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Effects of CO_2 enrichment on photosynthesis and photosynthate partitioning in soybean (*Glycine max*) leaves

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The short-term and long-term effects of CO_2 enrichment on certain aspects of photosynthesis and leaf carbohydrate metabolism were studied with soybean [*Glycine max* (L.) Merr.] plants. In general, both long-term and short-term CO_2 enrichment (300 ppm CO_2 above ambient) of soybean plants resulted in increased rates of photosynthesis (per unit leaf area) and starch accumulation. Leaf sucrose concentrations were increased slightly, but the rate of assimilate export and activity of sucrose phosphate synthase (EC 2.4.1.14) were usually not increased. Plant N-status affected the response of vegetative soybean 'Ransom' plants to short-term CO_2 enrichment. When plants were N-stressed (2 m*M* NO_3^- supplied), CO_2 enrichment resulted in increased rates of both starch accumulation and export. As N-supply was increased, partitioning of carbon into starch in CO_2-enriched atmospheres increased at the expense of assimilate export. When plants were grown with high-N (20 m*M* NO_3^-), the rate of assimilate export from CO_2-enriched leaves was reduced below the rate observed with plants maintained at ambient CO_2. The reduction in export rate was associated with decreased activities of sucrose phosphate synthase in leaf extracts. The activity of sucrose phosphate synthase in leaf extracts was closely associated with partitioning of carbon between starch and sucrose in leaves, and with the rate of assimilate export.

Additional key words – Assimilate export, N-nutrition, starch, sucrose, sucrose phosphate synthase.

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Introduction

Atmospheric CO_2 enrichment is typically associated with increased rates of leaf photosynthesis and total plant dry matter accumulation. However, increased photosynthetic rates (unit leaf area)$^{-1}$ may not persist for long periods at high atmospheric CO_2 concentrations (Clough et al. 1980). Hence, there is a need to distinguish between the short-term and long-term effects of CO_2 enrichment on photosynthetic processes.

It is also generally recognized that the starch content of leaves increases with increasing CO_2 concentration (Madsen 1968, Apel 1976, Cave et al. 1981). However, there are conflicting reports as to the extent to which the extra carbon fixed (as a result of CO_2 enrichment) is used for export compared to storage (as starch) in leaves. Ho (1977) reported increased rates of photosynthesis and carbon transport in leaves of tomato plants grown under CO_2 enrichment, compared to plants grown at ambient CO_2. He concluded that enriched plants have a higher efficiency of carbon transport when transferred to, or grown at, elevated CO_2. In contrast, Finn and Brun (1982) suggested that the majority of the additional reduced carbon, provided by CO_2 enrichment of soybean plants, was stored as leaf starch and was not available for transport to distant

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sinks (roots and nodules). Thus, soybean and tomato plants may respond differently to CO_2 enrichment.

In soybean leaves, starch and sucrose are the principal end-products of photosynthesis. It has been postulated that the rate of sucrose formation indirectly controls the rate of starch formation (Silvius et al. 1979). Sucrose-P synthase (SPS) is a key control point in the sucrose formation pathway (Harbron et al. 1981, Amir and Preiss 1982) and the activity of SPS in leaf extracts appears to be related to the capacity of the leaf to form sucrose. Consequently, leaf starch accumulation was correlated negatively with SPS activity in leaf extracts from different plant species (Huber 1981, 1983) including selected soybean cultivars (Huber and Israel 1982). One interpretation of the results is that the rate of sucrose formation is limited, perhaps by the activity of SPS, and is operating at near maximal velocity under atmospheric CO_2 levels. In the present study, we have used CO_2 enrichment to test this postulate.

The present study was undertaken with soybean 'Bragg' and 'Ransom' plants to study the effects of CO_2 enrichment on CER and carbohydrate metabolism during short-term and long-term exposure to high CO_2, and with differing plant N-nutrition (short-term only). Nitrogen nutrition was included as a variable in this study because preliminary studies indicated that plant nitrogen supply also affected CER and photosynthate partitioning between starch and sucrose.

Abbreviations – CER, carbon exchange rate; SPS, sucrose phosphate synthase.

