Daily Variations of Photosynthetic Efficiency of Greenhouse Tomato Plants during Winter and Spring

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ABSTRACT. Daily and seasonal variations of photosynthetic activity, chlorophyll *a* (Chl-*a*) fluorescence and foliar carbohydrate content were studied in situ on greenhouse tomato (*Lycopersicon esculentum* Mill. 'Trust') plants grown under CO₂ enrichment and supplemental lighting. The objective of this study was to assess the effect of seasonal variation of the photosynthetic photon flux (PPF) on photosynthetic efficiency of tomato plants and to determine the presence or absence of photosynthetic down-regulation under greenhouse growing conditions prevailing in northern latitudes. During winter, the fifth and the tenth leaves of tomato plants showed low, constant daily photosynthetic activity suggesting a source limitation under low PPF. In winter, the ratio of variable to maximum Chl-*a* fluorescence in dark adapted state (F_v/F_m) remained constant during the day indicating no photoinhibition occurred. In February, an increase in photosynthetic activity was followed by a decline during March, April, and May accompanied by an increase in sucrose and daily starch concentrations and constant but high hexose level. This accumulation was a long-term response to high PPF and CO₂ enrichment which would be caused by a sink limitation. Thus, in spring we observed an in situ down-regulation of photosynthesis. The ratio F_v/F_m decreased in spring compared to winter in response to increasing PPF. The daily decline of F_v/F_m was observed particularly as a midday depression followed by a recovery towards the end of the day. This indicated that tomato leaves were subject to a reversible inhibition in spring. F_v/F_m was lower in March than in April and May even though PPF was higher in April and May than in March. These results suggest that tomato plants develop an adaptive and protective strategy as PPF increases in spring.

Many studies have been conducted on the effect of CO₂ enrichment on the physiology, growth, and productivity of plants. Over the short term, a rise in CO₂ concentration enhances photosynthesis of C₃ plants by stimulating carboxylation of Rubisco (Faria et al., 1996) and carbohydrate synthesis (Kramer, 1981), thereby increasing plant growth (Kimball, 1983). Over the long term, the beneficial effects of elevated CO₂ concentration are determined by the balance between carbohydrate production in source leaves and the overall capacity of the plant to use photoassimilates in sink organs (Gunderson and Wulschleger, 1994; van Oosten and Besford, 1994; Yelle et al., 1989a). In sink-limited plants, a loss of photosynthetic efficiency may be caused by a biochemical limitation of inorganic phosphate (P_i) and/or Ribulose 1,5-bisphosphate (RuBP) regeneration (Sage, 1990), and eventually by a down-regulation of photosynthesis involving a cascade of reactions that repress the expression of genes, thylakoid proteins, Rubisco, and Rubisco activase proteins (van Oosten and Besford, 1995; Yelle et al., 1989b).

The down-regulation of photosynthesis under high CO₂ is increased further by high irradiance and/or long photoperiods (Dorais et al., 1996; Stutte et al., 1996). Under high CO₂ concen-

tration and high irradiance, the photosynthetic rate is determined largely by the rate of regeneration of RuBP and the capacity of sucrose synthesis to regenerate P_i (von Caemmerer and Farquhar, 1981). Low cytoplasmic P_i levels may affect the transport of triose-phosphates out of the chloroplast, resulting in high starch levels that are not completely mobilized overnight (Highsmith, 1989; Topa and Cheeseman, 1992).

The significance of these physiological processes has rarely been considered for commercial greenhouse production of tomatoes (*Lycopersicon esculentum*) which in northern latitudes relies typically on CO₂ enrichment as well as supplemental lighting to stimulate growth and productivity (Dorais et al., 1993; Vezina et al., 1991). During the growing season, large variations of incident photosynthetic photon flux (PPF) occur especially in northern latitudes which may affect plant responses to elevated CO₂. Little attention has been paid to the daily variations of photosynthetic efficiency of greenhouse tomato plants during the entire period of production from November to May. The objectives of this work were to study daily variations of photosynthetic efficiency of tomato plants under different seasons and to determine the presence or absence of photosynthetic down-regulation in situ under greenhouse conditions prevailing in northern latitudes.

