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Influence of Elevated CO_2 on Growth of Soybean Plants[1]

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ABSTRACT

Continuing use of fossil fuels in industrialized countries has created a need to understand growth responses of major crop species to elevated concentrations of CO_2. An analysis was therefore undertaken of the growth of soybeans [*Glycine max* (L.) Merr. 'Bragg'] grown in pots in open top field chambers at six CO_2 concentrations ranging from 332 $\mu L\ L^{-1}$ (ambient) to 910 $\mu L\ L^{-1}$. Major growth response occurred with the first increments of added CO_2 with a maximum 66% increase in total vegetative dry matter at the 910 $\mu L\ L^{-1}$ CO_2 level. Dry weight increases were proportionate among vegetative plant parts, although the harvest index was found to decrease slightly. Greater absolute growth rates in elevated CO_2 treatments were associated with greater rates of branch and internode elongation, leaf initiation, and leaf expansion. Yield increases represented greater seed numbers per plant rather than larger seeds. Percentage protein of seed decreased with CO_2 enrichment. In the interval from day 5 to 2 weeks after planting, mean relative growth rate (RGR) increased asymptotically with CO_2 concentration. Of the two components of RGR, the mean net assimilation rate (NAR) increased dramatically and mean leaf area ratio (LAR) decreased. In the intervals from week 2 to 7 and from week 7 to 12, RGR became constant across CO_2 treatments as the positive response of NAR and the negative response of LAR became less pronounced. Both RGR and NAR fell through the vegetative growth phase at each CO_2 level. The adjustment in LAR resulted from a decrease in specific leaf area while leaf weight ratio remained unaffected by CO_2.

Additional index words: **Growth analysis, Growth characteristics, Morphology.**

INCREASING concentrations of global atmospheric CO_2 resulting from massive combustion of fossil fuels (Stuiver, 1978) has generated interest in evaluating the long term implications for the growth and yield of crop plants. The CO_2 concentration influences the rate of dry matter production through both its role as regulator of stomatal aperture and its role as biochemical substrate for photosynthesis. But the relationship between photosynthesis, growth, and yield is not straightforward (Evans, 1975; Kramer, 1981); hence the need for evaluating the influence of CO_2 concentration on growth itself.

The purpose of this experiment was to characterize the growth and development responses of soybean [*Glycine max* (L.) Merr. 'Bragg'] to increasing atmospheric CO_2 concentration in open top chambers (Rogers et al., 1983a, 1983b) under field conditions.

MATERIALS AND METHODS

Exposure System

The open top chamber (Rogers et al., 1983a, b) was a cylindrical (3 m diam × 2.4 m high) aluminum frame covered with PVC film "Roll-A Glass"[3] with a 45 degree frustum (2.1m diam opening) attached at the top. The bottom half of the cylinder was double-walled, the inner wall perforated for uniform air distribution into the chamber. A 0.75 HP axial fan mounted in a sheet metal plenum box with a particulate filter supplied air at 1.06 $m^3\ s^{-1}$. Pure CO_2 was injected into the air stream ahead of the fan to assist thorough mixing. A time-shared monitoring system sequentially sampled each of the 14 test plot atmospheres for 50 s (30 s settling time and 20 s of rapid sampling). Air samples entered the 0.63 cm O.D. polyallomer, black Impolene (Gould-Imperial Eastman) delivery lines through a 4 L damping vessel with a glass wool filter. A bank of three-way solenoids controlled by a microcomputer directed the flow streams, one at a time, to the CO_2 analyzer (Horiba PIR2000). Data were automatically acquired and the sampling manifold controlled by a Digital Equipment Co. (DEC) LSI-11 microcomputer. The most recent scan of CO_2 values was available in digital form to assist adjustment of flow rates into the chambers.

