

Responses of Selected Plant Species to Elevated Carbon Dioxide in the Field¹

H. H. ROGERS, G. E. BINGHAM, J. D. CURE, J. M. SMITH, AND K. A. SURANO²

ABSTRACT

It has become of interest to study long-term effects of CO₂ concentration on plant growth, because intensive burning of fossil fuels and destruction of forests promise to continue the recent rise in atmospheric partial pressures of CO₂ into the next century (Bolin, 1977; Stuiver, 1978). Effects of CO₂ enrichment on growth of crop and forest species were therefore studied for the first time in the field in open top exposure chambers at daytime mean CO₂ concentrations of 612, 936, 1292, and 1638 mg m⁻³, and in ambient control plots. Increased growth of plant parts of corn (*Zea mays* L. 'Golden Bantam'), soybean [*Glycine max* L. (Merr.) 'Ransom'], loblolly pine (*Pinus taeda* L.), and sweetgum (*Liquidambar styraciflua* L.) were recorded. Growth increases for soybean and sweetgum in elevated CO₂ atmospheres were due to increases in leaf area and photosynthesis per unit leaf area, and decreases in conductance and, therefore, water use. For corn, however, photosynthesis was unaffected by CO₂ enhancement, and growth stimulation appeared to be due to lowered conductance and increased water use efficiency alone.

Additional Index Words: corn, soybean, pine, sweetgum, photosynthesis, water use efficiency.

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The global rise in atmospheric CO₂ concentration is now a well-established phenomenon (Pearman, 1980). However, an assessment of future consequences of elevated CO₂ on plant systems is impossible with the present paucity of quantitative field data (Kramer, 1981), due largely to a lack of appropriate methodology. This report presents first season results of field studies in which large-scale, open top chambers were used to continuously expose representative crop—corn (*Zea mays* L.) and soybean [*Glycine max* L. (Merr.)]—and forest—loblolly pine (*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.)—species to varying concentrations of CO₂. In addition to being the two most abundant crops in the United States, corn and soybeans represent grasses and legumes. Loblolly pine and sweetgum represent the conifer and broadleaf groups and are competitive species. Our focus was the documentation of CO₂ effects on growth and on photosynthesis and water use efficiency, which are thought to most significantly modify growth under conditions of elevated CO₂.

MATERIALS AND METHODS

Experimental Design

The treatments consisted of four CO₂ concentrations: 612 mg m⁻³, 936 mg m⁻³, 1292 mg m⁻³, and 1638 mg m⁻³ (mg m⁻³ = 1.8 × ppm at 25°C) maintained in open top field chambers (described below) and an ambient control plot (no chamber). These five treatments were randomly arranged in each of three replicate blocks, making 15 plots in all. Four species were grown in each plot, each species occupying one quadrant of the plot. Two each of the crop plants, 'Golden Bantam' corn and 'Ransom' soybean, were grown per pot; the tree crops, loblolly pine and sweetgum, were grown one per pot. Six pots occupied each

quadrant. All pots contained 15.5 L of a 1:1:2 mix of sand, Metro-Mix 200³ (W. R. Grace and Co.) and a sandy clay loam. The plants received adequate fertilization and were watered at least once a day. Corn and soybean plants were exposed from planting (1 Aug. 1980) to maturity. Corn was harvested at 11 weeks; soybeans were harvested at 11 weeks to assess vegetative growth and at 18 weeks for final yield. Pine trees, about 1 y old, were actively growing outdoors at a tree production nursery prior to the study period. The trees plus soil were transplanted from 4-L to 16.5-L pots on 4 Aug. 1980. Nondestructive measurements were taken at 2 and 12 weeks, and harvest occurred at 13 weeks. Bare-rooted sweetgum trees, also about 1 y old, were taken from cold storage and planted in similar pots in the various CO₂ atmospheres on 5 Aug. 1980. Nondestructive measurements were made at 2 and 10 weeks, and harvest occurred at 12 weeks.

Measurements

At the harvests, plants were divided into leaf, stem, and root portions, and the parts were dried at 55 ± 5°C for 48 h prior to weighing. Measurements of harvestable yield for soybeans (pod, seed number, and weight) and for corn (ear number, size, and weight) were also taken. Seeds were analyzed for protein, fiber, and oil content by the micro-Kjeldahl method for protein N; the Tecator Fibertec System for fiber; and the Tecator Refatec System for oil (Assoc. of Official Anal. Chem., 1970). Leaf diffusive conductance and net photosynthesis of intact leaves of corn, soybean, and sweetgum were determined throughout daylight hours using a steady state minicuvette system (Bingham et al., 1980). Minicuvette conditions were controlled at 25 ± 0.1°C and 70 ± 1% relative humidity, and a photon flux density range of 1600–1800 μmol m⁻² s⁻¹ was maintained with supplemental light provided by 1000-W multivapor lamps with Plexiglas[®] ultraviolet shields. Carbon dioxide level was set equal to the level present in a given treatment. Measurements were made on the ear leaf of corn at the early kernel development stage, and on recently fully expanded leaves of soybean and sweetgum. The soybean plants were at the pod-filling stage during measurements. Gas exchange values are those of both leaf surfaces being measured jointly, and the results are expressed on a single surface-leaf area basis. Water use efficiency was calculated as milligrams CO₂ fixed per gram of water consumed. Wood volume for the tree species was calculated using the length and average mainstem diameter (measured at 10-cm intervals) as follows:

$$\text{wood volume} = (\text{mainstem length})(\text{mainstem diameter})^2/4.$$

The design was a randomized complete block and data were analyzed according to standard analysis of variance and regression techniques (Snedecor & Cochran, 1967).

Exposure System

A 12.7 Mg liquid CO₂ receiver equipped with a low-temperature, air-cooled condensing unit and vaporizers served as a CO₂ supply reservoir. Gas was delivered through copper tubing past a solenoid valve to a custom-made, high-volume dispensing manifold. The manifold consisted of three high-pressure regulators, each with three

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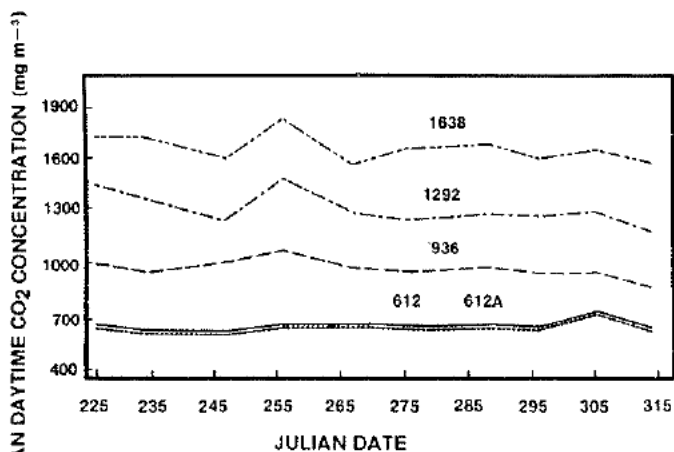


Fig. 1.—Mean daytime CO₂ concentrations by Julian date for the five treatments. Values were averaged from readings taken at 2-h intervals from 0600 to 2000 h every 10 d for 90 d.

single-stage line regulators and flow meters. Each flow meter provided two calibrated ranges, 0.708–11.320 and 7.245–36.224 L min⁻¹. A 0.95-cm (three-eighths inch) Impolene[®] (polyallomer, black; Gould Imperial-Eastman) tube led from each flow meter to the inlet of the exposure chamber.

The open top exposure chamber (Heagle et al., 1973, 1979; Rogers et al., 1983) was essentially a cylindrical, Al frame 3 m wide by 2.4 m high, covered with 2.03 × 10⁻⁴ m (8 mil) clear plastic film Roll-A-Glass[®] (Tenneco, Livingston Coating Corp., Charlotte, N.C.). This material nonselectively transmits approximately 94% of all wavelengths of light when new, and from 88% (washed) to 80% (unwashed) after one season's use (W. Cure, personal communication). The bottom half of each chamber cover was double-walled; the inner wall was perforated with 2.5-cm holes for gas distribution into the chamber. Carbon dioxide from the receiver was injected ahead of a 559 W axial fan mounted in a metal box equipped with a particulate filter, and mixing occurred in the box and delivery duct prior to chamber entry. Air speed (three changes of air per minute) was sufficient to hold temperature in the chamber to within at least 2°C of the ambient temperature and to assure true CO₂ concentration within the canopy. Since CO₂ was added in increments to ambient air, natural daily and seasonal fluctuations in concentration were maintained. Mean daytime CO₂ concentrations for the five treatments are shown in Fig. 1.

Polystyrene disc filter holders with custom-made glass fiber filters served as sampling intakes for the monitoring system and were located 1 m from the ground in the center of each of the 15 plots. Impolene lines delivered sample air to the sampling manifold in the field laboratory at 5 L min⁻¹. Each plot was monitored for 2 min every 20 min. Samples were drawn by a Metal Bellows pump through a flow meter and solenoid bank in which the solenoids were actuated by a digital timer such that one line was always being sampled while the remaining ones were being purged. A second pump diverted the current sample through a nondispersive Infrared Gas Analyzer (Horiba PIR 2000) with N serving as reference, and through a Dew Point Hygrometer (EG & G International, Inc., Model 880).