Materials and methods

Three separate studies were conducted with soybean [*Glycine max* (L.) Merr.] plants. The experimental protocol was similar in all of the studies reported herein. CERs and leaf carbohydrate concentrations were monitored over a given time interval (3 to 4 h) as specified in the text. At the beginning and end of the interval, leaf discs (4.0 cm^2) were taken for dry weight accumulation and carbohydrate analyses. During the interval, CERs, transpiration and stomatal resistance were measured. At the end of each interval, the trifoliolate leaves were harvested. Fresh weights and areas were recorded, and the leaves were sliced and frozen in dry ice for subsequent extractions of enzymes. CO_2 enrichment was performed in open top field chambers (Rogers et al. 1983) that provided constant CO_2 levels of 0, 75, 150, and 300 ppm CO_2 above ambient. Ambient CO_2 was 349 ± 12 ppm. All measurements were made with fully expanded leaves in the top of the canopy of four or twelve separate plants and on days that were sunny. Data presented are means ± SE from at least four replicate measurements.

Experiment 1: Long-term CO_2 enrichment
Seedlings of 'Bragg' soybean plants were grown from emergence in the field at different levels of CO_2. Plants were sampled at the early podfill stage (+0 and +300 ppm CO_2 levels) and again at about mid-podfill (all CO_2 levels tested).

Experiment 2: Short-term CO_2 enrichment
Seedlings of 'Ransom' and 'Bragg' soybeans were grown at ambient CO_2 in 6–1 pots filled with Perlite, and received nutrient solution daily containing 10 m*M* KNO_3 (Huber 1983). Plants were transferred to the open top chambers (+0 and +300 ppm CO_2) on the day of the experiment (day 40, vegetative stage).

Experiment 3: Effect of N-nutrition
Non-inoculated soybean 'Ransom' plants were grown in Perlite, and received nutrient solution (Huber 1983) containing 2, 5, 10 or 20 m*M* KNO_3. Plants were transferred to the open top chambers (+0 and +300 ppm) on the day of the experiment (day 40, vegetative stage). Visual inspection of the plants verified that total plant size increased with N-supply.

Photosynthesis, resistance, and assimilate export

In Experiment 1, CER, transpiration and stomatal resistance were measured simultaneously with a Li-Cor Model 6000 Portable Photosynthesis System. In Experiments 2 and 3, CERs were measured with an Anarad differential IR CO_2 analyzer equipped with a clamp-on Plexiglass cuvette enclosing a 10 cm^2 area of leaf. Air at the same temperature and CO_2 concentration of the open top exposure chamber (either 0 or 300 ppm above ambient, as indicated) was passed through the cuvette at a flow rate of 1.5 l min^{-1}. Differences between CO_2 concentration in incoming and exhaust air streams were monitored and used to calculate CERs. Stomatal resistances and transpiration rates were measured on the same leaves with a Li-Cor transient porometer.

Rates of photosynthesis, measured as mg CO_2, were expressed as mg CH_2O by multiplying by 0.68 (the molar ratio of the two forms of carbon). Estimates of mass carbon export rate were based on the difference between CER and dry weight accumulation of leaves (Terry and Mortimer 1972).

Dry weight and carbohydrate accumulation

Leaf discs were taken at 3 to 4 h intervals. The discs were freeze-dried and the observed dry weight accumulation was used to estimate export rate as described above. The lyophilized discs were then extracted with hot 80% (v/v) ethanol until the tissue was free of pigment. The supernatant was enzymatically analyzed for sucrose and hexoses by the method of Jones et al. (1977). The particulate fraction, containing starch, was suspended in 1.0 ml of 0.2 *M* KOH and placed in boiling water for 30 min. After cooling, the pH of the mixture was adjusted to about pH 5.5 with 200 µl of

1.0 *M* acetic acid. To each sample, 1.0 ml of dialyzed amyloglucosidase solution [from *Aspergillus oryzae* (Sigma), 35 units ml^{-1} in 50 m*M* Na^+-acetate buffer, pH 4.5] was added, and the tubes were incubated at 55°C for 15 min. After digestion, the tubes were placed in boiling water for 1 min, centrifuged, and the glucose in the supernatant was analyzed enzymatically using hexokinase and glucose-6-phosphate dehydrogenase (Jones et al. 1977).