Experimental Procedure

Soybean plants were grown from seed in pots in open top chambers (Rogers et al., 1983a, b) at six different atmospheric CO_2 concentrations: 332, 428, 534, 623, 772, and 910 $\mu L\ L^{-1}$ (seasonal daytime mean). Plants were also grown in plots outside the chambers under ambient atmospheric conditions for comparison. There were two replicates of each treatment, or 14 plots in all. Plants were grown singly in 16.5 L pots containing 15 L of a 1:1:2 mixture by volume of sand, Metro-Mix 220 (W.R. Grace Co.), and a sandy clay loam soil. The 20 pots occupied the central portion of the 3m-diam chamber, leaving an access around the perimeter of the chamber area of about 44 cm. Therefore the plant density was approximately 5.7 plants m^{-2}. The seeds were inoculated with a commercial *Rhizobium* preparation and were watered when tensiometer gauges (Irrometer Co., Riverside, Calif.) within pots reached 25 to 35 centibars (0.025 − 0.035 MPa). A N-free nutrient solution was applied weekly (Israel, 1981).

Destructive harvesting took place at 2, 7, 12, and 16 weeks after planting, corresponding to seedling, anthesis, early pod fill, and maturity stages. Leaf area was obtained photometrically. The plants were divided into roots, stems plus petioles, leaf blades, pod walls, and seeds. Branch length and branch number were recorded and the plants were dried at 55 ± 5°C for 72 h prior to weighing. Total weight in Table 1 represents vegetative growth, i.e., leaves, stems plus petioles, and roots. A more detailed breakdown of dry matter data is available (Rogers et al., 1982).

Data Analysis

Growth characteristics were calculated for the intervals 5 days to 2 weeks, weeks 2 to 7 and weeks 7 to 12. For calculation of mean relative growth rate (RGR), mean net assimilation rate (NAR), and mean leaf area ratio (LAR) over the intervals, plants in each replicate plot at each CO_2 level were ranked at the beginning and end of each interval in order of descending total dry weight and then paired,

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[3] Mention of trade or company name does not constitute a guarantee or warranty of the product by the USDA, or the North Carolina State Univ. and does not imply their approval to the exclusion of other products which may be suitable.

the largest with largest, etc. Calculations were then made for each pair of plants. These characteristics as well as leaf area ratio (LAR), specific leaf area (SLA), and leaf weight ratio (LWR) at the sampling points at weeks 5, 7, and 12 were calculated according to Kvet et al. (1971).

RGR = kg kg^{-1} (plant) day^{-1}
NAR = g m^{-2} (leaf area) day^{-1}
LAR = m^2 (leaf area) kg^{-1} (plant);
LWR = kg (leaf) kg^{-1} (plant);
SLA = m^2 (leaf area) kg^{-1} (leaf).

For the growth characteristics in the first interval it was assumed that at 5 days all plants weighed 0.142 g dry weight (mean dry weight per seed at planting) and had cotyledonary photosynthetic area of 3.5 cm^2.

Seeds were analyzed for protein, fiber and oil content by the Micro-Kjeldahl Method for protein N, Tecator Fibertec System for fiber and Tecator Refatec System for oil the (Assoc. of Official Anal. Chem., 1970).

The experimental design was a randomized complete block with two replicate blocks of seven CO_2 treatments. The experimental unit was the plot to which CO_2 levels were randomly assigned within each block. Either 10 or 20 plants were harvested at each sampling date, half from each plot at each CO_2 level. For the primary data in Tables 1 and 2 the treatment sum of squares was further partitioned to test for a chamber effect and linear and quadratic regressions on CO_2 concentrations. Significance of the model terms ($\alpha = 0.05$) was tested with an F statistic from the analysis of variance with 1 and 6 df. The R^2 measures the proportion of the treatment sum of squares accounted for by the chamber, linear, and quadratic effects.

RESULTS

Growth, Morphology, and Yield.

Growth enhancement was observed for the soybean plants grown under elevated CO_2 as early as the first sampling at 2 weeks (Table 1). Although the first increments of CO_2 added to the ambient concentration seemed to result in greater increases in growth than subsequent CO_2 increments at all three sampling dates, the quadratic terms in the regression models for total dry weight or leaf area against CO_2 concentration were not statistically significant.

Plants harvested at 12 weeks after planting had

Table 1. Vegetative growth of Bragg soybeans grown in ambient plots and in open top field chambers at various CO_2 concentrations.