Materials and Methods

PLANT MATERIAL AND GROWTH CONDITIONS. Seeds of 'Trust' tomato were sown 15 June 1995 and seedlings transplanted 14 July 1995 on 7.5 × 20 × 90 cm rockwool slabs (Grodan, Agro-

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Dynamics Inc., Milton, Ontario, Canada) in a Venlo glasshouse (Serres du St-Laurent Inc., Portneuf, Quebec, Canada, long. 71.4 W and lat. 46.7 N) at a density of 2.8 plants/m². Plants were fertilized with a nutrient solution (electrical conductivity 2.2 mS·cm⁻¹) containing the following nutrients (in mM): 12 N, 1.6 P, 8.5 K, 4 Ca, 1.8 Mg, 1.2 Cl and in (μM) 35.8 Fe, 7.3 Mn, 3 Zn, 3.1 Cu, 46 B, and 0.5 Mo), using a drip irrigation system. Carbon dioxide enrichment at 1000 μmol·mol⁻¹ was achieved during daytime using CO₂ produced by the combustion of natural gas. An infrared analyzer (Priva Computer, Beamsville, Ontario, Canada) was used to control CO₂ concentration in the greenhouse. Supplemental lighting of 100 μmol·m⁻²·s⁻¹ photosynthetically active radiation (*PAR*) was provided by high pressure sodium lamps (HPS, P.L. 780/N 400, P.L. Lighting Systems Canada Inc., Ontario, Canada). The total photoperiod used was progressive, set at 14 h in September, and then increased progressively to 17 h in December and January. Thereafter, it was shortened progressively from February to April (Iraqi et al., 1997). Lamps were turned off 30 min before the beginning of the natural dark period, or automatically when natural *PPF* measured inside the greenhouse at the top of the canopy exceeded 320 μmol·m⁻²·s⁻¹. Day/night temperatures were maintained at 19 ± 2/17 ± 2 °C.

PHOTOSYNTHETIC PHOTON FLUX. Hourly *PPF* was monitored each month from November to May. In our present study, we refer to the winter months as November, December, January, and February and to the spring months as March, April, and May. The ambient *PPF* received by tomato plants is the sum of natural *PPF* and supplemental lighting provided by HPS lamps (Fig. 1). Light transmission through the glasshouse was estimated at 65%. Seasonal changes in *PPF* were measured throughout the growing period of tomato plants, beginning in November and ending in May (Fig. 1). Supplemental lighting contributed on average 62% of the total light available to tomato plants for the winter (November to February) and 15% on average for the spring (March to April). In winter, *PPF* did not reach high levels and supplemental lighting continued throughout this period. However, from March *PPF* increased by midday to 120% the level measured in February and reached high levels (up to 1200 μmol·m⁻²·s⁻¹) in April and May.

PHOTOSYNTHETIC MEASUREMENTS. Diurnal measurements of the net photosynthetic rate at ambient light intensity (*P_N*) were performed under incident *PPF* received by tomato plants. Measurements of CO₂ assimilation rate were performed at 4 h intervals, on the fifth and the tenth developed leaves from the apex of tomato plants, using a portable photosynthesis system (LI-6200, LI-COR, Inc., Lincoln, Neb.). To determine the maximum photosynthetic rate at saturating light intensity (*P_{max}*), a red light emitting diode (LED) supplying a *PPF* of 800 μmol·m⁻²·s⁻¹ was used. Photosynthetic measurements were taken every 4 h after artificial lighting was turned on up to the beginning of the dark period. Photosynthetic measurements were repeated monthly from November 1995 to May 1996 on the fifth and the tenth leaves from a sample of 10 tomato plants chosen randomly in the greenhouse. Average of 10 measurements was calculated as well as the SE.

