CO₂-enhanced Foliar Deformation of Tomato: Relationship to Foliar Starch Concentration

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Abstract. Two cultivars of greenhouse tomato (*Lycopersicon esculentum* Mill.) were grown with ambient or 1000 µl CO₂/liter during Jan.-June 1987 and 1988. In both years, CO₂-enrichment increased foliar deformation and foliar starch, but during the season, foliar starch levels decreased while deformation increased. 'Laura' had more deformation, while 'Michigan-Ohio' had higher foliar starch concentration. During an entire season, there was no significant relationship between foliar starch concentration and deformation severity. Foliar C exchange rates in the lower canopy were not affected by severity of deformation. Data from these experiments do not support the hypothesis that excess foliar starch is responsible for foliar deformation at elevated CO₂.

Foliar deformation responses to elevated CO₂ have been observed in various crops (DeLucia et al., 1985; Ito, 1978; Van Berkel and Van Uffeln, 1975). Mortensen (1987) reviewed many observations of injuries to cultivated plants associated with CO₂ enrichment. Van Berkel (1981) investigated chlorosis and foliar "die-off" in *Gerbera* under elevated CO₂ (600-4500 µl-liter⁻¹) and found a direct correlation between CO₂ concentration and these responses. Nagoaka et al. (1974) reported that tomato leaves became thickened, twisted, and purple at 1000 to 1500 µl CO₂/liter, especially under high light intensity. Madsen (1974) reported deformed tomato leaves at elevated CO₂ (650-3200 µl-liter⁻¹) and noted that the intensity of deformity increased with increasing CO₂ concentration.

In greenhouse tomato in the southeastern United States, foliar deformation in response to high CO₂ appears as a combination of discolorations, reminiscent of K, Mn, and Mg deficiencies (Sprague, 1964), and tight inrolling and malformation of the leaf lamina (Fig. 1). Deformation generally begins in the lower canopy and progresses to the upper canopy during the season.

Foliar deformation has generally been attributed to high foliar starch concentrations (Bradley and Janes, 1985; Woltz, 1968). Madsen (1974) attributed tomato foliar deformation with CO₂ enrichment to excess foliar starch. He observed higher starch accumulation in leaves of CO₂-enriched plants in one 24-h period (Madsen, 1968). He also found much larger starch granules and chloroplast damage in the form of compressed grana in CO₂-enriched tomato plants (Madsen, 1971). Madsen (1974) concluded that high starch concentrations had caused the chloroplast breakdown. Madsen, however, did not make a seasonal comparison of foliar starch concentration with foliar deformation. A detailed hypothesis for the mechanisms by which chloroplast damage results in foliar growth deformation has not been advanced.

If chloroplast breakdown resulted in leaf deformation, foliar deformation might have been associated with reduced net photosynthesis. If excess foliar starch causes foliar deformation, any treatments that affect foliar starch concentration should also affect foliar deformation. Carbon dioxide enrichment, sink strength manipulations, cultivar differences, and increased night temperatures might all affect foliar starch concentrations and, therefore, foliar deformation.

This report examines seasonal foliar starch concentrations, carbon exchange rates, and foliar deformation in two cultivars of greenhouse tomato grown at elevated or ambient CO₂ concentrations, with or without sink reduction treatments or increased night temperature.

Materials and Methods

I. Cultural. 'Michigan-Ohio' and 'Laura' greenhouse tomatoes were seeded and grown to transplant size in a glasshouse using standard water and fertilization practices. Seedlings were transplanted into 18.9- or 9.4-liter black polyethylene growbags (Hydro-Gardens, Colorado Springs, Colo.) filled with 50% Pro-Mix BX (Premier Brands, New Rochelle, N.Y.) and 50% aged, 95-mm mesh pine bark (v/v). Experiments were conducted in either two large (1987) or four small (1988) polyethylene-covered greenhouses in Raleigh, N.C. One large house in 1987 and two small houses in 1988 were enriched to 1000 µl CO₂/liter. The remaining houses were at ambient CO₂. Rockbed storages (Willits and Peet, 1981) in the enriched houses allowed CO₂ enrichment to extend into the warm season. Average hours of CO₂ enrichment per day were 7.34 in 1987 and 8.54 in 1988. Details of greenhouse construction, CO₂ enrichment, rockbed storage systems, and environmental controls were reported by Willits and Peet (1989).