	Week 2		Week 7		Week 12				
CO_2	Total dry wt	Leaf area	Total dry wt	Leaf area	Total dry wt	Leaf area	Height	Branch length	Branch no.
µL L^{-1}	g	cm^2	g	cm^2	g	cm^2	cm	cm	
331†	0.40	69	19.7	1 941	70.0	6 261	66	308	18.7
332	0.36	69	24.0	2 870	82.0	7 273	74	349	21.0
428	0.47	85	27.6	2 909	86.4	7 835	80	453	23.2
534	0.51	85	32.2	3 378	118.2	8 750	90	598	27.6
623	0.52	82	34.0	3 189	133.5	8 930	89	581	26.2
772	0.56	83	31.4	2 969	124.3	9 447	89	665	31.6
910	0.61	99	36.6	3 615	140.2	10 419	94	706	34.0
n	10	10	10	10	20	20	10	10	10
$S_{\bar{x}}$‡	0.02	4	2.2	227.35	9.64	179.9	2.7	39.0	1.75
CV	14.0	15	15.6	17.5	14.2	14.8	9.9	16.2	14.8
b_0§	0.40 ± 0.02	69 ± 4	19.7 ± 2.2	2 982	70.6 ± 7.0	6 261 ± 181.6	64.3 ± 2.0	308.1 ± 27.3	18.7 ± 1.3
b_{chamber}	0.009 ± 0.03	4.8 ± 5.2	6.3 ± 2.7	NS	17.3 ± 8.5	1 132.8 ± 220.8¶	12.3 ± 2.3	51.9 ± 41.2	2.7 ± 1.6
b_{linear}	0.37 ± 0.04	35 ± 9	18.0 ± 4.6	NS	100 ± 10	5 151 ± 377	31.0 ± 3.9	1 140 ± 240	22.0 ± 2.9
$b_{\text{quadratic}}$	NS	NS	NS	NS	NS	NS	NS	0.96 ± 0.37	NS
R^2	0.96	0.74	0.88	NS	0.87	0.99	0.95	0.99	0.98

† Ambient plot (no chamber).

‡ $S_{\bar{x}}$ and CV from ANOVA.

§ Curves were fitted against CO_2 added to ambient concentration (332 ppm). Note: linear and quadratic coefficients and their standard errors should be multiplied by 10^{-3}.

¶ Significant F (0.95 level) for chamber effect.

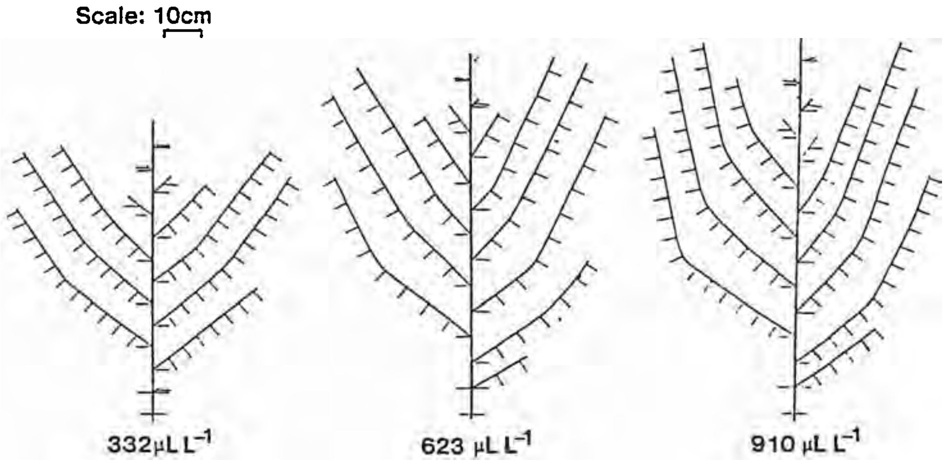

Fig. 1. Schematic diagram of the effects of CO_2 concentration on soybean morphology. Center axis = mainstem; horizontal lines = cotyledonary, primary and mainstem leaves; diagonal lines = secondary branches; lines normal to these = leaves.

Table 2. Reproductive growth and seed composition for Bragg soybeans grown in ambient plots and in open top field chambers at various CO_2 concentrations.

