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Photosynthesis and Stomatal Conductance with CO_2-Enrichment of Container- and Field-Grown Soybeans[1]

N. Sionit, H. H. Rogers, G. E. Bingham, and B. R. Strain[2]

ABSTRACT

The present experiment was an attempt to study the differences between photosynthetic responses of pot-grown and field-grown soybean [*Glycine max* (L.) Merr., 'Bragg'] plants to atmospheric CO_2 enrichment at six levels of irradiance and four leaf temperatures. Plants were grown in field soil or in pots containing an artificial substrate at five elevated atmospheric CO_2 levels and two water regimes in open top field chambers. Under well-watered conditions plants grown in the pots had lower stomatal conductances and lower rates of net photosynthesis than plants grown in the field. However, the field-grown plants responded to a less extent to increasing atmospheric CO_2 concentration than pot-grown plants. The photosynthesis-irrdiance relationships were linear in the field-grown plants and curvilinear in the pot-grown plants. At the highest irradiance level tested (1400 μmol m^{-2} s^{-1}), the field-grown plants had maximum net photosynthetic rates of 43 and 48 mg CO_2 dm^{-2} h^{-1} at 332 and 623 μL L^{-1} CO_2, respectively. The pot-grown plants were irradiance saturated at a level of 700 μmol m^{-2} s^{-1} and net leaf photosynthetic rates were 18 and 28 mg CO_2 dm^{-2} h^{-1} at 332 and 623 μL L^{-1} CO_2, respectively. Water stress caused a reduction in both stomatal conductance and net photosynthetic rate in the leaves of pot-grown plants. The effect of leaf temperature on net photosynthethis and stomatal conductance depended upon the atmospheric CO_2 concentration and rooting media. High temperature increased net photosynthetic response to CO_2 enrichment at high CO_2 concentrations but not at low CO_2 concentrations.

Additional index words: Glycine max, **Photosynthesis-irradiance relationships, Photosynthesis-leaf temperature, Field CO_2 chamber.**

PHOTOSYNTHESIS and stomatal resistance have been shown by several investigators (11,12,17) to increase when plant leaves are subjected to high levels of CO_2 for short periods of time under laboratory conditions (15). However, when exposed to elevated CO_2 for the entire growing period, photosynthesis in some plants was shown to decline below that of non-enriched plants (5, 11, 19, 26). This decline in photosynthesis may be the result of several stress effects such as those of irradiance level and limited rooting media that often exist in laboratory experiments.

The effects of CO_2 enrichment under field conditions remain poorly understood. Uncertainties in results showing interactions of CO_2 enrichment with limiting levels of soil water, temperature, irradiance, and size of rooting media in short-term laboratory experiments raise questions of the effects of a long-term global CO_2 increase on field-grown plants. The present experiment was designed to study the photosynthetic and stomatal responses to atmospheric CO_2 enrichment of soybean under field conditions when grown in pots (with limited rooting media) or in the field soil (with access to unrestricted soil resources). We sought to determine whether CO_2 enrichment would yield proportionally greater photosynthetic enhancement in container- and field-grown soybeans as irradiance and leaf temperature increased.

MATERIALS AND METHODS

Soybean plants (*Glycine max* L. Merr., 'Bragg') were grown in open top field chambers (22) at different atmospheric CO_2 concentrations. Each chamber consisted of a cylindrical aluminum frame (3 m in diameter × 2.4 m in height) covered with PVC film Roll-A-Glass with a 45 degree frustrum attached at the top. Air was supplied with the desired CO_2 concentration into the chambers through perforations in the inner wall of the lower half of the chambers. The chambers had mean seasonal daytime air CO_2 concentrations [± 1 standard deviation (SD)] of 332 ± 11, 428 ± 30, 534 ± 37, 623 ± 46, or 910 ± 65 μL L^{-1}. An LSI-11 minicomputer, manufactured by Digital Equipment Corporation, Maynard, Mass., was used to log data and assist in controlling CO_2 injection in each chamber.

