Responses of Greenhouse Tomatoes to Summer CO_2 Enrichment

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Abstract

To evaluate the feasibility of summer CO_2 enrichment for greenhouse tomato production in South-western Ontario, the largest and most concentrated greenhouse vegetable production area in North America, its effects on leaf photosynthesis, fruit yield and quality of long tomato crops planted in January were investigated in six greenhouse compartments over three summers from 2005 to 2007. Due to strong ventilation in the summer seasons, higher than ambient concentration of CO_2 was only achieved on sunny days before 10–11 a.m. when outside global solar radiation was less than 400–500 W m^{-2} (depending on ventilation setting) or after 6–7 p.m. or on overcast days when outside global solar radiation was less than 200 W m^{-2}. In summer 2005, the warmest on record in South-western Ontario, the leaf photosynthesis of the CO_2-enriched plants partially acclimated to high levels of CO_2. However, the leaf photosynthesis of the CO_2-enriched plants did not show any acclimation in summers of 2006 and 2007, a normal and a cooler than usual summer. The photo-assimilate gains with high concentration of CO_2 under high light intensity was much larger than under low light intensity, and the response of leaf photosynthesis to CO_2 did not change during the course of the day from early morning to late afternoon. Therefore, CO_2 enrichment will be more effective under strong solar radiation and the enrichment in the afternoon would be as effective as in the morning, if same concentration of CO_2 could be achieved with same amount of CO_2 supplied. Summer CO_2 enrichment to a level above the ambient did not affect fruit quality. It reduced fruit yield in August 2005, did not change fruit yield in summer 2006, and slightly increased fruit yield in summer 2007. High fruit load increased fruit yield per unit of area but it did not improve the crop response to CO_2 enrichment. Therefore, high temperature stress and the inability to achieve higher than ambient concentration CO_2 under high solar radiation due to strong ventilation, might have limited the crop response to summer CO_2 enrichment.

INTRODUCTION

Greenhouse CO_2 enrichment has been practiced by tomato growers since the 1960's in the Netherlands and later in England (Nederhoff, 1994). Many researchers have demonstrated the beneficial effects of atmospheric CO_2 enrichment in greenhouse crop production (Long et al., 2004). Short-term CO_2 enrichment increased photosynthetic rates of C3 plants because high concentrations of CO_2 inhibit photorespiration (Drake et al., 1997). Increased carbon uptake resulting from the stimulation of leaf photosynthesis by CO_2 enrichment could alter the balance of carbohydrate supply and sinks, and thereby cause an increase in non-structural carbohydrates (Drake et al., 1997). Such accumulations of carbohydrates in the leaves may cause a long-term reduction in photosynthetic capacity per unit leaf area (acclimation) (Drake et al., 1997). Therefore, the response of long tomato crops to CO_2 enrichment may be limited by the acclimation of photosynthetic capacity. Furthermore, the response to CO_2 enrichment may also vary with climate, greenhouse ventilation, fruit load and plant density (Nederhoff, 1994).

Research conducted in northern Europe has shown that greenhouse tomato production may benefit from summer CO_2 enrichment (Nederhoff, 1994) and many European commercial greenhouse growers have started to adopt the practice. The climate in South-western Ontario, Canada (the largest and most concentrated greenhouse vegetable production area in North America), especially in the summer, is quite different from that of northern Europe. Solar radiation and air temperature are higher and the greenhouse is more frequently ventilated than in northern Europe. Therefore, the practice of summer CO_2 enrichment needs to be carefully examined before it is used in commercial production in South-western Ontario.

The objectives of this study were to investigate the effects of summer CO_2 enrichment on growth, photosynthesis, fruit yield and quality on greenhouse tomato crops after a long-term of winter CO_2 enrichment and under conditions of strong solar radiation, high air temperature and extended periods of ventilation.

