Duration of CO₂ Enrichment Influences Growth, Yield, and Gas Exchange of Two Tomato Species

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Abstract. Lycopersicon esculentum Mill. cv. Vedettos and *Lycopersicon chmielewskii* Rick, LA 1028, were exposed to two CO_2 concentrations (330 or 900 $\mu mol \cdot m^{-3}$) for 10 weeks. The elevated CO_2 concentration increased the relative growth rate (RGR) of *L. esculentum* and *L. chmielewskii* by 18% and 30%, respectively, after 2 weeks of treatment. This increase was not maintained as the plant matured. Net assimilation rate (NAR) and specific leaf weight (SLW) were always higher in CO_2-enriched plants, suggesting that assimilates were preferentially accumulated in the leaves as reserves rather than contributing to leaf expansion. Carbon dioxide enrichment increased early and total yields of *L. esculentum* by 80% and 22%, respectively. Carbon exchange rates (CER) increased during the first few weeks, but thereafter decreased as tomato plants acclimated to high atmospheric CO_2. The relatively constant concentration of internal CO_2 with time suggests that reduced stomatal conductance under high CO_2 does not explain lower photosynthetic rates of tomato plants grown under high atmospheric CO_2 concentrations. Leaves 5 and 9 responded equally to high CO_2 enrichment throughout plant growth. Consequently, acclimation of CO_2-enriched plants was not entirely due to the age of the tissue. After 10 weeks of treatment, leaf 5, which had been exposed to high CO_2 for only 10 days, showed the greatest acclimation of the experiment. We conclude that the duration of exposure of the whole plant to elevated CO_2 concentration, rather than the age of the tissue, governs the acclimation to high CO_2 concentrations.

Carbon dioxide enrichment of greenhouses and the projected doubling of the atmospheric CO_2 concentration within the next century (Gates et al., 1983; Lemon, 1983) have stimulated interest in the long-term effects of high CO_2 levels on plant growth. The enhancement of photosynthesis, growth, and yield by increasing the concentration of CO_2 in the atmosphere has been shown for many species (Kimball, 1983). Carbon dioxide enrichment to 1000 $\mu mol \cdot m^{-3}$ increased yields and plant dry weight of tomato plants by 30% (Slack, 1986) and 36% (Yelle et al., 1987), respectively. Cucumber (Dennis, 1980), lettuce (Knecht and O'Leary, 1983), and many ornamental species (Mortensen, 1987) also responded positively to CO_2 enrichment. However, a side-effect of long-term growth in a CO_2-enriched environment is diminished photosynthetic efficiency of leaves. Declines in photosynthesis were demonstrated for tomatoes (Hurd, 1968; Hicklenton and Joliffe, 1980), cucumbers (Aoki and Yabuki, 1977; Frydrich, 1976; Peet et al., 1986), and several other species (Mauney et al., 1978; Mortensen, 1983; Wong et al., 1979). For instance, Aoki and Yabuki (1977) reported that CO_2 enrichment increased the photosynthetic rate of cucumbers by 76% after 1 day of treatment. However, as enrichment continued, the photosynthetic rate at the high CO_2 concentration rapidly decreased below that of the control level. Although this effect is well-known, there is no consensus yet on the physiological and biochemical causes.

Several reasons have been proposed to explain plant acclimation to high CO_2 concentrations: decreases in stomatal conductance (Peet et al., 1986), reduced Rubisco activity (Peet et al., 1986; Spencer and Bowes, 1986; Vu et al., 1983), and buildup of carbohydrates (Clough et al., 1981; Sasek et al., 1985).

The present study compared the long-term response of two tomato species, *L. esculentum* and *L. chmielewskii,* to elevated atmospheric CO_2. These species differ greatly in their sink metabolism and carbohydrate assimilation. Yelle et al. (1988) showed that *L. chmielewskii* accumulated less starch than *L. esculentum.* This difference was related to a lower level of ADP glucose pyrophosphorylase and a higher level of phosphorylase in *L. chmielewskii* fruits. A low level of invertase and a nondetectable level of sucrose synthase in *L. chmielewskii* were associated with the high level of sucrose in its fruits. *L. chmielewskii* had twice the soluble solids content in the fruits as *L. esculentum.* There were three objectives in this study: 1) assess whether the sink metabolism and carbohydrate assimilation of *L. chmielewskii* would prevent the long-term loss of efficiency resulting from CO_2 enrichment; 2) verify whether the loss of efficiency was due to the age of the tissue rather than the time of exposure to high CO_2 levels; 3) determine the relationship between stomatal conductance and internal CO_2 concentrations on the carbon exchange rates associated with CO_2 acclimation.

