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Communication

Short-Term and Long-Term Responses of Crassulacean Acid Metabolism Plants to Elevated CO_2[1]

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ABSTRACT

For the leaf succulent *Agave deserti* and the stem succulent *Ferocactus acanthodes*, increasing the ambient CO_2 level from 350 microliters per liter to 650 microliters per liter immediately increased daytime net CO_2 uptake about 30% while leaving nighttime net CO_2 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 CO_2 per liter compared with 350 microliters per liter. Based on these results plus those at 500 microliters per liter, net CO_2 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 CO_2 level up to 650 microliters per liter.

The atmospheric level of CO_2 has been steadily increasing since the beginning of the Industrial Revolution, in large measure reflecting the accelerating consumption of fossil fuels. Specifically, the ambient CO_2 level is estimated to have been about 270 $\mu l\ L^{-1}$ in 1850, is currently about 350 $\mu l\ L^{-1}$, and is predicted to reach 650 $\mu l\ L^{-1}$ before 2100 (2, 3, 10, 21). Compared with 350 $\mu l\ CO_2\ L^{-1}$, many agronomic C_3 plants would be expected to increase productivitiy about 30% at 650 $\mu l\ CO_2\ L^{-1}$ with little or no increase expected for C_4 plants (8, 10, 18, 22). Very little work has so far been done on the response of CAM plants to elevated CO_2 (1, 10). For the CAM leaf succulent *Agave vilmoriniana*, long-term (6 months) increases in dry weight were not significantly enhanced when the ambient CO_2 level was raised from 350 to 675 $\mu l\ L^{-1}$ for plants receiving water twice per week (5). When the plants received water on average once per week, increasing the CO_2 level from 350 to 675 $\mu l\ L^{-1}$ 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 CO_2 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 CO_2 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 CO_2 level from 350 to 650 $\mu l\ L^{-1}$ on both short-term net CO_2 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 CO_2 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 $\mu mol\ m^{-2}\ s^{-1}$ for 12 h each day, leading to a total daily PAR of 26 mol m^{-2} (essentially saturating for net CO_2 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 CO_2 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 gas 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 CO_2 level, which was either 350 $\mu l\ L^{-1}$ (the average value for the environmental chambers) or 650 $\mu l\ L^{-1}$. The CO_2 level was measured with an Anarad AR-500R IR gas analyzer. Gas exchange over 24-h periods was repeated twice at each CO_2 level for each species with comparable results.

For the long-term experiments on CO_2 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 CO_2 levels of 350, 500, or 650 $\mu l\ L^{-1}$. 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 CO_2 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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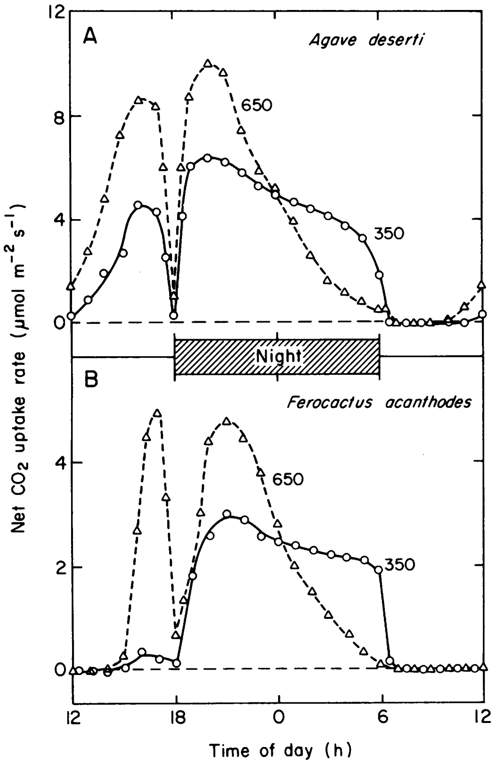

FIG. 1. Net CO_2 uptake rates over a 24-h period at ambient (350 μl L^{-1}) and elevated (650 μl L^{-1}) CO_2 levels for *A. deserti* (A) and *F. acanthodes* (B). The CO_2 levels were indicated in μl L^{-1} next to the curves for 1.5-year-old plants of *A. deserti* and 2-year-old plants of *F. acanthodes*.