There were two groups of chambers at adjacent locations in the field. In one location soybean seeds were planted in rows 95 cm apart in 0.6 ha of the field. There were approximately 10 plants on 1 m of a row. Open top chambers were placed on plants at random positions 6 days after planting. The plants were kept well watered by irrigating with the trickle method. All cultural practices were kept similar on plants outside and inside the chambers except for the CO_2 concentration inside the treatment chambers. In another location, each chamber contained 20 plants grown singly in 16.5 L plastic pots in a 2:1:1 mixture by volume of sandy clay loam soil: sand: metromix 220 (W.R. Grace and Co., Cambridge, Mass.). The plants were placed approximately 30 cm apart. Plants were divided into two groups of 10 in each chamber and were subjected to two watering regimes. One group of plants, considered as the controls, was irrigated when soil tensiometers, installed in the middle of the pots, reached −0.025 to −0.030 MPa. Another group of plants, considered as water-stressed plants, was irrigated when soil tensiometers reached −0.07 to −0.08 MPa. There were two replicate chambers of each of the five CO_2 treatments at each location. Five hundred mL of a N-free nutrient solution (13) was applied to each pot weekly during the entire growing period.

Net photosynthetic rate and stomatal conductance measurements were made on the middle leaflet of the third or fourth trifoliate leaves from the top of the main stem with a steadystate mini-cuvette system developed by Bingham et al. (1). The plants were at the pod formation (R3 through R5 stages according to Fehr and Caviness, 1977) during the measurements. During all measurements, the natural light was supplemented with a 1000 W multivapor lamp with Plexiglas ultraviolet shields located on top of plant canopy inside the chambers. Carbon dioxide concentration in the cuvette was set at that present in a given treatment. Leaf temperature in the cuvette was kept constant at 25 ± 0.5°C except in the study of the effect of variable temperature on photosynthesis where the temperature was kept at 20 ± 0.5, 25 ± 0.5, 30 ± 0.5, or 35 ± 0.5°C. Vapor pressure deficit in the cuvette was controlled and maintained at 8.0 ± 0.15 g m^{-3} at all temperature and irradiance levels. Gas exchange values are from both surfaces of a leaflet measured jointly and expressed on a single surface area basis.

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[2] Senior research scientist, Botany Dep., Duke Univ., Durham, N.C., associate professor, USDA-ARS, Botany Dep., North Carolina State Univ., Raleigh, N.C., associate professor, Univ. of California, Lawrence Livermore Lab., Livermore, Calif., and professor of botany, Botany Dep., Duke Univ., Durham, NC, respectively.

RESULTS AND DISCUSSION

Stomatal conductance of soybean leaves decreased with increasing CO_2 concentration in the atmosphere (Fig. 1). Under well-watered conditions, plants grown in pots had slightly lower stomatal conductance at low CO_2 concentrations than those grown in the field soil and both reached the same value at 623 $\mu L\ L^{-1}$ CO_2. The difference in the stomatal conductances of container- and field-grown plants may have resulted from the stress effect on root growth imposed by limited rooting media in the pots. Ritchie (22) concluded that the difference in the root system of pot- and field-grown corns was a major reason for the significant differences observed in their stomatal resistance and evaporation rates. Louwerse (17) concluded from his studies on sunflower, barley, and maize that the stomatal behavior was only partly species specific and depended mainly on growing conditions. He emphasized the importance of stomatal regulation during water stress. Hall and Schulze (10) found that leaf conductance of cowpeas decreased with decreasing available water in pots in a greenhouse.

The change in stomatal conductance of well-watered pot-grown plants declined relatively linearly with each increasing increment of CO_2 within the range of our treatment levels. Water-stressed plants grown at 623 $\mu L\ L^{-1}$ CO_2 had significantly lower stomatal conductance than those grown at lower CO_2 concentrations. Hofstra and Hesketh (12) found a progressive decrease in stomatal conductance in soybean leaves in response to increases in atmospheric CO_2 concentration up to 1000 $\mu L\ L^{-1}$.