CHL-*a* FLUORESCENCE MEASUREMENTS. Chlorophyll *a* (Chl-*a*) fluorescence induction kinetics were determined on 10 samples of fifth and tenth leaves each of which were used for photosynthetic measurements. Fluorescence measurements were made 1 h after the lamps were turned on, and every 4 h thereafter throughout the 24-h period. Chl-*a* fluorescence was measured during a 1 s flash of bright red light (3250 μmol·m⁻²·s⁻¹ centered at 650 nm) using a plant efficiency analyzer (PEA, Hansatech Ltd., Norfolk,

United Kingdom) as described by Strasser et al. (1995). Measurements were performed after a 20 min dark acclimation period. The minimal (*F_o*) and the maximal (*F_m*) unquenched yields of Chl-*a* fluorescence were determined in dark acclimated leaves. From these fluorescence levels, the maximum quantum yield of photosystem II (PSII) photochemistry was estimated by the ratio of variable to maximum fluorescence in dark adapted leaves *F_v*/*F_m* (where *F_v* = *F_m* - *F_o*). Measurements were made on the fifth and the tenth leaves from a sample of 10 tomato plants chosen randomly in the greenhouse. Average of 10 measurements was calculated as well as the SE.

CARBOHYDRATE ANALYSIS. Soluble sugar (glucose, fructose, and sucrose) and starch concentrations were analyzed as described by Ozburn et al. (1973) on the same fifth and tenth leaves used for photosynthetic and Chl-*a* fluorescence measurements (10 samples each). They were collected at 4-h intervals over a 24-h period, frozen immediately in liquid nitrogen (N₂) and stored at -80 °C until use. Leaves were ground in liquid N₂ with a mortar and pestle. Glucose, fructose, and sucrose were determined using high performance liquid chromatography (HPLC, Waters Co. Milford, Mass.; Sugar-PAK column 6.5 × 300 mm using Waters 600E pump). Sugar concentrations were expressed as mg·g⁻¹ fresh weight (FW). To digest the starch on the pellets, amyloglucosidase (EC 3.2.1.3), supplied by Sigma Chemical Co. (St. Louis, Mo.), was added to samples and incubated in a water bath at 50 to 55 °C for 3 h. Glucose content was determined using the YSI 7200 (Yellow Springs Inc., Ohio.). The final starch concentration per sample was expressed as mg glucose/g FW. Leaf sampling for carbohydrate analyses was conducted 1 h after the lamps were turned on, and every 4 h thereafter for 24 h. Analysis were made on the fifth and the tenth leaves from a sample of 10 tomato plants chosen randomly in the greenhouse. Average of 10 measurements was calculated as well as the SE.

Results

SEASONAL CHANGES OF PHOTOSYNTHESIS. For each month from November to May, *P_N* were measured on the fifth and the tenth leaves at regular intervals during a sunny day (Fig. 2). From November to January, *P_N* values of both the fifth and the tenth leaves were relatively low (4 to 6 μmol·m⁻²·s⁻¹) and did not show significant variations during the day. From February to April, maximum *P_N* was reached at the highest *PPF* recorded during the day. In contrast, in May *P_N* reached its maximum after only 4 h of light period (0900 HR), whereas maximum *PPF* was reached 4 h after 0900 HR (at 1300 HR).

The *P_{max}* of the fifth and the tenth leaves were constant from November to January. From February to May, large daily differences of *P_{max}* were observed despite the same saturating light (Fig. 3). But in February, *P_{max}* reached 17 μmol·m⁻²·s⁻¹ and 10 μmol·m⁻²·s⁻¹ for the fifth and the tenth leaves, respectively, after 8 h of light (1000 HR). Maximum *P_{max}* was reached at 1100 HR in March and then earlier in April and May (0900 HR) before *PPF* reached its maximum. The increase in *PPF* during these months did not increase *P_{max}* proportionally, since *P_{max}* increased significantly from January to February, then decreased from March, since *P_{max}* was lower in spring than in February despite higher *PPF*.