Extraction and assay of SPS

The frozen leaf tissue was ground with a Polytron high speed homogenizer in a medium (8.0 ml of medium/g fresh weight) containing 50 m*M* HEPES-NaOH (pH 7.2), 5 m*M* $MgCl_2$, 1 m*M* EDTA, 2.5 m*M* DTT, 2% (w/v) PEG-20, and 1% (w/v) BSA. The brei was then filtered through eight layers of cheesecloth, and cells were disrupted by passage through a French pressure cell (330 kg cm^{-2}). Debris was pelleted by centrifugation at 38 000 *g* for 10 min and enzyme assays were conducted on the supernatant.

Sucrose-P synthase was assayed by measurement of fructose-6-P-dependent formation of sucrose (+ sucrose-P) from UDP-glucose (Huber 1981). The assay mixture (70 µl) contained 7.5 m*M* UDP-glucose, 7.5 m*M* fructose-6-P, 15 m*M* $MgCl_2$, 50 m*M* HEPES-NaOH (pH 7.5), and an aliquot of leaf extract. Mixtures were incubated at 25°C, and reactions were terminated after 10 min by addition of 70 µl 1.0 *M* NaOH. Unreacted fructose-6-P (or fructose) was destroyed by placing the tubes in boiling water for 10 min. After cooling, 0.25 ml of 0.1% (v/v) resorcinol in 95% ethanol and 0.75 ml of 30% (w/v) HCl were added, and the tubes incubated at 80°C for 8 min. The tubes were allowed to cool, and the A_{520} was measured.

Results

Long-term effects

'Bragg' soybean plants were grown from emergence in the field at ambient CO_2 or with CO_2 enrichment (300 ppm above ambient). Fully expanded leaves in the top of the canopy were sampled when plants were in the early podfill stage. Leaves of CO_2-enriched plants had higher rates of carbon fixation per unit leaf area compared to control (ambient) plants. However, CO_2 enrichment had no significant effect on rates of mass carbon export. The extra-carbon assimilated under CO_2 enrichment was largely partitioned into starch, which

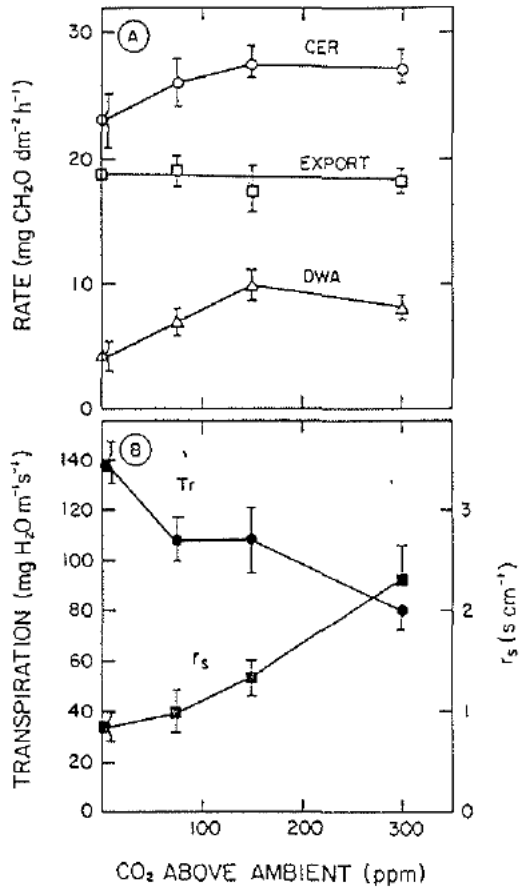

Fig. 1. Effect of long-term CO_2 enrichment of soybean 'Bragg' plants on A) carbon exchange rate (CER), export rate and dry weight accumulation (DWA) rate and B) transpiration (Tr) rate and stomatal resistance (r_s). Plants were grown in the field from emergence at the indicated CO_2 level, and leaves in the top of the canopy were sampled when plants were at the mid-podfill stage. Measurements were made over a 4 h interval, from 11 00 to 15 00 h.

Tab. 1. Long-term effects of CO_2 enrichment on the rates of carbon fixation, export, and changes of carbon metabolism in leaves of field-grown soybean 'Bragg' plants. Plants were grown from emergence with or without CO_2 enrichment. Fully expanded leaves in the top of the canopy were sampled between 09 00 and 15 00 h when plants were in early podfill. SPS activity (µmol $dm^{-2}h^{-1}$) was measured in leaves harvested at 15 00 h. All values are means ± SE of 12 determinations. DWA, dry weight accumulation.

