Plant Physiol. (1986) 80, 63–67
0032-0889/86/80/0063/05/$01.00/0

# Acclimation to High $CO_2$ in Monoecious Cucumbers[1]

## II. CARBON EXCHANGE RATES, ENZYME ACTIVITIES, AND STARCH AND NUTRIENT CONCENTRATIONS

Received for publication June 17, 1985 and in revised form July 30, 1985

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### ABSTRACT

**Carbon exchange capacity of cucumber (*Cucumis sativus* L.) germinated and grown in controlled environment chambers at 1000 microliters per liter $CO_2$ decreased from the vegetative growth stage to the fruiting stage, during which time capacity of plants grown at 350 microliters per liter increased. Carbon exchange rates (CERs) measured under growth conditions during the fruiting period were, in fact, lower in plants grown at 1000 microliters per liter $CO_2$ than those grown at 350. Progressive decreases in CERs in 1000 microliters per liter plants were associated with decreasing stomatal conductances and activities of ribulose bisphosphate carboxylase and carbonic anhydrase. Leaf starch concentrations were higher in 1000 microliters per liter $CO_2$ grown-plants than in 350 microliters per liter grown plants but calcium and nitrogen concentrations were lower, the greatest difference occurring at flowering. Sucrose synthase and sucrose-P-synthase activities were similar in 1000 microliters per liter compared to 350 microliters per liter plants during vegetative growth and flowering but higher in 350 microliters per liter plants at fruiting. The decreased carbon exchange rates observed in this cultivar at 1000 microliters per liter $CO_2$ could explain the lack of any yield increase (MM Peet 1986 Plant Physiol 80: 59–62) when compared with plants grown at 350 microliters per liter.**

Growth rates and yield of most plants including gynoecious, seedless cucumbers (*Cucumis sativus* L.) grown commercially in greenhouses, increase with an increase in $CO_2$ concentration (see summary in Kimball [15]). There have been no previous studies, however, on $CO_2$ enrichment effects on field-type monoecious, seeded cucumbers. These cucumbers differ from greenhouse cucumbers in that only one or two fruit generally develop at a time, apparently because the first-pollinated fruit prevents subsequent fruit from developing. This inhibition was reported as early as 1928 (31), and was described in 1934 (19), and subsequently but has still not been explained (see citations in Uzcategui and Baker [32]). Pharr *et al.* (24) suggested that carbohydrate production limits fruit development in the seeded outdoor cultivar Calypso, as they estimated 40% of the canopy would be required to support growth of one fruit.

In a recent study (22) on the monoecious seeded cultivar, Chipper, however, $CO_2$ enrichment (1000 $\mu$l $L^{-1}$) did not increase dry weight beyond the first 16 d after planting compared to control plants grown at 350 $\mu$l $L^{-1}$ $CO_2$ and final fruit weight and number did not differ. Similar results were seen in a preliminary study with the same cultivar grown at 675 and 350 $\mu$l $L^{-1}$ $CO_2$. In both studies considerable leaf necrosis appeared in the high-$CO_2$-grown plants.

We report here on the effects of high $CO_2$ concentration during growth of a field-type monoecious cucumber on gas exchange, starch, and nutrient concentrations and the activities of several enzymes possibly rate-limiting to carbon fixation and partitioning (SPS,[2] SS, RuBPCase, and CA).

## MATERIALS AND METHODS

Seeds of cucumbers (*Cucumis sativus* cv Chipper) were germinated and grown in the controlled environment chambers of the Southeastern Plant Environmental Laboratory at Duke University. From the time of planting, a 12 h, 26/20°C thermoperiod, 65 to 70% RH, and 500 $\mu$E $m^{-2}$ $s^{-1}$ irradiance at pot level were maintained. $CO_2$ concentration was 350 or 1000 $\mu$l $L^{-1}$ $CO_2$. Plant density was 97 $m^{-2}$ before transplanting (15 d) and 10.8 $m^{-2}$ thereafter. Growth media was a 1:1:1 (v:v:v) mixture of gravel, vermiculite, and calcined clay, which is a heated, pulverized soil conditioner prepared by International Minerals Corporation.

Pots were watered to the drip point once daily with half strength Hoagland solution until 33 d after seeding at which time plants were sprayed with iron chelate because of their light green leaf color. After d 33, watering was increased to 3 times daily.

