

References and Notes

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Changes in Carbon Fixation, Tuberization, and Growth Induced by CO_2 Applications to the Root Zone of Potato Plants

Abstract. *The root systems of potato plants (Solanum tuberosum L. var. Russet Burbank) treated with CO_2 for 12 hours showed an increase in dry matter as early as 2 days after the treatment. When treated plants were allowed to grow for 3 to 6 weeks there was a substantial increase in tuberization. In addition, there was an increase in stolon length, number of tubers per stolon, and overall dry weight after the enrichment of the root zone with CO_2 . Plants treated with CO_2 showed higher concentrations of malic and citric acids and of the cations Mg^{2+} and Ca^{2+} . The effect of CO_2 was more dramatic when CO_2 was applied to the root zone than when it was applied to the shoots.*

Terrestrial plants have been credited with fixing about 25 billion metric tons of CO_2 per year (1). Atmospheric CO_2 concentrations appear to be limiting with respect to photosynthesis, because most C_3 plants (2) are capable of significantly greater rates of CO_2 fixation in the presence of higher concentrations of CO_2 than are present in ambient air. Carbon dioxide enrichment of the air increases yields of greenhouse-grown vegetable and flower crops (3, 4), but CO_2 enrichment of the air for field crops would not be practical. We have investigated the feasibility of increasing plant productivity by applying CO_2 to underground plant parts.

The response of plants to high concentrations of CO_2 depends on the species. The root growth of *Pisum sativum*, *Vicia faba*, *Phaseolus vulgaris*, and *He-*

lianthus annua were completely inhibited by high CO_2 , whereas *Avena sativa* and *Hordeum vulgare* were unaffected (5). Potato plants are particularly well suited to CO_2 enrichment of the root zone because of their ability to tolerate high concentrations of CO_2 without the roots being damaged.

Potato plants were propagated by taking 1-cm plugs from the "eye" area of the tuber (*Solanum tuberosum* L. var. Russet Burbank). The plugs were arranged in holes bored into Styrofoam sheets and floated on water with continuous aeration in the dark for 2 weeks. When sprouts were 6 to 8 cm in length, they were detached from the plug and surface-sterilized in 10 percent sodium hypochlorite solution. The sterilized plants were transferred to 3-liter contain-

ers with full-strength Hoagland nutrient solution (6) and kept in a growth chamber under 16 hours of light (21.1°C) and 8 hours of darkness (15.6°C). Containers were covered with black polyethylene (5 mil in thickness) to keep light (which would inhibit tuberization) from reaching the bottom portion of the plant. Plants were grown for 3 weeks with continuous aeration. Nutrient solutions were changed weekly. After the 3-week growing period, uniform plants were selected for each treatment. The root zones of potato plants were aerated for varying time intervals with a gas stream that was 45 percent CO_2 with 21 percent O_2 and 34 percent N_2 . Plant roots were immersed in aerated nutrient solution while stolons and tubers were suspended above the solution. Carbon dioxide enrichment was restricted to the root zones by isolating the roots in an airtight chamber with an outlet attached to a 25 percent sodium hydroxide trap for escaping CO_2 , and the nutrient solution was maintained at a constant pH (5.5). All CO_2 experiments were conducted when the shoots were exposed to the light unless otherwise stated. We found that the 12-hour treatment period showed the best results with respect to dry matter increase and also the tuberization response.

Plants that had CO_2 applied to the roots showed a significant increase in shoot dry weight as early as 2 to 6 days after the treatment (Table 1). When plants were allowed to grow for 3 to 6 weeks after the CO_2 treatment, there was also a significant increase in the underground biomass (Fig. 1 and Tables 2 and 3). Three weeks after the 12-hour CO_2 treatment, stolons of the treated plants were not only longer than untreated controls, but also had multiple tubers as opposed to the single tubers per stolon typical of controls (Fig. 1 and Table 2).

