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Effects of Water Stress on Photosynthesis and Carbon Partitioning in Soybean (*Glycine max* [L.] Merr.) Plants Grown in the Field at Different CO_2 Levels[1]

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ABSTRACT

The effects of water stress and CO_2 enrichment on photosynthesis, assimilate export, and sucrose-P synthase activity were examined in field grown soybean plants. In general, leaves of plants grown in CO_2-enriched atmospheres (300 microliters per liter above unenriched control, which was 349 ± 12 microliters per liter between 0500 and 1900 hours EST over the entire season) had higher carbon exchange rates (CER) compared to plants grown at ambient CO_2, but similar rates of export and similar activities of sucrose-P synthase. On most sample dates, essentially all of the extra carbon fixed as a result of CO_2 enrichment was partitioned into starch. CO_2-enriched plants had lower transpiration rates and therefore had a higher water use efficiency (milligrams CO_2 fixed per gram H_2O transpired) per unit leaf area compared to nonenriched plants. Water stress reduced CER in nonenriched plants to a greater extent than in CO_2-enriched plants. As CER declined, stomatal resistance increased, but this was not the primary cause of the decrease in assimilation because internal CO_2 concentration remained relatively constant. Export of assimilates was less affected by water stress than was CER. When CERs were low as a result of the imposed stress, export was supported by mobilization of reserves (mainly starch). Export rate and leaf sucrose concentration were related in a curvilinear manner. When sucrose concentration was above about 12 milligrams per square decimeter, obtained with nonstressed plants at high CO_2, there was no significant increase in export rate. Assimilate export rate was also correlated positively with SPS activity and the quantitative relationship varied with CER. Thus, export rate was a function of both CER and carbon partitioning.

The principal end products of leaf photosynthesis are starch and sucrose. Starch accumulates in leaves as a temporary reserve form of carbon and is the principle component of dry weight accumulation in mature leaves, whereas sucrose is the transport form of carbohydrate and is available for export. Mass carbon export rate, calculated as the difference between CER[2] and dry weight accumulation of leaves during the light period (28), provides an estimate of the rate of photosynthetic sucrose formation *in situ*. When CER is restricted (*e.g.* low irradiance), export rate can be maintained by mobilization of reserves (9–11). One of the principal determinants of export rate is leaf sucrose concentration (7, 9, 23), which is a function of both CER and the partitioning of carbon among end products.

The enzyme SPS may be involved in the regulation of carbon partitioning in leaves in two different ways (14). SPS is activated by glucose-6-P and inhibited by Pi (6), and the concentration of these metabolites changes as a function of CER (26). Thus, metabolic regulation of SPS may coordinate the rate of sucrose formation in the cytosol with the rate of C-assimilation in the chloroplast when CERs are low. However, when CER is high (light-saturated), sucrose formation may be limited by the maximum activity of SPS (12, 13, 24, 25). Consequently, short-term CO_2 enrichment of soybean plants did not result in increased rates of export even though CER was increased (14).

In addition to using CO_2 enrichment as a system to study carbon partitioning (14) and the interaction between C and N metabolism (8), the long-term effects of CO_2 supply are also of interest because global CO_2 is increasing (16). In particular, plant growth is often enhanced by CO_2 enrichment, but the effects are not necessarily related to sustained increases in CER (20). Rather, increased water use efficiency may also be involved (16, 20).

The present study was conducted to obtain more information on the interactions between CO_2 enrichment and plant water stress, both of which are known to affect carbohydrate concentrations in leaves (1, 4, 5, 17, 18). Specific objectives were to determine the long-term effects of CO_2 enrichment on (a) CER and photosynthate partitioning and (b) SPS activity in leaves of nonstressed *versus* water-stressed plants. The study was conducted over a 2-week period when plants were in early podfill. The plants were grown in the field from emergence at ambient CO_2 or with CO_2 enrichment (300 ppm above ambient). The stressed plants had been subjected continuously to cycles of stress, and measurements were conducted during two drying cycles.

MATERIALS AND METHODS

Seeds of soybean (*Glycine max* [L.] Merr. cv 'Bragg') were planted on June 6, 1983 on an Appling-Cecil[3] association soil.