MATERIALS AND METHODS

Three experiments were conducted in six double-poly greenhouses (70 m^2 each) from Jan. to Sept. in 2005, 2006 and 2007, at the Greenhouse and Processing Crops Research Centre (GPCRC), Agriculture and Agri-Food Canada, Harrow (41º N), Ontario, Canada. Regular (non-grafted) and grafted tomato plants of several beefsteak tomato cultivars (Rapsodie (2005), Macarena (2006) and Big-Dena (2006 and 2007) and one cluster tomato cultivar Clarance (2006) were used in the experiments. Tomato transplants were planted onto sleeved rockwool slabs (50 x 20 x 10 cm^3, Fibrex Insulation Inc., Sarnia, ON, Canada) on troughs hanging 75 cm above the ground in the greenhouses, at a density of 2.7 plants m^{-2} in January. Day/night heating temperature was set at 19/18ºC while the threshold temperature for ventilation was set at 25ºC. The temperature settings were adjusted through the growing season according to recommendations by the Ontario Ministry of Agriculture, Food and Rural Affairs (2001). Ventilation was implemented in the greenhouse compartments by roof openings (natural ventilation) and by forced fan ventilation. When the ventilation requirement calculated by the Argus Climate Control Computer (Argus Control System Ltd., White Rock, BC, Canada) for these compartments was more than 50% (2005 and 2006) or 75% (2007), one of the two exhausted fans in the compartment was automatically turned on, which substantially increased air exchange rate, bringing the greenhouse CO_2 concentration down to the ambient level (380 µl L^{-1}).

Tomato plants were trained to a single stem by removal of side shoots on the main stem according to commercial practices. To determine if fruit load is a limiting factor for tomatoes to respond to summer CO_2 enrichment, three different fruit loads were applied in each of the six compartments in 2007 by varying stem density and cluster fruit pruning. A side shoot from the main stem in one of every 4 plants was allowed to develop on March 27 to increase the stem density to 3.4 stems m^2. Two cluster fruit pruning methods (3 fruit or 4 fruit per cluster) were started on June 1. The combination of stem density and fruit pruning allowed the following three fruit loads: (1) - 8.1 fruit $cluster^{-1}$ m^{-2} (3 fruit $cluster^{-1}$*2.7 stems m^{-2}), (2) - 10.8 fruit $cluster^{-1}$ m^{-2} (4 fruit $cluster^{-1}$*2.7 stem m^{-2}), and (3) - 13.6 fruit $cluster^{-1}$ m^{-2} (4 fruit $cluster^{-1}$*3.4 stems m^{-2}).

Carbon Dioxide Enrichment

From January to May, all six compartments were supplemented with liquid CO_2 at 1000 µl L^{-1} when the calculated ventilation requirement by the Climate Control Computer was less than 10%, 400 µl L^{-1} when above 10%, and discontinued when above 20%. In June, three summer CO_2 treatments were applied to the six greenhouse compartments (randomized complete block design with two replicates) during daytime. The three CO_2 treatments were applied in summer of 2005 as following:

- Control - ambient concentration of CO_2 (380 µl L^{-1}), no CO_2 enrichment.
- Enrich1 - 800 µl L^{-1} when ventilation requirement was <10%, 400 µl L^{-1} when between 10% and 50%, and ambient concentration when >50%.
- Enrich2 - 1200 µl L^{-1} when ventilation requirement was <10%, 500 µl L^{-1} when

between 10% and 50%, and ambient concentration when >50%.

In summer of 2006, the Enrich 1 and Enrich2 were modified to increase the CO_2 concentration difference between the enriched treatments during the ventilation period:

- Enrich1 - 1000 µl L^{-1} when ventilation requirement was <20%, 400 µl L^{-1} when between 20% and 50% and ambient concentration when >50%.
- Enrich2 - 1000 µl L^{-1} when ventilation requirement was <20%, 800 µl L^{-1} when between 20% and 50% and ambient concentration when >50%.

In summer 2007, the ventilation threshold for stopping CO_2 enrichment was increased to 75% for increasing the duration of CO_2 enrichment. The Enrich1 and Enrich2 in 2007 were applied as following:

- Enrich1 - 600 µl L^{-1} when ventilation was <20%, 400 µl L^{-1} when between 20% and 75% and ambient concentration when >75%.
- Enrich2 - 1000 µl L^{-1} when ventilation requirement was <20%, 600 µl L^{-1} when between 20% and 75% and ambient concentration when >75%.

Plant Growth Measurement

Plant growth parameters (leaf area, dry weight, specific leaf area, and leaf chlorophyll of the 5^{th} and 10^{th} fully expanded leaf) were measured several times in each summer. Leaf area was measured by a Li-Cor 3100 leaf area meter (Li-Cor, Lincoln, Nebraska, USA). Leaf dry weight was determined after drying at 60ºC for 2 weeks. Leaf chlorophyll was measured with a SPAD-502 chlorophyll meter (Minolta Corporation, New Jersey, USA).