RESULTS

Effect on Growth of Field Crops

Growth of corn plants under elevated atmospheric CO₂ concentrations was increased, compared with plants grown at ambient levels (Table 1). Significantly greater growth was observed for most plant components at 936 mg m⁻³ CO₂; higher concentrations had little further stimulatory effect. Leaf dry matter did not appear to contribute to the total growth response. The greatest relative effect on the vegetative plants was observed in roots, then in stems, then in leaves. Among aerial parts, dry matter partitioning favored the ears slightly over the leaves and stems.

The effects of elevated CO₂ on the components of yield for corn plants are presented in Table 2. The marginal C (C fixed in excess of that fixed at 612 mg m⁻³; Gifford, 1980) in the reproductive structures appeared as both greater dry weight per ear and as a trend for greater average number of ears per plant, although the latter was not statistically significant. Seed quality (i.e., fat, protein, fiber, and moisture content) was not appreciably affected by CO₂ concentration (Table 3).

Increased dry matter accumulation was also observed in soybean plants grown under elevated atmospheric CO₂. Corn did not respond to CO₂ concentrations above 936 mg m⁻³; soybeans showed further increases in leaf and stem dry matter accumulation in the highest treatments (Table 1). Growth of all plant parts was stimulated by elevated CO₂, and the relative ranking of

Table 1—Growth of corn and soybean plants grown 11 weeks in ambient plots (612A) and open top field chambers under various CO₂ concentrations.†

	CO ₂ concentration					Standard error
	612A	612	936	1292	1638	
	mg m ⁻³					
	Corn					
Roots (grams dry wt plant ⁻¹)	8.7 a‡	7.4 a	15.8 c	12.4 b	15.1 bc	1.0
Leaves (grams dry wt plant ⁻¹)	9.2 a	11.1 ab	12.8 b	12.0 b	13.1 b	0.6
Stems (grams dry wt plant ⁻¹)	30.9 a	34.3 a	46.1 b	43.5 b	50.2 b	2.6
Total ears (grams dry wt plant ⁻¹)	27.6 a	32.5 a	45.5 b	48.6 b	44.8 b	3.0
Leaf area (m ² plant ⁻¹)	0.16 a	0.19 b	0.26 c	0.22 b	0.27 c	0.02
	Soybean					
Roots (grams dry wt plant ⁻¹)	6.3 a	5.1 a	10.0 b	10.5 b	12.8 b	0.9
Leaves (grams dry wt plant ⁻¹)	9.8 a	9.6 a	13.4 b	15.8 c	17.9 d	0.5
Stems (grams dry wt plant ⁻¹)	9.4 a	8.7 a	14.7 b	18.3 c	18.7 c	0.9
Total pods (grams dry wt plant ⁻¹)	17.3 a	18.0 a	26.9 b	29.4 b	27.9 b	1.4
Leaf area (m ² plant ⁻¹)	0.21 a	0.24 ab	0.27 bc	0.30 c	0.31 c	0.01

† For corn, n = 6 for root dry wt; n = 18 for leaf, stem, and ear dry wt; For soybean, n = 6 for all variables.

‡ Entries followed by the same letter within a row are not significantly different according to the Waller-Duncan k-ratio t-test.

Table 2—The components of yield for corn plants (week 11) and soybean plants (week 18) grown in ambient plots (612A) and open top field chambers under various CO₂ concentrations. †

CO ₂	Corn			Soybean		
	Market-able ear dry wt per plant	Ears per plant	Dry wt per ear	Seed dry wt per plant	Seeds per plant	Dry wt per seed
mg m ⁻³	g		g	g		mg
612A	27.5 b†	1.5 a	21.9 b	17.0 a	113.6 a	150 a
612	32.5 b	1.5 a	26.8 ab	21.4 a	131.0 a	163 b
936	45.6 a	1.6 a	30.5 ab	27.4 b	169.4 b	162 b
1292	48.6 a	1.7 a	31.1 ab	33.2 c	191.4 b	174 b
1638	44.8 a	1.5 a	33.3 a	32.4 bc	193.4 b	168 b
Standard error	3.0	0.2	3.0	1.8	10.4	4

† n = 18.

‡ Entries followed by the same letter within a column are not significantly different according to the Waller-Duncan *k*-ratio *t*-test.

treatment effects among plant parts was similar to that of corn (roots > stems > leaves). However, unlike corn, soybean plants partitioned relatively less marginal C fixed by week 11 into reproductive structures than any other plant parts.

The increase in soybean seed yield observed in high CO₂ treatments was due entirely to greater numbers of seeds per plant rather than greater seed size (Table 2). Chemical analysis indicated that the quality of this seed was unaffected by CO₂ treatment (Table 3), and variability tests described elsewhere confirmed this observation (Rogers et al., 1981).