Materials and Methods

Plant material. 'Vedettos' *(Lycopersicon esculentum)* and LA 1028 *(L. chmielewskii)* tomatoes were seeded in rockwool blocks (Grodania, Hedehusene, Denmark) on 15 Dec. 1987 and transplanted on 17 Jan. 1988 in 16 independent hydroponic systems (NFT). Tomato plants were grown in four identical glasshouse compartments (24 m^2). The CO_2 concentration within each compartment was maintained at 330 ± 50 (control, ambient concentration) or 900 ± 50 $\mu mol \cdot m^{-3}$. Each CO_2 treatment was repeated twice. Both species were repeated twice in each compartment. Each experimental unit was randomly distributed in each compartment and consisted of 20 plants.

Carbon dioxide levels were monitored and controlled by an infrared gas analyzer (Priva Computers, No. APBA 251 E CO_2 Monitor). The CO_2 was supplied from a pure liquid source during the photoperiod. Day and night temperatures were maintained at a minimum of 22 ± 2C and 17 ± 2C, respectively.

Forced ventilation was activated when air temperature reached 30C. During forced ventilation, CO_2 levels dropped to 500 $\mu mol \cdot m^{-3}$. Forced ventilation accounted for $\approx$ 1hr/day during the first half of the experiment and 2 hr/day during the second. Temperatures were measured using six thermocouples in each compartment; four for the nutrient solutions and two for air temperatures. Thermocouples were connected to a Minitrend 205 recorder (Doric Scientific). Supplemental lighting (150 $\mu mol \cdot s^{-1} \cdot m^{-2} PPF$) was supplied by high-pressure sodium lamps for a photoperiod of 16 hr.

Nutrient solutions contained (in $\mu l \cdot liter^{-1}$) 176 N, 46 P, 284 K, 140 Ca, 47 Mg, 2 Fe, 1 Mn, 0.4 Zn, 0.29 B, 0.03 Cu, and 0.06 Mo and were renewed every 5 days. Solutions were adjusted daily with H_2SO_4 to a pH of 5.8 and to an electric conductivity of 220 $dS \cdot cm^{-1}$ using a complete nutrient solution.

Vegetative growth and gas exchange. Fresh and dry weights of the leaves and stems and leaf areas were measured every 2 weeks for 10 weeks on four plants randomly sampled from each experimental unit. After each plant removal, the remaining plants were redistributed into the canopy to minimize patchy light distribution. Leaves and stems were dried for 48 hr at 70C before measurement of the dry weights. Leaf area was measured with a LI-COR portable area meter (LI-3000, LI-COR, Lincoln, Neb.). Relative growth rate (vegetative growth), net assimilation rate, and leaf area ratio were calculated as reported by Gardner et al. (1985). Ripe tomato fruits were harvested during 4 weeks from 16 Mar. to 15 Apr. Early yields corresponded to the first 3 weeks of harvest. For the last harvest date (15 Apr.), all green and red fruits of all sizes were picked and included in the total yield. Yield of *L. chmielewskii* is not reported because of frequent fruit abscission and high variability however, it was about 100 times lower than that of *L. esculentum,* with an average fruit size of $\approx$ 8g.

Gas exchange was measured every week for 10 weeks on the 5th and 9th leaves with a portable photosynthesis apparatus (LI-6000). Leaf 9 was considered as a fully expanded leaf, acting as a source leaf, while leaf 5 was not fully expanded and was considered as an importer of carbohydrates. Leaves were counted from the top of the plant, starting with the first leaf >2 cm. Photosynthetic rates were measured at the same CO_2 concentrations under which the plants were grown. The photosynthesis system monitored photosynthetic photon flux (PPF), relative humidity, leaf temperature, chamber air temperature and CO_2 concentration, initial internal leaf CO_2 concentration, stomatal conductance, and the net photosynthetic rate. The measurement period was 90 sec, with an air flow inside the l-liter leaf chamber of 6 $cm^3 \cdot s^{-1}$ and a leaf area of 28 cm^2. Each point is the average of four series of four measurements taken randomly during the mid-day (1000 to 1400 HR) in each experimental unit.