Soybean plants grown in the field had higher rates of leaf photosynthesis at all levels of CO_2 and in fact had a negligible response to CO_2 enrichment compared to plants grown in the pots (Fig. 2). The field-grown plants, which presumably had access to unrestricted soil resources, did not respond to CO_2 enrichment. On the other hand, net photosynthesis of well-watered plants grown in pots was almost two times higher at 910 than at 332 $\mu L\ L^{-1}$ CO_2. Water stress caused a reduction in net photosynthesis of pot-grown plants relative to well-watered controls at all but the lowest CO_2 level used. Field-grown plants had a lower photosynthetic rate when grown at 623 $\mu L\ L^{-1}$ than when grown at 534 $\mu L\ L^{-1}$ CO_2. This observation is in agreement with the findings of Hofstra and Hesketh (12) on soybean plants grown in controlled environment chambers. These investigators found accumulation of starch in the leaves of high CO_2 grown plants and calculated a negative correlation between photosynthetic rate and starch content in the mesophyll cells. Cave et al. (4) found that accumulation of large numbers of irregularly shaped starch grains in the chloroplasts of leaves of *Trifolium subterraneum* at 1000 $\mu L\ L^{-1}$ CO_2 probably altered the normal chloroplast structure and function. However, Hicklenton and Jolliffe (11) observed that the photosynthetic rate of tomato plants grown in greenhouses increased with increasing atmospheric CO_2 concentration up to 1000 $\mu L\ L^{-1}$ and decreased or remained unchanged only at concentrations higher than 1000 $\mu L\ L^{-1}$.

The responses of photosynthesis to increasing irradiance were not similar in all the treatments. The photosynthesis-irradiance relationships were linear in the field-grown plants and curvilinear in the pot-grown plants (Fig. 3). At the highest photosynthetic photon flux density (PPFD) level tested (1400 $\mu mol\ m^{-2}\ s^{-1}$) the field-grown plants had maximum net photosynthetic rates of 43 and 48 mg CO_2 $dm^{-2}\ h^{-1}$ at 332 and

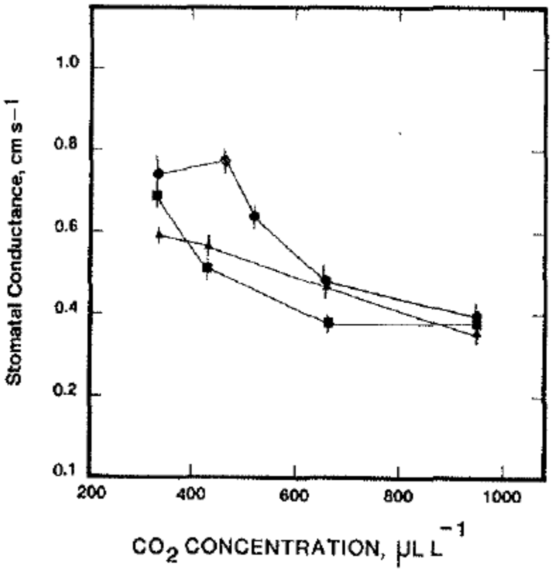

Fig. 1. Stomatal conductances of stressed (■) and well-watered (▲) soybean grown in pots and well-watered (●) soybean grown in field soil at several levels of enriched atmospheric CO_2. n = 4.

