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EFFECTS OF ATMOSPHERIC CO_2 CONCENTRATION ON PHOTOSYNTHETIC PERFORMANCE OF C_3 AND C_4 PLANTS

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CHEN X. M., ALM D. M. and HESKETH J. D. *Effects of atmospheric CO_2 concentration on photosynthetic performance of C_3 and C_4 plants.* BIOTRONICS **24**, 65–72, 1995. Four C_3 and C_4 plant species (soybean, sunflower, pigweed, and corn) were grown in the field to test photosynthetic performance at ambient (350 μmol CO_2 mol^{-1} air or ppm) and enriched (700 ppm) atmospheric CO_2 (*Ca*), particularly after plants were switched from the 700 to 350 ppm treatment and back. Comparing plants in a CO_2 enriched atmosphere with those at ambient, leaf water content increased for pigweed and corn, but was the same or less for the C_3 plants; leaf mass per unit area (kg m^{-2}) was less for C_4 plants and greater for C_3 plants, for the same comparison. At 700 ppm steady-state photosynthetic gas exchange (*Pn*) values were the same for C_4 species and were greater for C_3 species, while stomatal conductances (*gs*) were reduced in all comparisons, compared to plants at ambient CO_2 levels. Short term *Pn* values taken immediately after switching treatments were not significantly different from long term values for the same treatment, except for pigweed, where in both cases *Pn* after switching was 73% of the long term values. In all tested species, *gs* values were lowered when measured directly after being transferred to the other treatment. Continual gas exchange measurements, for up to 90 min after a transfer from long term CO_2 enrichment to ambient and back, indicated that the short term *Pn* value for pigweed, as pointed out above in the switching experiments, had not equilibrated to the change in treatment whereas that of corn had. *Pn* at 700 ppm continued at a rapid pace throughout the day for the C_3 species, that for the C_4 species being the same as at 350 ppm. *Pn* declined over the course of the day for the same light levels for all species and treatments, except for pigweed at 350 ppm. The decrease in *Pn* at 700 ppm suggested nonstomatal control in the C_3 species.

Key words: photosynthesis; stomatal conductance; CO_2-enrichment; soybean; corn; sunflower; pigweed; climate change.

INTRODUCTION

Photosynthesis in C_3 plants usually increases in response to an increase in atmospheric CO_2 concentration (*Ca*), but C_4 plants net leaf photosynthetic carbon dioxide exchange rate (*Pn*) is nearly saturated by CO_2 at current ambient CO_2

concentration (350 μmol CO_2 mol^{-1} air or ppm). In nearly all C_3 crop plants studied in the field, the capacity of the photosynthetic system is sufficient to allow a substantial and rapid increase in *Pn* with CO_2 enrichment (*5–8, 13*). Another frequently reported phenomena is that stomatal conductance to water vapor (*gs*) decreases in response to increases in atmospheric CO_2, in both C_3 and C_4 plants (*6, 10, 14*). Recently Chen et al. (*7*) reported changes of *Pn* and *gs* in soybean leaves acclimated to elevated CO_2 concentrations. Current knowledge about mechanisms controlling leaf photosynthetic performance at elevated CO_2 concentrations is still limited (*17*), and it is still useful to examine the photosynthetic behavior of both C_3 and C_4 species at ambient and enriched CO_2 conditions in order to contribute more towards an understanding of the potential impact of increasing atmospheric CO_2 concentration on agricultural- and eco-systems.

In this study, soybean, sunflower, pigweed and corn were grown in the field at both ambient (350 ppm) and elevated (700 ppm) CO_2 concentrations at Urbana. Gas exchange rates, short term and over the course of 65 to 90 min or over a day, were measured at both CO_2 levels throughout the entire period of the study. We also tried to examine mechanisms controlling photosynthetic acclimation to CO_2 enrichment for these species in order to test effects of long-term CO_2 exposure on stomatal responses reported earlier (*7*).