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[2] Abbreviations: CER, carbon exchange rate (mg CO_2 or $CH_2O/dm^2 \cdot h$); SPS, sucrose phosphate synthase.

[3] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the United States Department of Agriculture or the North Carolina Agricultural Research Service and does not imply its approval to the exclusion of other products that may also be suitable.

Plant density was about 15 plants/m^2. Rows were spaced 1 m apart and oriented in a north to south direction. No fertilization was recommended from soil analysis. Treflan was applied following recommended procedures. Plants were grown in transparent, open-topped chambers (3 m diameter; [21]) at ambient CO_2 or with CO_2 enrichment (300 μl/l CO_2 above ambient).

Stressed and nonstressed irrigation treatments were imposed when plants were in the vegetative stage. Irrigation was based on soil water potential measurements, obtained with tensiometers. Chambers received water when soil water potentials reached −0.2 bar (nonstressed) or −1 bar (stressed) at a depth of 46 cm for the first 2 months of the growing season, and −2 bar, at the same depth, thereafter. There were two replicate chambers for each CO_2 level and irrigation treatment. All photosynthetic measurements reported herein were made on fully expanded leaves at comparative nodes in the top of the canopy, when plants were in early reproductive development (August 30 to September 12, 1983). The interval studied corresponded to two drying cycles of the stress treatment.

The general experimental protocol was as follows. CERs, export rate, and leaf carbohydrate concentrations were monitored over two 3-h intervals of the day (0900–1200 h, 'AM' interval; 1200–1500 h, 'PM' interval). At the beginning and end of each interval, leaf discs (4 cm^2) were taken and within each time interval CERs were measured. At 1500 h, the remaining trifoliolate leaves were harvested, immediately frozen, and saved for enzyme analyses. All values reported are means of measurements made on six different leaves.

Photosynthesis and Export. CER, transpiration, and stomatal resistance were measured simultaneously with a Li-Cor model 6000 Portable Photosynthesis System, which also calculated leaf internal CO_2 concentration. Rates of photosynthesis, measured as mg CO_2 assimilated, 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 (7, 28).

Dry Weight and Carbohydrate Accumulation. Leaf discs were taken at 3-h intervals as described above. The discs were freeze-dried and the observed dry weight accumulation was used to estimate export rate. The lyophilized discs were then extracted with hot 80% ethanol until the tissue was pigment-free. The supernatant was analyzed for sucrose and hexoses, and the particulate fraction was analyzed for starch as previously described (22).

Extraction and Assay of SPS. Extraction of frozen leaf samples, and assay of SPS activity, were as previously described (22).

RESULTS

Gas Exchange. Both the stress and nonstress treatments received irrigation water on August 29, and the plants were monitored for the 13 d following. During the time interval studied, the nonstressed plots were kept well-watered, whereas the stressed plots were followed through two drying cycles. As stress intensity increased, leaves had altered angles but never showed visible signs of wilting. Changes in afternoon (1400–1500 h) leaf water potential during the first stress cycle are shown in Figure 1, A and D. As soil water depleted, afternoon leaf water potential decreased in stressed plants at ambient CO_2 (Fig. 1A) but not in CO_2-enriched plants (Fig. 1D). The increase in leaf water potential in stressed plants at ambient CO_2 between September 1 and 4 (Fig. 1A) was coincident with a period of relatively cool, humid, and cloudy days. It is evident that stomatal closure (Fig. 1, C and F) acted to reduce transpiration (Fig. 1, B and E) and thereby prevented loss of water rather than being simply a response to low leaf water potential. Supply of water to the stressed plants on the evening of September 7 resulted in increased transpiration and decreased stomatal resistance. Fluctuations in stomatal resistance of unstressed plants (Fig. 1, C and F) were not the result of decreased soil water but rather were associated with periods of high temperature and low RH.