Table 3 shows that root zone enrichment with CO_2 enhanced shoot weight. When potato shoots were treated with

Table 1. Effects of CO_2 enrichment of the root zone on dry matter content, organic acid, total chlorophyll, and mineral levels in nontuberizing potato plants. The CO_2 (45 percent CO_2 , 21 percent O_2 , and 34 percent N_2) was applied for 12 hours, at 2, 4, or 6 days before the plants were harvested. Control plants received ambient air. All plants were the same age at the time they were harvested. All values are expressed on a dry weight basis ($\pm$ standard error).

Days after CO_2 treatment	Plant dry weight (g)	Malic acid (mg/g)		Citric acid (mg/g)		Minerals* (total)					Total chlorophyll (mg/g)
		Leaf	Root	Leaf	Root	Ca^{2+} (mg/g)	Mg^{2+} (mg/g)	Mn^{2+} ($\mu\text{g/g}$)	K^+ (mg/g)	Cl^- ($\mu\text{g/g}$)	
Control	10.6 ± 2.3	9.2 ± 1.6	0.14 ± 0.005	4.3 ± 1.7	0.05 ± 0.003	43.7 ± 4.1	15.4 ± 0.25	2.5 ± 0.02	64.2 ± 1.6	928.4 ± 30.0	9.0 ± 0.46
2	14.9 ± 2.1	11.9 ± 0.63	1.4 ± 0.03	7.9 ± 2.3	0.29 ± 0.11	63.3 ± 4.9	12.5 ± 0.22	2.0 ± 0.01	61.0 ± 1.5	711.8 ± 26.5	9.7 ± 0.73
4	19.8 ± 4.5	15.2 ± 0.54	2.9 ± 0.86	10.9 ± 0.65	0.62 ± 0.28	76.8 ± 5.6	19.5 ± 0.28	2.1 ± 0.01	63.9 ± 1.5	681.3 ± 25.6	9.8 ± 0.95
6	25.8 ± 1.8	14.4 ± 0.29	3.9 ± 0.75	11.2 ± 0.38	1.1 ± 0.54	91.5 ± 6.2	18.4 ± 0.24	1.6 ± 0.01	69.7 ± 1.6	691.4 ± 25.8	12.7 ± 0.78

*Calcium, magnesium, and potassium ions were measured in milligrams, and manganese and chloride ions were measured in micrograms per gram of dry weight.

higher than normal concentrations of atmospheric CO₂, there was an increase in the tuber weight and the tuber number per plant remained the same. With CO₂ enrichment of the root zone there was a significant increase in the tuber weight and a highly significant increase in the number of tubers per plant (Fig. 1 and Tables 2 and 3).

In a subsequent experiment, the root zones of potato plants were treated with CO₂ for 12 hours and the effects were evaluated at 2, 4, and 6 days. There was a progressive increase in the total plant dry weight from 2 to 6 days (Table 1) which is indicative of an increase in photosynthesis or a decrease in photorespiration. The concentrations of several or-

ganic acids were measured by gas chromatography (7) and confirmed by mass spectrometry. Both malic and citric acids increased in treated plants in proportion to the increase in total dry weight (Table 1), indicating an increase in carbon fixation by the CO₂-treated plants. Through the use of autoradiography we showed that label from ¹⁴CO₂ was translocated from the roots to the shoots. The bulk of the ¹⁴C was found in malic acid. This work supports data from earlier studies (8) showing that when carbon is fixed by intact plant roots most of the label occurs in malate. By means of ¹⁴CO₂ incorporation studies, we found that approximately 18 percent of the dry matter increase came from CO₂ taken up through the roots (9).

Carbon dioxide treatment of root zones also selectively affected the uptake of minerals by the plants. This analysis was accomplished by neutron activation analysis and gamma-ray spectrometry with a high-resolution Ge(Li) detector and a programmable multi-channel analyzer. Total plant Ca²⁺ and Mg²⁺ increased, whereas Mn²⁺ and Cl⁻ decreased; K⁺ showed no change (Table 1). Chlorophyll levels as measured by acetone extraction (10) of treated plants increased in proportion to the increase in total dry weight. This increase lagged slightly behind the dry weight increase (Table 1).

Considering the worldwide economic and nutritional importance of potatoes, this research suggests the possibility of underground CO₂ enrichment as a means of increasing productivity, possibly by means of encapsulation of CO₂.