Thirty five, 42, and 58 d after seeding gas exchange was measured using a small, hand-held cuvette enclosing both upper and lower leaf surfaces Patterson *et al.* [21] for cuvette description) and a Beckman 865 IR gas analyzer. All measurements were made inside the growth chambers, selecting the uppermost fully expanded leaf on each of eight plants. Measurements were made during the middle of the photoperiod (1000–1530 h) during which period CER for individual plants did not vary greatly.

Measurement conditions for determining rates of photosynthesis were as close as possible to the growth conditions in the

[1] Paper No. 9930 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601. Supported in part by National Science Foundation grants DEB77-15845 to the Duke University Phytotron, DEB78-23640 to B. Strain, PCM76-20595 to P. J. Kramer and M. M. Peet, and PCM77-11142 to P. J. Kramer.

[2] Abbreviations: SPS, sucrose phosphate synthase; SS, sucrose synthase; RuBPCase, ribulose bisphosphate carboxylase; CA, carbonic anhydrase; CER, carbon exchange rate.

chamber. Although the cuvette was not cooled artificially, high flow rates (1–2 L $min^{-1}$) maintained leaf temperatures in the cuvette within ±0.5 to 1.0°C of ambient. The airstream was hydrated to a dew point equivalent to 62% RH. On d 42 and 58, the airstream consisted of 345 or 977 $\mu l\ L^{-1}$ $CO_2$ and 20% $O_2$ from cylinders. On d 35 bottled gas was not available and outdoor air (335 ± 20 $\mu l\ L^{-1}$ $CO_2$) was substituted. Photosynthesis was measured under chamber light conditions, which differed only slightly between measurement dates and between the two chambers. Measurement irradiances for the plants grown at 1000 $\mu l\ L^{-1}$ $CO_2$ averaged 544 ± 8.33, 525 ± 13, and 514 ± 17 $\mu E\ m^{-2}\ s^{-1}$ for the three harvests, respectively. For the plants grown at 350 $\mu l\ L^{-1}$ $CO_2$, measurement irradiances averaged 560 ± 11, 568 ± 19, and 508 ± 16 $\mu E\ m^{-2}\ s^{-1}$, respectively.

Stomatal conductances were measured with a LI-COR steady state porometer (LI-1600, LI-COR, Lincoln, NE) under the same irradiances as measurements of carbon exchange rates and more or less simultaneously. Total stomatal conductances ($1/r_t$) for the leaves were calculated from resistances of the upper and lower leaf surfaces using the formula:

$$1/r_t = 1/r_u + 1/r_l$$

where $r_t$ is total leaf resistance to diffusion of water vapor, $r_u$ is the resistance of the upper leaf surface only, and $r_l$ is the lower surface resistance only.

Stomatal conductances were used to correct photosynthetic rates for internal $CO_2$ concentration. Internal leaf $CO_2$ concentration ($C_i$) was calculated as:

$$C_i = C_e - 1.6\ \mathrm{CER}/g$$

where $C_e$ is the external $CO_2$ concentration, CER is net $CO_2$ uptake rate, and $g$ is the stomatal conductance to water vapor.

By 0830 h of the morning after completion of gas exchange measurements, the leaves used for gas exchange measurements were detached for analysis of RuBPCase, SPS, SS, and CA activities. Chl and starch contents were also determined. Chl was measured by the procedure of Arnon (2). Extracts for determination of SPS and SS activity were prepared as described in Camp *et al.* (4) and assayed by measurement of sucrose-P (+sucrose) formation from UDP-glucose and fructose-6-P (SPS) or fructose (SS) as described by Huber (12). RuBPCase activity was determined by the method of Perchorowicz *et al.* (23) with modifications as described in Camp *et al.* (5). For the starch assay, leaf samples were homogenized in 80% ethanol and starch was estimated as glucose released by amyloglucosidase treatment of the ethanol-insoluble fraction of leaf samples (13). All data are expressed on a fresh weight basis.

Nutrient concentrations were determined from leaf tissue harvested on d 36, 43, and 60. N was assayed by Kjeldahl digestion, K by flame photometer, P by a colorimetric assay using ascorbic acid and sodium molybdate, and Ca and Mg by atomic absorption spectrometry. Analyses were conducted by the North Carolina Department of Agriculture Plant Analysis Laboratory, which also provided guidelines for acceptable nutrient concentrations.