Results and Discussion

Growth analysis. Plants grown under high CO_2 levels showed a higher relative growth rate (RGR) than the plants grown at ambient CO_2 for the first 2 weeks of treatment (Fig, 1). The difference was greater for *L. chmielewskii* (30% higher) than *L. esculentum* (18% higher) for these first 2 weeks. Thereafter, the RGR of CO_2-enriched plants declined faster than the control. The greatest decline was found for *L. chmielewskii* grown under high CO_2. After 7 weeks of treatment, the RGRs of the 900- and 330-$\mu mol \cdot m^{-3}$-grown plants were identical for both species. After 10 weeks, the RGRs of CO_2-enriched plants were lower than the controls for *L. esculentum* and *L. chmielewskii.* Peet (1986) also observed higher RGRs for CO_2-enriched cu-
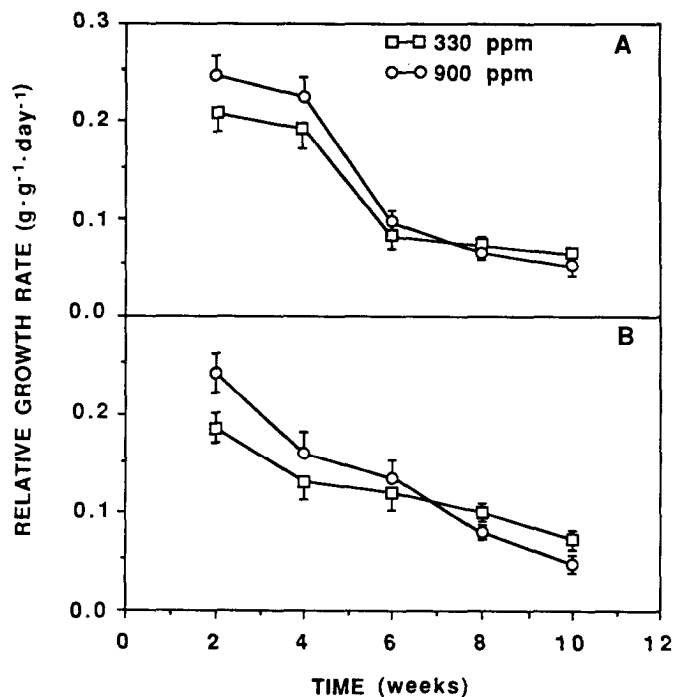

Fig. 1. Relative growth rate of *L. esculentum* (**A**) and *L. chmielewskii* (**B**) grown at 330 and 900 $\mu mol \cdot m^{-3}$ for 10 weeks. Each point represents the mean of four values $\pm$ SE.

cumber plants during the first 2 to 3 weeks. Thereafter, the RGR declined faster in CO_2-enriched plants. Mauney et al. (1978) reported that cotton, sorghum, soybean, and sunflower all had higher RGRs under CO_2 enrichment during the juvenile stage, but not during the mature stage.

Leaf areas were slightly greater for CO_2-enriched plants after 2 weeks (5.5% and 6.7% for *L. esculentum* and *L. chmielewskii,* respectively), but were similar thereafter (data not shown). The specific leaf weight (SLW) was higher under high CO_2 for all sampling dates (Fig. 2). After 2 weeks, the SLW had increased by 33% for *L. esculentum* and 27% for *L. chmielewskii,* whereas the corresponding values after 8 weeks were 51% and 53%. *L. chmielewskii* had a higher SLW at both CO_2 levels than *L. esculentum* (average of 18% higher). These results suggest that more photosynthates were stored per unit of leaf area in *L. chmielewskii* and at high CO_2. Sionit et al. (1981) and Imai and Murata (1976) previously showed that the increase in leaf area was not as important as the increase in leaf dry weight under high CO_2 levels.