MATERIALS AND METHODS

Soybean [*Glycine max* (L.) Merr. *cv.* Jack], sunflower [*Helianthus annuus* (L.) *cv.* Mammoth Russian], pigweed [*Amaranthus hybridus* (L.)], and corn [*Zea mays* (L.) *cv.* Pioneer 3921] were planted May 16, 1994. CO_2 enrichment (700 ppm v v^{-1}) treatments were applied during the daytime, using open-top chambers as reported earlier (*6*), from the 4th to 5th leaf stages to over 30 days. Very small pigweed seedlings were transplanted into treatment plots at 2–3 leaf stage on June 20, 1994 and CO_2 enrichment treatments were applied during the daytime for 20 days. An irrigation system was used to minimize the occurence of drought stress.

Leaf gas exchange rates and associated parameters were measured on new fully expanded leaves using LiCor 6,200 portable photosynthesis system (LI-COR, Lincoln, NE, U. S. A.).[1] Diurnal leaf gas exchange measurements were made at both CO_2 levels for all plant species to examine photosynthetic performance under natural field conditions.

Rapid responses of *Pn* and *gs* to changes in CO_2 concentrations were studied to examine any differences in patterns of response to sudden changes in CO_2. Plants exposed to a 700 ppm long-term CO_2 environment level were suddenly exposed to 350 ppm CO_2 in air, with frequent measurements of *Pn* until a steady

[1]Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the Univ. Illinois of the USDA and does not imply the approval of the named product to the exclusion of other products that may be suitable.

–state *gs* value was achieved, at which time the plants were exposed again to the 700 ppm treatment. Such changes in atmospheric CO_2 were imposed during morning hours (about 9:00–11:00 am) under clear skies for all four species.

Leaf water content and specific leaf weight were measured after 20 days of CO_2 enrichment for all four species. Leaves at similar morphological age were collected and 10 leaf discs were made by using a cork borer (1.4 cm in diameter). Immediately after fresh weights were measured, all leaf discs were oven dried for 24 hour at 70℃ to determine dry weight.

RESULTS AND DISCUSSION

Leaf water status

A number of reports have shown that plant response to CO_2 varies among different species (*3, 9, 17*). In this study, long–term CO_2 exposure resulted in increases (corn and pigweed), decreases (soybean) and no change (sunflower) in leaf water content, compared to that in ambient–grown plants (Table 1). In a similar comparison, the leaf dry mass per area was larger in soybean and sunflower, smaller in corn, and the same in pigweed, compared to that in ambient–grown plants (Table 1). As reported earlier (*6, 15*), nonstructural carbohydrates increased with CO_2 enrichment in soybean, contributing to the increase in leaf mass per unit area and the decrease in relative water content. Since C_3 species are CO_2–limited at current ambient CO_2 levels, *Pn* increases at higher CO_2 concentrations; however, higher *Pn* in sunflower at 700 ppm CO_2 (Table 2) did not result in a lower leaf water content, but the leaf mass per area was higher. Leaf area expansion might have been stimulated in plants growing at the higher CO_2 level, but no area measurements were taken. Both pigweed and corn are C_4 species showing no enhancement of *Pn* in the high CO_2 treatment; their increase in leaf water content might have been due to reduced *gs* and leaf transpiration rate (*E*) (Table 2). Leaf mass per area responded to CO_2 enrichment differently for the two C_4 species tested. Anatomic and metabolic differences among these species may contribute to leaf water content and leaf mass per area responses to CO_2 in different ways, and these may be key factors causing diversity in the way plants acclimate to elevated CO_2 concentrations.