CO_2	Pod dry wt per plant	Pod no. per plant	Harvest index	Seed oil	Seed protein	Seed fiber
$\mu L\ L^{-1}$	g			%		
331†	55.6	117	0.54	16.5	34.2	9.4
332	73.2	126	0.52	16.8	34.0	9.2
428	79.9	138	0.49	17.5	32.6	8.6
534	93.6	169	0.48	16.8	31.8	10.3
623	95.0	170	0.47	18.1	32.1	9.3
772	96.7	168	0.46	18.0	30.7	9.6
910	101.1	185	0.-	17.9	30.4	9.4
n	20	20	20	5	4	4
$S_{\bar{x}}$‡	6.3	18.7	0.01	0.75	0.38	1.02
CV	11.1	11.6	10.30	0.32	0.76	1.78
B_0§	59.5 ± 4.6	117.0 ± 6.7	0.54 ± 0.011	17.34	34.2 ± 0.4	9.34
$b_{chamber}$	21.9 ± 5.4¶	13.6 ± 16.0	−0.037 ± 0.012	NS	−0.71 ± 0.5	NS
b_{linear}	46.1 ± 9.2	121.3 ± 27.4	−0.10 ± 0.02	NS	−5.8 ± 0.8	NS
$b_{quadratic}$	NS	NS	NS	NS	NS	NS
R^2	0.97	0.95	0.97	NS	0.96	NS

† Ambient plot (no chamber).

‡ $S_{\bar{x}}$ and CV from ANOVA.

§ Curves were fitted against CO_2 added to ambient concentration (332 ppm). Note: linear and quadratic coefficients and their standard errors should be multiplied by 10^{-3}.

¶ Significant F (0.95 level) for chamber effect.

attained their maximum values for height and branch elongation and had ceased to initiate any new leaves or branches. Comparison of gross morphologies of 12 week-old plants grown in ambient, 623 and 910 $\mu L\ L^{-1}$ CO_2 (Fig. 1 and Table 1) illustrates the impact of elevated CO_2 on the form of the mature determinate soybean plant. Plants grown in 910 $\mu L\ L^{-1}$ CO_2 initiated at least 2 more mainstem nodes, 30 more leaves, and 13 more (primary plus secondary) branches than did plants in unenriched treatments (Fig. 1 and Table 1). However, mainstem height increments in higher CO_2 concentrations (Table 1) resulted from stimulation of internode elongation as well as from greater node numbers. The mean internode length of the 910 $\mu L\ L^{-1}$ plants was 6.3 cm compared with 5.5 cm in 332 $\mu L\ L^{-1}$ plants. Individual leaf expansion was slightly more rapid in the 3 highest CO_2 concentrations, requiring 6 to 7 days compared with 7 to 8 days in the lower CO_2 atmospheres (data not shown; see Rogers et al., 1982).

Reproductive yield per plant was also enhanced in high CO_2 atmospheres (Table 2). The increases in seed yield per plant with CO_2 enrichment were due to greater numbers of pods rather than greater weight per pod. Harvest index (seed dry weight/total top dry weight) decreased steadily with increasing CO_2. Seed protein as a percentage of seed dry weight decreased with increasing CO_2, although total seed protein per plant increased from 16.2 g at 332 $\mu L\ L^{-1}$ to 18.8 g at 910 $\mu L\ L^{-1}$ (Table 2). A trend towards increased oil concentration with increasing CO_2 was not statistically significant, and seed fiber was apparently unaffected (Table 2). Germination tests revealed no significant differences in germination or early seedling growth due to mother plant pretreatment with CO_2 enrichment.

Analysis of Growth

The RGR and its two component growth characteristics, the NAR and the LAR were plotted for the three vegetative growth intervals in Fig. 2 and 3. By 2 weeks LAR had increased much more in the low CO_2 treatments than in the high CO_2 treatments so that the arithmetic average LAR for the interval was inversely related to CO_2 concentration (Fig. 2). The LAR increased rapidly in the second interval (weeks 2–7) and then decreased in the third (weeks 7–12) but the inverse relationship to CO_2 concentration was maintained, becoming less pronounced with time. The NAR increased significantly with CO_2 concentration

