel, 1994). Indeed,

considerable genetic diversity with respect to low-temperature sensitivity exists among species of opuntias and even within a species (Nobel, 1988, 1990). Moreover, *O. ficus-indica* and other playopuntias are of increasing economic importance in arid and semi-arid regions of Mexico and other countries (Nobel, 1994; Pimienta-Barrios, 1994). Various species of *Stenocereus*, including *S. gummosus* (Brandege) Gibson & Horak, *S. griseus* (Haw.) Buxb., and *S. thurberi* (Engelm.) Buxb., are being evaluated as possible fruit crops in Israel (Nerd *et al.*, 1993); an air temperature of -7°C injured 51% of the stem surface area for *S. griseus* but less than 5% for the other two species (Nerd *et al.*, 1993), underscoring the limitations caused by low temperatures for the expansion of the cultivation of cacti and the genetic diversity within a genus. In any case, rising air temperatures and increasing atmospheric CO_2 concentrations accompanying global climate change should increase the opportunities for cultivation of agaves, cacti and other CAM plants of potential economic importance in arid and semi-arid regions.

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