Effects on Growth of Tree Species

Precise total growth measurements over the experimental period were not possible for pine or sweetgum, because these trees were already 1 y old when CO₂ treatments were imposed. Even though the dry weight data for pine plant parts, therefore, represent the combined growth of two seasons, effects of the CO₂ treatments present during only the second season were apparent. Root, stem, and needle dry weights all confirmed the growth-enhancing effect of continuous exposure to elevated CO₂ concentrations to the level of 936 mg m⁻³ (Table 4). Treatments above 936 mg m⁻³ had little further effect. Furthermore, dry weights of roots, stems, and needles at 1638 mg m⁻³ CO₂ were 162%, 138%, and 120%, respectively, of corresponding dry weights of 612 mg m⁻³ CO₂-grown plants, a ranking similar to the corn and soybean results.

Nondestructive measurements for pine were made at weeks 2 and 12 of treatment and should, therefore, reflect changes occurring only during exposure to the CO₂ treatments. Pine stem diameter, wood volume, and height over only 10 weeks of exposure showed a trend (not statistically significant) towards continuously increasing responses to CO₂ (Table 5). For pine trees, only differences in height were significant.

Sweetgum trees were exposed to elevated CO₂ concentrations for 8 weeks. In spite of variability and the short exposure period, trends were noted in the dry matter response of sweetgum plant parts (Table 4), as well as in stem diameter and wood density (Table 5).

Table 3—Seed quality of corn and soybean plants grown in ambient plots (612A) and open top field chambers at various CO₂ concentrations. †

CO ₂	Moisture	Fat	Protein		Crude fiber
			g/kg		
mg m ⁻³					
Corn					
612A	68 a†	43 a	191 a		31 a
612	69 a	43 a	172 a		31 a
936	65 a	40 a	165 a		24 a
1292	65 a	51 a	166 a		24 a
1638	65 a	49 a	171 a		27 a
Standard error	01	05	12		02
Soybean					
612A	62 a	187 a	342 a		50 a
612	62 a	201 b	433 a		50 a
936	64 a	198 ab	425 a		51 a
1292	63 a	197 ab	378 a		51 a
1638	63 a	194 ab	412 a		48 a
Standard error	02	01	68		02

† n = 6.

‡ Entries followed by the same letter within a column are not significantly different according to the Waller-Duncan *k*-ratio *t*-test.

Table 4—Dry weight of plant parts of 1-y-old pine and sweetgum trees grown 12 weeks in ambient plots (612A) or in open top field chambers under various CO₂ concentrations. †

CO ₂	Pine			Sweetgum		
	Root	Stem	Needle	Root	Stem	Leaf
mg m ⁻³	g					
612A	--	31.7 ab†	48.4 a	--	26.1 a	29.5 a
612	33.4	30.4 a	51.7 a	29.1	35.1 a	38.7 ab
936	--	36.6 bc	63.6 b	--	30.6 a	36.2 ab
1292	--	40.2 c	64.9 b	--	35.2 a	44.3 ab
1638	54.0	42.0 c	62.0 b	44.8	44.8 a	54.9 b
Standard error	1.6	1.8	2.8	2.7	5.0	5.4

† n = 6 for root dry wt; n = 18 for all other variables.

‡ Entries followed by the same letter within a column are not significantly different according to the Waller-Duncan *k*-ratio *t*-test.

Table 5—Percentage increase† in nondestructive growth indices and final wood density of 1-y-old loblolly pine and sweetgum trees grown in ambient plots (612A) or in open top field chambers under varying CO₂ concentrations. ‡

CO ₂	Stem diameter	Wood volume	Height	Wood density
mg m ⁻³	kg m ⁻³			
Loblolly pine				
612A	74 a§	209 a	21 a	578 a
612	65 a	203 a	28 ab	599 a
936	83 a	258 a	42 bc	576 a
1292	83 a	273 a	39 abc	567 a
1638	89 a	323 a	55 c	577 a
Standard error	6.8	40.2	6.2	32
Sweetgum				
612A	50 a	125 a	39 a	773 b
612	49 a	176 a	80 a	634 a
936	95 b	294 a	84 a	816 bc
1292	92 b	264 a	77 a	842 bc
1638	78 ab	256 a	77 a	910 c
Standard error	10	47	22	40

† Final-Initial/Initial × 100; Initial = 2 weeks for both species; Final = 12 weeks for pine and 10 weeks for sweetgum trees.

‡ n = 18.

§ Entries followed by the same letter within a column are not significantly different according to the Waller-Duncan *k*-ratio *t*-test.