	Rate (mg CH_2O $dm^{-2}h^{-1}$)				Sucrose concentration (mg dm^{-2})		
CO_2	CER	DWA	Starch accumulation	Export	09 00 h	12 00 h	SPS activity
Ambient	30.3±0.8	13.0±1.1	11.2±0.4	17.3±1.8	6.5±0.3	10.5±0.9	57±5
300 ppm above ambient	37.1±1.2	21.7±1.6	19.3±2.5	15.4±2.8	12.0±0.7	21.0±1.2	57±6

was the principal component of dry weight accumulation in leaves. Under both CO_2 regimes, leaf sucrose concentration increased during the morning hours (Tab. 1), and thereafter remained relatively constant (results not shown). At all sampling times, leaves of CO_2-enriched plants had higher concentrations of sucrose compared to control leaves. The activity of SPS in leaf extracts was similar in plants grown with or without CO_2 enrichment (Tab. 1).

The trends identified in Tab. 1 were also observed in plants at a later stage of reproductive development (about mid-podfill). By the second sampling date, CERs of leaves had decreased somewhat, but the effect of CO_2 enrichment was still observed. CER increased with CO_2 enrichment up to 150 ppm CO_2 above ambient, but export rate remained relatively constant at about 18 mg CH_2O $dm^{-2}h^{-1}$ (Fig. 1A). The extra carbon fixed as a result of CO_2 enrichment accumulated in leaves (dry weight accumulation, Fig. 1A), primarily as starch (data not shown). As is often observed, CO_2 enrichment resulted in increased stomatal resistance and decreased rates of transpiration (Fig. 1B).

Short-term effects

Transfer of vegetative soybean plants grown at ambient CO_2 to CO_2-enriched atmospheres (300 ppm above ambient) also resulted in increased rates of photosynthesis. In most respects, cultivars 'Bragg' and 'Ransom' responded similarly although 'Ransom' had higher CERs than did 'Bragg'. With both cultivars, CO_2 enrichment resulted in increased rates of leaf dry weight and starch accumulation, and increased leaf sucrose concentrations (Tab. 2). CO_2 enrichment had no significant effect on export rate with 'Bragg' plants, but resulted in a slight decrease in export with 'Ransom' plants. The effect of CO_2 enrichment on rates of export were reflected in the activities of SPS in leaf extracts. Leaf extracts of 'Bragg' plants had lower SPS activities compared to 'Ransom' and CO_2 enrichment had no effect on enzyme activity. In contrast, SPS activity was reduced in leaves of 'Ransom' after a 4 h exposure to CO_2 enrichment (Tab. 2).