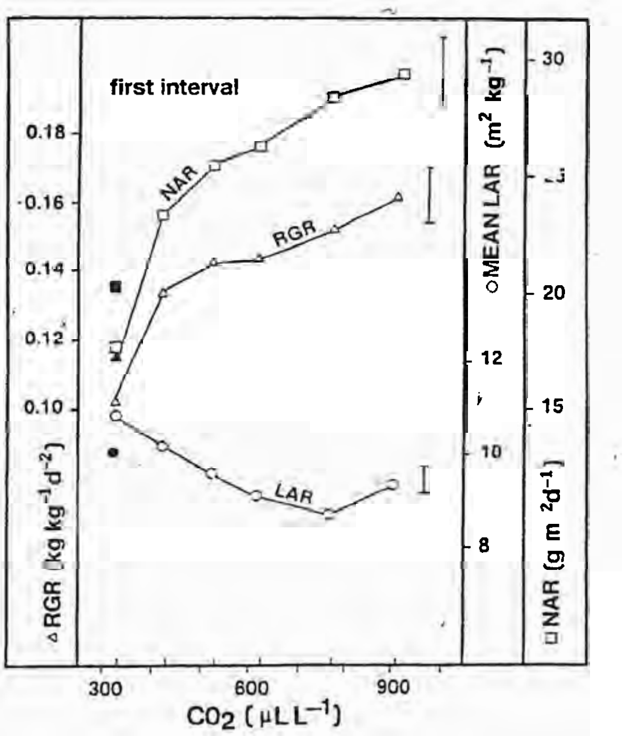

Fig. 2. Mean RGR, NAR, and LAR for soybean plants grown in ambient plots (closed symbols) and open top field chambers (open symbols) at various CO_2 concentrations during the interval day 5 to 2 weeks. Vertical bars denote one standard error.

in the first interval (note the difference in scale for NAR between Fig. 2 and 3), increasing from 17.6 g $m^{-2}day^{-1}$ at 332 μL L^{-1} CO_2 to 29.4 g $m^{-2}day^{-1}$ at 910 μL L^{-1}, a 73% increase. The mean RGR, the product of NAR and LAR, increased from 0.10 to 0.16 or 58%, over the same CO_2 concentration range. While NAR at all CO_2 levels adjusted downwards in the second and third intervals, the decrease with time was greater in the high CO_2 atmospheres so that by the third interval the CO_2 effect was no longer statistically significant. Thus the RGR became constant across CO_2 treatments for most of the vegetative growth phase due to changes in both LAR and NAR.

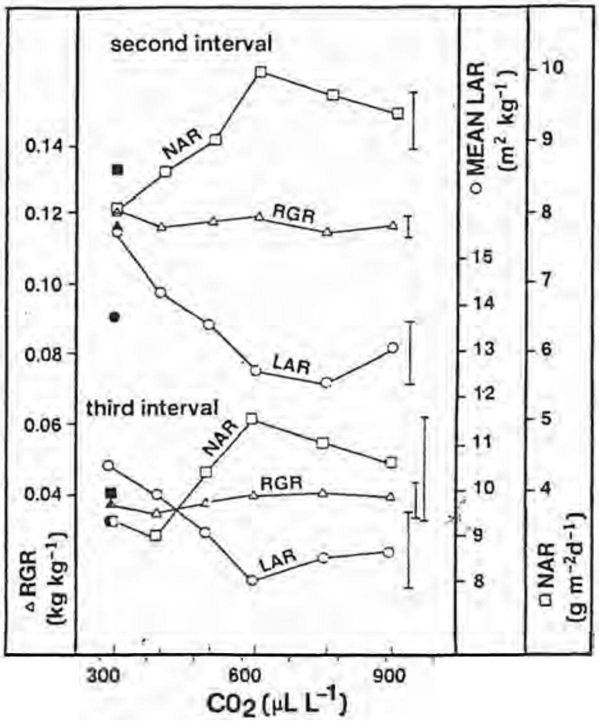

Fig. 3. Mean RGR, NAR, and LAR for soybean plants grown in ambient plots (closed symbols) and open top field chambers (open symbols) at various CO_2 concentrations during the intervals weeks 2 to 7 and weeks 7 to 12. Vertical bars denote one standard error.

The adjustment in LAR occurred through a change in SLA rather than through a change in relative allocation of dry matter to leaves, or LWR. In Fig. 4, data for weeks 2, 7, and 12 show the LWR, although falling with time, remained essentially constant with CO_2 concentration, whereas SLA fell with both time and CO_2 concentration. Since LAR is the product of the other 2 characteristics, the LAR curve assumed the shape of the SLA curve.

In general, the effect of CO_2 on all the growth characteristics diminished as CO_2 concentration increased.