Gas exchange behavior

Recent reports have shown that long–term CO_2 enrichment results in photosynthetic and stomatal acclimation (*1, 4, 7*). Although several hypotheses have been proposed for mechanisms involved (*4*), the causes for acclimation are still not clear because of conflicting reported responses in the literature among different species (*2, 5, 6, 18*). Table 2 shows photosynthetic gas exchange of C_3 and C_4 leaves grown at ambient and elevated CO_2 concentrations in open top chambers for 20 days. *Pn* of both treatments were measured at the other treatment level in order to compare short term effects. Pn of corn was not affected by CO_2 enrichment, although *gs* differed greatly, especially for ambient

Table 1. Effects of elevated CO_2 on leaf water status.

Plants	Leaf Water Content (%)	Leaf dry mass per unit area (kg m^{-2})
Soybean (A)*	73.50a**	0.039a
Soybean (E)	68.71b	0.056b
Pigweed (A)	71.35a	0.066a
Pigweed (E)	74.28b	0.065a
Corn (A)	71.86a	0.047a
Corn (E)	73.18b	0.043b
Sunflower (A)	79.60a	0.043a
Sunflower (E)	80.46a	0.048b

*A and E represent ambient and enriched plants 20 days after CO_2 treatment, respectively. Each value is the mean of ten measurements.
**Letter difference between two treatments within same species indicates a significant difference at 0.05 level.

Table 2. Photosynthetic gas exchange of C_3 and C_4 leaves at ambient and elevated CO_2 concentrations.

Plants	Growing/ Measuring Conditions	*Pn* [μmol (CO_2) m^{-2} s^{-1}]	*gs* [mol (H_2O) m^{-2} s^{-1}]	*E* [mmol (H_2O) m^{-2} s^{-1}]
Pigweed	A/A*	47.28b**	0.63c	0.012c
	E/E	48.94b	0.43b	0.010b
	E/A	35.90a	0.41b	0.009b
	A/E	34.54a	0.24a	0.006a
Soybean	A/A	23.28a	1.02d	0.015c
	E/E	42.18b	0.89c	0.014c
	E/A	21.99a	0.52b	0.010b
	A/E	35.09b	0.28a	0.007a
Sunflower	A/A	31.92a	1.73d	0.016b
	E/E	47.69b	1.47c	0.016b
	E/A	35.19a	1.27b	0.014a
	A/E	48.70b	0.89a	0.013a
Corn	A/A	40.89a	0.64c	0.013c
	E/E	42.85a	0.47b	0.011c
	E/A	41.94a	0.42b	0.009b
	A/E	39.92a	0.18a	0.006a

*A and E represent ambient (350 ppm) and enriched (700 ppm) CO_2 levels, respectively. Measurements were made 20 days after CO_2 treatments under field conditions. Each set of values is the mean of ten measurements.
**Letter difference between measuring conditions within same species for each parameter indicates a significant difference at 0.05 level.

grown leaves suddenly exposed to elevated CO_2 concentrations, where it was only 0.28 of the value measured at ambient CO_2 levels. Pigweed, the other C_4 plant, had lower *Pn* in leaves measured at the new CO_2 concentration (35 vs. 48 μmol CO_2 m^{-2} s^{-1}, Table 2), with a lower *gs* value only for the ambient grown pigweed leaves measured at elevated CO_2 levels (0.24 vs. 0.43, A/E vs. E/E, Table 2). For both C_3 species tested, *Pn* did not respond statistically to a change in measured CO_2 concentration. *gs* in soybean leaves was much less immediately after exposure to elevated CO_2 concentrations (0.28 vs. 0.89, A/E vs. E/E). *gs* of ambient growm sunflower was not as sensitive to elevated CO_2 (0.89 vs. 1.47, A/E vs. E/E, Table 2) as that for the other tested species. It has been reported (7) that *gs* in soybean becomes less sensitive to elevated CO_2 after long-term CO_2-enrichment, as seen in Table 2 for all four species. Similar responses were reported for *Maranthes corymbosa* (*1*). Most of recorded evidence for negative photosynthetic acclimation to long-term CO_2 exposure was for plants grown in CO_2-enriched air and suddenly exposed to ambient concentrations; such negative responses could have been caused by low *gs* values (*4*).