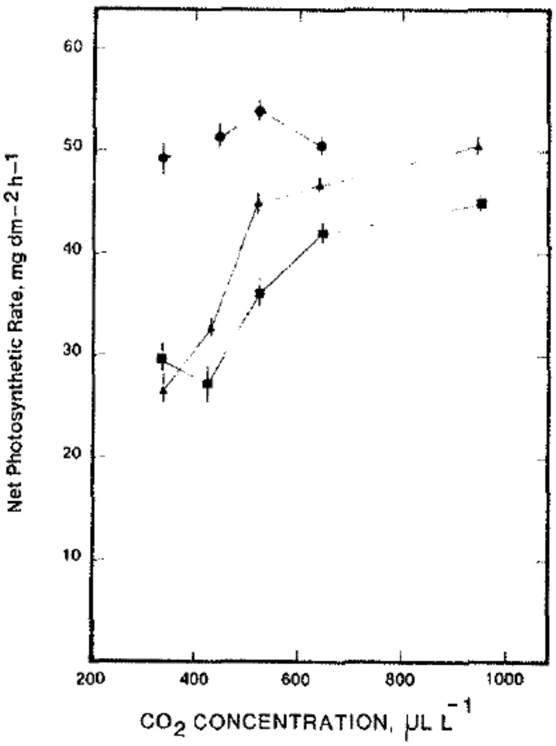

Fig. 2. Net photosynthetic rates in the leaves of stressed (■) and well-watered (▲) soybean grown in pots, and well-watered (●) soybean grown in field soil at several levels of enriched atmospheric CO_2. No measurement was made on field grown plants at 910 $\mu L\ L^{-1} CO_2$. n = 4.

623 μL L^{-1} CO$_2$, respectively. Net photosynthesis of the plants in pots were irradiance saturated at the level of 700 μmol m^{-2} s^{-1}, where net photosynthetic rates were 18 and 28 mg CO$_2$ dm^{-2} h^{-1} at 332 and 623 μL L^{-1} CO$_2$, respectively. Brun and Cooper (2) found that photosynthesis of the leaves of soybean plants was saturated at about 350μmol m^{-2} s^{-1} when grown at 300 μL L^{-1}CO$_2$, but were not saturated at the highest PPFD level tested (1130 μmol m^{-2} s^{-1}) when grown at 1670 μL L^{-1}CO$_2$. These plants were growing in aerated nutrient culture under greenhouse conditions and had optimum levels of nutrients.

There is considerable information in the literature on the response of stomata to atmospheric CO$_2$ concentration and irradiance (17, 20, 24). In sunflower (8) and barley (17), the stomata remained open when photosynthesis was varied by increasing irradiance at constant atmospheric CO$_2$ concentration. Our data (Fig. 4) shows that field-grown soybean had higher stomatal conductance and hence greater rate of photosynthesis (Fig. 3) than container-grown soybean in response to increasing irradiance at either low or high levels of atmospheric CO$_2$.

However, net photosynthetic rates of soybean plants grown in pots at low or high CO$_2$ levels were limited at 700 μE m^{-2} s^{-1} PPFD while stomatal conductances continued to increase with irradiance. Thus, it appears that stomata of soybean in our experiment were more sensitive to changes in irradiance than those of sunflower and barley in the experiments either of Gourdiaan and van Laar (8) or Louwerse (17).

Although net photosynthetic rates of soybean leaves have been reported by several investigators to be lower than those of many other C$_3$ crop plants (6), it has been observed that increasing CO$_2$ concentration at high irradiances greatly increased net photosynthesis of soybean (2, 12). The interacting effects of CO$_2$ concentration and irradiance on the rate of net photosynthesis observed in the present experiment are unique because of the fact that, within the range of irradiance levels tested, the photosynthesis of pot-grown plants became limited at a moderate irradiance level but those of field-grown plants increased linearly with increasing irradiance at both levels of CO$_2$. Patterson (18) observed higher photosynthetic rates in cotton plants grown in the field than in plants grown in pots in

