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Short Communication

Growth Response of a Succulent Plant, *Agave vilmoriniana*, to Elevated CO_2[1]

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ABSTRACT

Large (about 200 grams dry weight) and small (about 5 grams dry weight) specimens of the leaf succulent *Agave vilmoriniana* Berger were grown outdoors at Phoenix, Arizona. Potted plants were maintained in open-top chambers constructed with clear, plastic wall material. Four CO_2 concentrations of 350, 560, 675, and 885 microliters per liter were used during two growth periods and two water treatments. Small and large plants were grown for 6 months, while a few large plants were grown for 1 year. Wet-treatment plants received water twice weekly, whereas dry-treatment plants received slightly more water than they would under natural conditions. Plant growth rates in all treatments were significantly different between small and large specimens, but not between 6 month and 1 year large plants. Only the dry-treatment plants exhibited statistically different growth rates between the CO_2 treatments. This productivity response was equivalent to a 28% and 3-fold increase when mathematically interpolated between CO_2 concentrations of 300 and 600 microliters per liter for large and small plants, respectively.

As a result of the clear-cutting of forests associated with the expansion of agriculture, plus an ever-accelerating usage of fossil fuels, the CO_2 concentration of Earth's atmosphere has been steadily rising. The preindustrial level of CO_2 is believed to be in the vicinity of 265 $\mu l\ L^{-1}$ (14), while the current level is in excess of 340 $\mu l\ L^{-1}$ (7). Recently the United States National Academy of Sciences suggested that a nominally doubled level of 600 $\mu l\ L^{-1}$ will probably be reached sometime near the year 2070 (3). One potential ramification of this phenomenon is a likely increase in global vegetative productivity (5). Indeed, from an analysis of over 700 prior experimental observations on plant growth and development, Kimball (9, 10) has concluded that the bulk of the world's agronomic C_3 plants may well experience a one-third increase in productivity at a CO_2 concentration of 600 $\mu l\ L^{-1}$. Although there is still some uncertainity about the potential increases in productivity of natural ecosystems (13), this conclusion is supported by recent detailed studies which suggest that the stimulatory effect of atmospheric CO_2 enrichment is already manifesting itself in an increasing amplitude of the seasonal CO_2 concentration cycle of the globe (1, 8).

One group of plants which has not been studied in this regard is that composed of the leaf and stem succulents which utilize CAM. This fact is evident in the most recent review of this subject wherein Black (2) has stated that "no long-term growth work has been done with CO_2 enrichment and the production of CAM plants." Thus, we conducted the following preliminary experiment to initiate research in this area.

MATERIALS AND METHODS

Plant Material. The plant selected for study was the leaf succulent *Agave vilmoriniana* Berger, a taxon common in Sonora and south Sinaloa, Mexico. It was grown outdoors at Phoenix, AZ, in open-top chambers constructed of clear, plastic wall material (6). Growth periods were 6 months or 1 year and there were two water treatments. A group of large plants, having initial dry weights of 191 ± 77 g each, were obtained from a local nursery. Small plants, having initial dry weights of 5 ± 2 g each, were obtained as bulbils from a single plant at the Desert Botanical Garden, Phoenix.

At the start of the experiment (June 1984) soil was washed from the roots of each individual plant and it was then weighed and replanted in a 1:1 mixture of sand and commercial potting soil. The large plants were placed in 7.5-L pots while the small plants were placed in 1.5-L pots. Two plants of each size and water treatment were weighed and then oven-dried to determine the plants' initial dry weight percentages. Of the remaining plants, 30 to 32 large and 12 to 14 small plants were placed in each of four chambers with an area in each chamber equally divided between wet and dry treatments. One chamber was not enriched with CO_2, having a mean CO_2 concentration of 350 $\mu l\ L^{-1}$. Three chambers were enriched to mean CO_2 concentrations of 560, 675, and 885 $\mu l\ L^{-1}$. Throughout most of the experiment, the wet treatment was characterized by twice-a-week watering. Watering was continued until water discharged from the bottom of the pot. The dry treatment was watered once-a-week. In early September, however, the dry treatment was changed to biweekly watering as natural precipitation increased. From November to the end of the experiment no extra water was given to the dry treatment plants beyond that which they received as rainfall.