DISCUSSION

We observed a 66% increase in total vegetative dry matter at the 910 μL L^{-1} CO_2 level based on regression values (Table 1). This stimulation of growth after 12 weeks in elevated CO_2 atmospheres is in general agreement with results from other CO_2 enrichment studies with soybeans. Patterson and Flint (1980) grew soybeans for 45 days in growth cabinets and reported 24 and 74% increases at 600 and 1,000 μL L^{-1} CO_2, respectively. Cooper and Brun (1967) obtained 61 and 71% increases for two varieties after 38 days in 350 and 1350 μL L^{-1} CO_2 in growth cabinets within a greenhouse. Hardy and Havelka (1975) reported a 49% increase in total dry matter of soybeans grown in CO_2 enriched atmospheres (800–1200 μL L^{-1}) during reproductive phase. Also Hardman and Brun (1971), who provide the only other season-long CO_2 enrichment study, show a 64% increase in total dry weight of plants grown in the ground at 1200 μL L^{-1} vs. 425 μL L^{-1}. Of the published studies of soybean growth under CO_2 enrichment, our results depart substantially only from those of Mauney et al. (1978) who report a 380% stimulation of total dry matter production at 630 μL L^{-1} vs. 330 μL L^{-1}.

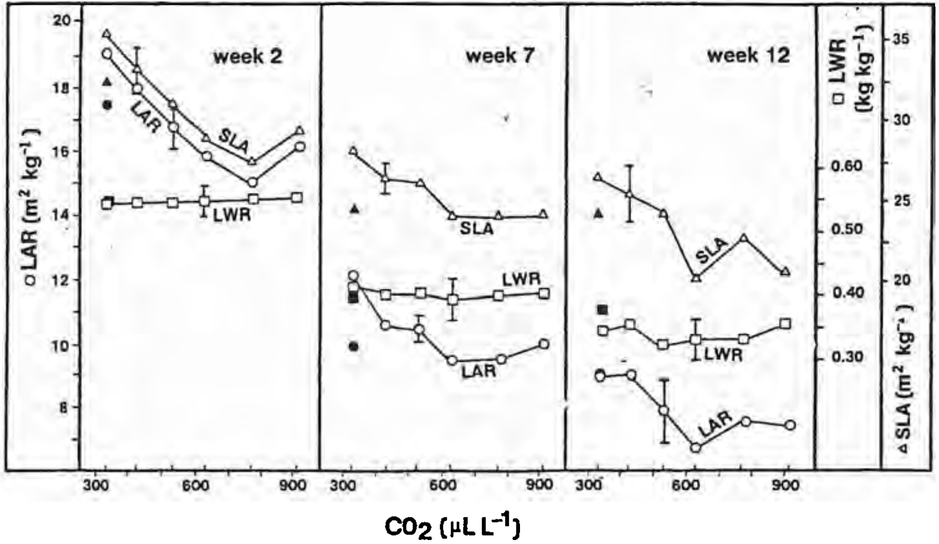

Fig. 4. LAR, LWR, and SLA for soybean plants grown in ambient plots (closed symbols) and open top field chambers (open symbols) at various CO_2 concentrations at 2, 7, and 12 weeks. Vertical bars denote one standard error.

The increased size of the vegetative plant in high CO$_2$ atmospheres was primarily due to higher net assimilation rate (see below) and higher absolute growth rate. The higher growth rate was due to higher rate of leaf initiation, also observed for soybeans in high CO$_2$ growth cabinets by Hofstra and Hesketh (1975). Greater node numbers represent both additional sites for pod initiation and additional leaf area to support pod development. However, a slight delay in anthesis and a slower transition from vegetative to reproductive phase were also observed in higher CO$_2$ treatments. Since flowering puts an upper limit on vegetative growth of determinate soybeans, potential capacity for reproductive development (i.e., leaf area) was increased by the slower transition from vegetative to reproductive growth as well (Tables 1 and 2). Hesketh and Hellmers (1973) have also reported delayed flowering in four other crop species under CO$_2$-enriched growth chamber conditions. Although Cooper and Brun (1967) did not observe any effect of CO$_2$ enrichment on flowering of soybean, the varieties used in their study were indeterminate.

