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

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Abstract. Lycopersicon esculentum Mill. cv. Vedetos and Lycopersicon chmielewskii Rick, LA 1028, were exposed to two CO₂ concentrations (330 or 900 µmol·m⁻²) for 10 weeks. The elevated CO₂ 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 CO₂-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 CO₂. The relatively constant concentration of internal CO₂ with time suggests that reduced stomatal conductance under high CO₂ does not explain lower photosynthetic rates of tomato plants grown under high atmospheric CO₂ concentrations. Leaves 5 and 9 responded equally to high CO₂ enrichment throughout plant growth. Consequently, acclimation of CO₂-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 CO₂ for only 10 days, showed the greatest acclimation of the experiment. We conclude that the duration of exposure of the whole plant to elevated CO₂ concentration, rather than the age of the tissue, governs the acclimation to high CO₂ concentrations.

Carbon dioxide enrichment of greenhouses and the projected doubling of the atmospheric CO₂ concentration within the next century (Gates et al., 1983; Lemon, 1983) have stimulated interest in the long-term effects of high CO₂ levels on plant growth. The enhancement of photosynthesis, growth, and yield by increasing the concentration of CO₂ in the atmosphere has been shown for many species (Kimball, 1983). Carbon dioxide enrichment to 1000 µmol·m⁻² 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 CO₂ enrichment. However, a side-effect of long-term growth in a CO₂-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 CO₂ enrichment increased the photosynthetic rate of cucumbers by 76% after 1 day of treatment. However, as enrichment continued, the photosynthetic rate at the high CO₂ 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 CO₂ 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).

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Materials and Methods

Plant material. ‘Vedetos’ (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 m²). The CO₂ concentration within each compartment was maintained at 330 ± 50 (control, ambient concentration) or 900 ± 50 µmol·m⁻² Each CO₂ 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 CO₂ Monitor). The CO₂ was supplied from a pure liquid source during the photoperiod. Day and night temperatures were maintained at a minimum of 22 ± 2°C and 17 ± 2°C, respectively.
Forced ventilation was activated when air temperature reached 30°C. During forced ventilation, CO₂ levels dropped to 500 µmol·m⁻². Forced ventilation accounted for ≈1 hr/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 µmol·s⁻¹·m⁻²·PPF) was supplied by high-pressure sodium lamps for a photoperiod of 16 hr.

Nutrient solutions contained (in µl·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 H₂SO₄ to a pH of 5.8 and to an electric conductivity of 220 dS·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 70°C 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 8 g.

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 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 CO₂ concentrations under which the plants were grown. The photosynthesis system monitored photosynthetic photon flux (PPF), relative humidity, leaf temperature, chamber air temperature and CO₂ concentration, initial internal leaf CO₂ concentration, stomatal conductance, and the net photosynthetic rate. The measurement period was 90 sec, with an air flow inside the 1-liter leaf chamber of 6 cm³·s⁻¹ and a leaf area of 28 cm². 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 CO₂ levels showed a higher relative growth rate (RGR) than the plants grown at ambient CO₂ 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 CO₂-enriched plants declined faster than the control. The greatest decline was found for L. chmielewskii grown under high CO₂. After 7 weeks of treatment, the RGRs of the 900- and 330-µmol·m⁻²-grown plants were identical for both species. After 10 weeks, the RGRs of CO₂-enriched plants were lower than the controls for L. esculentum and L. chmielewskii. Peet (1986) also observed higher RGRs for CO₂-enriched cu-

![Fig. 1. Relative growth 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.](image)

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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 concluded 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$^{-2}$ (average of 57% lower) than those grown at 330 µmol·m$^{-2}$. 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,

![](image1.png)

**Fig. 2.** Specific leaf weight of *L. esculentum* (A) and *L. chmielewskii* (B) grown at 330 and 900 µmol·m$^{-2}$ for 10 weeks. Each point represents the mean of four values ± se.

![](image2.png)

**Fig. 3.** Net assimilation rate of *L. esculentum* (A) and *L. chmielewskii* (B) grown at 330 and 900 µmol·m$^{-2}$ for 10 weeks. Each point represents the mean of four values ± se.

(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 concluded 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.

**Table 1.** Flowering date and yields of *Lycopersicon esculentum* grown under 330 or 900 µmol·m$^{-2}$ CO$_2$ for 10 weeks.$^*$

| Criterion | 330 | 900 | Increase (%) |
|-----------|-----|-----|--------------|
| Flowering date | 4 Feb. | 28 Jan. | 80 |
| Early yields (kg/plant) | 1.95 ± 0.31 | 3.51 ± 0.49 | 22 |
| 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 | 22 |
| Average fruit weight (g) | 91.05 ± 9.37 | 103.83 ± 9.89 | 22 |

$^*$Each value is a mean of eight plants ± se.

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CO₂ 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 CO₂ enrichment throughout plant growth, which suggests that the loss of efficiency of CO₂-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 (≈10 to 15 days old). Our results indicate that it is the duration of exposure of the whole plant to elevated CO₂ concentration, rather than the time of exposure of the tissue, that governs the acclimation to high CO₂ concentration.

Spencer and Bowes (1986) compared the effects of CO₂ 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 CO₂. Acclimation of these plants under high CO₂ level was more related to the time of exposure at high CO₂ than the age of the plant. In addition, our results suggest that the time of exposure of the mother plant to high CO₂ greatly influences the acclimation of the young plant tissues exposed to high CO₂, only for very short periods of time. The loss of photosynthetic efficiency of old leaves exposed for a long time to high CO₂ seems to be transmitted to young leaves exposed only for a short period.

As reported for many C₃ species, the beneficial effects of CO₂ 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 CO₂-enriched plants decreases more rapidly than the control. Both *L. esculentum* and *L. chmielewskii* acclimated to high CO₂. These results suggest that the specific mechanisms involved in the sink metab-

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 represents the mean of four values ± SE.

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though tomato plants lost some of their photosynthetic efficiency under high CO

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