Carbon Dioxide Enrichment in ‘Virosa’ Tomato Plant: Responses to Enrichment Duration and to Temperature

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Abstract. Responses of the tomato (*Lycopersicon esculentum* Mill. cv. Virosa) plant to elevated CO₂ concentrations applied throughout the photoperiod or part of it were studied under two temperature regimes. Plants were exposed to CO₂ at 340 (control), 700, and 1000 µl·liter⁻¹. The highest concentration was applied only at 22/16C (day/night) and 700 µl·liter⁻¹ at 22/16C and 25/16C. Transpiration rates were lower and photosynthetic rates were higher under elevated CO₂ than at the ambient level. Biomass production was higher only for plants grown at 700 µl·liter⁻¹ and 25/16C. Concentrations of macronutrients were lower in plants exposed to 1000 µl CO₂/liter than in the control plants. Intermittent CO₂ was applied using two timing methods. In method 1, plants were exposed to 4- or 8-hour high-CO₂ concentrations during their 12-hour photoperiod. In method 2, plants were exposed for 3.5 days of each week to 700 µl CO₂/liter. Only two of the 8-hour exposures resulted in greater growth than the controls. The lack of higher growth for CO₂-enriched plants at 22/16C was attributed to a higher dark respiration rate and to a lack of efficient transport of photosynthates out of leaves.

Carbon dioxide enrichment is a common practice in protected cultivation of tomatoes (Nederhoff and De Graaf, 1993). Although its effects on growth, yield, and physiological attributes of the plant have been researched extensively, there are aspects of CO₂ enrichment that have been relatively neglected. These aspects, which we focused on, include intermittent CO₂ application and interaction with temperature (Mortensen, 1987). These variables have economic implications for production. We hypothesized that CO₂ enrichment is more beneficial during the early hours of the photoperiod than during middle or late hours. If this is true, enrichment throughout the entire photoperiod could be obviated. This hypothesis was based on a previous finding that photosynthetic rate was maximal during early hours in a constant environment (Behboudian, 1977), similar to the experimental conditions of this study.

As O₂ inhibition of photosynthesis increases with temperature, the effect of CO₂ enrichment will increase with increasing temperature within a certain range (Mortensen, 1987). Growers are often advised to increase ventilation temperature by 2 to 4C when CO₂ enrichment is used (Mortensen, 1987). However, data on temperature responses of plants under CO₂ enrichment are scarce (Rozema, 1993), and temperature programs for various greenhouse crops should be reassessed (Mortensen, 1987). Therefore, we studied tomato plant responses to elevated CO₂ with a 3C difference in day temperature. ‘Virosa’ was used because it is a popular greenhouse cultivar in New Zealand. In these initial studies, the focus was on early vegetative growth.

Materials and Methods

These experiments were performed in the National Climate Laboratory at HortResearch, Palmerston North, New Zealand. For each experiment, seedlings were transplanted singly into 4.4-liter plastic pots containing sterilized 70% coarse sand, 15% vermiculite, 15% peat growing medium. Plants were kept in a shadehouse for 1 week before being transferred to the appropriate walk-in controlled-environment room. One room was assigned to each CO₂-temperature treatment and up to four were used simultaneously. The position of the plants, which were placed on trolleys in each room, was rotated twice a week within the trolley and the trolleys were also rotated in