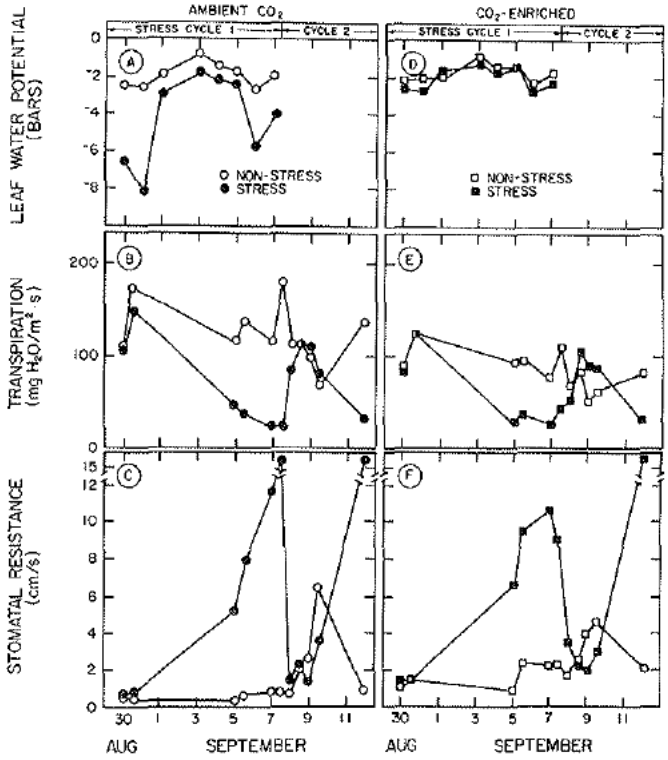

FIG. 1. Changes with time in leaf water potential (A, D), transpiration rate (B, E), and stomatal resistance (C, F) of soybean plants grown at ambient CO_2 (left panel) or with CO_2 enrichment (300 ppm CO_2 above ambient, right panel). Nonstressed plants (○, □) were well-watered throughout, whereas the bar at the top of the figure shows that stressed plants (●, ■) received water on August 29 and the evening of September 7. Each point is the mean of six determination.

Over the time interval studied, CER of unstressed plants tended to decrease (Fig. 2), as is often observed with determinate cultivars during reproductive development (15). However, at all sampling dates, leaves of CO_2-enriched plants had higher CER (per unit leaf area) compared to nonenriched (ambient CO_2) plants (Fig. 2). The increase in CER ranged from 4 to 8 mg CH_2O/dm·h, which corresponded to a relative increase of 17 to 27% of the rate at ambient CO_2. CERs of stressed plants decreased as water availability was reduced. The adverse effect of the water stress on CER was greater with plants at ambient CO_2. When stressed chambers were rewatered, CERs were restored on the following day to rates comparable to the nonstressed plants. The second cycle of stress resulted in similar decreases in CERs.

Because transpiration rate tended to change in parallel with CER, within treatments, water use efficiency (mg CO_2 fixed/g H_2O transpired) remained relatively constant with time (Fig. 3). However, because CO_2-enriched plants had higher CERs and lower transpiration rates, water use efficiency was greater compared to nonenriched plants. At each CO_2 level, the stress treatment tended to slightly reduce water use efficiency relative to nonstressed plants.

Similarly, the internal partial pressure of CO_2 was higher in CO_2-enriched plants than in nonenriched plants, and in both cases, remained relatively constant with time (Fig. 4). Importantly, internal CO_2 concentrations were similar in stressed and nonstressed leaves. Thus, stomatal closure was not the principal factor responsible for the observed reduction in CER in stressed plants.

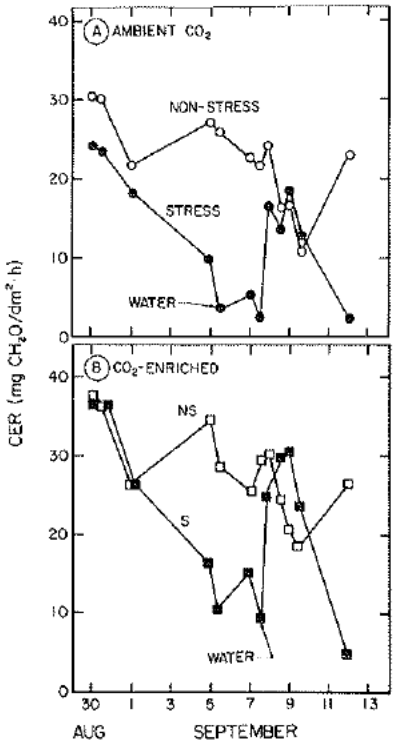

FIG. 2. Changes with time in CER of stressed (●, ■) and nonstressed (○, □) soybean plants grown at ambient CO_2 (A) or with CO_2 enrichment (B). Stressed treatments received water as indicated.