SEASONAL VARIATIONS OF CHL-*a* FLUORESCENCE. Daily patterns of variation of the maximal photochemical efficiency of PSII estimated by the Chl-*a* fluorescence ratio *F_v*/*F_m* were studied each month. The ratio *F_v*/*F_m* remained constant (0.82 to 0.86) during the daily cycle of November, December, January, and February,

for both the fifth or the tenth leaves (Fig. 4). However, in spring the ratio F_v/F_m decreased at midday especially for the fifth leaves where F_v/F_m reached the lowest values in March (0.77), and recovered in the evening. In April and May, F_v/F_m showed a similar pattern during midday but did not reach as low values as recorded in March, although PPF was higher in April and May than in March.

SEASONAL CHANGES OF CARBOHYDRATE. Sucrose content of tomato leaves was significantly lower in winter than in spring months (Fig. 5). Leaf sucrose concentrations were related to seasonal and daily changes of PPF . We also observed higher initial concentrations of sucrose at the beginning of the diurnal period in spring than in winter. Leaf hexose content was fairly constant during the day for all months (Fig. 6). However, in spring, hexose content in leaves increased up to 4 fold compared to winter months. Starch concentration in leaves behaved differently over the course of the day in winter compared to spring (Fig. 7). Starch concentration remained constant during the day in November to February. However, there was a seasonal increase

in leaf starch content in spring, and initial content of leaves in starch at the beginning of the photoperiod in spring was greater than in winter. From March, plants exposed to high PPF accumulated starch during the light period.

Discussion

Many researchers have studied the effects of CO_2 enrichment, supplemental lighting, and photoperiod on growth, yield, development, and physiology of greenhouse crops. However, little work has been done on the influence of seasonal variations of light on tomato plants grown under supplemental lighting and CO_2 enrichment in terms of photosynthetic efficiency and carbohydrate leaf content. The present research demonstrates the relationship between seasonal variations of PPF on photosynthetic parameters (P_N , P_{max} , and $Chl-a$ fluorescence) and leaf carbohydrate concentration.

From November to January, photosynthetic activity was lim-

Fig. 1. Hourly variations of total PPF (closed squares) received by tomato plants. Values are the sum of natural PPF (open squares) plus artificial PPF provided by HPS lamps ($100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), from November to April. Nonshaded areas represent the total photoperiods. The dashed horizontal line represents the $320 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ level at which lamps were automatically turned off.

Fig. 2. Diurnal variations of P_N of the fifth (closed squares) and the tenth (open squares) leaves of tomato plants from November to May. Measurements were taken four times a day at 4-h intervals, starting 1 h after the beginning of the photoperiod. Data are the mean values of 10 independent measurements $\pm$ SE. In some cases the standard error bar is obscured by the symbol.

ited by the low natural *PPF* received by plants (Figs. 2 and 3). In winter, artificial lighting contributed significantly to the total *PPF* received by the canopy (Fig. 1), so photosynthetic activity was constant during the day since artificial *PPF* irradiance was unchanged. Under northern latitudes, use of supplemental lighting in winter is beneficial for greenhouse tomato plants as shown previously (Demers et al., 1998; Dorais et al., 1993; Vezina et al., 1991). In our present study, the contribution of supplemental lighting to the total *PPF* received by plants was higher in winter (62% in average) than in spring (15% in average). Although supplemental lighting was used, photosynthetic activity of tomato plants remained low suggesting a source limitation during winter when plants were subject to low *PPF*. Sage (1990) suggested that at subsaturating irradiance, as prevailed during winter in the present study, when electron transport limits photosynthesis, the activity of Rubisco is down-regulated to balance the limiting rate of RuBP regeneration.