the room. Nights were at 16 ± 0.5C in all experiments and the days were either 22 ± 0.5C or 25 ± 0.5C, depending on the experiment. Relative humidity was kept at 70% ± 5%. Average photosynthetic photon flux (PPF) was 710 µmol·m⁻²·s⁻¹ at the plant level. The lighting system for each room consisted of 4 × 1000-W Sylvania Metalarc high-pressure discharge lamps (GTE Products Corp., Manchester, N.H.) together with 4 × 1000-W Philips tungsten iodide lamps. The photoperiod was from 0900 to 2100 HR. Plants were irrigated at 0600, 1800, and 2400 HR with a mineral nutrient solution supplied by an automatic application system. The solution contained (in ppm) 105.1 N, 15.5 P, 119.0 K, 32.1 S, 100.2 Ca, 2.1 Fe, 24.3 Mg, 0.25 B, 0.25 Mn, 0.01 Cu, 0.02 Zn, 0.005 Mo, 1.8 Cl, and 1.02 Na. Normal CO₂ concentration for control plants was 340, and for enriched treatments it was either 700 or 1000 µl·liter⁻¹. Enrichment was achieved by using bottled food-grade CO₂ regulated by a solenoid and controlled to within 50 µl·liter⁻¹ of the set point by a Binos-1 infrared gas analyzer (Leybold-Heraeus GmbH, Hanau, Germany). Intermittent CO₂ was applied by one of two timing methods. In method 1, plants were exposed to a CO₂ enrichment during either their first, second, or third 4 h of the 12-h photoperiod. In addition, 8-h exposures also were used by a combination of any two of the 4-h intervals. In method 2, plants were kept for 3.5 days of each week in the high-CO₂ (700 µl·liter⁻¹) room and for the remainder of the week in the ambient-CO₂ room.

Photosynthesis, transpiration, and dark respiration were measured on the youngest fully expanded single leaves, using a LI-COR 6200 system (LI-COR, Lincoln, Neb.). Whole-plant transpiration was measured gravimetrically. Leaf area was determined using a LI-COR 3100 area meter. Concentration of macronutrients was measured in the top eight leaves, which were dried at 65C before they were ground, using one sample per plant. Nitrogen was analyzed by Kjeldahl digestion and colorimetry; P by sulphuric acid digestion and colorimetry; K, Mg, and Ca by nitric acid digestion and either atomic absorption or emission spectrophotometry; and S by sodium hypobromite digestion followed by hydrogen sulphide reduction and colorimetry. This research consisted of several experiments, the specifics of each are presented with the results for clarity. The *t* test was used for comparison of two means, and analysis of variance was used for comparing several means. These analyses were done using Minitab and SAS statistical packages.

Results

The first experiment on intermittent application of 1000 µl CO₂/liter showed that 4-h exposures neither increased total plant dry mass nor leaf area compared to the ambient control (Table 1). Leaf expansion was restricted in the continuously enriched treatment. Two of the 8-h exposures resulted in higher plant dry mass than the control. We

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then tested whether the lack of response to enrichment in this experiment might have been due to either the mode of intermittent CO₂ application (as discussed below) or to the CO₂ concentration used (1000 µl·liter⁻¹). We investigated these alternatives by holding plants either in normal (340 µl·liter⁻¹) or high (700 µl·liter⁻¹) CO₂ levels, or for half the week at the normal level followed by half the week at the high-CO₂ level. The day/night cycle was again 22/16C. After 37 days, the leaf areas (m² ± SE, n = 5) for control, continuously enriched (photoperiod only), and partially enriched treatments were 0.91 ± 0.03, 0.71 ± 0.03, and 0.88 ± 0.04, respectively. The corresponding plant dry masses (g ± SE) were 91.5 ± 5.1, 102.4 ± 4.8, and 90.7 ± 2.2. Continuous enrichment significantly reduced leaf area compared to the other two treatments. A possible reason for the lack of a positive response to elevated CO₂ was the limited growth potential under the low day temperature. Therefore, the initial experiment (Table 1) was repeated with 25C days. In these conditions, leaf area was significantly smaller with all elevated CO₂ concentrations, as was total plant dry mass with 4-h exposures, compared to the control (Table 2). Continuous exposure to elevated CO₂ resulted in a significant increase in total plant dry mass.