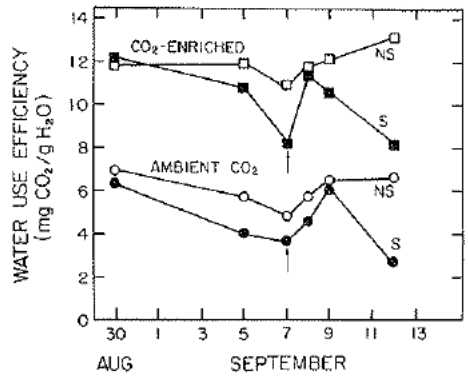

FIG. 3. Changes with time in water use efficiency of stressed (S) and nonstressed (NS) soybean plants grown at ambient CO_2 or with CO_2 enrichment. Arrows indicate application of water to stress treatments.

Photosynthate Partitioning. In general, rates of mass carbon export from leaves were less affected by CO_2 enrichment and water stress than were CERs. In nonstressed leaves, export rates were often higher in the afternoon than in the morning, and although some variation was observed with sample date, export rates were not generally increased by CO_2 enrichment of nonstressed plants (Fig. 5). Over the time interval studied, mean export rates were 14.3 ± 1.0 and 15.9 ± 1.0 mg $CH_2O/dm^2 \cdot h$ for nonstressed leaves of nonenriched and CO_2-enriched plants, respectively. In both stress treatments, export rate decreased as available soil moisture declined and CER was restricted. However, the change in export rate was less compared to the reduction in CER (Fig. 2). Irrigating stressed plants resulted in a transient recovery of high export rates, which coincided with recovery of CERs. At all sample dates, stressed plants grown with CO_2 enrichment had somewhat higher export rates compared to stressed plants at ambient CO_2. Over the time interval studied,

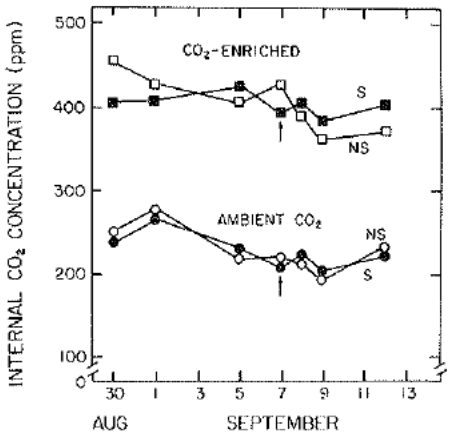

FIG. 4. Internal CO_2 concentration in leaves of stressed (S) and nonstressed (NS) soybean plants grown at ambient CO_2 or with CO_2 enrichment. Arrows indicate application of water to stress treatments.

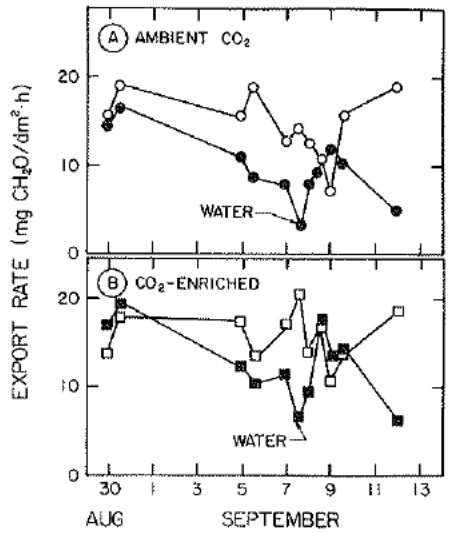

FIG. 5. Changes in export rate of stressed (S) and nonstressed (NS) soybean plants grown at (A) ambient CO_2 or (B) with CO_2 enrichment. Stressed treatments received water as indicated. Each point is the mean of six determinations.

mean export rates from stressed leaves were 9.3 ± 1.3 and 13.3 ± 1.2 mg $CH_2O/dm^2 \cdot h$ for nonenriched and CO_2-enriched plants, respectively. Thus, export of assimilates was less sensitive to water stress than was photosynthesis, and CO_2 enrichment tended to moderate the effects of the stress.