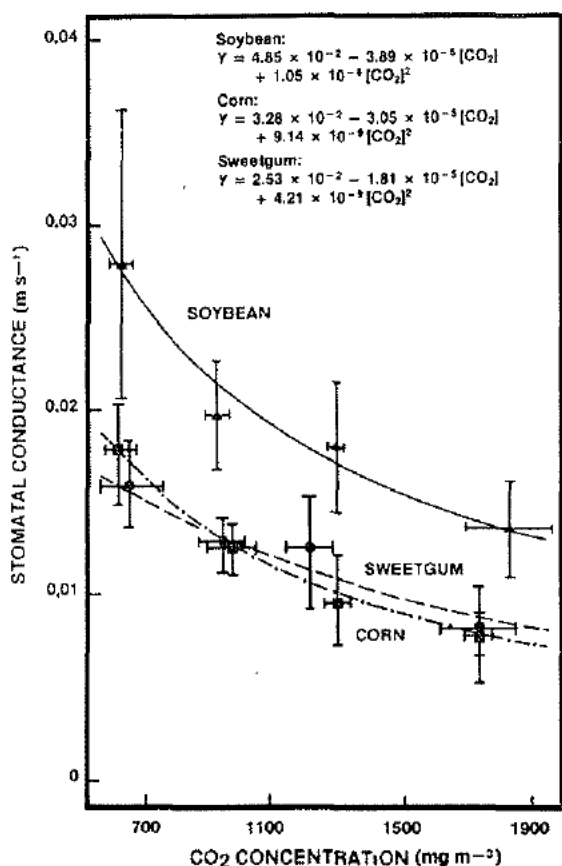


Fig. 2—Stomatal conductances of soybean, corn, and sweetgum at various CO_2 concentrations. Vertical and horizontal bars indicate \pm one standard deviation for conductance and CO_2 concentrations. Each point represents from 4 to 32 readings taken throughout the day.

Physiological Measurements

Stomatal conductance values, measured on recently fully expanded leaves of sweetgum, of soybean during the pod-filling stage and on the ear leaf of corn during early kernel development stage all displayed a similar decrease in enriched CO_2 atmospheres (Fig. 2). With soybean, the most dramatic decrease was observed between ambient and $936 \text{ mg m}^{-3} \text{ CO}_2$, with smaller decreases in higher CO_2 treatments. Conductance for corn was much lower than for soybean under similar conditions, and its response to CO_2 concentration was also curvilinear (Fig. 2). Data for sweetgum approached linearity. Thus, the species' differences in conductance decreased with increasing CO_2 concentration.

Gas exchange measurements (Fig. 3) show the increase in photosynthesis with increasing CO_2 concentration expected for soybean and sweetgum plants, which assimilate CO_2 via the Calvin cycle (so-called "C3" plants) and the lack of response for corn, which assimilates CO_2 via the 4-carbon dicarboxylic acid cycle (a "C4" plant) (Black et al., 1969). Water use efficiencies for the three species appear in Fig. 4. For sweetgum and soybean, this agronomic index increased in high CO_2 atmospheres, because photosynthetic rates increased and transpiration rates decreased in those treatments. Due to the lack of photosynthetic response for corn, the increased water use efficiency of this species was attributed to lowered transpiration alone.

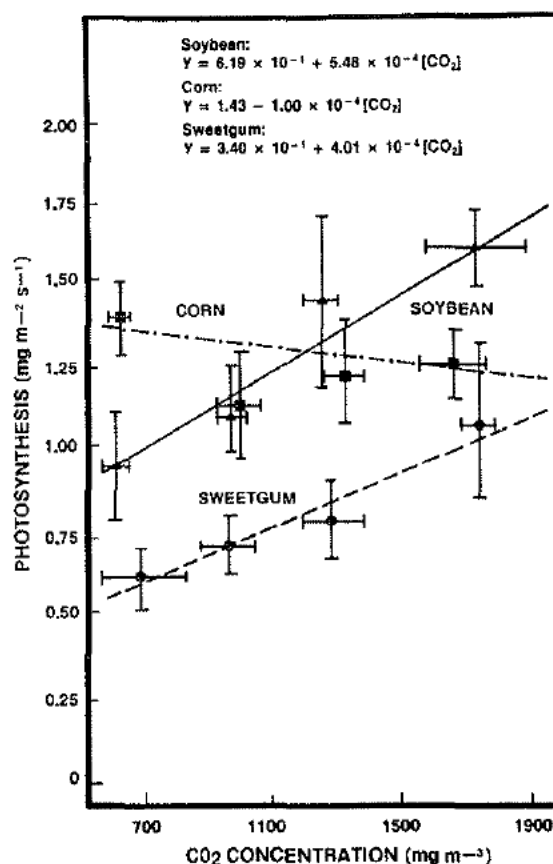


Fig. 3—Net photosynthesis at various CO_2 concentrations for soybean, corn, and sweetgum. Vertical and horizontal bars indicate \pm one standard deviation for photosynthetic rate and CO_2 concentration. Each point represents from 4 to 28 readings taken throughout the day.