In 1987, day and night heating began at 21 and 16C, respectively. Cooling began at 25, 27, and 28C for low-vent, high-vent, and evaporative cooling pad, respectively. In 1988, greenhouse temperatures were the same until the increased night temperature treatments were initiated at a plant age of 10 weeks. At that point, all temperatures remained the same, except the night heat temperature, which was increased in one of the two enriched and one of the two nonenriched houses. In those two houses, night heating was increased so it would begin at 21 instead of 16C.

Plants were grown for 20 (1987) or 18 weeks (1988) under the treatments. The growing apex of all plants was removed

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Abbreviation: CER, carbon exchange rate.

Fig. 1. Foliar deformation of leaf from a tomato plant grown in a greenhouse at $1000 \mu\text{l CO}_2/\text{liter}$. Leaf is from the lower third of the canopy.

after the sixth flower cluster had set at least one fruit. All axillary leaf growth was removed weekly.

Using drip irrigation, a modified Hoagland's solution (Hoagland and Arnon, 1950) was injected three times daily for a total of 1.5 liters, but waterings were increased or decreased depending on crop evapotranspiration. Fertilizer was delivered at each watering. Initial concentrations were (in ppm) 90 N, 45P, 195 K, 155 Ca, and 44 Mg. At apex removal, N and Ca were raised to 125 and 185 ppm, respectively. Two weeks before crop removal, N and K were raised to 165 and 310 ppm, respectively. Foliar samples and fertilizer solutions were analyzed for nutrient content every 2 to 3 weeks.

In 1987, after 7 weeks, 144 plants of each cultivar were transplanted into 18.9- or 9.4-liter (reduced bag size) black polyethylene grow bags. On half of the plants, fruit was removed from all clusters, except for the two largest fruit on each cluster when both had diameters of at least 1 cm. The design was a split plot within each greenhouse. Whole plots were factorial combinations of bag size (9.4 and 18.9 liters) and fruit removal treatment (yes vs. no); subplots were the cultivars.

Each of the four treatment $\times$ cultivar combinations was replicated three times within each greenhouse, giving 12 whole plots. Each whole plot had two rows (one row per cultivar) of six plants in each row on 56-cm centers. Each grow bag contained one plant. Data were tested by analysis of variance. A pooled error term was constructed from subplot replications following verification by F tests that error-term pooling was justifiable.

In 1988, after 5 weeks, 128 plants of each cultivar were transplanted into the 18.9-liter grow bags. Thirty-two plants of each cultivar were grown in each of four small, polyethylene-covered greenhouses. The design was a split plot with whole plots of CO_2 (two houses enriched and two at ambient) and subplots of cultivar. There were eight subplots in each house: four replications of each cultivar. Data were tested by analysis of variance.

II. Foliar deformation severity rating. A visual rating of foliar deformation severity was developed to allow comparison of relative foliar deformation with other measured criteria. Severity was rated weekly on a scale of 0 to 3, where 0 = none, 1 = low, 2 = moderate, and 3 = severe. Relative severity was rated on the basis of a visual estimate of the area of foliage affected and the degree of deformation in the affected area. Regression analysis was used to compare deformation severity with foliar starch concentrations and foliar C exchange rates (CER). In 1987, ratings of severity of foliar discoloration and foliar malformation were made on the lower, middle, and upper canopies of all plants independently by two individuals. For each canopy region, correlation analysis was used to compare ratings given by the two individuals and to compare malformation with discoloration ratings. In 1988, ratings of general foliar deformation (reflecting both malformation and discoloration) were made on the lower and upper canopies of all plants. Because deformation increased cumulatively and consistently during the season in both years, only the ratings that were taken concurrently with other data are presented.