Water stress and CO_2 enrichment affected the concentration of starch in leaves, and the accumulation of starch during the photoperiod (Fig. 6). Over the time interval studied, photosynthetic starch formation (difference between PM and AM concentrations) was always observed in the nonstressed plants, but absolute accumulation tended to decrease with time (Fig. 6, A and C). In CO_2-enriched (nonstressed) plants, the AM concentration of starch was higher and the amount of starch accumulated during the day was greater than in nonenriched plants.

As soil water availability decreased, the AM concentration of starch decreased and accumulation during the day was restricted. On September 5 and 7, when stress was greatest, leaves of CO_2-enriched plants exhibited little change in starch during the day (Fig. 6D), whereas leaves of nonenriched plants mobilized their starch reserves during the day (Fig. 6B).

The concentration of soluble sugars in leaves was also affected by CO_2 enrichment and water stress. Figure 7 shows the change

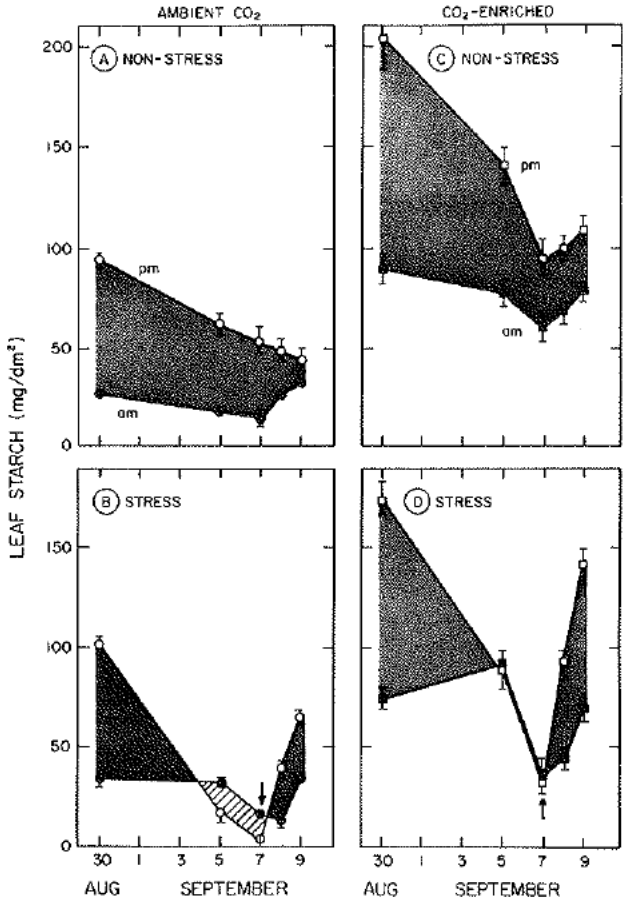

FIG. 6. Diurnal changes in starch concentration in leaves of nonstressed (A, C) and stressed (B, D) soybean plants, at ambient CO_2 (left panel) or with CO_2 enrichment (right panel). Measurements were made at 0900 h (AM; ●, ■) and 1500 h (PM; ○, □). Starch accumulation is indicated by the dotted areas, whereas net starch mobilization during the day is indicated by the cross-hatched area in (B). Each point is the mean of six determinations ± SE. Arrows in (B) and (D) indicate application of water to stress treatments.

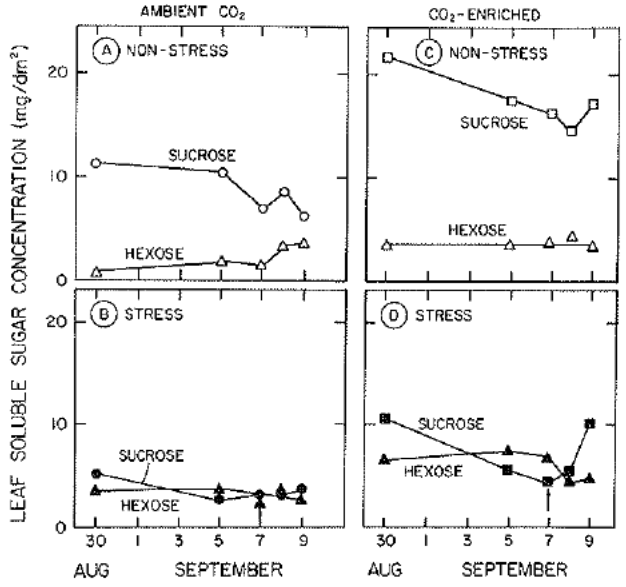

FIG. 7. Effects of CO_2 enrichment and water stress on the concentrations of sucrose and hexose sugars in soybean leaves at 1500 h. Arrows indicate application of water to stress treatments. Each point is the mean of six determinations.