Further treatments were imposed to determine if plant growth, in terms of dry mass, was improved under some durations of elevated CO₂ and increased temperature. With 25C days, a significant increase of shoot dry mass occurred at 700 µl CO₂/liter compared to ambient (Table 3). In contrast, with elevated CO₂ and 22C days, root dry mass was higher than the control. Leaf area was reduced with plants exposed to elevated CO₂ at both temperatures.

Whole-plant and single-leaf transpiration were always significantly lower at the elevated CO₂ concentration compared to the ambient in either 22/16C or 25/16C (day/night). For example, whole-plant rates (kg·m⁻²·s⁻¹ × 10⁶ ± SE, n = 8) in 700 µl CO₂/liter at 22/16C (day/night) were 18.2 ± 1.19, 22.8 ± 1.08, and 16.6 ± 0.67 for hour 1, hour 5, and hour 9 of the photoperiod, respectively; the corresponding values for plants at 340 µl CO₂/liter were 25.3 ± 0.75, 28.7 ± 0.72, and 26.3 ± 0.81. Photosynthesis of plants at the differing CO₂ and day temperature treatments was measured at various stages during the photoperiod. On one occasion, the values for plants in 1000 µl CO₂/liter and 22/16C (day/night) were 20.4, 21.3, and 21.9 µmol·m⁻²·s⁻¹ for hour 1, hour 5, and hour 10 of the photoperiod, respectively; the corresponding values for plants in the ambient CO₂ concentration were 13.6, 13.7, and 13.2 µmol·m⁻²·s⁻¹. The differences between ambient and elevated CO₂ were highly significant (*P* ≤ 0.01). For plants growing in 700 µl CO₂/liter and with days of 25C, photosynthetic rates for the above hours were 22.4, 20.2, and 21.5 µmol·m⁻²·s⁻¹, respectively; the corresponding values for the control plants were 11.7, 12.0, and 15.0 µmol·m⁻²·s⁻¹, with the same differences being significant at *P* ≤ 0.01. With intermittent CO₂ exposures, photosynthesis of plants during exposure to the elevated CO₂ concentration was significantly higher than

the values measured during the exposure to the ambient CO₂ concentration (Fig. 1). Dark respiration rates (measured during the fourth hour of the dark period under ambient conditions) for plants exposed to daytime CO₂ concentrations of 340 or 700 µl·liter⁻¹ were 2.7 ± 0.2 and 4.1 ± 0.7 µmol·m⁻²·s⁻¹, respectively.

No visual nutrient deficiency symptoms were observed in any plants. However, concentrations (on a dry-weight basis) of N, P, K, S, Ca, and Mg in recently matured leaves were significantly lower in plants grown with CO₂ at 1000 than at 340 µl·liter⁻¹ (Table 4).

Discussion

Plants grown with days at 22C were generally characterized by a lack of growth response to CO₂ enrichment, despite having significantly higher photosynthetic rates, possibly because of acclimation of photosynthesis under prolonged CO₂ enrichment, as previously reported in tomatoes (Besford, 1993; Yelle et al., 1989, 1990). A striking feature of our research was the smaller leaf area in CO₂-enriched plants than in control plants (Tables

1–3). The specific leaf weight (leaf weight per unit leaf area) was always higher in enriched than in control plants. Tripp et al. (1991) reported that yield increases observed among eight tomato genotypes grown at 1000 µl CO₂/liter were independent of carbon exchange rate because of a change in partitioning from root to fruit. In our experiment, root dry matter accumulation was not affected by elevated CO₂ concentrations (Tables 1–3), but it was greater at 22C than at 25C (Table 3). Shoot dry mass was higher than for the control only for the continuously enriched CO₂ plants at 25C (Tables 2 and 3).