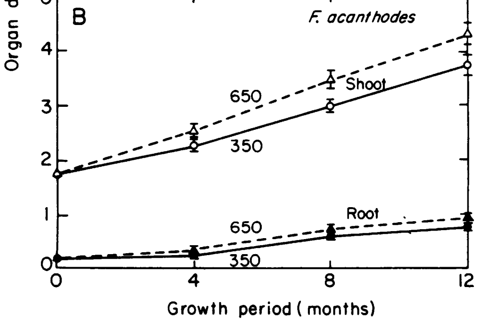

FIG. 2. Influences of ambient (350 μl L^{-1}) and elevated (650 μl L^{-1}) CO_2 levels on growth of *A. deserti* (A) and *F. acanthodes* (B), as indicated by changes in organ dry weight. Six matched plants initially 1-year-old for *A. deserti* and 1.5-year-old for *F. acanthodes* were harvested for each species at 4-month intervals under 350 or 650 μl CO_2 L^{-1} for shoot and root dry weight determinations (with the indicated SD).

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 21.21 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 CO_2 L^{-1} were compared using the Student's t test; plant dry weights at all three CO_2 levels were analyzed using ANOVA with pairwise comparisons by Tukey's method.

RESULTS AND DISCUSSION

For the short-term experiments on net CO_2 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 CO_2 level of 350 μl L^{-1} or were suddenly exposed to 650 μl CO_2 L^{-1}. Such near doubling of the ambient CO_2 level caused the maximal rate of nocturnal net CO_2 uptake to increase about 50% for both species (Fig. 1). The higher rates at 650 μl CO_2 L^{-1} were maintained only during the first half of the night and indeed the rate at the elevated CO_2 level became less than the net CO_2 uptake rate at 350 μl L^{-1} during the second half of the night for both species (Fig. 1). Hence, the total net CO_2 uptake integrated over the whole night was little affected by ambient CO_2 level, amounting to 202 mmol CO_2 m^{-2} at 350 μl L^{-1} and 207 mmol CO_2 m^{-2} at 650 μl L^{-1} for *A. deserti* (Fig. 1A) and 101 mmol CO_2 m^{-2} at 350 μl L^{-1} and 103 mmol CO_2 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 CO_2 uptake over a 10-h night increased only 2% upon raising the ambient CO_2 level from 340 to 700 μl L^{-1} (16). Hence, the amount of CO_2 acceptor was insufficient, the malate pool became filled, or the available energy supply could not maintain the high initial rates of net CO_2 uptake at the elevated CO_2 level over the entire night.

In contrast to the small immediate effect of external CO_2 level on the total CO_2 uptake at night, raising the CO_2 level from 350 to 650 μl L^{-1} caused the daytime CO_2 uptake by *A. deserti* to increase from 54 mmol m^{-2} to 130 mmol m^{-2} (Fig. 1A). Also, the maximal rate of net CO_2 uptake was nearly doubled at the higher ambient CO_2 level for *A. deserti*. Even though 2-year-old plants of *F. acanthodes* exhibited little daytime CO_2 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 CO_2 L^{-1} (Fig. 1B); daytime net CO_2 uptake increased from 3 mmol m^{-2} at the low CO_2 level to 31 mmol m^{-2} at the high level. Daytime CO_2 uptake by CAM plants is evidently by the C_3 pathway (9, 20), which is known to have higher rates at elevated CO_2 levesl (3, 10). However, raising the CO_2 level from 350 to 650 μl L^{-1} does not even double the net CO_2 uptake rate of C_3 plants, while the enhancement in daytime net CO_2 uptake observed here at elevated CO_2 levels was 2.5- to 10-fold.

Long-term experiments with elevated CO_2 led to effects comparable to those of the short-term experiments. Specifically, shoots of *A. deserti* increased by 2.72 g at 350 μl CO_2 L^{-1} and by 3.47 g at 650 μl L^{-1} (Fig. 2A), leading to a 28% higher growth at the elevated CO_2 level (differences were significant at $P < 0.01$). Shoots of *F. acanthodes* increased by 1.96 g at 350 μl CO_2 L^{-1} and 2.54 g at 650 μl L^{-1} (Fig. 2B) or by 30% more at the elevated CO_2 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 CO_2 L^{-1} than at 350 μl L^{-1}. In all cases, root and shoot growth at an intermediate CO_2 level of 500 μl L^{-1} was approximately halfway between. Thus, as the CO_2 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 CO_2 level was raised from 350 to 650 μl L^{-1}, both the short-term net CO_2 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 CO_2 level was caused by mainly an increase in daytime net CO_2 uptake for both species. It is predicted that, after a period of adjustment during which glucan levels build up providing sufficient acceptor for nocturnal CO_2 binding and other adjustments occur (9, 17, 19), most of the effect of increased ambient CO_2 level would eventually be on nocturnal CO_2 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 CO_2 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 CO_2 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 CO_2 level from 350 to 500 μl L^{-1} and by another 12% at 650 μl L^{-1}, in general agreement with comparable studies on C_3 plants (8). In any case, based on the present study the net CO_2 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 CO_2 up to 650 μl L^{-1}.

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