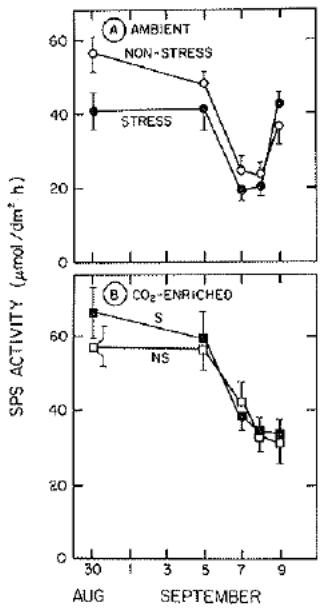

FIG. 8. Changes in SPS activity in stressed (S) and nonstressed (NS) leaves of soybean plants grown at (A) ambient CO_2 or (B) with CO_2 enrichment. Each point is the mean of six determinations ± SE from leaves harvested at 1500 h.

in sugar concentration in leaves harvested at 1500 h over the time interval from August 30 to September 9. In nonstressed leaves, sucrose concentration increased substantially during the day (from 0900 to 1500 h), whereas hexose concentration either increased or decreased slightly during the day (data not shown). However, sucrose concentration always exceeded hexose concentration, and CO_2-enriched leaves had higher sucrose concentrations than did nonenriched leaves (Fig. 7, A and C). In stressed leaves, the concentration of sucrose was lower whereas hexose was slightly greater relative to nonstressed leaves (Fig. 7, B and D).

Factors Related to Export Rate. The activity of SPS in leaves tended to decrease over the time interval studied, and activities were usually similar in leaves of nonenriched (Fig. 8A) and CO_2-enriched plants (Fig. 8B). Mean activities of SPS in leaves of stressed plants at ambient CO_2 tended to be lower than activities in nonstressed plants (Fig. 8A), but at most sample dates the differences were not significant.

In addition to examining trends over time, it is also of interest to correlate changes in related parameters. For example, the relationships between dry weight accumulation, export rate, and CER are shown in Figure 9. Over all the data, no net dry weight or starch accumulation was observed when CER was reduced to about 10 mg $CH_2O/dm^2 \cdot h$ (Fig. 9, A and C). When CER was reduced below this value, a net loss of leaf dry weight and starch was observed. Thus, at low CER (<10 mg $CH_2O/dm^2 \cdot h$), export exceeded concurrent assimilation, and was supported by mobilization of reserves (Fig. 9, B and D). Mean starch mobilization rates as high as 5 mg $CH_2O/dm^2 \cdot h$ were observed in stressed plants. However, by the end of the first stress cycle, starch reserves in stressed leaves of plants at ambient CO_2 were essentially depleted (<5 mg CH_2O/dm^2; Fig. 6B) and thus export rate was limited by availability of reserves. The relationship between export rate and CER was similar for plants at ambient CO_2 (Fig. 9B) and elevated CO_2 (Fig. 9D). However, the lines had slightly different slopes, which reflects the fact that for a given export