III. Carbohydrate sampling. Foliage was sampled throughout the growing season for carbohydrates. Leaf disks were taken from the lower third of the canopy, where deformation severity developed earliest and most severely. One disk was taken from the terminal leaflet of one leaf of each of five (1987) or four (1988) plants within each treatment group. All samples were freeze-dried and stored in a dessicator at 25°C until analysis. In 1987, samples were taken from 9-, 13-, 19-, and 23-week-old plants. Time of sampling was 0900 and 1600 HR. Leaf disks from one group were collected into a glass vial, held no more than 0.5 h on ice, and then frozen at -20°C . Samples were randomly chosen from two of the three replicates, resulting in 64 samples per sampling date. Results of one sampling for each treatment group are therefore the means of four samples (two replicates in the morning and two in the late afternoon), each made up of five leaf disks per sample. In 1988, foliar samples were taken at 12, 17, and 23 weeks. Samples were taken at 0600, 1200, and 1800 HR. The four leaf disks from each group were collected into snap-cap glass vials on dry ice. This procedure resulted in two vials of four disks each for each cultivar (one from each CO_2 treatment replication, i.e., one per whole-plot replication) at each sampling time for a total of 72 samples.

IV. Starch. Leaf disks from each sample were ground in 3 ml of 80% ethanol using a Brinkman Polytron homogenizer (Brinkman Instruments, Westbury, N.Y.). Samples were then prepared and analyzed for starch content as reported by Robbins and Pharr (1987).

V. Soluble sugars. Ethanolic extracts from sample preparation

for starch analysis were prepared for soluble sugar analysis as reported by Robbins and Pharr (1987). Aliquots were then analyzed for sucrose, fructose, and glucose by the method of Jones et al. (1977).

VI. *Net photosynthesis (CER)*. CERs were measured using an LCA-2 portable leaf chamber analyzer system (Model A120; Analytical Development Corp., Andover, Mass.). All readings were taken between 0900 and 1500 HR using natural light in the greenhouses during clear, full-sun conditions. Light levels ranged from 700 to 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Measurements were made at the CO_2 levels at which plants were grown. Readings were taken on unshaded terminal leaflets of leaves in the lower third of the canopy on the same date and on the same leaves that were sampled for starch. CERS are presented as milligrams of CO_2 per square decimeter per hour.

In 1987, CERS were measured on 9-, 13-, 19-, and 23-week-old plants. Readings from weeks 9 and 13 were taken before pruning treatments began and on one leaf from each of 10 plants in each treatment group. Readings from weeks 19 and 23 were taken after pruning treatments began on one leaf from six plants in each treatment group.

In 1988, CERS were measured at 8, 13, and 18 weeks on eight plants from each cultivar in each of the four greenhouses.

Results

I. *Foliar deformation*. Deformation ratings from the two individuals in 1987 were highly and significantly correlated for the middle and lower canopy, but not the upper canopy (Table 1). Ratings of malformation and discoloration were also significantly correlated in the lower and middle canopy, but not in the upper canopy. Both malformation and discoloration appeared earliest and became most severe in the lower canopy.

Table 1. Relationships between foliar deformation ratings by two persons (Rater 1 and Rater 2), between ratings of foliar malformation and foliar discoloration, and between deformation in the lower, middle, and upper canopy regions of two cultivars of greenhouse tomato grown at ambient (≈ 350) or 1000 $\mu\text{l CO}_2/\text{liter}$ in 1987. Correlation coefficients (r values) and their significance (P values) are shown for each relationship.

Comparison	Rating type	Canopy region	r^2	P
Rater 1 vs. Rater 2	Malformation	Lower	0.90	0.0001
		Middle	0.94	0.0500
		Upper	0.00	1.0000
Rater 1 vs. Rater 2	Discoloration	Lower	0.90	0.0001
		Middle	0.90	0.0001
		Upper	0.67	0.0050
Lower vs. middle canopy ^y	Malformation	---	0.84	0.0001
Lower vs. middle canopy ^y	Discoloration	---	0.96	0.0001
Middle vs. upper canopy ^y	Malformation	---	0.12	0.6500
Middle vs. upper canopy ^y	Discoloration	---	0.93	0.0001
Malformation vs. discoloration	---	Lower	0.93	0.0001
	---	Middle	0.93	0.0001
	---	Upper	0.15	0.5800

^yn = 16.

^yResults all from one rater.