Leaf Photosynthesis

The CO_2 photosynthetic response curves were measured on the 6^{th} (counted from the top leaf longer than 10 cm) fully expanded leaf with a Li-Cor 6400 portable photosynthesis system equipped with a 6400-02B LED light source and a 6400-01 CO_2 injector system (Li-Cor, Lincoln, Nebraska, USA) in all three summers. The system can control light, temperature, humidity and CO_2 concentrations in the leaf chamber. A minimum of three plants in each greenhouse compartment were used for these measurements. The CO_2 photosynthetic response curves at two levels of photosynthetically active radiation (PAR, 300 and 1000 µmol m^{-2} s^{-1}) were determined at three time periods: at early morning (7:00–9:00), around noon (11:00–13:00) and in late afternoon (17:00–19:00).

Fruit Harvest and Quality Evaluation

Fruit reaching the breaker stage were harvested twice a week and graded according to commercial grading standards (Ontario Ministry of Agriculture, Food and Rural Affairs, Regulation 378/90, 1987). The fruit harvested in 2007 was also rated for russeting (cuticle cracking) and radial cracking according to the rating scales of Hao and Papadopoulos (2003). For quality analysis, 4 large or extra-large fruit of grade#1 in breaker stage were randomly selected from each plot, and then stored at 20ºC and 70% relative humidity until the table-red stage. Fruit dry matter content was measured by drying sliced fruits at 65ºC for three weeks. Soluble solid content was measured with a portable digital refractometer (model PR-101, Atago Co., Tokyo, Japan) in homogenized fruit samples. Fruit firmness was tested by constant area compression test with an Instron Model 4411 Testing machine (Instron Canada, Burlington, ON, Canada). The fruit used for firmness test was kept at 20ºC for one day to allow them to ripe to the pink stage. Three pericarp specimens from each fruit were taken around the fruit equator and over the locule using a 12-mm core borer. The maximum force for tissue collapse/failure (MF) and the total energy required for tissue collapse of these specimens were recorded.

RESULT AND DISCUSSION

Greenhouse CO_2 Concentration and Climate

The daytime average CO_2 concentration for the summer CO_2 enrichment period (July and August in 2005, June to August in 2006 and 2007) was 370, 430 and 452 µl L^{-1} in 2005, 381, 455 and 533 µl L^{-1} in 2007 for Control, Enrich1 and Enrich2, respectively. In 2006, it was 373 and 470 µl L^{-1} for Control and Enrich2 (Enrich1 treatment was not applied due to severe pest infestation in the compartments planned for the treatment). Thus, increasing the ventilation threshold for stopping CO_2 enrichment and the CO_2 concentration settings during the ventilation period led to higher CO_2 concentration during daytime. Higher than ambient concentration of CO_2 achieved by the summer enrichment was mostly in the morning with the peak concentration at 7–8 a.m. Based on the diurnal CO_2 concentration averaged over the summer enrichment period, the CO_2 concentration inside the CO_2-enriched compartments was only higher than the ambient concentration from 6:00 to 11:00 for about 5 hours in summers of 2005 and 2006. In summer of 2007, after increased ventilation threshold for CO_2 enrichment from 50% to 75%, additional two more hours of higher-than ambient concentrations were achieved from 19:00 to 21:00. The CO_2 concentration inside all compartments was at the ambient level between 12:00 to 18:00. In summers of 2005 and 2006, the CO_2 enrichment in the morning usually stopped after the outside global solar radiation reached about 400 W m^{-2} while in 2007 it stopped only after the outside global solar radiation reached about 500 W m^{-2}. Higher than ambient concentration of CO_2 was achieved by the CO_2 enrichment when outside global solar radiation was below 200 W m^{-2} on overcast days in all 3 years and in the late afternoon on sunny days in 2007 only. The summer of 2005 was the warmest on record, while summer of 2006 was normal and summer of 2007 was cooler than usual for South-western Ontario (http://ontario.hazards.ca/historical/heat_Ontario-e.html, Environment Canada).