Net assimilation rates (NAR) of the high-CO_2-grown plants were always higher than those of the ambient-grown plants (Fig. 3 A and B). After 2 weeks of treatment, NAR at 900 $\mu mol \cdot m^{-3}$ was 43% higher for *L. esculentum* and 58% for *L. chmielewskii* than for the controls. After 8 weeks, the NAR at high CO_2 was still significantly higher for *L. chmielewskii,* but not for *L. esculentum.* The increase in leaf dry weight (data not shown) relative to leaf area explains the higher NAR as compared to RGR under high CO_2 levels. These results suggest that assimilates were preferentially accumulated as reserves in the leaves rather than contributing to canopy enlargement. This particular partitioning, which resulted in thicker leaves under high CO_2 levels, was more evident in *L. chmielewskii* than *L. esculentum.*

L. esculentum plants grown under high CO_2 concentrations flowered 7 days earlier than those grown under ambient CO_2
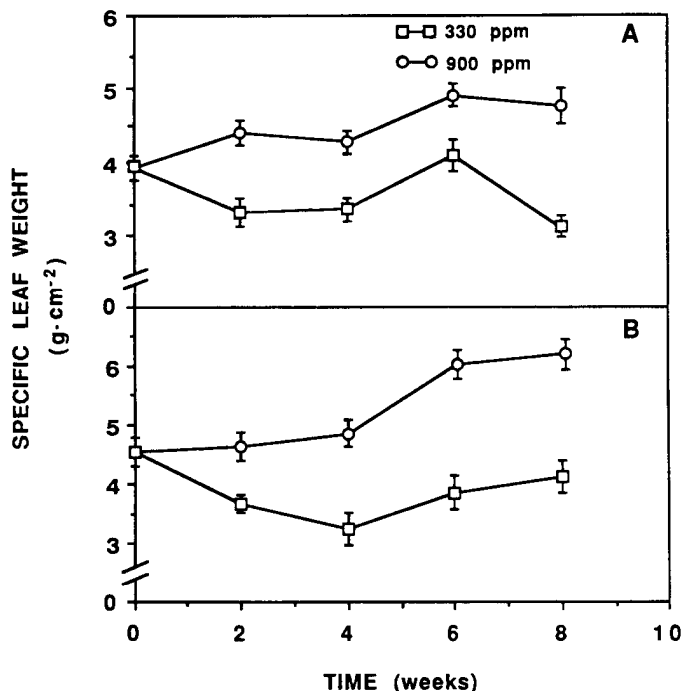
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Fig. 2. Specific leaf weight of *L. esculentum* (**A**) and *L. chmielewskii* (**B**) grown at 330 and 900 μmol·m^{-3} for 10 weeks. Each point represents the mean of four values ± SE.
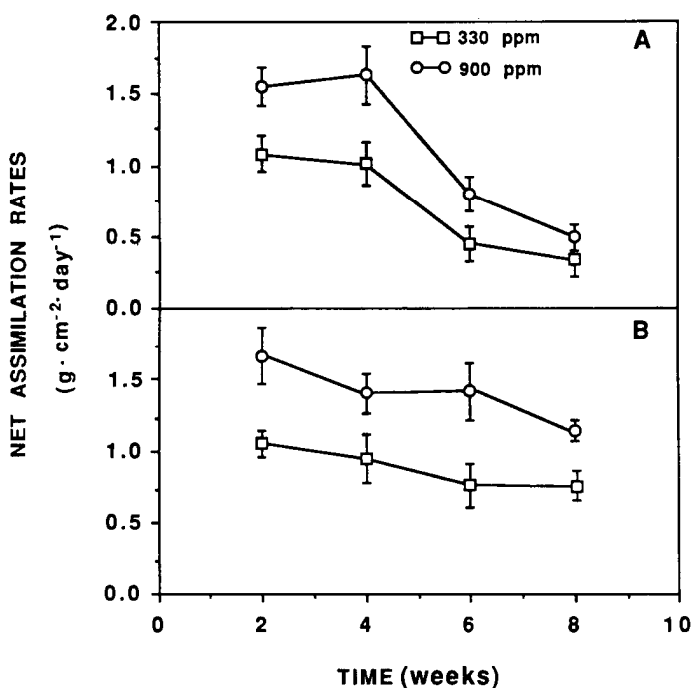

Fig. 3. Net assimilation rate of *L. esculentum* (**A**) and *L. chmielewskii* (**B**) grown at 330 and 900 μmol·m^{-3} for 10 weeks. Each point represents the mean of four values ± SE.