In February, as natural *PPF* increased, the contribution of

supplemental lighting decreased and tomato plants exhibited a higher P_N and P_{max} compared to November to January. In contrast, from March to May, both P_N and P_{max} decreased although *PPF* increased. Under high irradiance and CO_2 -enriched conditions, our photosynthetic data showed a decline from March until May. This is consistent with acclimation of photosynthesis observed frequently under CO_2 -enriched atmosphere, where an initial stimulation of photosynthesis is followed by a decrease (Bowes, 1991) that usually involves a decline of Rubisco activity (Stitt, 1991; van Oosten and Besford, 1995; Yelle et al., 1989b).

Our data showed that the tenth tomato leaves had always lower P_N and P_{max} versus the fifth leaves. Morphologically, the fifth leaf represents 45% to 60% of its final area (data not presented). On tomato plants the light-saturated rate of photosynthesis reached a maximum at 60% leaf expansion for plants in all growth conditions (from CO_2 levels of 350 to 1400 $\mu mol \cdot mol^{-1}$) and then declined to half or less of the maximum value when the leaf was mature (van Oosten and Besford, 1995).

Fig. 3. Diurnal variations of P_{max} of the fifth (closed squares) and the tenth (open squares) leaves of tomato plants from November to May. Measurements were taken four times a day at 4-h intervals, starting 1 h after the beginning of the photoperiod. Data are the mean values of 10 independent measurements $\pm$ SE. In some cases the standard error bar is obscured by the symbol.

Fig. 4. Daily variations of F_v/F_m of the fifth (closed squares) and the tenth (open squares) leaves of tomato plants from November to May. Measurements were taken six times a day at 4-h intervals, starting 1 h after the beginning of the photoperiod. Data are the mean values of 10 independent measurements $\pm$ SE. In some cases the standard error bar is obscured by the symbol.

Under winter conditions, the F_v/F_m ratios of the fifth and the tenth leaves were constant and similar during the photoperiod (Fig. 4). F_v/F_m ratio is closely related to maximum PSII quantum yield (Butler, 1977) and correlated to the maximum photosynthesis quantum yield (Demmig and Björkman, 1987). The F_v/F_m ratio constitutes a diagnostic probe for photoinhibition (Demmig and Björkman, 1987). Quenching, resulting from photoinhibition, is often expressed as a decrease in the ratio F_v/F_m recorded when a dark period of 15 to 20 min follows a high light exposure (Krause and Weis, 1991). In winter, F_v/F_m showed a constant pattern suggesting that no photoinhibition of photosynthesis occurred during winter.

The increase of *PPF* in spring was accompanied by changes in *Chl-a* fluorescence parameters. The F_v/F_m ratio decreased and reached lower midday values than those observed in winter. In spring, the F_v/F_m response to seasonal changes of *PPF* suggests that tomato leaves were subject to photoinhibition (Powles, 1984). However, this photoinhibition was reversible as F_v/F_m

recovered at the end of the day possibly representing a protective strategy from excessive light (Gilmore, 1997), so reducing the probability of permanent photooxidative damage. This protection strategy and adaptation towards high irradiance developed progressively throughout the season. In April and May, F_v/F_m was higher than that observed in March, although *PPF* was higher in April and May than in March.

Our P_N and P_{max} data showed a decrease in photosynthetic capacity of leaves in spring (Figs. 2 and 3) resulting in part from photoinhibition. Recently, photoinhibition and reduced photosynthetic efficiency were measured on cork oak (*Quercus suber* L.) (García-Plazaola et al., 1997), sugarcane [*Miscanthus floridulus* (Labill.) Warb.] (Kao et al., 1998), and tomato (*Lycopersicon hirsutum* Dunal) (Jung et al., 1998). In the present study, we noted that the tenth leaves were less affected by photoinhibition than fifth leaves, as the tenth leaves had higher F_v/F_m . Baker and Bowyer (1994) reported that under high *PPF*, the upper but not the lower leaves in the canopy became photoinhibited.