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Table 2. The effects of 12-hour CO₂ enrichment of root zones on tuberization in *Solanum tuberosum* L. 3 weeks after treatment. Control plants were treated with ambient air applied to both the roots and shoots; the enriched plants were treated with 45 percent CO₂ applied to the roots, and with ambient air applied to the shoots. Values are expressed as means $\pm$ standard error (dry weight basis).

Treat- ment	Tuber weight (g)	Total number of tubers	Number of tubers per stolon	Stolon length (cm)	Root weight (g)	Shoot weight (g)
Control	10.4 $\pm$ 3.8	7.0 $\pm$ 1.2	1.0 $\pm$ 0	2.0 $\pm$ 0.76	6.3 $\pm$ 1.6	32.8 $\pm$ 5.0
CO ₂	22.5 $\pm$ 6.0*	51.0 $\pm$ 11.3*	7.0 $\pm$ 0.68†	25.0 $\pm$ 0.27†	9.5 $\pm$ 2.8	56.6 $\pm$ 1.4*

*Significant at the 95 percent confidence level.

†Significant at the 99 percent confidence level.

Table 3. The effects of 12-hour CO₂ enrichment of root zones on tuberization in *Solanum tuberosum* L. 6 weeks after treatment. Control and enriched plants were treated as in Table 2. Values are expressed as means $\pm$ standard error (dry weight basis).

Treat- ment	Tuber weight (g)	Total number of tubers	Number of tubers per stolon	Root weight (g)	Shoot weight (g)
Control	77.4 $\pm$ 9.6	30.0 $\pm$ 13.0	1.0 $\pm$ 0	127.1 $\pm$ 23.0	412.3 $\pm$ 41.0
CO ₂	139.8 $\pm$ 10.0*	152.0 $\pm$ 8.6†	6.0 $\pm$ 1.2†	113.2 $\pm$ 10.6	538.9 $\pm$ 22.4*

*Significant at the 95 percent confidence level.

†Significant at the 99 percent confidence level.

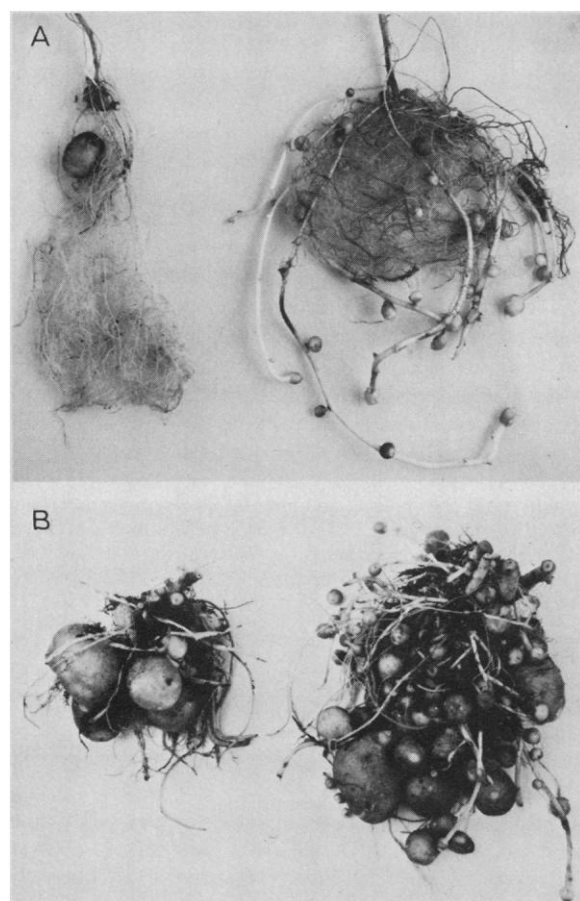


Fig. 1. The effects of 12-hour CO₂ enrichment of root zones on stolon elongation, tuber initiation, and growth in *Solanum tuberosum* L. (A) 3 weeks and (B) 6 weeks after treatment. Controls are at left and CO₂-treated plants at right.