Table 1. Flowering date and yields of *Lycopersicon esculentum* grown under 330 or 900 μmol·m^{-3} CO_2 for 10 weeks.[z]

	CO$_2$ concn (μmol·m^{-3})		
Criterion	330	900	Increase (%)
Flowering date	4 Feb.	28 Jan.	
Early yields (kg/plant)	1.95 ± 0.31	3.51 ± 0.49	80
Total yields (kg/plant)	6.92 ± 0.95	8.41 ± 1.02	22
Number of fruits/plant	76.00 ± 8.41	81.00 ± 8.53	6.6
Average fruit weight (g)	91.05 ± 9.37	103.83 ± 9.89	14

[z]Each value is a mean of eight plants ± SE.

cluded that the preferential increase of leaf thickness, as opposed to leaf expansion under high CO_2, suggests that the extra assimilates were stored in the leaves rather than translocated into the developing fruits. Similarly, we found that high CO_2 increased leaf dry weight more than leaf area.

Gas exchange rate. The carbon exchange rates (CER) were significantly higher in CO_2-enriched plants for the early sampling dates. After 1 week of treatment, CO_2 enrichment increased the CER of leaf 5 by 37% for *L. esculentum* and 38% for *L. chmielewskii* (Fig. 4 A and B). However, long-term growth at elevated CO_2 concentrations resulted in diminished CER (Fig. 4 C and D). The decrease was faster and more pronounced for *L. chmielewskii* for both leaves. After 6 weeks, no beneficial effect of CO_2 enrichment on CER was measured for either species. For both species, most of the decline in photosynthesis of CO_2-enriched plants occurred during the first 6 weeks of treatment; thereafter, the differences stabilized. Aoki and Yabuki (1977) found that the decline of photosynthesis under CO_2 enrichment was faster in lower (older) leaves of cucumber plants. With tomato, we found a similar decline in both the younger (5th) and older (9th) leaves.

Stomatal conductance of leaves 5 and 9 of the two tomato species was lower for plants grown at 900 μmol·m^{-3} (average of 57% lower) than those grown at 330 μmol·m^{-3}. The difference between the two CO_2 treatments gradually increased throughout the experiment (Fig. 5). Stomatal conductance of the 5th leaf of *L. chmielewskii* and *L. esculentum* decreased by 84% and 36% over the course of the experiment. In leaf 9, the average decline due to CO_2 enrichment was the same (54%) in both species. Our results agree with those reported by Peet et al. (1986), Havelka et al. (1984), and Spencer and Bowes (1986), who measured a significant decrease of stomatal conductance of leaves grown under high CO_2 concentration.

The stomatal conductance of high-CO_2-grown plants showed the same trend of decline as the photosynthetic rates. These results suggest that the acclimation of plants to high CO_2 concentration may be attributed to a partial closure of the stomata. However, in contrast to photosynthesis and stomatal conductance, internal CO_2 levels were similar for both types of leaves grown in a given CO_2 concentration (Table 2). Since internal CO_2 was not reduced over the course of the experiment (data not shown), we believe that reduced stomatal conductance does not account for the decrease in photosynthesis seen in high-CO_2-grown plants. Our results suggest that the decline of photosynthesis of high-CO_2-grown plants results from a lower rate of use of the internal CO_2. Spencer and Bowes (1986) also found a simultaneous decrease of photosynthesis and stomatal conductance, resulting in a constant internal CO_2 concentration during plant development. In tomatoes, even though the partial closure of the stomata did not affect the carbon exchange rate,