## RESULTS

**Gas Exchange Rates.** CERs of all plants were measured both at 977 and 345 $\mu l\ L^{-1}$ $CO_2$ except for the initial (vegetative) sampling date when only CER at 345 $\mu l\ L^{-1}$ $CO_2$ was measured. CER of 1000 $\mu l\ L^{-1}$-grown plants measured at a $CO_2$ concentration near growth levels (977 $\mu l\ L^{-1}$) declined from the flowering to the fruiting stage while CER of 350-grown plants measured near growth levels (345 $\mu l\ L^{-1}$) increased 20% from the vegetative to the fruiting stage (Fig. 1). Thus, under growth conditions CERs in the two treatments were similar at flowering but actually

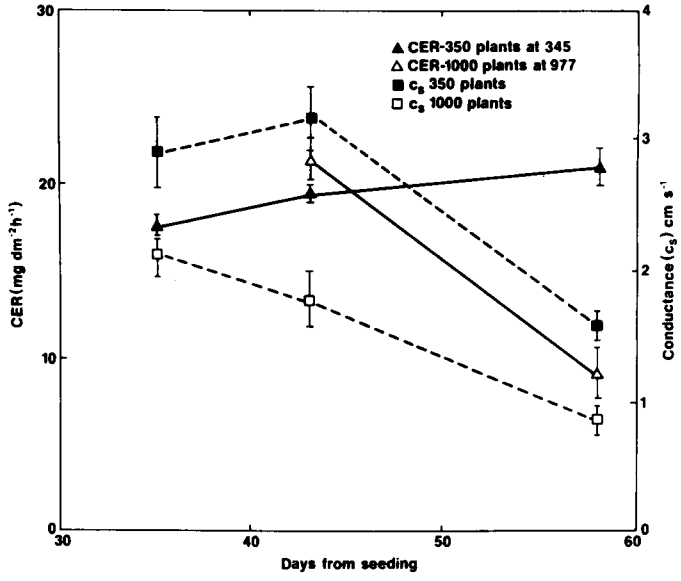


FIG. 1. *In situ* carbon exchange rates (CER, mg $CO_2$ $dm^{-2}$ $h^{-1}$) and stomatal conductances ($C_s$, cm $s^{-1}$) of cucumbers grown at 350 (▲, ■) $\mu l\ L^{-1}$ $CO_2$ or 1000 $\mu l\ L^{-1}$ $CO_2$ (△, □).

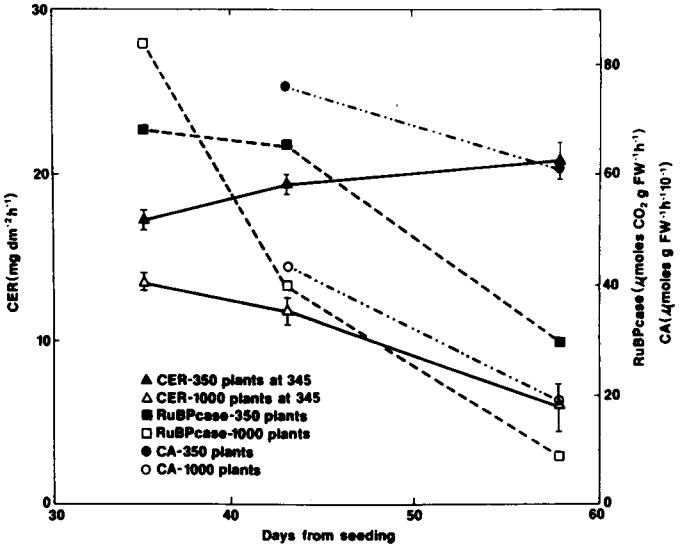


FIG. 2. CER measured at 345 $\mu l\ L^{-1}$ $CO_2$ and activities of RuBPCase ($\mu mol\ CO_2\ g^{-1}$ fresh wt $h^{-1}$) and CA ($\mu mol\ g^{-1}$ fresh wt $h^{-1}$ $10^{-1}$) for plants grown at 350 $\mu l\ L^{-1}$ $CO_2$ (▲, ■, ●) or 1000 $\mu l\ L^{-1}$ $CO_2$ (△, □, ○).