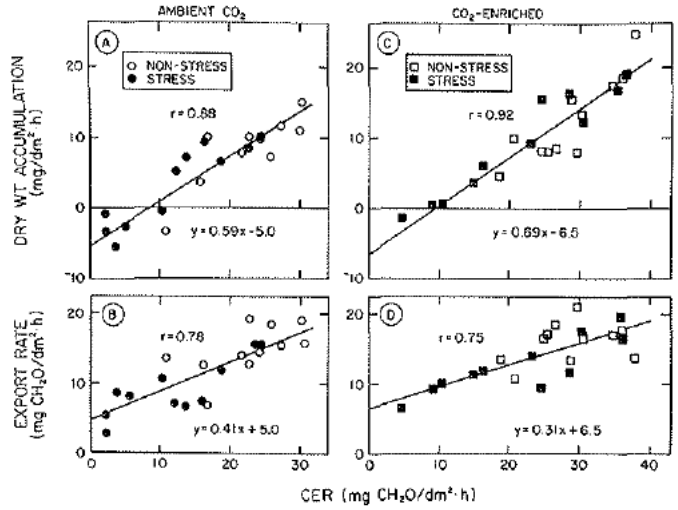

FIG. 9. Relation between CER and dry weight accumulation rate (A, C) and export rate (B, D) of leaves from plants grown at ambient CO_2 (left panel) or with CO_2 enrichment (right panel). Correlations are significant at the 1% level.

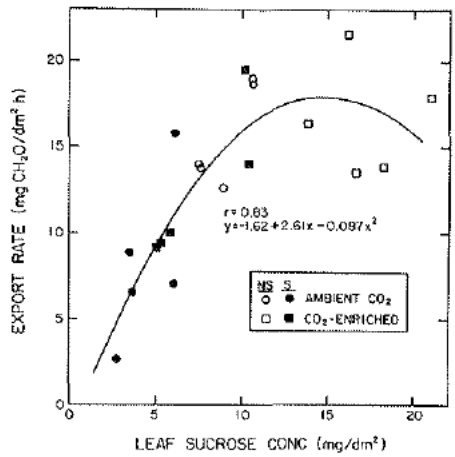

FIG. 10. Relation between export rate and leaf concentration of sucrose in leaves of soybean plants.

rate, CO_2-enriched leaves had higher CERs compared with nonenriched plants.

In addition to CER, leaf sucrose concentration and SPS activity were also important factors that were associated with export rate. Figure 10 compares export rate with leaf sucrose concentration. Over all the data obtained with the four treatments, export rate increased with leaf sucrose concentration up to about 12 mg sucrose/dm². Thereafter, export rate plateaued at a value of about 17 mg CH_2O/dm²·h. The highest concentrations of sucrose were observed in nonstressed leaves of CO_2-enriched plants and all of the data points fell above the 'threshold' value of 12 mg/dm².

Figure 11 compares mean daily export rate with the activity of SPS in leaves. The data points segregated into two groups depending on CER (less than or greater than 15 mg CH_2O/dm²·h). Within each group, export rate was correlated positively with the activity of SPS in leaf extracts.

DISCUSSION

In general, CO_2-enriched plants had higher CERs than did nonenriched plants (Fig. 2), but the extra carbon assimilated was

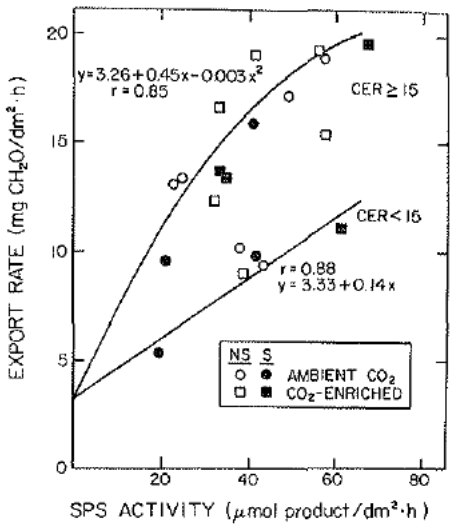

FIG. 11. Relation between mean daily export rate (average of rates in AM and PM intervals) and SPS activity in leaves of soybean plants harvested at 1500 h. Best fit lines were by quadratic or linear regression as shown.

partitioned largely into starch (Fig. 6) and thus was not available for immediate export (Fig. 5). In both CO_2-enriched and nonenriched plants, the imposed water stress had a greater effect on CER than on export, and both parameters were less affected by stress in CO_2-enriched plants. The greater apparent stress-tolerance of CO_2-enriched plants was associated with a higher water use efficiency (Fig. 3) and thus CO_2-enriched plants maintained higher leaf water potentials than did nonenriched plants (Fig. 1, A and D). However, other factors such as root mass and volume may also be responsible for the differences noted.

