Communication

Short-Term and Long-Term Responses of Crassulacean Acid Metabolism Plants to Elevated CO₂

PARK S. NOBEL* AND TERRY L. HARTSOCK
Department of Biology and Laboratory of Biomedical and Environmental Sciences, University of California, Los Angeles, California 90024

ABSTRACT

For the leaf succulent Agave deserti and the stem succulent Ferocactus acanthodes, increasing the ambient CO₂ level from 350 microliters per liter to 650 microliters per liter immediately increased daytime net CO₂ uptake by about 30% while leaving nighttime net CO₂ uptake of these Crassulacean acid metabolism (CAM) plants approximately unchanged. A similar enhancement of about 30% was found in dry weight gain over 1 year when the plants were grown at 650 microliters CO₂ per liter compared with 350 microliters per liter. Based on these results plus those at 500 microliters per liter, net CO₂ uptake over 24-hour periods and dry weight productivity of these two CAM succulents is predicted to increase an average of about 1% for each 10 microliters per liter rise in ambient CO₂ level up to 650 microliters per liter.

The atmospheric level of CO₂ has been steadily increasing since the beginning of the Industrial Revolution, in large measure reflecting the accelerating consumption of fossil fuels. Specifically, the ambient CO₂ level is estimated to have been about 270 μL L⁻¹ in 1850, is currently about 350 μL L⁻¹, and is predicted to reach 650 μL L⁻¹ before 2100 (2, 3, 10, 21). Compared with 350 μL CO₂ L⁻¹, many agronomic C₃ plants would be expected to increase productivity about 30% at 650 μL CO₂ L⁻¹ with little or no increase expected for C₄ plants (8, 10, 18, 22). Very little work has so far been done on the response of CAM plants to elevated CO₂ (1, 10). For the CAM leaf succulent Agave vilmoriniana, long-term (6 months) increases in dry weight were not significantly enhanced when the ambient CO₂ level was raised from 350 to 675 μL L⁻¹ for plants receiving water twice per week (5). When the plants received water on average once per week, increasing the CO₂ level from 350 to 675 μL L⁻¹ increased the growth rate of plants initially 5 g in dry weight over 300% and increased those initially 191 g in dry weight about 30% (5).

The responses of net CO₂ uptake to water status, temperature, and photosynthetically active radiation are known for certain desert CAM plants, namely the leaf succulent Agave deserti and the stem succulent Ferocactus acanthodes (11–14). Moreover, their predicted productivities based on CO₂ responses are in close agreement with field productivities determined upon harvesting and dry weight measurements (13, 14). These two CAM species were selected to investigate the influence of raising the CO₂ level from 350 to 650 μL L⁻¹ on both short-term net CO₂ exchange and long-term changes in dry weight.

MATERIALS AND METHODS

Agave deserti Engelm. (Agavaceae) was grown from seed for 6 months under well-watered conditions in a glasshouse in Los Angeles. One-year-old seedlings of Ferocactus acanthodes (Lemaire) Britton and Rose (Cactaceae) were obtained from a commercial nursery. All seedlings were then transplanted into washed sand and maintained in an M-31 Environmental Growth Chamber with day/night air temperatures of 25°C/15°C (near optimal for net CO₂ uptake by these species) (12, 13) until used for the short-term or the long-term experiments. PAR (400 to 700 nm, determined with a Licor LI-190S quantum sensor) in the planes of the shoot surfaces averaged 600 μmol m⁻² s⁻¹ for 12 h each day, leading to a total daily PAR of 26 mol m⁻² (essentially saturating for net CO₂ uptake for these species (12, 13). The plants were watered weekly with 0.1-strength Hoagland No. 1 solution supplemented with micronutrients (4) so that the soil water potential in the root zone was always above −0.5 MPa (measured with Wescor PT 51-05 soil thermocouple psychrometers).