The higher rate of dark respiration measured for CO₂-enriched plants could explain the absence of growth response to CO₂ enrichment at 22C. The respiration rates measured are similar to those of Bunce (1990), who reported an increase in the dark respiration for CO₂-enriched tomato plants and suggested that accumulation of carbohydrates in CO₂-enriched leaves is the reason for the higher rate of dark respiration. In separate experiments (unpublished data), we pulse-fed leaf 10 (counted acropetally) of 90-day-old plants for

Table 1. Growth responses of tomatoes to ambient (A, 340 µl·liter⁻¹) or high (H, 1000 µl·liter⁻¹) CO₂ concentrations in a 12-h photoperiod, either in the first (H, A, A), second (A, H, A), or third (A, A, H) 4 h, or in a combination of these.

Treatment ^y	Leaf area ^z (m ²)	Dry mass ^z		
		Total plant (g)	Shoot (g)	Root (g)
A, A, A	0.12 ab ^x	11.6 cd ^x	10.3 bc ^x	1.3 a ^x
H, H, H	0.11 b	12.4 a–d	11.1 a–c	1.3 a
H, A, A	0.12 ab	12.0 b–d	10.5 bc	1.5 a
A, H, A	0.12 ab	11.3 d	9.9 c	1.4 a
A, A, H	0.12 ab	12.3 a–d	10.7 a–c	1.6 a
H, H, A	0.12 ab	13.3 ab	11.8 a	1.5 a
H, A, H	0.12 ab	13.6 a	12.0 a	1.6 a
A, H, H	0.12 ab	13.2 a–c	11.6 ab	1.6 a

^zMeans of eight replicate plants.

^yEnrichment occurred for 20 days at 22/16C (day/night).

^xMean separation within each column by Duncan's multiple range test, *P* ≤ 0.05.

Table 2. Growth responses of tomatoes to ambient (A, 340 µl·liter⁻¹) or high (H, 700 µl·liter⁻¹) CO₂ concentrations in a 12-h photoperiod, either in their first (H, A, A), second (A, H, A), or third (A, A, H) 4 h. Plants were 64 days old from seeding at harvest.

Treatment ^y	Leaf area ^z (m ²)	Dry mass ^z		
		Total plant (g)	Shoot (g)	Root (g)
A, A, A	0.61 a ^x	58.5 b ^x	51.5 b ^x	7.1 a ^x
H, H, H	0.45 b	65.5 a	57.3 a	8.2 a
H, A, A	0.47 b	52.2 c	44.9 c	7.4 a
A, H, A	0.47 b	49.9 c	42.4 c	7.2 a
A, A, H	0.46 b	49.9 c	43.5 c	6.4 a

^zMeans of eight replicate plants.

^yEnrichment was for 30 days at 25/16C (day/night).

^xMean separation within each column by Duncan's multiple range test, *P* ≤ 0.05.

Table 3. Growth responses of tomatoes to elevated CO₂ at two-day temperature regimes of 22 or 25C (night temperature = 16C). Plants were 64 days old from seeding at harvest.

CO ₂ concn (µl·liter ⁻¹)	Temp ^y (°C)	Leaf area ^y (m ²)	Dry mass ^z		No. flower trusses ^z	No. laterals ^z
			Shoot (g)	Root (g)		
340	25	0.61 ab ^x	51.4 b ^x	7.1 b ^x	7.3 a ^x	6.1 a ^x
700	25	0.45 c	58.0 a	8.3 ab	7.1 a	6.1 a
340	22	0.64 a	55.5 ab	10.5 a	4.9 b	7.7 a
700	22	0.54 b	55.1 ab	11.0 a	4.3 b	6.6 a

^zMeans of eight replicate plants.

^yEnrichment was for 31 days.

^xMean separation within each column by Duncan's multiple range test, *P* ≤ 0.05.

Fig.1. Effect of air CO₂ concentration on photosynthesis in single leaves of tomato during a 12-h photoperiod. Exposure to elevated CO₂ (700 μl·liter⁻¹) occurred during either the first (left), second (center), or third (right) 4 h of the photoperiod. For the remaining 8 h, the plants were exposed to ambient CO₂ concentration (340 μl·liter⁻¹). Plants were grown at 25/16C (day/night). Carbon dioxide enrichment was applied over 30 days. Bars on histograms represent twice standard error of means, based on eight replicate plants.