Gas exchange dynamics after changes in atmospheric CO_2

Few studies on the dynamics of leaf photosynthetic responses to elevated CO_2 have been reported (*7, 15, 16*). Fig. 1a–d shows *Pn, gs* and *Ci* (CO_2 concentration in the substomatal air space after leaves from the long term 700 ppm treatment were transferred into ambient air (350 ppm) and subsequently back to 700 ppm. There are inconsistencies in the data but in general *gs* and *Pn* in the C_4 species dropped quickly after the change from high to low CO_2 and did not recover for some 20 min. When transferred back to the original treatment *gs* in corn dropped immediately but *Pn* did not, while both dropped slowly in pigweed despite a high *Ci.* The data in Table 2 show that corn had recovered from the change in CO_2 (no change in *Pn*) while pigweed had not.

In the C_3 species, *Pn* changed rapidly after switching plants from 700 to 350 ppm, or from 350 back to 700 ppm (Fig. 1c, d), with *Pn* increasing after exposure to 350 ppm as *gs* increased, over a 25–30 min period. After the switch back to 700 ppm, *gs* had recovered after 30 min in soybean but not after 20 min in sunflower; *Pn* recovered immediately in soybean and had reached 90% of the original value in sunflower.

We did not have time to study the short-term dynamics of a switch in atmospheric CO_2 from 350 to 700 ppm (A/E). There are inconsistencies within the data set reported here and between it and an earlier one for soybean alone. In the earlier soybean study we let the plants equilibrate to the new atmospheric CO_2 concentration for 24 h after the switch; *gs* of the A/E switch was roughly 50% of the E/E *gs* value (0.438) after 24 h in that study; *gs* seemed to have recovered in our dynamic study within 20 min after such a switch, but *gs* is known to oscillate dramatically after such a treatment, and in this case the plants were returning to the CO_2 level they had been previously exposed to for 20 days.