To measure short-term influences of CO₂ levels, shoots of 1.5-year-old plants of A. deserti and 2-year-old plants of F. acanthodes were sealed into a modified Siemens, null-point, closed-circuit glass flow system (15). The conditions were the same as in the environmental chamber, including a water vapor content of 10 g m⁻³ (determined with a Cambridge Systems EG&G 880 dewpoint hygrometer), except for the CO₂ level, which was either 350 μL L⁻¹ (the average value for the environmental chambers) or 650 μL L⁻¹. The CO₂ level was measured with an Anarad AR-500R 1R gas analyzer. Gas exchange over 24-h periods was repeated twice at each CO₂ level for each species with comparable results.

For the long-term experiments on CO₂ effects, 1-year-old plants of A. deserti and 1.5-year-old plants of F. acanthodes were removed from the sand, the fresh weights were determined, and then the seedlings were sent to the Duke University Phytotron, Durham, NC, for growth in glasshouses controlled at local mean air temperatures and CO₂ levels of 350, 500, or 650 μL L⁻¹. The plants were again grown in washed sand and watered weekly with 0.1-strength Hoagland solution No. 1 supplemented with micronutrients (4). At 4-month intervals, six plants of each species were harvested under each CO₂ level.

Shoot and root dry weights of the harvested plants were determined by drying in a forced-draft oven at 80°C until no further weight change occurred. The 1-year-old plants of A. deserti selected for the long-term studies had an initial fresh weight within 2% of 12.32 g; based on measurements of 12

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plants, the mean initial shoot dry weight was 0.921 g (8.2% of the shoot fresh weight) and the mean initial root dry weight was 0.136 g (12.5% of the root fresh weight). The 1.5-year-old plants of F. acanthodes selected for the long-term studies had an initial fresh weight within 2% of 21.2 g; again based on measurements of 12 plants, the mean initial shoot dry weight was 1.778 g (8.9% of the shoot fresh weight) and the mean initial root dry weight was 0.185 g (15.2% of the root fresh weight). To provide additional precision, final dry weights were adjusted up or down by the same percentage that the initial fresh weight was less or more, respectively, than the mean values for each species (the maximum adjustment was 2%). Such root and shoot dry weights at 350 and 650 μL CO₂ L⁻¹ were compared using the Student’s t test; plant dry weights at all three CO₂ levels were analyzed using ANOVA with pairwise comparisons by Tukey’s method.

RESULTS AND DISCUSSION

For the short-term experiments on net CO₂ uptake, plants of the same mean age as those used for the long-term experiments on growth (1.5 years old for A. deserti and 2 years old for F. acanthodes) were either kept at the average ambient CO₂ level of 350 μL L⁻¹ or were suddenly exposed to 650 μL CO₂ L⁻¹. Such near doubling of the ambient CO₂ level caused the maximal rate of nocturnal net CO₂ uptake to increase about 50% for both species (Fig. 1). The higher rates at 650 μL CO₂ L⁻¹ were maintained only during the first half of the night and indeed the rate at the elevated CO₂ level became less than the net CO₂ uptake rate at 350 μL L⁻¹ during the second half of the night for both species (Fig. 1). Hence, the total net CO₂ uptake integrated over the whole night was little affected by ambient CO₂ level, amounting to 202 mmol CO₂ m⁻² at 350 μL L⁻¹ and 207 mmol CO₂ m⁻² at 650 μL L⁻¹ for A. deserti (Fig. 1A) and 101 mmol CO₂ m⁻² at 350 μL L⁻¹ and 103 mmol CO₂ m⁻² at 650 μL L⁻¹ for F. acanthodes (Fig. 1B). This is in agreement with previous studies on somewhat older plants of A. deserti, where net CO₂ uptake over a 10-h night increased only 2% upon raising the ambient CO₂ level from 340 to 700 μL L⁻¹ (16). Hence, the amount of CO₂ acceptor was insufficient, the malate pool became filled, or the available energy supply could not maintain the high initial rates of net CO₂ uptake at the elevated CO₂ level over the entire night.