Table 4. Concentration (percent dry weight) of N, P, K, S, Ca, and Mg in tomato leaves at ambient (340 μl·liter⁻¹) and at 1000 μl CO₂/liter at 22/16C (day/night). Plants were 64 days old from seeding at harvest.

CO ₂ concn (μl·liter ⁻¹)	Nutrient					
	N	P	K	S	Ca	Mg
340	2.57 ± 0.12 ^z	0.18 ± 0.01 ^z	2.96 ± 0.15 ^z	0.56 ± 0.04 ^z	1.88 ± 0.09 ^z	0.54 ± 0.03 ^z
1000 ^y	1.42 ± 0.05	0.12 ± 0.01	1.81 ± 0.05	0.31 ± 0.03	1.26 ± 0.11	0.37 ± 0.03

^zMeans of 10 replicate plants ± SE.

^yEnrichment was for 31 days.

10 min with ¹⁴CO₂ between the second and third hours of the photoperiod and then measured the proportion of ¹⁴C-labeled assimilates after 30 min, 3 h, and at the end of light and dark periods in leaves 8, 9, 10, and truss 1. For all these measurement times, leaf 10 had a lower proportion of ¹⁴C-labeled assimilates in control than in CO₂-enriched plants, while the opposite was true for the other organs. A lower rate of translocation in enriched than in control plants is a possible reason for the lack of positive growth response to CO₂ enrichment. Rozema (1993) observed that the higher photosynthetic rate for wheat at 700 than at 350 μl CO₂/liter did not result in a higher growth rate for the former treatment. He hypothesized that a lower translocation rate at the prevailing low temperature (10–14C) might have been the reason. In our CO₂-enriched plants, photosynthates accumulated in leaves as reserves rather than contributing to leaf expansion, as also observed previously by Yelle et al. (1990) for two species of tomato.

The lower transpiration rate at the elevated CO₂ concentration is solely due to stomatal closure, as shown by Nederhoff and De Graaf (1993), whose analysis included other environmental factors affecting transpiration, such as radiation, air humidity, and leaf temperature. They concluded that stomatal conductance of tomatoes decreases by ≈3% for every 100-μl·liter⁻¹ increase in CO₂ concentration in the range of 300 to 1200 μl·liter⁻¹. The lower concentration of macronutrients (Table 4) in the CO₂-enriched plants is associated with

their lower transpiration rate (Glass, 1989) than of the control plants. Kuehny et al. (1991) reported that, on a dry-weight basis, foliar concentrations of N, P, K, S, Ca, and Mg were lower in chrysanthemums [*Dendranthema × grandiflorum* (Ramat.) Kitamura] at elevated CO₂ levels. Starch concentration was higher at the high CO₂ level, and when it was subtracted from the leaf dry weights, the differences in concentration of these mineral elements between high and normal CO₂ treatments disappeared. Possibly, mineral element concentrations were similarly diluted in our research for plants exposed to elevated CO₂. These lower concentrations were still above the deficient range reported for tomato (Madsen, 1975). We, therefore, doubt that the lack of growth response to CO₂ enrichment at 22C was due to nutrient deficiency. Nutrient deficiency would possibly result in a lower rate of photosynthesis as shown for K-deficient tomato plants by Behboudian and Anderson (1990). No such effect was observable in this experiment. Kimball et al. (1993), in reviewing the effects of increasing atmospheric CO₂ on vegetation, concluded that plants growing in nutrient-poor soils will also respond to elevated CO₂, although the response may be reduced under very severe nutrient deficiency. Some studies have indicated that root restriction in potted plants might prevent positive responses to CO₂ enrichment. Growth in cotton (*Gossypium hirsutum* L.) plants grown in 0.4-liter pots was less than in those grown in 1.7-liter pots when exposed to 650 μl CO₂/liter (Thomas and Strain,

1991). However, McConnaughay et al. (1993) questioned the relevance of the root restriction–CO₂ enrichment hypothesis without paying due attention to the nutritional status of the plant that was overlooked in some studies. We did not regard root restriction as being a problem in our experiment. The 4.4-liter pots were much bigger than those used in some root-restriction studies (McConnaughay et al., 1993; Thomas and Strain, 1991), and in some experiments the root mass was too small (Table 1) to have been restricted by 4.4-liter pots.