(Table 1). The early (first 3 weeks of harvest) and total yields were increased by 80% and 21.5%. Slack (1986) reported that CO_2 enrichment increased total yield of greenhouse tomato by ≈30%. Calvert and Slack (1975) showed that the major effect of high CO_2 was on the earliness and pointed out that the beneficial effect of CO_2 was mainly on the first truss. They con-
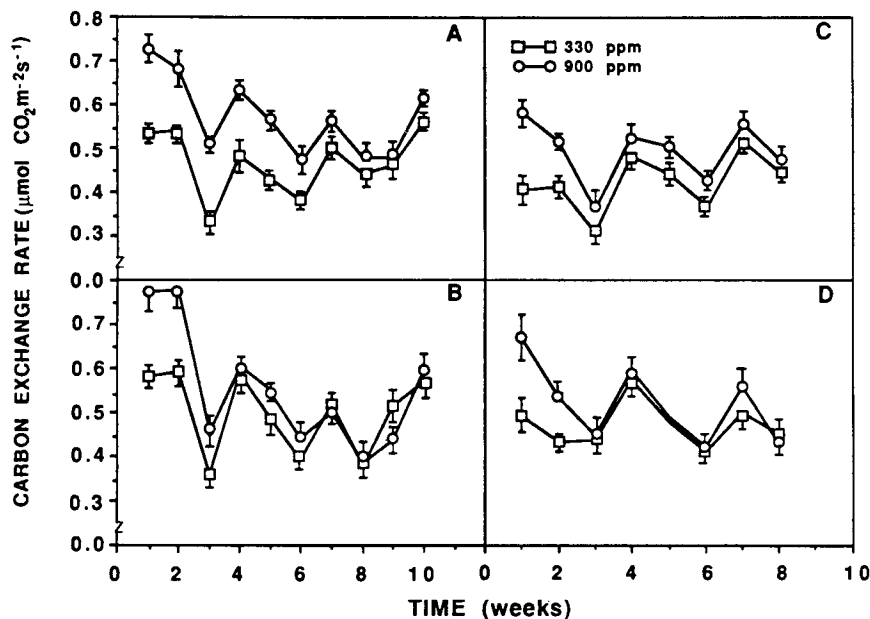
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Fig. 4. Carbon exchange rates of two tomato species grown at 330 and 900 μmol·m^{-3} for 10 weeks. (A) Leaf 5 of *L. esculentum*. (B) Leaf 5 of *L. chmielewskii*. (C) Leaf 9 of *L. esculentum*. (D) Leaf 9 of *L. chmielewskii*. Each point represents the mean of four values ± SE.

Fig. 5. Stomatal conductance of two tomato species grown at 330 and 900 μmol·m^{-3} for 10 weeks. (A) Leaf 5 of *L. esculentum*. (B) Leaf 5 of *L. chmielewskii*. (C) Leaf 9 of *L. esculentum*. (D) Leaf 9 of *L. chmielewskii*. Each point respresents the mean of four values ± SE.
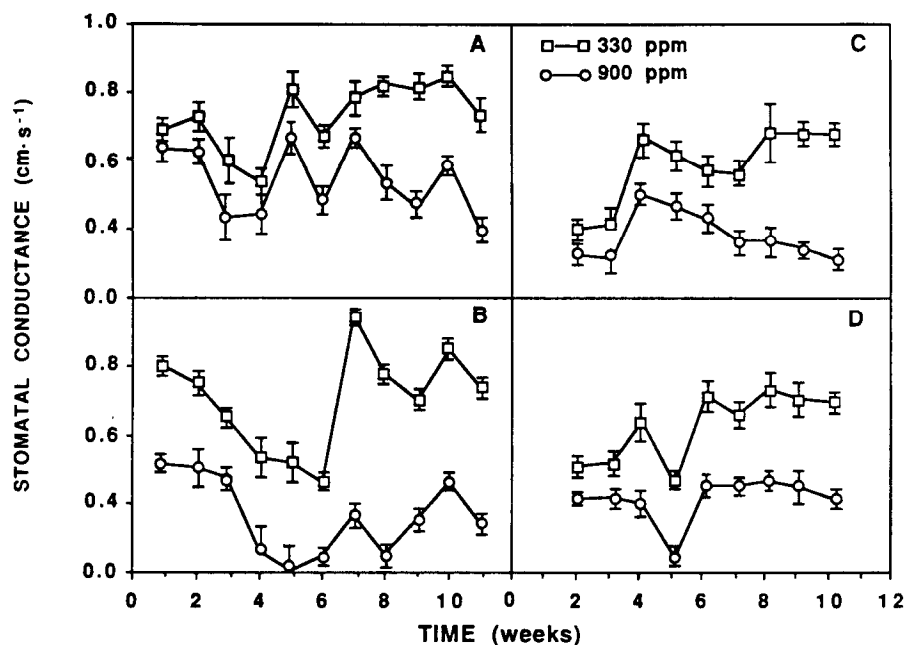
CO_2 enrichment may have sufficiently reduced transpiration and lowered nutrient uptake (Madsen, 1975) to indirectly cause the acclimation of plants.