DISCUSSION Chamber System

Our goal in this and subsequent studies was an accurate assessment of probable crop behavior as global atmospheric CO_2 concentration rises. This paper reports on the first use of field-scale test atmospheres to study the growth of several crop species exposed for extended periods in known CO_2 concentrations under conditions close to field conditions. Most of the variables recorded confirmed the similarity of conditions between the ambient plots and ambient chambers. Differences in dry matter accumulation of plant parts, in seed quality, and in the components of yield of the annual crops were not statistically significant, except for slightly smaller soybean seed size and greater oil content in the ambient plot and slightly decreased leaf area for corn (Tables 1, 2, and 3). Wood density was greater for sweetgum in the ambient plot than in the ambient chamber, but otherwise, the chambers had little apparent effect on the growth of the two tree species (Tables 4 and 5). The differences that were recorded are scattered and do not suggest a patterned response to the presence of the chamber, and we believe they are errors that occasionally result from use of multiple comparison tests of significance. The system, therefore, provides the most valid conditions reported to date in which to run dose-response field studies of CO_2 enrichment and to evaluate the physiological bases for these responses.

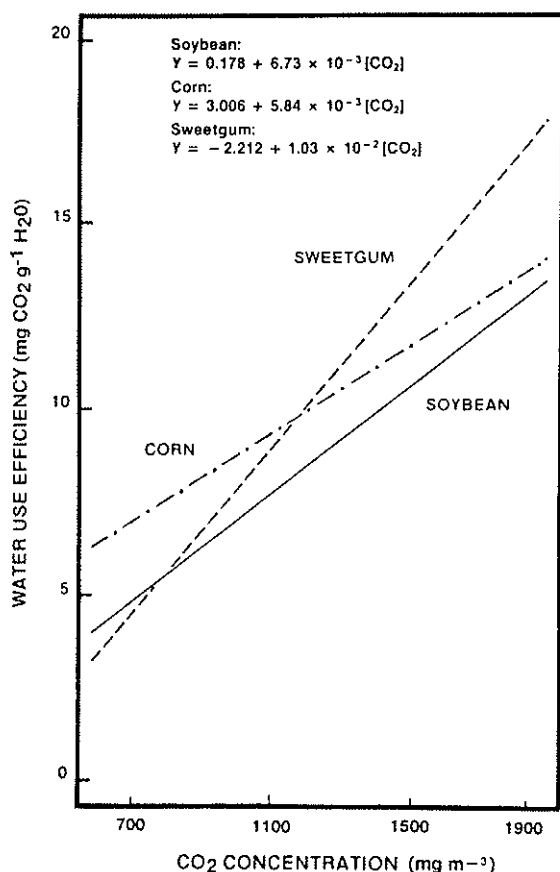


Fig. 4—Least squares fits for water use efficiencies calculated for samples in Fig. 2 and 3.

Plant Responses

The partitioning of assimilate in CO_2 treatments above ambient favored roots very slightly for all four species studied (Tables 1 and 4). Similar observations were made by Imai and Murata (1976) for rice (*Oryza sativa* L.) but not for corn, and by Kriedemann et al. (1976) for *Vitis* but not for *Leea* grown under high temperatures. Furthermore, root/shoot ratios of ponderosa pine (*Pinus ponderosa* Laws.) and blue spruce (*Picea pungens* Engelm.) seedlings were shown to be unaffected by $2160 \text{ mg m}^{-3} \text{ CO}_2$ for 12 months (Tinus, 1972) and treatments of very high CO_2 for up to three months were without effect on the root/shoot ratio of Douglas fir (*Pseudotsuga menziesii*) (Leadem, 1979).⁴ Root/shoot ratios were actually decreased in CO_2 -enriched wheat plants (*Triticum aestivum* L.) grown under both adequate and limiting moisture conditions (Gifford, 1977, 1979a). As suggested by Gifford (1980), there is probably a strong interaction between the effect of CO_2 concentration and other environmental variables on the partitioning of the marginal C.

Our results with the crop species grown in open top field chambers confirm in general the findings from controlled environment studies (Patterson & Flint, 1980) and from glasshouse studies (Imai & Murata, 1976; Wong, 1979, 1980; Carlson & Bazzaz, 1980) concerning the relatively greater C assimilation and growth

responses of C3 plants and the relatively greater stomatal response of C4 plants to CO_2 enrichment. When attempting to relate instantaneous physiological measurements to overall crop behavior, many factors must be considered. Leafiness may be much more important than assimilation rate per unit leaf area, and treatments promoting early differences in leaf expansion may thereby greatly influence final productivity (Kramer, 1980; Neales & Nicholls, 1978). In this study, leaf area was observed to be higher for soybeans at 5 weeks (data not shown), and by 11 weeks was approximately 28% greater in the 1638 mg m^{-3} treatment than in the ambient chamber (Table 1). For corn, on the other hand, there was only a trend towards increased leaf area in all treatments at or above 936 mg m^{-3} . In his comparison of C3 [cotton (*Gossypium hirsutum* L.)] and C4 (corn) responses to CO_2 enrichment at four N concentrations, Wong (1979) found a 60% increase in leaf area for cotton and only a 10%, nonsignificant increase in corn leaf area at 1152 mg m^{-3} vs. 594 mg m^{-3} .