Fig. 5. Daily variations of sucrose concentration on the fifth (closed squares) and the tenth (open squares) leaves of tomato plants from November to May. Samples were taken six times a day at 4-h intervals, starting 1 h after the beginning of the photoperiod. Data are the mean values of 10 independent measurements $\pm$ SE. In some cases the standard error bar is obscured by the symbol.

Fig. 6. Daily variations of hexose concentration on the fifth (closed squares) and the tenth (open squares) leaves of tomato plants from November to May. Samples were taken six times a day at 4-h intervals, starting 1 h after the beginning of the photoperiod. Data are the mean values of 10 independent measurements $\pm$ SE. In some cases the standard error bar is obscured by the symbol.

During winter months, when tomato plants were under low *PPF* and CO_2 enriched atmosphere, we observed low and constant daily concentrations of sucrose (Fig. 5), hexoses (Fig. 6), and starch (Fig. 7). Sage (1990) reported that sucrose synthesis was regulated downward following reductions in irradiance due in part to changes in the level of fructose-2,6-bisphosphate and in some cases by modulation of the activity of sucrose phosphate synthase. In spring, our results showed an increase in daily sucrose and starch contents and an increase up to 4 fold of hexose concentrations in spite of its constant pattern at the same period where we observed a decrease in photosynthetic activity (Figs. 2 and 3). Under high irradiance and high CO_2 concentrations, as prevailed in our experiment during spring, the decline of photosynthetic efficiency of plants was caused by an accumulation of starch (Bowes, 1991; Galtier et al., 1995; Stitt, 1991; Yelle et al., 1989a). Over the long term, growth under CO_2 enrichment leads to a change in the sink-source balance of the plant. Van Oosten

and Besford (1994) suggested that accumulation of carbohydrate occurred progressively as a result of an insufficient sink strength. Thus, this suggests that in spring a sink limitation results from high levels of CO_2 and light. So, carbohydrate accumulates in the source leaves as the rate of photosynthesis exceeds the capacity of the sinks to utilize the photosynthate for growth (Stitt, 1991). A limitation of the transport capacity of photoassimilates from sources to sinks can further increase accumulation of carbohydrate in leaves and then can be at the origin of changes in gene expression enzyme activity and protein content leading consequently to a negative feedback on the assimilation rate (Krapp et al., 1993).

At high CO_2 and saturating light, photosynthesis is limited by the rate of regeneration of the substrate of carboxylation, RuBP. The latter is determined by the rate of electron transport that provides the NADP and ATP to drive the Calvin cycle. ATP synthesis in turn, may be restricted by the availability of P_i (Galtier et al., 1995). When light and CO_2 are not limiting, photosynthesis rate is determined by the capacity of sucrose synthesis to generate P_i (Stitt, 1991). The decrease of P_i concentration in cytoplasm and stroma induces a reduction of triose-phosphates output from the chloroplast, leading consequently to starch accumulation (Dorais et al., 1996; Faria et al., 1996; Sawada et al., 1989; Yelle et al., 1989a). This would suggest that decline of photosynthesis of tomato plants during spring was caused by carbohydrate accumulation that could induce changes in gene expression of Rubisco and its activity, leading consequently to the down-regulation of photosynthesis.

In conclusion, during winter, low photosynthetic rates were observed suggesting source limitation of tomato plants under low *PPF* and high CO_2 concentrations. High F_v/F_m ratio values indicated that during winter tomato plants were not subject to photoinhibition. Corresponding to low photosynthetic rates, low carbohydrate contents were found both in the fifth and the tenth leaves. In contrast to November, December, and January, we measured an increase in photosynthetic activity during February followed by a decline in March, April, and May. In spring, we measured daily accumulation of sucrose and starch and high constant level of hexoses as a long-term response to high *PPF* levels and high CO_2 enriched atmosphere. This accumulation of carbohydrate was suggested to be caused by sink strength limitation (van Oosten and Besford, 1994). So, we conclude that under greenhouse conditions in northern latitudes, photosynthetic down-regulation in situ caused by an accumulation of carbohydrate in leaves occurred in spring but not in winter.

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