Leaf Photosynthesis

The CO_2-enriched plants did not show any acclimation (reduction in photosynthetic capacity) in summers of 2006 and 2007. The CO_2 response curves of leaf photosynthesis determined at both low (300 µmol m^{-2} s^{-1} PAR) and high (at 1,000 µmol m^{-2} s^{-1} PAR) light intensities were similar between the control and CO_2-enriched plants in the morning and around noon. In the afternoon, the increase in leaf photosynthesis of CO_2-enriched plants with increasing CO_2 was even faster than the control plants. In the summer of 2005, the warmest on record, the plants in CO_2-enriched compartments partially acclimated to high levels of CO_2; the leaf photosynthesis rates of the CO_2-enriched plants at CO_2 levels higher than 400 µl L^{-1} were lower than the plants in the control compartments. This acclimation of photosynthesis was only partial since it did not completely eliminate the increase of leaf photosynthesis with the high concentration of CO_2; the photosynthetic rate with Enrich2 at 800 µl L^{-1} of CO_2 concentration was still higher than that of Enrich1 at 600 µl L^{-1} of CO_2, which was higher than that of Control at 400 µl L^{-1} of CO_2. The photosynthesis response curves below 400 µl L^{-1} were similar between the control and CO_2-enriched plants. The increase of leaf photosynthetic rates with high concentrations of CO_2 under strong light intensity (1,000 µmol m^{-2} s^{-1} PAR) was much larger than at low light intensity (300 µmol m^{-2} s^{-1} PAR), indicating that CO_2 enrichment is more effective if high concentration of CO_2 could be achieved under strong light conditions. The CO_2 response curves of leaf photosynthesis (acceleration rate and saturation point) did not change during the course of day from early morning to late afternoon for most of the cultivars tested with the CO_2-enriched plants. Therefore, there was no feed-back inhibition of leaf photosynthesis in the afternoon due to the accumulation of carbohydrates. Thus, CO_2 enrichment in the afternoon would be as effective as in the morning if same CO_2 concentration could be achieved with same amount of CO_2 supplied.

Plant Growth

"Short Leaves Syndrome" (SLS) as reported by Nederhoff (1994) was observed on the CO_2-enriched plants in summer 2005. Those plants with SLS had short, thick, curled and somewhat crisp, dark grey-green leaves and low specific leaf area. Tomato SLS usually occurs under conditions of high light intensity and high CO_2 concentration and low plant density (Nederhoff, 1994). However, no SLS was observed in summers of 2006 and 2007 (a normal and a cooler than usual summer). Therefore, the occurrence of SLS was probably more related to high temperature stress in the summer. Summer CO_2 enrichment reduced specific leaf area in 2005, but it did not affect it in 2006 and 2007. The effects of the summer CO_2 enrichment on plant growth were quite small in 2006 and 2007; most of its effects on growth parameters were not statistically significant ($P>0.05$, Analysis of Variance). Summer CO_2 enrichment increased total vegetative biomass in one of the three cultivars tested (cv. Macarena) in 2006, and the leaf area and dry weight in 2007. The CO_2 enrichment reduced the number and fresh weight of green fruits set and developed during the month of July 2005, a month with the highest solar radiation and temperature, but it did not affect (2006) or only slightly increased (2007) the number and fresh weight of green fruits on the plant at the end of the experiment. High fruit load in 2007 increased leaf area, dry weight and total vegetative biomass per unit of area but it did not affect the response of the plant growth to summer CO_2 enrichment.

Fruit Yield and Quality

Marketable fruit yield in August 2005 was reduced by the summer CO_2 enrichment; most of these fruits set and developed in the month of July, a month with the highest solar radiation and air temperature for South-western Ontario. Summer CO_2 enrichment did not affect fruit yield in summer 2006 (a regular summer season) and slightly increased fruit yield in summer 2007 (a cooler than usual summer season). High fruit load significantly increased fruit yield on per unit area but it did not improve the fruit yield response to summer CO_2 enrichment. The largest yield increase with summer CO_2 enrichment actually occurred at the low fruit load treatment (8.1 fruit $cluster^{-1}$ m^{-2} (3 fruit $cluster^{-1}$*2.7 stems m^{-2})). Therefore, fruit load was not a limiting factor for the tomato crop to respond to summer CO_2 enrichment. The high temperature stress and the inability to achieve higher than ambient concentration of CO_2 under strong solar radiation when it is more effective for photosynthesis, due to strong greenhouse ventilation, might be the limiting factors. Summer CO_2 enrichment did not affect fruit dry matter content, pH, soluble solid content, and fruit russetting and radial cracking in all three years.

CONCLUSIONS

Leaf photosynthesis of tomato plants in general did not acclimate during summer CO_2 enrichment unless under high temperature stress. The photo-assimilate gains with high concentration of CO_2 was much larger under high than under low light intensity and the photosynthesis response to CO_2 did not change during the course of the day from early morning to late afternoon. Thus, CO_2 enrichment will be more effective under strong solar radiation and the CO_2 enrichment in the afternoon would be as effective as in the morning, if same CO_2 concentration could be achieved with same amount of CO_2 supplied. Carbon dioxide enrichment to a level above the ambient in summer did not or only slightly increase fruit yield. High fruit load increased fruit yield per unit area but it did not improve the response of the plants to CO_2 enrichment. High temperature stress and the inability to achieve higher than ambient concentration of CO_2 under high solar radiation might have limited the crop response to summer CO_2 enrichment.

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