lower in the 1000 $\mu l\ L^{-1}$-grown plants at fruiting. During vegetative growth, CERs under growth conditions were probably higher in 1000 $\mu l\ L^{-1}$-grown than 350 $\mu l\ L^{-1}$-grown plants since CER at 345 $\mu l\ L^{-1}$ $CO_2$ in 1000 $\mu l\ L^{-1}$-grown plants was only slightly (23%) lower than CER at 345 $\mu l\ L^{-1}$ in 350 $\mu l\ L^{-1}$ $CO_2$-grown plants (Fig. 2). Differences in photosynthetic capacity when plants from both treatments were measured at 345 $\mu l\ L^{-1}$ increased with time. By flowering, CERs of 1000 $\mu l\ L^{-1}$-grown plants were 39% and by fruiting they were 56% lower than CERs in 350 $\mu l\ L^{-1}$-grown plants. Similar trends were seen when CERs were compared at 977 $\mu l\ L^{-1}$ (data for 350-grown plants measured at 977 $\mu l\ L^{-1}$ not shown).

On all sampling dates, stomatal conductances (Fig. 1) were lower in 1000 $\mu l\ L^{-1}$-grown plants than in 350 $\mu l\ L^{-1}$ plants. In 1000 $\mu l\ L^{-1}$-grown plants, conductances showed the same pattern of decline from the vegetative to fruiting (third) sampling date as did photosynthetic rates measured at 345 $\mu l\ L^{-1}$ (Fig. 2). In the

350 $\mu$l $L^{-1}$ plants, conductances and CER at 345 both increased slightly from the vegetative to flowering sampling periods. While CER continued to increase in the fruiting period, conductances declined drastically.

Intercellular $CO_2$ levels (Table I) in the 350 $\mu$l $L^{-1}$-grown plants were similar during vegetative growth and flowering, but declined at fruiting because of lower conductances. Intercellular $CO_2$ level ($C_i$) cannot be calculated for the 1000 $\mu$l $L^{-1}$ grown plants for the vegetative period, but $C_i$s were similar at flowering and fruiting. In this case, proportional declines in conductance and photosynthesis resulted in similar intercellular $CO_2$ levels.

**Enzyme Activities.** Carbonic anhydrase (Fig. 2) was measured only at flowering and fruiting. On both dates, activities were much higher in 350 $\mu$l $L^{-1}$-grown plants than in those from the 1000 $\mu$l $L^{-1}$ $CO_2$ treatment. For both treatments, activities declined from flowering to fruiting, but the decline was greater in the 1000 $\mu$l $L^{-1}$ $CO_2$-grown plants than in the 350 $\mu$l $L^{-1}$-grown plants.

RuBPCase activities (Fig. 2) were higher in 1000 compared to 350 $\mu$l $L^{-1}$-grown plants during vegetative growth, but were much lower thereafter. RuBPCase activities, like CER at 345 $\mu$l $L^{-1}$ and conductances, declined in the 1000 $\mu$l $L^{-1}$ plants from vegetative growth to fruiting. In the 350 $\mu$l $L^{-1}$-grown plants, RuBPCase activities were similar during vegetative growth and flowering, but then declined during fruiting.

SPS activity (Fig. 3) was higher in the 1000 $\mu$l $L^{-1}$ plants than in the 350 $\mu$l $L^{-1}$-grown plants during vegetative growth, similar at flowering, and lower during fruiting. In both treatments, SPS activities were higher during vegetative growth than at flowering. In the 1000 $\mu$l $L^{-1}$ treatment, activities then declined slightly at the time of fruiting, while in the 350 $\mu$l $L^{-1}$ treatment they increased again, although not to the level found in the leaves during vegetative growth.

The changes in SS activity (Fig. 3) with time and the differences between the treatments were somewhat similar to those in SPS activities. For both enzymes, activities were higher in 1000 $\mu$l $L^{-1}$-grown plants than the 350 $\mu$l $L^{-1}$ grown plants during vegetative growth and flowering, but the reverse was true at fruiting. For both enzymes, the activities of 350 $\mu$l $L^{-1}$-grown plants were lowest at flowering, while the activities of 1000 $\mu$l $L^{-1}$-grown plants were lowest at fruiting. Patterns of change in the two enzymes differed most conspicuously in the 350 $\mu$l $L^{-1}$-grown plants, where highest SPS activity was found during vegetative growth, while SS activity was highest at fruiting.