Seed protein values in our experiment, which decreased with increasing atmospheric CO$_2$ (Table 2), are at variance with those of Hardy and Havelka (1975) who reported that CO$_2$ enrichment had no effect on pod N concentration. The N concentration of leaves sampled at week 12 decreased with increasing CO$_2$ (data not shown), a finding in agreement with observations of Hardy and Havelka (1975). Concentrations of P, K, and Ca also decreased in this foliar tissue, but Mg, Fe, Mn, Zn, Cu, and B concentrations were unaffected (see Rogers et al., 1982).

In this study of soybean growth in pots under field chamber conditions the effectiveness of successive increments of added CO$_2$ on the growth characteristics (RGR, NAR, LAR, and SLA) at any interval appeared to diminish at the higher CO$_2$ concentrations (Fig. 2, 3, and 4). In other growth chamber studies where the effects of multiple CO$_2$ concentrations on growth characteristics were observed, asymptotic responses to CO$_2$ enrichment were reported for wheat (*Triticum aestivum* L.) (Neales and Nicholls, 1978) and tomato (*Lycopersicon esculentum*; Hurd and Thornley, 1974), and NAR and RGR were smaller at 900 μL L^{-1} than at 600 μL L^{-1} for asters *Callistephus chinensis* (Hughes and Freeman, 1967; Hughes and Cockshull, 1968). Likewise, the influence of elevated CO$_2$ on the changes with time of these characteristics resembles the results of the above studies for wheat, tomato, and asters as well as for soybeans under greenhouse conditions (Mauney et al., 1978) and growth cabinet conditions (Patterson and Flint, 1980). As in these other studies, the highest values for the growth characteristics were obtained during early development, followed by a gradual decline termed ontogenetic drift (Kvet et al., 1971).

Very early in development, when differences in LAR across CO$_2$ treatments were relatively small, changes in RGR were determined largely by its other component, NAR, which was initially greatly stimulated in high CO$_2$ concentrations (Fig. 1). In the second and third intervals, however, RGR appeared unaffected by CO$_2$. In studies where multiple harvests have permitted estimation of instantaneous values for the growth characteristics, RGR and/or NAR have been shown to be increased by high CO$_2$ initially, only to decrease as fast or faster than for control plants. Such a pattern was described by Neales and Nicholls (1978) for wheat, by Hurd (1968) for tomato, by Hughes and Cockshull (1969) for aster and by Thomas et al. (1975) for tobacco (*Nicotiana tobaccum* L.). In the wheat study (Neales and Nicholls, 1978), the analysis of variance for all data showed no CO$_2$ effect per se, but a highly significant CO$_2$ × time interaction. Such a pattern may underlie the apparently constant RGR calculated over rather long intervals (35 days) in this study. The initial increase and subsequent steeper decline in RGR and NAR observed for high CO$_2$ plants have also been observed for plants treated with high light intensity (Hurd, 1968) or greater daily light integral (Hurd and Thornley, 1974). thus the adjustments in growth characteristics have tended to equalize RGR, at least for CO$_2$ and light treatments, as growth diminishes with time.

This equalizing of RGR occurred through adjustment of both NAR and LAR. The steeper drop in NAR with time in CO$_2$-enriched treatments may have been due to a shading effect, since total leaf area per plant was greater in high CO$_2$ grown plants than in low CO$_2$ grown plants (Table 1). Possibly there were adjustments in CO$_2$ uptake rates in the upper canopy as well, an area which has not been sufficiently investigated. The adjustment in leaf area ratio has been reported for the tomato, wheat, and aster studies referenced above and appears to be a widespread response of plants, raising questions as to the partitioning of assimilate towards leaf area vs. leaf thickness. The decrease in SLA of soybeans with increasing atmospheric CO$_2$ concentration has been related to additional cell layers of the leaf (Hofstra and Hesketh, 1975). This has also been observed for soybean, sweetgum (*Liquidambar styraciflua* L.), and pine (*Pinus taeda* L.) by Thomas and Harvey (1983). These results suggest that as soybean plants develop, two important mechanisms serve to modify or buffer an initially striking growth response to elevated CO$_2$, 1) a dampening of the stimulation of NAR through self shading (and perhaps through a more direct effect on photosynthesis) and 2) a downshift in the LAR resulting from reduced SLA and altered leaf anatomy.

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