Leaves 5 and 9 responded similarly to high CO_2 enrichment throughout plant growth, which suggests that the loss of efficiency of CO_2-enriched plants was not caused by tissue aging. Our data also demonstrated that leaf 5 was less efficient in 10-week-old plants than in 1-week-old plants, even though leaf 5 was young tissue ($\approx$ 10 to 15 days old). Our results indicate that it is the duration of exposure of the whole plant to elevated CO_2 concentration, rather than the time of exposure of the tissue, that governs the acclimation to high CO_2 concentration.

Spencer and Bowes (1986) compared the effects of CO_2 enrichment on mature and immature tissues. Both mother and daughter plants of water hyacinth had the same temporary enhancement of photosynthesis when exposed to high CO_2. Ac-

climation of these plants under high CO_2 level was more related to the time of exposure at high CO_2 than the age of the plant. In addition, our results suggest that the time of exposure of the mother plant to high CO_2 greatly influences the acclimation of the young plant tissues exposed to high CO_2 only for very short periods of time. The loss of photosynthetic efficiency of old leaves exposed for a long time to high CO_2 seems to be transmitted to young leaves exposed only for a short period.

As reported for many C_3 species, the beneficial effects of CO_2 enrichment on CER was most effective during short-term exposure. However, our results show that the photosynthetic efficiency was not maintained throughout plant growth. Consequently, the photosynthetic efficiency of CO_2-enriched plants decreases more rapidly than the control. Both *L. esculentum* and *L. chmielewskii* acclimated to high CO_2. These results suggest that the specific mechanisms involved in the sink metab-

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Table 2. Internal CO_2 concentration of *Lycoperisicon esculentum* and *L. chmielewskii* grown under two CO_2 concentrations.

Species	CO_2 treatments ($\mu mol \cdot m^{-3}$)	Internal CO_2 concn[z] ($\mu mol \cdot m^{-3}$) Leaf 5	Leaf 9
L. esculentum	330	265 ± 7	257 ± 8
	900	766 ± 22	716 ± 31
L. chmielewskii	330	254 ± 7	261 ± 8
	900	701 ± 27	727 ± 26

[z]Each value is a mean of four replications ± SE and the average of 10 weeks of experiment. Measurements were taken weekly.

olism and carbohydrate assimilation of *L. chmielewskii* cannot eliminate, nor attenuate, the long-term decline of photosynthesis of plants exposed to high CO_2 concentrations. However, even though tomato plants lost some of their photosynthetic efficiency under high CO_2 concentrations, early and total yields of *L. esculentum* were increased by more than 80% and 21%, respectively.

The results reported here demonstrate that stomatal conductance decreased significantly at high CO_2, while internal CO_2 remained constant throughout tomato plant growth. Consequently, the partial closure of stomata cannot explain the acclimation of plants to high CO_2 level. An increased mesophyll resistance rather than stomatal resistance seems a more likely explanation for the long-term decline of photosynthesis with extended use of high CO_2 concentration.

This study found that leaves 5 and 9 responded similarly to high CO_2 concentrations, which suggests that aging and/or differential sink : source ratios of the two leaves are not primary explanations of the long-term decline. In addition, this result implies that the time of exposure of the whole plants to high CO_2 concentration was more critical than the time of exposure of a specific tissue. The loss of photosynthetic efficiency that gradually appears as tomato plants were exposed to high CO_2 level seems to be transmitted to young tissue.

Further research is needed to verify if there is a relationship between leaf ontogeny and the time of exposure to high CO_2 concentrations. Long-term studies are required to evaluate if very young leaves become acclimated due to the acclimation of older leaves. Furthermore, fundamental research should be undertaken to specify the relationships among sugar metabolism, Rubisco activity, and the loss of photosynthetic efficiency to specify the biochemical and physiological reasons underlying the efficiency loss.

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