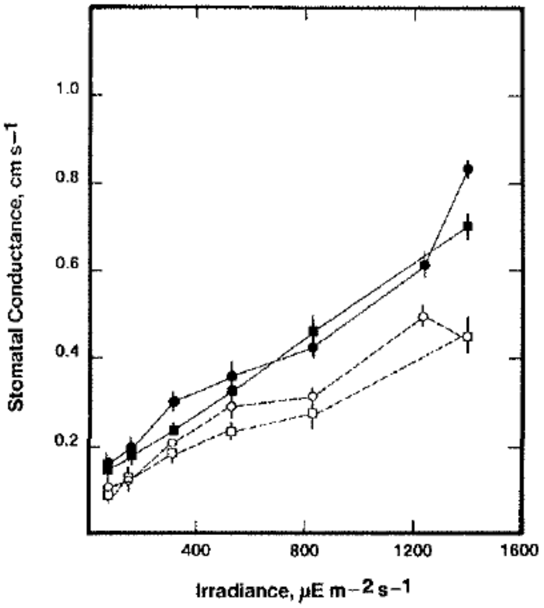

Fig. 4. Changes in stomatal conductance of well-watered pot-grown (■ at 332; □ at 623 μL L^{-1}CO$_2$), and field-grown (● at 332; and ○ at 623 μL L^{-1}CO$_2$) soybean plants in response to different levels of irradiance. n = 4.

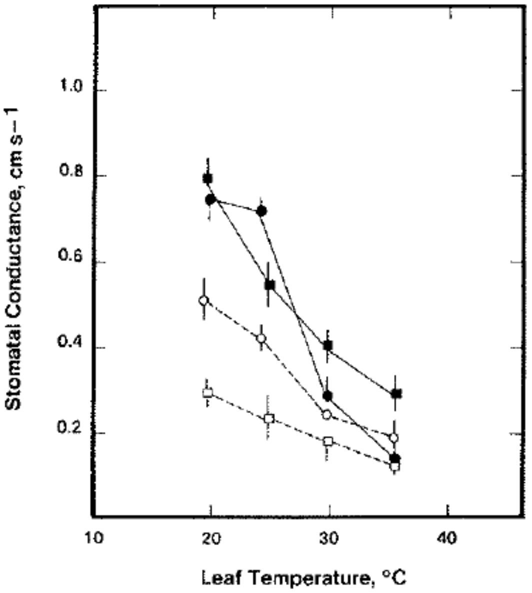

Fig. 5. Changes in stomatal conductance of well-watered pot-grown (■ at 332; □ at 623 μL L^{-1}CO$_2$), and field-grown (● at 332; ○ at 623μL L^{-1}CO$_2$) soybean plants in response to increasing leaf temperature. n = 3.

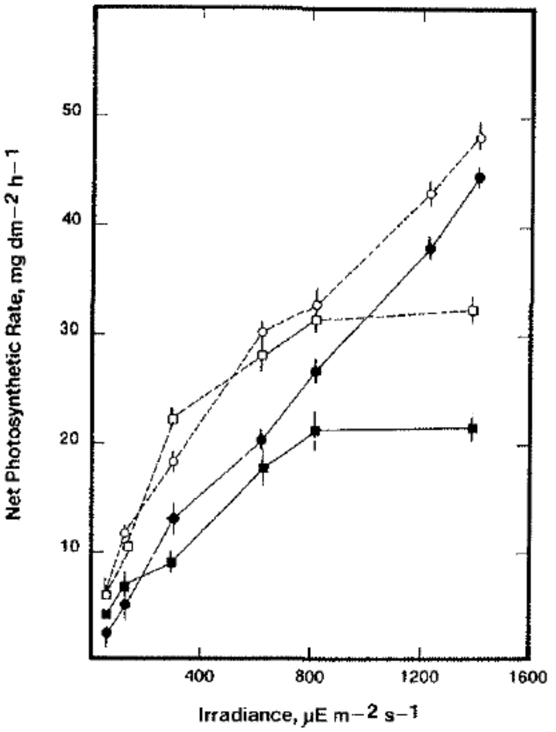

Fig. 3. Net photosynthesis-irradiance response curves of well-watered pot-grown (■ at 332; □ at 623 μL L^{-1}CO$_2$), and field -grown (● at 332; ○ at 623 μL L^{-1}CO$_2$) soybean plants. n = 4.

controlled environments at several irradiance levels. Our observations indicate that greater increases in photosynthetic productivity of soybean plants at saturated irradiance levels should be obtained by increasing the CO_2 content of the atmosphere when plants are grown in the field with minimum limitations to root growth.