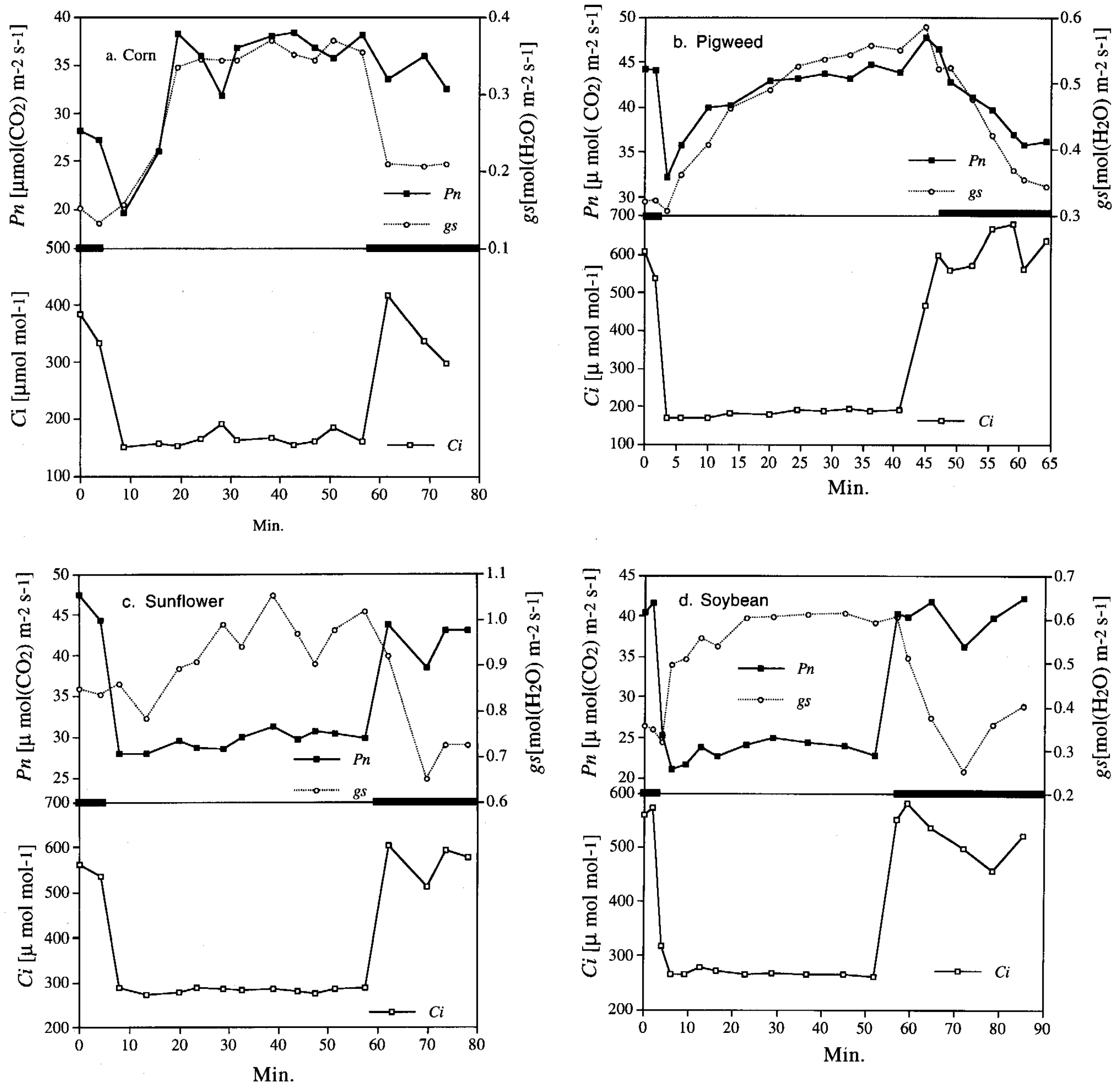

Fig. 1. Dynamics of leaf photosynthetic response to changes in atmospheric CO_2 concentration in a. corn (9 July), b. pigweed (1 July), c. sunflower (9 July) and d. soybean (30 June). Solid square, open diamonds and open squares represent net photosynthetic CO_2 exchange rate (*Pn*), stomatal conductance (*gs*) and intercellular CO_2 concentration (*Ci*), respectively. Dark bars indicate the time period when leaves were at 700 ppm level, and time period between dark bars indicates time period when leaves were at 350 ppm level. Plants had been exposed to 700 ppm for 20 days before these treatments were imposed. Each value is the mean of three measurements.

Diurnal patterns

In general *Pn* for corn and pigweed were the same over the course of a clear day, with *gs* drifting downward over time except for pigweed at 350 ppm. Pn at 700 ppm generally pararalled that at 350 ppm for the C_3 species, with some decline in *Pn* for both treatments in sunflower and soybean as the day progressed. Solar noon is at 1,300 daylight saving time at the Urbana longitude.