However, discoloration appeared earlier and became more severe than malformation. Ratings in the upper canopy were not well correlated because deformation was minimal. Owing to the high correlation between malformation and discoloration in 1987, a general deformation rating was made in 1988 that integrated these effects. Deformation in 1988 again appeared earliest and became most severe in the lower canopy. Because ratings were most highly correlated with each other in the lower canopy, only those data are presented.

II. *Foliar deformation and foliar carbohydrates*. Carbon dioxide enrichment dramatically increased deformation in both years, although some foliar deformation occurred in all plants (Figs. 2A and 3A). Carbon dioxide enrichment also increased foliar starch concentrations in both years. However, foliar deformation increased during the season, while foliar starch concentrations decreased early and then mostly remained unchanged or increased on an area basis (Figs. 2B and 3B). Seasonal starch concentrations followed similar trends on a dry-weight basis (data not shown). Regression analysis using linear and quadratic models showed no significant relationship between foliar starch concentration and deformation severity ($r^2 = 0.06$) (data not shown). There were no treatment effects on foliar soluble sugar concentrations. There was no apparent relationship between foliar soluble sugar concentration and foliar deformation (data not shown).

III. *Foliar deformation and cultivar*. Carbon dioxide enrich-

Fig. 2. Foliar deformation (A) and starch concentration (mg glucose/ dm^2 leaf area) (B) of two greenhouse tomato cultivars grown at ambient (≈ 350) or 1000 $\mu\text{l CO}_2/\text{liter}$ in 1987 (M = 'Michigan-Ohio', L = 'Laura'). For each deformation rating, n = 36 plants; for each starch concentration, n = 4 samples.

Fig. 3. Foliar deformation (A) and starch concentration (mg glucose/dm² leaf area) (B) of two greenhouse tomato cultivars grown at ambient (≈ 350) and 1000 $\mu\text{l CO}_2/\text{liter}$ in 1988 (M = 'Michigan-Ohio', L = 'Laura'). For each deformation rating, $n = 64$ plants; for each starch concentration, $n = 6$ samples.

ment increased deformation severity differentially between cultivars in both years (Figs. 2A and 3A). At ambient CO_2 concentration, there was only a very small difference in deformation severity or foliar starch concentration between cultivars. With CO_2 enrichment, cultivar differences were magnified. 'Laura' showed more severe deformation than 'Michigan-Ohio' with CO_2 enrichment. Late in the season in both years, 'Michigan-Ohio' contained more foliar starch than 'Laura'. After week 13, 'Laura' showed more deformation than 'Michigan-Ohio' (Figs. 2B and 3B). In both years as the season progressed, 'Laura' developed the most severe deformation, while 'Michigan-Ohio' developed the highest foliar starch concentration.

IV. *Foliar deformation and sink manipulation.* Sink reduction treatments (fruit removal and smaller bag size in 1987) did not affect foliar deformation at any time during the season. Fruit removal had no effect on foliar starch. Plants grown in small bags had higher foliar starch concentrations at 9 weeks (Table 2), but not thereafter. Increased night temperature had no effect on foliar deformation or foliar starch concentration (data not shown).

V. *Foliar deformation and CER.* CERs in lower leaves were generally low, except for those sampled at 9 weeks in 1987. Carbon dioxide enrichment increased CERs only slightly (Table 3). Increases and decreases in CERs were not always associated with similar changes in deformation severity. Regression analysis using linear and quadratic models showed no significant relationship between CERs and deformation severity ($r^2 = 0.13$) (data not shown).

Table 2. Foliar starch concentrations for two cultivars of greenhouse tomato grown at ambient (≈ 350) or 1000 $\mu\text{l CO}_2/\text{liter}$ in 18.9- or 9.4-liter grow bags for 9-week-old plants. Deformation was rated 0 for all plants.