In contrast to the small immediate effect of external CO₂ level on the total CO₂ uptake at night, raising the CO₂ level from 350 to 650 μL L⁻¹ caused the daytime CO₂ uptake by A. deserti to increase by 54 mmol m⁻² to 130 mmol m⁻² (Fig. 1A). Also, the maximal rate of net CO₂ uptake was nearly doubled at the higher ambient CO₂ level for A. deserti. Even though 2-year-old plants of F. acanthodes exhibited little daytime CO₂ uptake, as has been noted previously for similar-aged plants of this species (7) and as is the case for other stem succulents (9), uptake was again much higher at 650 than at 350 μL CO₂ L⁻¹ (Fig. 1B); daytime net CO₂ uptake increased from 3 mmol m⁻² at the low CO₂ level to 31 mmol m⁻² at the high level. Daytime CO₂ uptake by CAM plants is evidently by the C₃ pathway (9, 20), which is known to have higher rates at elevated CO₂ levels (3, 10). However, raising the CO₂ level from 350 to 650 μL L⁻¹ does not even double the net CO₂ uptake rate of C₃ plants, while the enhancement in daytime net CO₂ uptake observed here at elevated CO₂ levels was 2.5- to 10-fold.

Long-term experiments with elevated CO₂ led to effects comparable to those of the short-term experiments. Specifically, shoots of A. deserti increased by 2.72 g at 350 μL CO₂ L⁻¹ and by 3.47 g at 650 μL CO₂ L⁻¹ (Fig. 2A), leading to a 28% higher growth at the elevated CO₂ level (differences were significant at P < 0.01). Shoots of F. acanthodes increased by 1.96 g at 350 μL CO₂ L⁻¹ and 2.54 g at 650 μL L⁻¹ (Fig. 2B) or by 30% more at the elevated CO₂ level (P < 0.01). Root dry weight increased 29% more for A. deserti (P < 0.01) and 28% more for F. acanthodes.
(P < 0.01) at 650 μL CO₂ L⁻¹ than at 350 μL L⁻¹. In all cases, root and shoot growth at an intermediate CO₂ level of 500 μL L⁻¹ was approximately halfway between. Thus, as the CO₂ level was raised from 350 to 500 to 650 μL L⁻¹, plant dry weight after 1 year increased by 3.63, 4.19, and 4.60 g for A. deserti and by 2.55, 2.96, and 3.29 g for F. acanthodes, respectively (all pairwise comparisons were significantly different at P < 0.05 for both species).

As the ambient CO₂ level was raised from 350 to 650 μL L⁻¹, both the short-term net CO₂ uptake over 24 h and the long-term dry weight gain over 1 year were enhanced by about 30% for the leaf succulent A. deserti and the stem succulent F. acanthodes. The short-term effect immediately after raising the CO₂ level was caused by mainly an increase in daytime net CO₂ uptake for both species. It is predicted that, after a period of adjustment during which glaucan levels build up providing sufficient acceptor for nocturnal CO₂ binding and other adjustments occur (9, 17, 19), most of the effect of increased ambient CO₂ level would eventually be on nocturnal CO₂ uptake for such CAM plants.

The approximately three-fold higher growth rates per unit dry weight for A. deserti than for F. acanthodes (Fig. 2) reflect the higher surface area per unit volume (6, 7) and the inherently higher net CO₂ uptake rates of A. deserti (Fig. 1) (11, 12). This study did not support results for well-watered A. vilmoriniana, where growth was enhanced an average of only 1% by raising the ambient CO₂ level from 350 to 675 μL L⁻¹, but was similar to results on large plants of this species under drier conditions (5). Growth of A. deserti and F. acanthodes was increased about 16% upon raising the ambient CO₂ level from 350 to 500 μL L⁻¹ and by another 12% at 650 μL L⁻¹, in general agreement with comparable studies on C₃ plants (8). In any case, based on the present study the net CO₂ uptake and productivity of CAM plants would be expected to increase an average of about 1% for each 10 μL L⁻¹ rise in atmospheric CO₂ up to 650 μL L⁻¹.

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LITERATURE CITED


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