**Starch Levels.** Starch levels (Fig. 3) in 1000 $\mu$l $L^{-1}$-grown plants exceeded those in 350 $\mu$l $L^{-1}$ plants on all sampling dates. Changes in starch levels with time differed in the two treatments, however, and were not related in any obvious way to changes in rates of photosynthesis. In the 1000 $\mu$l $L^{-1}$ plants, starch levels peaked at the time of flowering (d 43) and were lowest at fruiting. In the 350 $\mu$l $L^{-1}$-grown plants, tissue starch levels were similar throughout the entire measurement period.

**Leaf Necrosis.** In both a preliminary study (spring 1980) and the study reported here, by d 44 $CO_2$ enriched plants appeared lighter green than controls and had a pronounced yellow margin on most leaves. In enriched treatments, older leaves in particular had a blotchy, light-green appearance with some interveinal necrosis. In both experiments, one or two of the oldest leaves had withered in the enriched treatment, but not in the control treatment. In the second experiment which incorporated higher levels of enrichment (1000 *versus* 675 $\mu$l $L^{-1}$) the tendency for lighter leaves in enriched plants was more pronounced, and plants appeared smaller and more spindly in some cases than 350 $\mu$l $L^{-1}$-grown plants. Chlorosis also appeared earlier, showing up by d 33 in the 1000 $\mu$l $L^{-1}$ plants. In the first experiment, although color was lighter, plant vigor was not noticeably decreased in the 675 $\mu$l $L^{-1}$ plants compared to 350 $\mu$l $L^{-1}$-grown plants.

**Nutrient Concentrations.** Nutrient concentrations (Fig. 4) in all the tissues analyzed were within or slightly above those considered normal (3.5–4.5% N, 0.35–0.65% P, 3.5–5.0% K, 1.5–4.0% Ca, and 0.2–0.4% Mg) by the North Carolina Department of Agriculture. During vegetative growth and flowering, concentrations of all elements, but particularly calcium, were considerably lower in the 1000 $\mu$l $L^{-1}$-grown compared to 350 $\mu$l $L^{-1}$-grown plants. By fruiting, however, they were similar in the two treatments. Starch concentrations above 20 $\mu$g $g^{-1}$ fresh

Table I. *Intercellular $CO_2$ Concentration for Cucumber Plants Grown at 350 and 1000 $\mu$l $L^{-1}$ $CO_2$*

| $CO_2$ Level | Intercellular $CO_2$ concentration ($C_i$) | | |
|---|---|---|---|
| | Vegetative | Flowering | Fruiting |
| | $\mu l\ L^{-1}$ | | |
| 350 | 321 | 325 | 313 |
| ± SE | 1.0 | 1.0 | 2.0 |
| 1000 | | 979 | 982 |
| ± SE | | 2.0 | 4.0 |

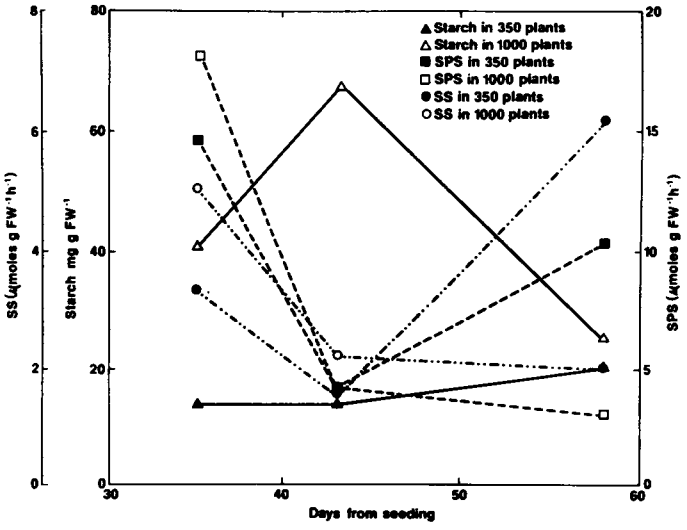


FIG. 3. Starch concentrations (mg $g^{-1}$ fresh wt), SS and SPS activities ($\mu$mol $g^{-1}$ fresh wt $h^{-1}$) in leaves from cucumber plants grown at 350 (▲, ■, ●) and 1000 $\mu$l $L^{-1}$ $CO_2$ (△, □, ○).