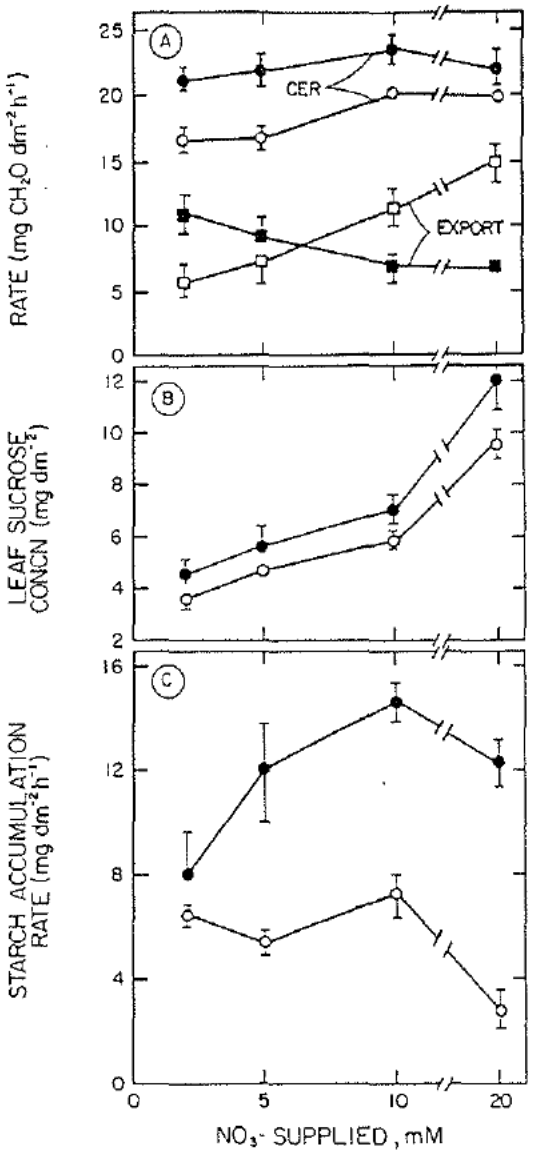

Fig. 2. Effect of short-term CO_2 enrichment of soybean 'Ransom' plants on A) carbon exchange rate (CER) and export rate; B) leaf sucrose concentration and C) starch accumulation rate. Plants were grown outdoors in pots at different levels of N (supplied as nitrate as indicated). Vegetative plants were maintained at ambient CO_2 (open symbols) or transferred to CO_2-enriched atmospheres (closed symbols, 300 ppm CO_2 above ambient) at 08 00 h on the day of the experiment. Measurements were made over a 4 h interval, from 09 00 to 13 00 h.

Tab. 2. Effects of short-term CO_2 enrichment on photosynthetic carbon metabolism in leaves of soybean 'Bragg' and 'Ransom' plants. Plants were grown in pots at ambient CO_2. Plants were maintained at ambient or transferred to high CO_2 on the day of the experiment. The most recently fully expanded leaves of vegetative plants were sampled between 09 00 and 13 00 h. SPS activity (μmol $dm^{-2}h^{-1}$) was measured in leaves harvested at 13 00 h. Values are means of 4 experiments ± SE. DWA, dry weight accumulation; ND, not determined.

Cultivar	CO_2 (ppm)	Rate (mg CH_2O $dm^{-2}h^{-1}$)				Sucrose concentration	SPS
		CER	DWA	Starch	Export	(mg dm^{-2})	activity
Bragg	Ambient	12.5±1.3	8.2±2.3	ND	4.3±0.4	4.3±0.3	21.6±3.0
	+300 ppm	18.6±2.3	12.9±1.5	ND	5.7±1.0	6.2±0.2	20.4±2.0
Ransom	Ambient	20.0±0.1	8.8±1.5	7.3±0.8	11.2±1.2	5.2±0.4	52.0±4.0
	+300 ppm	23.4±2.0	16.2±1.1	14.5±1.0	7.0±2.0	7.5±0.8	38.0±3.0

Influence of N-nutrition

A short-term study was conducted to determine the interaction between plant N-status and short-term CO_2 enrichment with soybean 'Ransom' plants. N-supply affected both CER and photosynthate partitioning. At ambient CO_2, as N-supply was increased, CER and export rate increased, whereas starch accumulation rate tended to decrease (Fig. 2A). The increase in export rate was associated with increased leaf sucrose concentrations (Fig. 2B) and increased activities of SPS (Fig. 3).

The effects of CO_2 enrichment on photosynthetic parameters were influenced by plant N-status. CERs were increased regardless of N-status, but the effect of CO_2 enrichment on photosynthate partitioning depended on nutrition. At low N-supply, CO_2 enrichment resulted in a substantial increase in export rate, relative to control leaves (Fig. 2A), and only a small increase in starch accumulation rate (Fig. 2C). As N-supply was increased, CO_2 enrichment caused a significant reduction in assimilate export rate (Fig. 2A) with the result that starch accumulation rate was increased significantly (Fig. 2C). Short-term exposure of plants to CO_2 enrichment also resulted in rapid (within 4 h) changes in the activity of SPS in leaf extracts. The primary effect of elevated CO_2 was to reduce the SPS activity in leaves of plants grown with high-N (Fig. 3).

Control of export rate

In the experiments conducted in the present study, differences among cultivars or changes in export rate with CO_2 enrichment were associated with variation in SPS activities in leaf extracts. Figure 4 compares export rate with SPS activity in leaves of soybean plants from the