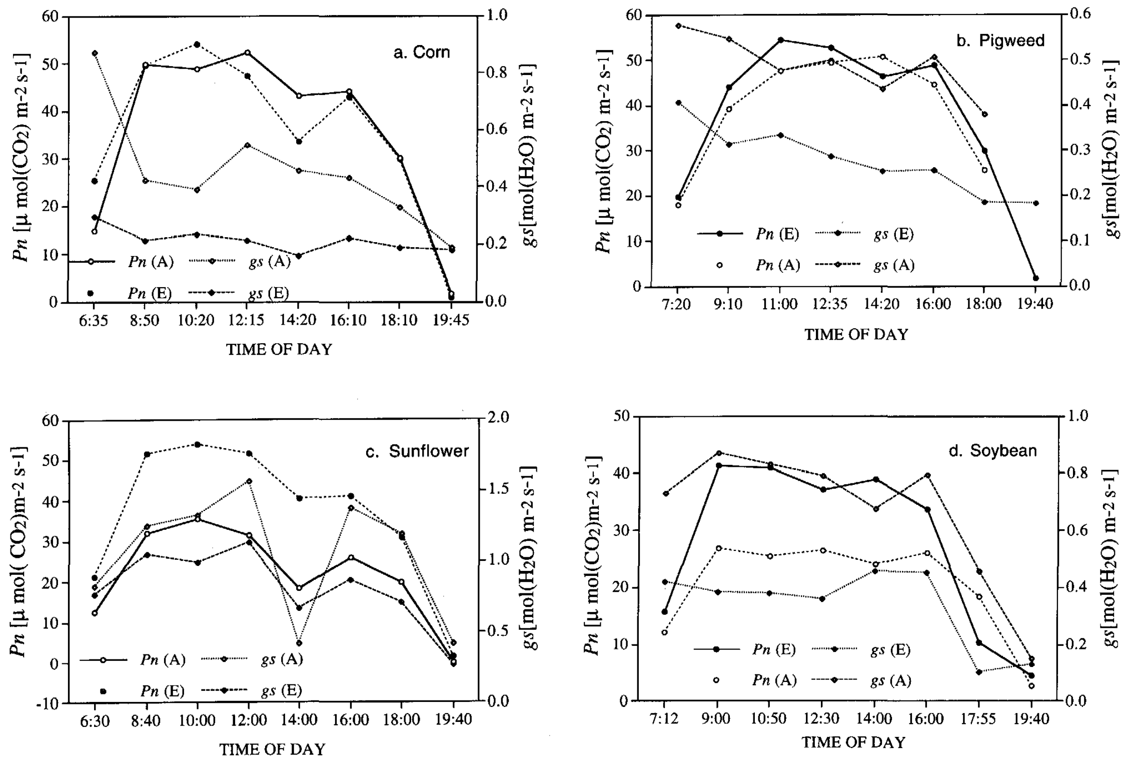

Fig. 2. Diurnal variation of leaf photosynthesis (*Pn*) and stomatal conductance (*gs*) in a. corn (16 June), b. pigweed (30 June), c. sunflower (16 June) and d. soybean (30 June). *Pn* (A), *Pn* (E), *gs* (A) and *gs* (E) represent photosynthesis and stomatal conductances measured at ambient (350 ppm) and enriched (700 ppm) CO_2 levels, respectively. Each value is the mean of three measurements. Irradiance levels [μmols (photon) m^{-2} s^{-1}] at the beginning, midday and at the end were 494, 2145 and 55 for corn; 657, 2018 and 111 for pigweed; 398, 2208 and 131 for sunflower and 496, 1994 and 149 for soybean.

There was a decline in *gs* in sunflower but *gs* increased over the day in soybean. Since increasing *Ca* should overcome limitations to CO_2 flux into the leaf imposed by decreases in *gs* seen here in sunflower, some of the decline in *Pn* might well have been caused by nonstomatal factors, as it certainly must have been for soybean. We conclude from this experiment that under good irrigation, *Pn* at 700 ppm continues at a rapid pace throughout the day in C_3 species after 20 days at this CO_2 level, although there was a general decline in *Pn* over the day at both 350 and 700 ppm in both species.

CONCLUSIONS

In this paper we show that sunflower behaves generally like soybean in the way it responds to CO_2 treatments, with the exception of the higher *gs* values for sunflower. While *Pn* in C_4 species is the same at 350 and 700 ppm *Ca*, sudden changes in *Ca* (E/A, A/E) cause changes in *Pn* and *gs* that sometimes revert slowly to the original levels. *Pn* in irrigated plots proceeds at a fast pace over the course of a clear day. *gs* is often slow to reach a new equilibrium value after a change in *Ca*, and sometimes may limit *Pn* while doing so. While results from field studies are sometimes inconsistent because of uncontrolled plant and environmental conditions, such results are valuable for analyzing results from plants grown under more carefully controlled conditions.

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