At 25C, CO₂ at 700 μl·liter⁻¹ resulted in greater plant dry-matter accumulation than at 22C, with the increase occurring in shoots and not in roots (Table 3). However, control plants growing in ambient CO₂ concentration at 22C produced more dry matter than those at 25C. The lower temperature appears to be better for total dry-matter production with this cultivar under ambient CO₂, but a higher temperature should be used if CO₂ enrichment is adopted. This recommendation supports the statement by Mortensen (1987) that, under elevated CO₂ concentration, optimum temperature for growth is increased.

Commercial enrichment of CO₂ is normally carried out for the entire photoperiod. In Great Britain, enrichment of commercially produced tomatoes is achieved by applying 1000 μl CO₂/liter from sunrise to 1.5 h before sunset (Slack, 1986). Provided similar results were produced, shorter durations of CO₂ application would be an attractive economic alternative. This possibility was the basis of our intermittent CO₂ experiments. At 22C, dry-matter production was unchanged by 4-h exposures to 1000 μl CO₂/liter compared to continuous exposure (Table 1). However, an 8-h exposure produced significantly higher dry matter than ambient CO₂. With days at 25C and CO₂ at 700 μl·liter⁻¹, a 4-h exposure resulted in significantly less dry-matter production than the continuously exposed control (Table 2), although the photosynthetic rate during the enrichment period was significantly higher (Fig. 1). Diminution of dry-matter production occurred possibly because of the manner in which the 4-h enrichment was imposed. Plants had to be shifted from the ambient to the high-CO₂ room, which did not take more than 2 min. However, their stomata might have closed during the move and subsequently needed adjustment time in the high-CO₂ conditions. Photosynthesis was measured 45 min after the plants were shifted. At the end of 4 h, plants were shifted back to the ambient-CO₂ conditions and had to undergo a similar adjustment. Possibly, the total photosynthetic production throughout the photoperiod for these plants was lower than the control plants, resulting in less growth. For plants undergoing the 8-h exposures (Table 1), the situation would have been redressed by longer exposure to higher CO₂ concentration and a better opportunity for photosynthates to move out of leaves compared to the continuous enrichment.

Plants growing at 22/16C and 700 μl CO₂/liter for 3.5 days of each week did not produce more dry matter than those growing at ambient CO₂. Continuous exposure to 700 μl CO₂/liter

resulted in significant increases in growth at 25/16C but not at 22/16C (day/night). One possibility is that the higher temperature improved translocation of photosynthates, thus producing more dry matter (Rozema, 1993).

Although CO₂ enrichment is a common practice in greenhouse production of tomatoes, they might be less responsive than some other C₃ plants. They ranked 18th in Poorter's (1993) review in which he compared 19 C₃ crop species in their response to enrichment (600–720 µl·liter⁻¹). Poorter (1993) cited numerous studies, involving the same species, in which the degree of response differed, presumably reflecting cultivar differences. Lakso et al. (1984) reported marked cultivar difference in photosynthetic responses of tomato plants to enriched CO₂ concentration. In our studies, 'Virosa' did not show favorable growth responses to enhanced CO₂ concentrations at its optimal day temperature of 22C. Although significant growth responses occurred at 25C, the extra cost of doubling the CO₂ concentration and raising the temperature might not have been compensated for by improved vegetative growth. However, the ultimate test of the variables we used must consider production of marketable fruit.

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