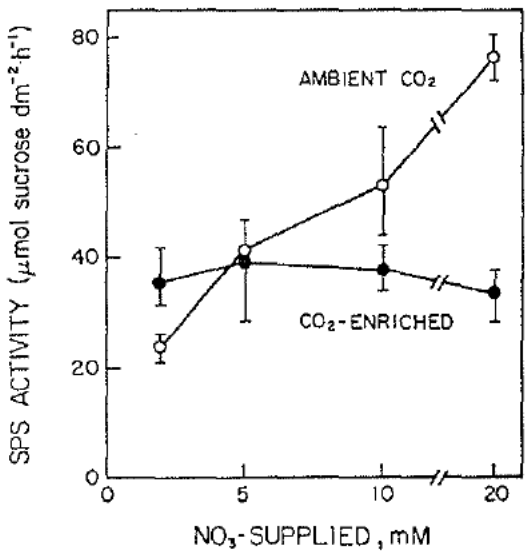

Fig. 3. Effect of short-term CO_2 enrichment of vegetative soybean 'Ransom' plants on the activity of SPS in leaves harvested at 13 00 h. Legend as in Fig. 2.

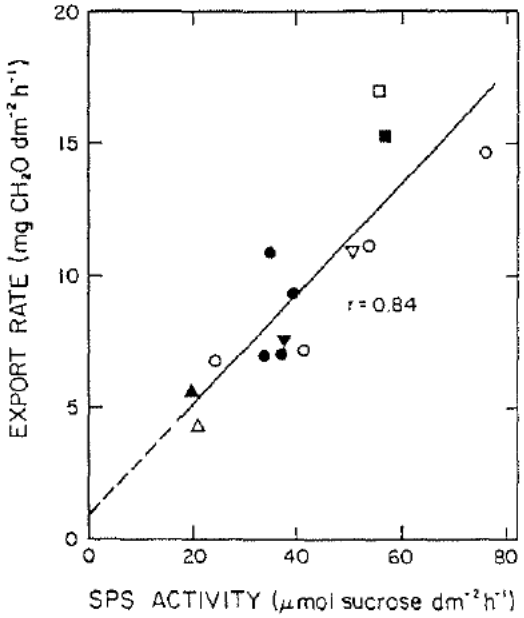

Fig. 4. Relation between export rate and activity of SPS in leaf extracts of soybean at ambient CO_2 (open symbols) and at elevated CO_2 (closed symbols). Key: (○, ●) 'Ransom' N-nutrition; (□, ■) 'Bragg' field grown plants; (▽, ▼) 'Ransom' vegetative stage; (△, ▲) 'Bragg' vegetative stage. Data from Tabs 1 and 2, and Fig. 3. The correlation is significant at the 0.01 level.

different experiments. In general, export rate was correlated positively ($r = 0.84$) with SPS activity, for plants at ambient CO_2 as well as elevated CO_2. Over all, export rate was also correlated positively with CER, but the correlation was not as high ($r = 0.70$, data not shown).

Differences in assimilate export rate were sometimes associated with variation in leaf sucrose concentration, which is thought to be one of the primary determinants of export rate (Ho 1976). As shown in Fig. 5, export rate was correlated positively ($r = 0.92$) with sucrose concentration in leaves of plants monitored at ambient CO_2, but a separate relation existed between the two parameters for leaves of plants subjected to CO_2 enrichment ($r = 0.66$, not significant). Different lines resulted because, in general, CO_2 enrichment increased leaf sucrose concentration slightly while export rate either remained the same or decreased relative to the comparable plants at ambient CO_2.

Discussion

In the different esperiments conducted in the present study, CO_2 enrichment (300 ppm above ambient) caused an increase in CER (unit leaf area)$^{-1}$ of 20 to 30%. However, under most conditions, CO_2 enrichment did not result in increased rates of assimilate export in the light. Rather, the additional carbon fixed was largely partitioned into starch and accumulated in leaves. The only situation encountered where the ex-