CO ₂ (μl·liter ⁻¹)	Cultivar	Bag size (liters)	Starch (mg glucose/ dm ² leaf)
1000	Michigan-Ohio	18.9	94
		9.4	132
	Laura	18.9	110
		9.4	133
350	Michigan-Ohio	18.9	90
		9.4	120
	Laura	18.9	96
		9.4	130
LSD (<i>P</i> = 0.05)			27.5

Discussion

Collectively, data from these experiments do not support the hypothesis that excess foliar starch is responsible for foliar deformation in tomato. If high foliar starch concentrations caused foliar deformation in tomato, one might expect a strong correlation between foliar starch concentrations and foliar deformation. Our repeated samplings of the lower canopy during an entire growing season in 1987 and 1988 showed that CO_2 enrichment increased foliar deformation and foliar starch. However, opposing trends in starch and deformation were found. Seasonal increases in CO_2 -enhanced deformation of greenhouse tomato were found, while seasonal decreases in leaf starch concentration were observed in the same leaves (Figs. 2 and 3). This seasonal decrease in foliar starch concentration of leaves from the lower third of the canopy contrasts with a seasonal increase of foliar starch in the upper canopy observed by Yelle et al. (1989). This difference emphasizes the importance of sampling position, especially during long-term studies. Within a particular canopy region, however, there appears to be no relationship between foliar starch concentration and foliar deformation over the entire growing season.

These data do not preclude the possibility that foliar starch reached a threshold concentration that triggered the foliar deformation response. Once triggered, foliar deformation might continue regardless of foliar starch concentration fluctuations throughout the season. In that case, treatments increasing foliar starch would be expected to increase deformation. Reduced bag size in 1987 elevated foliar starch early in the season but did not increase deformation. These results do not support the hypothesis that foliar starch reached a threshold concentration that triggered a continuing foliar deformation response.

Sasek et al. (1985) found that long-term CO_2 enrichment was associated with increased foliar starch, inhibition of photosynthesis, and deformation of leaves in cotton. They hypothesized that the "feedback inhibition" of photosynthesis associated with CO_2 enrichment was probably due to elevated foliar starch because, when plants were returned to ambient CO_2 concentrations, photosynthetic recovery was associated with a reduction in foliar starch. In tomato, however, there was no apparent relationship between seasonally repeated measures of CER and foliar deformation. All CERs measured were low, but there was no seasonal reduction in CER associated with increased foliar starch or increased deformation in either year.

Sink reduction was not associated with increased deformation. There was no effect of fruit removal on foliar deformation or foliar starch. Reduced grow-bag size in 1987 significantly

Table 3. CER, foliar starch concentrations, and foliar deformation ratings throughout the season for two cultivars of greenhouse tomato grown at ambient (≈ 350) and 1000 $\mu\text{l CO}_2/\text{liter}$ in 1987 and 1988.

Plant age (weeks)	CO ₂ (μl·liter ⁻¹)	Cultivar ^z	CER (mg CO ₂ / dm ² per hour)	Starch (mg glucose/ dm ² leaf)	Deformation ^y
1987					
9	1000	M	7.7	113.0	0.0
		L	19.6	121.8	0.0
	350	M	20.6	105.3	0.0
		L	17.9	112.9	0.0
13	1000	M	8.7	51.7	1.8
		L	6.1	40.3	2.3
	350	M	8.7	15.8	1.0
		L	5.7	21.8	1.0
19	1000	M	8.9	100.9	2.0
		L	7.7	53.1	2.3
	350	M	2.8	14.5	1.0
		L	10.1	15.0	1.0
23	1000	M	1.6	72.1	2.0
		L	-0.4	37.1	2.4
	350	M	2.3	34.0	1.0
		L	1.0	22.8	1.2
LSD (<i>P</i> = 0.05)			4.3	21.0	0.1
1988					
9	1000	M	0.9	133.8	0.4
		L	4.7	162.3	0.5
	350	M	0.5	55.7	0.2
		L	-2.0	57.8	0.1
17	1000	M	6.1	71.9	1.2
		L	6.9	80.0	1.6
	350	M	0.5	10.7	0.8
		L	0.0	13.5	0.8
23	1000	M	4.4	129.2	2.0
		L	-1.6	90.7	2.7
	350	M	-0.0	31.8	1.7
		L	-0.2	17.5	1.7
LSD (<i>P</i> = 0.05)			4.3	38.3	0.1

^zM = 'Michigan-Ohio'; L = 'Laura'.

^y0 = None; 3 = severe.

elevated foliar starch early in the season but had no effect on foliar deformation at any time. These results, too, do not support the hypothesis that high starch causes foliar deformation.