Over the time interval monitored, CERs of nonstressed plants declined. Superimposed on this time-dependent change was the effect of water stress which increased in intensity during the drying cycles. In stressed leaves, stomatal closure (Fig. 1) was not solely responsible for the reduction in CER, because internal CO_2 concentration was not substantially reduced relative to nonstressed leaves (Fig. 4). As water stress intensity increased, CERs were progressively reduced.

Over all of the treatments, export rate tended to change less than did CER. Maintenance of export capacity in stress-adapted plants has been documented previously (2, 27). Export rate was "buffered" by mobilization of reserves (*e.g.*, starch) when CERs were low (Fig. 9). Similar relationships have been reported in short-term studies (6–9 h) when CO_2 assimilation was varied with irradiance (7, 10). It is important to note, however, that in the present study, all measurements were made when irradiance was high. Variation in CER was the result of developmental changes, CO_2 enrichment, and the imposed water stress. In a recent study with two soybean cultivars grown in a growth chamber, Fader and Koller (7) reported that net accumulation of dry matter occurred when CERs were greater than 1.3 to 1.9 mg CH_2O/dm²·h and at an extrapolated CER of zero, export rates (supported by reserve mobilization) were 0.6 to 1.5 mg CH_2O/dm²·h. In the present study with field-grown plants, net accumulation of dry matter occurred when CERs exceeded about 10 mg CH_2O/dm²·h, and extrapolated rates at zero CER were about 6 mg CH_2O/dm²·h (Fig. 9). Thus, the relationship between CER and export rate was qualitatively similar in the two studies, but rates reported herein with field-grown plants were much higher.

Leaf sucrose concentration was correlated positively with export rate when sucrose concentration was below about 12 mg/dm²; but above this threshold concentration, the two parameters

were not related (Fig. 10). Previous studies have also identified positive correlations between sucrose concentration and export rate in short-term experiments when CERs were light-limited (7, 10, 23). Leaf sucrose can be compartmented into transport and nontransport pools within the leaf (19); 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 (nontransport) pool of sucrose in leaves, because total leaf sucrose concentration was increased, but export rate was not.

Export rate was also correlated with the activity of SPS in leaf extracts (Fig. 11). However, the relation between these two parameters was dependent on CER. A given activity of SPS was associated with a higher export rate when CER was high (>15 mg $CH_2O/dm^2 \cdot h$). The observed interaction with CER may be rationalized as follows. Spinach leaf SPS is activated by glucose-6-P and inhibited by Pi (6). In studies with spinach leaf protoplasts, Stitt *et al.* (25) reported that cytosolic [glucose-6-P] decreased as CER was reduced. It is likely that cytosolic [Pi] increased as the concentration of P-esters such as glucose-6-P decreased. Thus, the activity of SPS *in situ* would be expected to decrease as CER declined. It is important to note that the activity of SPS measured *in vitro* in leaf extracts would not reflect this metabolic regulation. Assuming that soybean leaf SPS is regulated similarly to the enzyme from spinach, it might be expected that the relationship between export rate and SPS activity would vary depending on CER. Water stress has been shown to reduce the activity of certain enzymes such as nitrate reductase (3). However, SPS activity in the present study was not substantially reduced by water stress and maintenance of enzyme activity was associated with sustained export capacity.

The observation that long-term CO_2 enrichment of soybean plants during reproductive development results in increased CERs but did not increase export rates is consistent with our previous short-term studies with vegetative plants (14). In addition, Finn and Brun (8) observed that the majority of the additional carbon fixed during short-term(<36 h) CO_2 enrichment of vegetative soybean plants was stored as starch in leaves and thus was unavailable for export and use in nodule N_2 fixation. Tomato plants respond differently to CO_2 enrichment. Ho (10) reported that CO_2-enriched tomato plants had higher CERs and higher export rates compared to nonenriched plants. When vegetative plants were transferred from ambient CO_2 to CO_2-enriched atmospheres, CERs increased immediately; but export rate increased only slightly on the first day of transfer but continued to increase for the next 5 to 10 days (11). Thus, tomato and soybean plants may respond similarly to short-term CO_2 enrichment (<24 h) but appear to acclimate to long-term enrichment (days to weeks) in different ways.

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