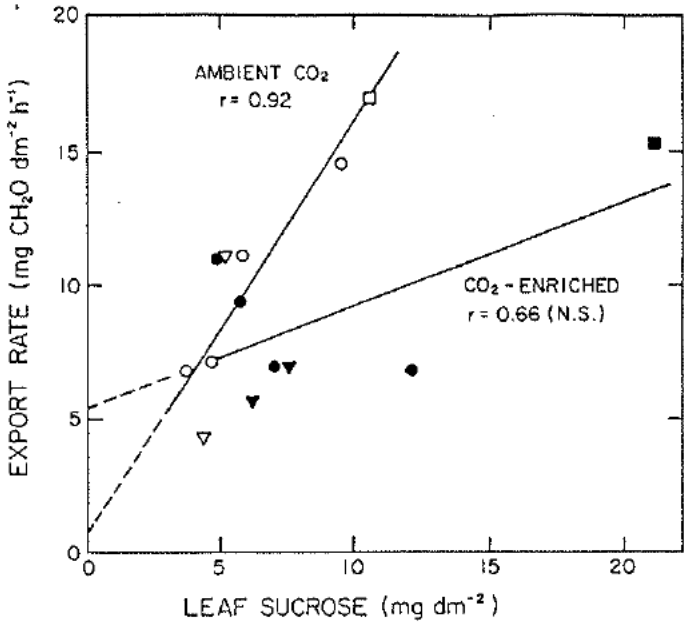

Fig. 5. Relation between export rate and leaf sucrose concentration. Open symbols denote plants maintained at ambient CO_2, and closed symbols correspond to CO_2 enrichment. Key to symbols as in Fig. 4.

port rate was increased as a result of short-term CO_2 enrichment was with vegetative plants grown with a limiting level of N (2 m*M* NO_3^-, Fig. 2A). Under these conditions, the rate of starch (and leaf dry matter) accumulation was increased only slightly, and much of the additional fixed carbon was exported.

Conversely, when plants were grown with high levels of N (10 to 20 m*M* NO_3^-), short-term CO_2 enrichment resulted in a decrease in export rate compared to control plants, that was associated with decreased activities of SPS in leaf extracts (Fig. 3). Thus, CO_2 enrichment resulted in changes in photosynthate partitioning such that leaves accumulated more starch than could be accounted for simply in terms of the increase in CER. It is not known how CO_2 enrichment causes these changes, or how long these effects persisted.

CO_2 enrichment usually resulted in a slight increase in leaf sucrose concentration (Tabs 1 and 2, Fig. 2B). The increase in sucrose concentrations, as a result of CO_2 enrichment, however, was not typically associated with increased rates of export. Thus, different relationships between export rate and leaf sucrose concentration were observed for plants at ambient CO_2 versus elevated CO_2 (Fig. 5). Our results with plants at ambient CO_2 are consistent with the earlier report (Ho 1976) that leaf sucrose concentration is one of the principal factors affecting export rate. Elevated CO_2 apparently affects the distribution of sucrose between transport and 'non-transport' pools in the leaf; only the transport pool would be expected to affect the rate of export. Thus, CO_2 enrichment may have affected the size of the storage (non-transport) pool of sucrose in leaves because total leaf sucrose concentration was increased, but the export rate was not. This is consistent with a recent report (Geiger et al. 1983) that increased leaf sucrose in sugar beet, produced in response to elevated CO_2, was compartmented mainly in the vacuole. The sucrose that is directly available for export is probably the sucrose in the cytoplasm and in the minor vein phloem (Geiger et al. 1983).

In general, our results are consistent with previous studies on the effects of CO_2 enrichment on soybeans, but contrast with the effect on tomato. Several studies (Nafziger and Koller 1976, Mauney et al. 1979, Finn and Brun 1982) have reported that CO_2 enrichment increased starch content of soybean leaves, but not sucrose concentrations. None of the studies, however, attempted to quantitate the increase in starch accumulation in relation to CER, as was done in the present study. However, Finn and Brun (1982) concluded that the additional photosynthate provided by CO_2 enrichment was retained as starch because of "inefficient partitioning into sucrose." The results presented herein substantiate this point.

In contrast, additional photosynthate produced by CO_2 enrichment of tomato leaves is apparently partitioned between both starch and sucrose, because CO_2 enrichment of tomato plants resulted in substantial increases in leaf sucrose concentration and also increased carbon transport (Madsen 1968, Ho 1977, 1978). Considerable differences may exist among species in both the short-term and long-term effects of CO_2 enrichment.

In general, the results obtained with soybean in the present study suggest that the rate of sucrose formation in leaves at ambient CO_2 and saturating irradiance is limited by some factor(s) other than provision of carbon skeletons. Previous studies with soybeans and other species (Silvius et al. 1979, Huber 1981) have suggested that the activity of SPS in leaf extracts is associated with the partitioning of carbon between starch and sucrose. The results obtained with soybean plants grown under different conditions and subjected to CO_2 enrichment support, but do not prove, a causal relation between SPS activity and assimilate export rate (Fig. 5). The basis for the reduction in SPS activity at high CO_2 (Fig. 4 and Tab. 2) will require further studies.

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