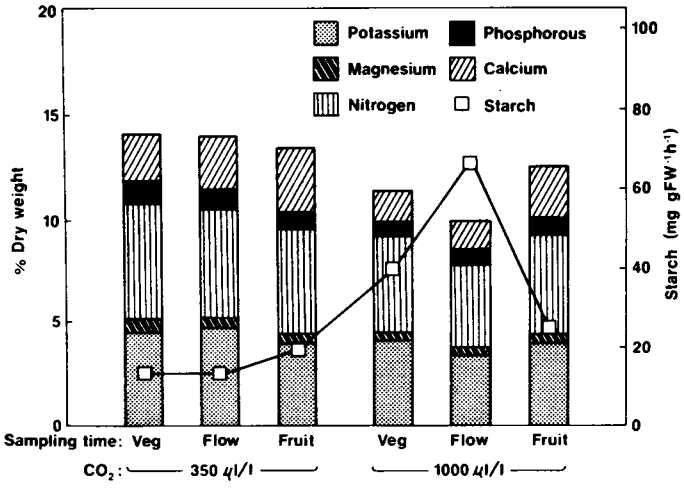


FIG. 4. Nutrient concentrations (% dry weight) and starch concentration in leaves grown at 350 or 1000 $\mu$l $L^{-1}$ $CO_2$ and harvested during vegetative growth, flowering or fruiting.

weight were associated with lower nutrient levels, as seen during vegetative growth and flowering in the enriched plants. The percent change in starch was greater than the percentage change in dry weight, however.

## DISCUSSION

When photosynthetic rates of high and low $CO_2$-grown plants have been measured at the same $CO_2$ concentration, lower rates of enriched plants have been recorded in many crops (34, 36) including cucumbers (1, 8). In most of these studies *in situ* (*ie.* measured at growth $CO_2$ concentration) CERs were still higher in enriched plants, but in beans (*Phaseolus vulgaris* L.) (34), *in situ* CER in high $CO_2$ grown plants was similar to or less than that of 'normal' $CO_2$ grown plants even when measured at high and low $CO_2$ concentrations, respectively, a result similar to that seen in the present study at flowering and fruiting. In soybeans (7) and cucumbers (14), as in the present study, differences between photosynthetic rates under ambient $CO_2$ of high and low $CO_2$ grown plants increased with time.

Photosynthetic reductions with time in $CO_2$ enriched plants in this study were associated with decreased CA and RuBPCase activities (Fig. 2). Lower CA activities in $CO_2$ enriched plants have been reported in bean (25) and cotton (6). Lower RuBPCase activities have been reported in $CO_2$ enriched bean (25), cotton, maize (36), and soybean (35). There are also reports, however, of only slightly lower photosynthetic capacity and similar RuBPCase activities in wheat (9) and of higher RuBPCase and photosynthesis in $CO_2$-enriched tomatoes (10, 11).

Variations in photosynthetic response to high $CO_2$ levels exists not only between species, but between experimental treatments with a single species. Container-grown soybeans showed a much greater photosynthetic response to $CO_2$ level than did field-grown plants (30). In low nitrogen-grown cotton, ambient plants had higher photosynthetic rates at all intercellular $CO_2$ partial pressures, but in high nitrogen-grown plants this occurred only at low partial pressures (36).

A direct relation between increases above a critical level in carbohydrate concentration and declines in $CO_2$ assimilation was recently shown in wheat (3). High starch levels were associated with lowered CER compared to controls in $CO_2$ enriched soybeans (20) and defruited cucumber (24). Higher starch concentrations in $CO_2$-enriched plants compared to 350 $\mu l\ L^{-1}$ plants were associated with reduced CER during vegetative growth and flowering in the present study. At fruiting, however, starch concentrations were similar in the two treatments, but CER was greatly reduced in enriched plants compared to 350 $\mu l\ L^{-1}$-grown plants.