A related consideration is the possible effect of CO_2 concentration on leaf area duration. In this study, with only one, short season's growth, senescence appeared to occur similarly for both crop species in all treatments, although Chang (1975) reported hastened senescence in cotton plants grown in elevated CO_2 . In spite of late bud break, senescence appeared to occur normally for sweetgum. However, pine trees in the higher CO_2 treatments continued active growth after those in the ambient control chambers were becoming dormant in late October.

In general, measurements of net photosynthesis and conductance performed on leaves at or near the top of the canopy related well to growth responses to CO_2 treatments. Photosynthesis per unit leaf area increased linearly for the two C3 species measured (soybean and sweetgum), whereas corn showed no statistically significant response (Fig. 3). These results are in agreement with the measurements of Carlson and Bazzaz (1980) in which photosynthesis for soybean and sunflower (*Helianthus annuus* L.) grown under natural light conditions was stimulated by elevated CO_2 , and that of corn was not. However, in the latter study, growth of corn was also unaffected; in the present study, growth was enhanced by about 50% by all CO_2 concentrations at or above 936 mg m^{-3} . This increase in corn growth may have been due in part to a small cumulative effect of increased leaf area (Table 1), but probably more important was the decrease in stomatal conductance (61% at 1638 mg m^{-3}) and transpiration rate, and increased water use efficiency observed in elevated CO_2 treatments (Fig. 2 and 4). For the C3 species, however, there was a pronounced enhancement by CO_2 of C fixation rates (68 and 77% for soybean and sweetgum, respectively, at 1638 mg m^{-3}) and a lesser effect (45 and 54%, respectively) on conductance. For these species, therefore, CO_2 enhancement of leaf expansion, photosynthetic rate per unit area, and increased water use efficiency probably all contributed significantly to greater dry matter production.

Our work with the tree species, which must be considered preliminary, demonstrates the potential usefulness of field studies of longer duration on the growth responses of woody species to elevated CO_2 . Little other such work has been done. Krizek et al. (1971) reported

⁴C. L. Leadem. 1979. Effects of carbon dioxide and day length on growth, development and hardiness of Douglas fir. Ph.D. Dissertation. University of British Columbia, Vancouver.

greater node number, stem length, branching, and leaf area of birch (*Betula pendula* Roth) and crabapple [*Malus toringoides* (Rehder) Hughes] seedlings grown for 4 weeks in 3600 mg m⁻³ CO₂. Growth of Douglas fir was observed to increase at 1800 mg m⁻³ and to decrease at higher CO₂ concentrations in controlled environment experiments up to 12 weeks in duration (Leadem, 1979).⁴ Funsch et al. (1970) reported a doubling of height, stem diameter, and crown width for white pine (*Pinus strobus* L.) grown 4 months in 1800 mg m⁻³ CO₂. Tinus (1972) reported growth data for ponderosa pine and blue spruce seedlings cultured at ambient and at 2160 mg m⁻³ CO₂ in a greenhouse with artificially extended long photoperiods. Growth responses of these two species at 12 months appeared similar, but observations made over several natural seasons may be required to determine possible species-specific changes in the timing of reproductive cycles or dormancy. There is a need to document differences among individual tree species in direct response to CO₂ enrichment.

Another prerequisite for accurately anticipating the response of mixed stands to CO₂ enrichment is knowledge of relative sensitivities of species to other environmental stresses under conditions of high CO₂ (Botkin et al., 1973). In both agricultural and natural ecosystems, suboptimal levels of some environmental factor(s) such as water, temperature, nutrients, or light are generally present. The relative enhancement of plant growth by CO₂ has been shown to vary in relation to these, at least for some species (Gifford, 1979b, 1980). Our ongoing and future studies include improvement of our field-oriented methodology so as to document CO₂ × stress interactions on plant development.