In January 1985, all but 10 of the large plants and all of the small plants in each treatment were harvested. All soil was washed from their roots and final dry weights determined. The 5 remaining large plants in each watering treatment were grown for another 6 months. Those plants were harvested in June 1985.

Statistical Analysis. Plant growth rates were analyzed to determine which means were statistically different at a probability greater than that predicted by the F value. This was done using a one-way ANOVA and Tukey's least statistical difference test. The two tests were done by computer using the statistical analysis system.

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Table I. *Dry Matter Accumulation Rates in Specimens of Agave vilmoriniana Grown in Elevated CO_2*

Size	Treatments[a] H_2O	Treatments[a] CO_2	Growth Rate[b]
			mg dry wt gm^{-1} dry wt d^{-1}
Small ($n = 26$)	W	1	4.56 ± 0.87 A
		2	4.88 ± 1.50 A
		3	4.96 ± 2.58 A
		4	5.63 ± 1.66 A
Small ($n = 24$)	D	1	1.13 ± 3.11 A
		2	2.46 ± 1.93 A
		3	4.91 ± 1.87 B
		4	5.19 ± 2.11 B
Large ($n = 60$)	W	1	2.21 ± 0.70 A
		2	2.03 ± 0.50 A
		3	2.06 ± 0.66 A
		4	1.92 ± 0.63 A
Large ($n = 64$)	D	1	1.89 ± 0.93 A
		2	2.18 ± 0.81 A
		3	2.46 ± 0.56 AB
		4	2.78 ± 0.76 B

[a] Treatments: W, wet; D, dry; 1, 350 $\mu l\ L^{-1}$; 2,560 $\mu l\ L^{-1}$; 3, 675 $\mu l\ L^{-1}$; 4, 885, $\mu L\ L^{-1}$ [b] Growth rates followed by a different letter are significantly different at P = 0.05.

RESULTS AND DISCUSSION

Our results indicate that the mean growth rate of all small plants, 4.7 ± 2.1 mg dry weight per g dry weight per d, was significantly different from that of all large plants, 2.2 ± 0.7 mg dry weight per g dry weight per d, at a P = 0.0001. This difference is due in part to the relative ratios of dry weight to fresh weight, being 2-fold higher in the small plants. Between the 6-month and 1-year grown large plants there was no significant difference in growth rates between the water and CO_2 treatments at a P = 0.05. Hence, their productivity responses were merged for all subsequent analyses.

In this study, CO_2-induced productivity differences were evident between the two water treatments for both plant sizes (Table I). Unexpectedly, growth was enhanced for the dry treatment plants only. The productivity enhancement of the large, dry plants was equivalent to a 28% increase when mathematically interpolated between CO_2 concentrations of 300 and 600 $\mu l\ L^{-1}$. This interpolation utilized a linear regression model derived from all of the data where $n = 16$ in each CO_2 treatment. The linear regression equation was $y = 0.0017\ (x) + 1.27$ and the $r^2 = 0.40$. Their growth response to elevated CO_2 is comparable to the one-third increase in productivity observed in C_3 plants (9, 10). The productivity enhancement of the small, dry plants was equivalent to a 3-fold increase when mathematically interpolated between the same CO_2 concentrations used above. This interpolation also utilized a linear regression model derived from all of the data where $n = 5$ to 6 in each CO_2 treatment. The linear regression equation was $y = 0.0079\ (x) - 1.60$, and the $r^2 = 0.56$. The estimated negative *y*-axis intercept is the result of a small sample size wherein three of the bulbils decreased in dry weight in the 135-d period.

We conclude from this initial observation that in arid and semiarid climates, dry-treatment leaf succulents like *Agave vilmoriniana* should respond positively to atmospheric CO_2 enrichment. In similar studies where water was limiting, Gifford (4) and Sinoit *et al.* (12) have previously reported an increased effect of high CO_2 on yield relative to control yields (low CO_2, low water). Cultivated succulents which receive irrigation, *e.g. Agave sisilana*, may prove to be less responsive to CO_2 enrichment. Such a response is strikingly different than that observed in most well watered C_3 plants (11). This study needs to be supported by more detailed analyses of the plants' water relations and gas exchange patterns during growth with ambient and elevated CO_2.

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