While CO₂ enrichment increased both foliar deformation and foliar starch concentrations, there was no correlative relationship between them. Therefore, a causal relationship between excess foliar starch and foliar deformation in greenhouse tomato at elevated CO₂ is unlikely. Carbon dioxide enrichment probably increases both foliar starch and foliar deformation through separate mechanisms. Because deformation symptoms resemble certain nutrient deficiencies, future research could investigate relationships between plant nutrition and foliar deformation at elevated CO₂ concentrations.

Literature Cited

- Bradley, F.M. and H.W. Janes. 1985. Carbon partitioning in tomato leaves exposed to continuous light. *Acta Hort.* 174:293-302.
- Delucia, E. H., T.W. Sasek, and B.R. Strain. 1985. Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric CO₂. *Photosynthesis Res.* 7:175-184.
- Hoagland, D.R. and D.I. Amen. 1950. The water-culture method for growing plants without soil. *California Agr. Expt. Sta., Univ. of California, Berkeley, Circ.* 347.
- Ito, T. 1978. Physiological aspects of CO₂-enrichment to cucumber plants grown in greenhouses. *Acta Hort.* 87:139-146.
- Jones, M. G. K., W.H. Outlaw, Jr., and O.H. Lowry. 1977. Enzymic assay of 10⁻¹ to 10⁻³ moles of sucrose in plant tissues. *Plant Physiol.* 60:379-383.
- Madsen, E. 1968. Effect of CO₂ concentration on the accumulation of starch and sugar in tomato leaves. *Physiol. Plant.* 21:168-175.
- Madsen, E. 1971. Cytological changes due to the effect of CO₂-concentration on the accumulation of starch in chloroplasts of tomato leaves. *Royal Veterinary and Agricultural Univ., Copenhagen, Denmark, Yearbook 1971:191-194.*
- Madsen, E. 1974. Effect of CO₂-concentration on growth and fruit production of tomato plants. *Acta. Agr. Scandinavia* 24:242-246.
- Mortensen, L.M. 1987. Review: CO₂ enrichment in greenhouses. *Crop responses. Scientia Hort.* 33:1-25.
- Nagoaka, M., K. Takahashi, K. Arai, T. Hanada, and H. Yoshioka. 1974. Effects of light intensity, night temperature and CO₂ concentration on the growth and yield of glasshouse tomato. *Bul. Veg. Ornamental Crops Res. Sta. A, Ishinden-Ogoso.* 6:105.
- Robbins, N.S. and D.M. Pharr. 1987. Regulation of photosynthetic carbon metabolism in cucumber by light intensity and photosynthetic period. *Plant Physiol.* 85:592-597.
- Sasek, T.W., E.H. DeLucia, and B.R. Strain. 1985. Reversibility of photosynthetic inhibition in cotton after long term exposure to elevated CO₂ concentrations. *Plant Physiol.* 78:619-622.
- Sprague, H.B. 1964. *Hunger signs in crops.* 3rd ed. David McKay, New York.
- Van Berkel, N. 1981. Three physiological disorders in glasshouse cultivation. *Acta Hort.* 119:77-90.
- Van Berkel, N. and J. Van Uffeln. 1975. CO₂ nutrition of spring cucumbers in the Netherlands. *Acta Hort.* 51:213-224.
- Willits, D.H. and M.M. Peet. 1981. CO₂ enrichment in a solar energy collection/storage greenhouse. *Paper 81-4525, Amer. Soc. Agr. Eng.* 15-18 Dec. 1981.
- Willits, D.H. and M.M. Peet. 1989. Predicting yield responses to different greenhouse CO₂ enrichment schemes: Cucumbers and tomatoes. *Agr. For. Meteorol.* 44:275-293.
- Woltz, S.S. 1968. Influence of light intensity and photosynthate export from leaves on physiological leaf roll of tomatoes. *Proc. Fla. State Hort. Soc.* 81:208-211.
- Yelle, S., R.C. Beeson, Jr., M.J. Trudel, and A. Gosselin. 1989. Acclimation of two tomato species to high atmospheric CO₂. I. Sugar and starch concentrations. *Plant Physiol.* 90:1465-1472.