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LITERATURE CITED

- Association of Official Analytical Chemists. 1970. Official methods of analysis. 11th Ed. Assoc. of Official Anal. Chem., Washington, D.C.
- Bingham, G. E., P. I. Coyne, R. B. Kennedy, and W. L. Jackson. 1980. Design and fabrication of a portable minicuvette system for measuring leaf photosynthesis and stomatal conductance under controlled conditions. UCRL-52895. Lawrence Livermore Laboratory, Livermore, Calif.
- Black, C. C., T. M. Chen, and R. H. Brown. 1969. Biochemical basis for plant competition. *Weed Sci.* 17:338-344.
- Bolin, B. 1977. Changes of land biota and their importance for the carbon cycle. *Science* 196:613-615.
- Botkin, D. B., J. F. Janak, and J. K. Wallis. 1973. Estimating the effects of carbon fertilization on forest composition by ecosystem simulation. p. 328-344. *In* G. M. Woodwell and E. V. Pecan (ed.) Carbon and the biosphere. National Technical Information Service, Springfield, Va.
- Carlson, R. W., and F. A. Bazzaz. 1980. The effects of elevated CO₂ concentrations on growth, photosynthesis, transpiration and water use efficiency of plants. p. 609-623. *In* J. J. Sigh and A. Deepak (ed.) Environmental and climatic impact of coal utilization. Academic Press, New York.
- Chang, C. W. 1975. Carbon dioxide and senescence in cotton plants. *Plant Physiol.* 55:515-519.
- Funsch, R. W., R. H. Mattson, and G. R. Mowry. 1970. CO₂-supplemented atmosphere increases growth of *Pinus strobus* seedlings. *Forest Sci.* 16:459-460.
- Gifford, R. M. 1977. Growth pattern, carbon dioxide exchange and dry weight distribution in wheat growing under differing photosynthetic environments. *Aust. J. Plant Physiol.* 4:99-110.
- Gifford, R. M. 1979a. Growth and yield of CO₂-enriched wheat under water-limited conditions. *Aust. J. Plant Physiol.* 6:367-378.
- Gifford, R. M. 1979b. Carbon dioxide and plant growth under water and light stress: implications for balancing the global carbon budget. *Search* 10:316-318.
- Gifford, R. M. 1980. Carbon storage by the biosphere. p. 167-181. *In* G. I. Pearman (ed.) Carbon dioxide and climate: Australian research. Australian Academy of Science, Canberra.
- Heagle, A. S., D. E. Body, and W. W. Heck. 1973. An open-top field chamber to assess the impact of air pollution on plants. *J. Environ. Qual.* 2:365-368.
- Heagle, A. S., R. B. Philbeck, H. H. Rogers, and M. B. Letchworth. 1979. Dispensing and monitoring ozone in open-top field chambers for plant effects studies. *Phytopathology* 69:15-20.
- Imai, K., and T. Murata. 1976. Effect of carbon dioxide concentration on growth and dry matter production of crop plants. I. Effects on leaf area, dry matter, tillering, dry matter distribution ratio, and transpiration. *Proc. Crop Sci. Soc. Jpn.* 45:598-606.
- Kramer, P. J. 1980. The role of physiology in crop improvement. p. 51-62. *In* Richard C. Staples and Ronald J. Kuhn (ed.) Linking research to crop production. Plenum Press, New York.
- Kramer, P. J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience* 31:29-33.
- Kriedemann, R. E., R. J. Sward, and W. J. S. Downton. 1976. Vine response to carbon dioxide enrichment during heat therapy. *Aust. J. Plant Physiol.* 3:605-618.
- Krizek, D. T., R. H. Zimmerman, H. H. Klueter, and W. A. Bailey. 1971. Growth of crabapple seedlings in controlled environments: effect of CO₂ level, and time and duration of CO₂ treatment. *J. Am. Soc. Horticult. Sci.* 96(3):285-288.
- Neales, T. F., and A. O. Nicholls. 1978. Growth responses of young wheat plants to a range of ambient CO₂ levels. *Aust. J. Plant Physiol.* 5:45-59.
- Patterson, D. T., and E. P. Flint. 1980. Potential effects of global atmospheric CO₂ enrichment on the growth and competitiveness of C3 and C4 weed and crop plants. *Weed Sci.* 28:71-72.
- Pearman, G. I. 1980. The global carbon cycle and increasing levels of atmospheric carbon dioxide. p. 11-20. *In* G. I. Pearman (ed.) Carbon dioxide and climate: Australian research. Australian Academy of Science, Canberra.
- Rogers, H. H., G. E. Bingham, J. D. Cure, W. W. Heck, A. S. Heagle, J. M. Smith, K. A. Surano, and J. F. Thomas. 1981. 1980 Report: field studies of plant responses to elevated carbon dioxide levels. Prepared for the Dep. of Energy, Washington, D.C.
- Rogers, H. H., W. W. Heck, and A. S. Heagle. 1983. A field technique for the study of plant responses to elevated carbon dioxide concentrations. *J. Air Pollut. Control Fed.* 33:42-44.
- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa University Press, Ames.
- Stuiver, M. 1978. Atmospheric carbon dioxide and carbon reservoir changes. *Science* 199:253-258.
- Tinus, R. W. 1972. CO₂-enriched atmosphere speeds growth of ponderosa pine and blue spruce seedlings. *Tree Planters Notes* 23:12-15.
- Wong, S. C. 1979. Elevated atmospheric partial pressure of CO₂ and plant growth. *Oecologia* 44:68-74.
- Wong, S. C. 1980. Effects of elevated partial pressure of CO₂ assimilation and water use efficiency in plants. p. 159-166. *In* G. I. Pearman (ed.) Carbon dioxide and climate: Australian research. Australian Academy of Science, Canberra.