Attempts have been made by several investigators (9,14,21,25) to quantify the relationship between stomatal conductance, photosynthesis, and leaf temperature in conjunction with increasing CO_2 concentration in the air surrounding the leaves. Different observations have been made on different species of plants depending on environmental conditions. Caldwell et al. (3) reported increasing stomatal conductance of C_4 species of *Atriplex* with increasing temperature under controlled environmental conditions. However, Ku et al. (16) observed that the stomatal conductance of potato (*Solanum tuberosum*) plant (C_3) decreased sharply in response to an increase in leaf temperature above 25°C. In our experiment, temperatures above 20°C caused significant decreases in stomatal conductance in all treatments (Fig. 5). Temperature increases had a much greater effect in reducing stomatal conductance at low rather than high levels of CO_2 for both field- and pot-grown plants. Increasing leaf temperature from 20 to 35°C decreased stomatal conductance of pot-grown plants by 60 and 40% at 332 and 623 $\mu L\ L^{-1} CO_2$, respectively.

The effect of leaf temperature on net photosynthesis depended greatly on atmospheric CO_2 concentration and root growth media (Fig. 6). At lower CO_2 levels, increasing leaf temperature had no significant effect on net photosynthesis of either field- or pot-grown plants in spite of decreasing stomatal conductance. However, at higher CO_2 levels, increasing leaf temperature from 20 to 30°C increased net photosynthesis of field-grown plants to a greater extent (36.6%) than that of pot-grown plants (7.5%). High temperatures increased the percentage response to CO_2 enhancement by increasing net photosynthesis at high CO_2 concentrations and decreasing it slightly at low CO_2 concentrations.

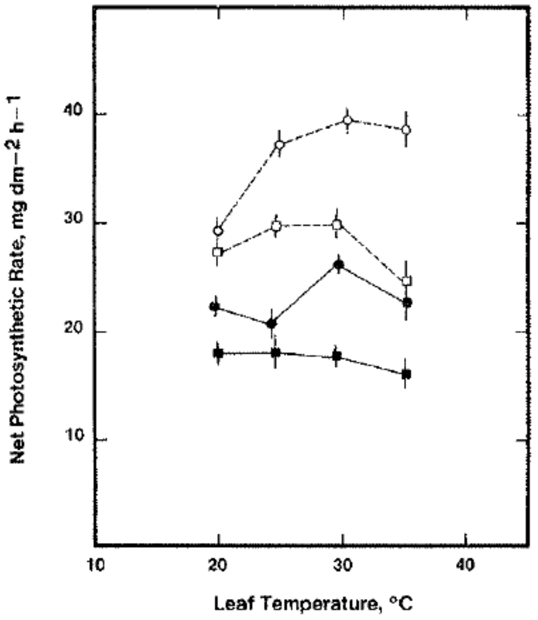

Fig. 6. Changes in net photosynthetic rate of leaves of well-watered pot-grown (■ at 332; □ at 623 $\mu L\ L^{-1} CO_2$), and field-grown (● at 332; ○ at 623 $\mu L\ L^{-1} CO_2$) soybean plants in response to increasing leaf temperature. n = 3.

From our observations in the present experiment on soybean grown in large pots or in the field, it is concluded that stress imposed on plants by confining the roots may alter the magnitude of the photosynthetic response to atmospheric CO_2 enrichment.

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