SPS activities are negatively correlated with starch levels in soybeans (13). We did not see this correlation, possibly because in the present study, leaf starch concentration was measured in the early morning rather than at the end of the photoperiod. Changes in starch reported here strongly reflect differences in the extent of starch mobilization at night and thus might not parallel SPS changes as closely as daytime starch changes. There were, however, some similarities between SPS activities and *in situ* CER. At flowering, both photosynthetic rates *in situ* and SPS activities were similar in the two treatments and at fruiting, *in situ* photosynthetic rates and SPS activities in 1000 $\mu l\ L^{-1}$ plants were both only a third that of 350 $\mu l\ L^{-1}$ $CO_2$ plants. SS activities showed somewhat the same pattern as SPS activities. They were 32% higher initially in the 1000 $\mu l\ L^{-1}$ treatments, but more than 3 times as high in the 350 $\mu l\ L^{-1}$ treatments by the last sampling (at fruiting). The patterns of change in SPS and SS activities with time are similar to those reported by Huber and Israel in soybeans (13).

In addition to having depressed enzyme activities, $CO_2$-enriched plants had lower stomatal conductances as has also been observed in studies with $CO_2$-enriched soybeans (27). Lower conductances at fruiting reduced intercellular $CO_2$ levels in 350 $\mu l\ L^{-1}$ plants, but did not reduce $C_i$ in 1000 $\mu l\ L^{-1}$ plants because of the proportional decline in CER. Since intercellular $CO_2$ was not reduced in the high $CO_2$ grown plants at fruiting, the decreased stomatal conductances did not account for the decreases in photosynthesis seen in these plants from flowering to fruiting.

Reductions in tissue nutrient concentrations of $CO_2$ enriched plants have been reported in greenhouse cucumbers (14), lettuce (16), and beans (25). Lower stomatal conductances in $CO_2$ enriched plants may reduce transpiration sufficiently to affect nutrient uptake as suggested by Madsen (18) for tomatoes. This linkage between transpiration and nutrient uptake is not important at natural soil fertility levels (29), but at high nutrient levels such as those we used, low transpiration may be a factor in reducing nutrient uptake (28).

The physiological significance of lower nutrient concentrations in $CO_2$ enriched plants is unclear. In studies using greenhouse cucumber (14), lettuce (16), beans (25), and in our study, all nutrients were within the adequate range, although the necrosis we observed resembled K deficiency. In other studies where cucumbers were $CO_2$ enriched under bright conditions for extended periods of time, similar necroses have been reported (14). van Berkel (33) reported that 'glassiness' in cucumbers was promoted by high root pressure which causes air to be driven from the intercellular spaces. Madsen (17) attributed progressive deformation of $CO_2$-enriched tomato plants to the accumulation of starch in the leaves.

**Conclusions.** Lack of a sustained growth or a yield increase in this cultivar when grown at 1000 $\mu l\ L^{-1}$ $CO_2$ was caused by an increasing depression of carbon exchange capacity such that by the time plants were flowering, *in situ* photosynthetic rates were similar in both 350 and 1000 $\mu l\ L^{-1}$ plants and by fruiting CER was actually higher in the 350 $\mu l\ L^{-1}$ plants than in the 1000 $\mu l\ L^{-1}$ plants. We expected that development of fruits between d 43 and 58 would stimulate photosynthetic rates in enriched plants. This was not the case, however, even though leaf starch did decline. This reduction in starch (or other carbohydrates) might have eventually led to a recovery in CER as it was associated with an increase in relative growth rates on an area basis (22), but the lack of successful pollinations after d 51 in both treatments indicated plants were past a 'window' in fruit set. Such a window was also seen in a similar cultivar given flower removal treatments in the greenhouse (26).

The implications of this study relative to the cause of first fruit inhibition are unclear since at the time of flowering, photosynthetic rates were similar in the two treatments. Possibly if the plants had not been exposed to higher $CO_2$ until fruit set, the response would have been greater. In lettuce (16) and tomatoes (18) restricting enrichment to the period of most rapid growth has also been suggested as a means of increasing response. Fruit number per plant in monoecious seeded cucumber appears inelastic, however, and may be controlled internally rather than by carbohydrate supply. When we raised carbohydrate supply by $CO_2$ enrichment, leaf area/fruit increased from 11.3 to 12.7 $dm^2$/fruit rather than remaining the same or decreasing. Similarly, when Ramirez (26) removed fruit for 21 d before allowing fruit set, the area per fruit increased to 18.5 $dm^2$ compared to 13 in controls.

*Acknowledgments*—For seed, the original suggestion to conduct the experiment and subsequent comments, I am indebted to Dr. D. Mason Pharr, Department of Horticultural Science, North Carolina State University. Excellent assistance in all phases of the research was provided by Dr. Elizabeth Flint and members of the Duke University Phytotron staff.

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