

# Relationship of Photosynthetic Rate to Growth and Fruiting of Cotton, Soybean, Sorghum, and Sunflower<sup>1</sup>

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## ABSTRACT

Cotton (*Gossypium hirsutum* L.), sorghum (*Sorghum bicolor* L.), soybean (*Glycine max* L.), and sunflower (*Helianthus annuus* L.) plants were exposed during daylight hours to an atmosphere enriched with CO<sub>2</sub> to 630 ppm (v:v) (HiCO<sub>2</sub>) in a glasshouse. Temperature was controlled continuously to produce a daily maximum of 35 C and a minimum of 21 C. Days were cloudless and long, May to August, in Phoenix, Ariz. Average CO<sub>2</sub> exchange rate (CER) increased 15% for cotton, 2% for sorghum, 41% for soybean, and 7% for sunflower compared to the CER of these species at 330 ppm CO<sub>2</sub> (LoCO<sub>2</sub>). The increase in CER was not statistically significant for sorghum and sunflower. Measurements of relative growth rate (RGR) and net assimilation rate (NAR) showed that the growth rate of all species increased during the juvenile stage (10d-30d) in the enriched atmosphere. RGR and NAR were not higher in the enriched atmosphere after the juvenile stage, but cotton and soybean plants maintained their larger size and greater absolute growth.

Final dry weights of cotton and soybean increased 110 and 380%, respectively, in HiCO<sub>2</sub> compared to LoCO<sub>2</sub>. Lint yield of cotton was increased 180% by HiCO<sub>2</sub> on a per-plant basis and 88% on a unit leaf area basis. Because of growth limitations imposed by terminal flowers, the final size of sorghum and sunflower plants in HiCO<sub>2</sub> was not significantly larger than in LoCO<sub>2</sub>. These results imply that selection for CER will not effectively increase yield of determinate species such as sunflower and sorghum, but may effectively increase yield of indeterminate species such as cotton and soybean, if a sensitive assay for CER can be found.

**Additional index words:** Relative growth rate, Net assimilation rate, CO<sub>2</sub> enrichment, Determinate species, Indeterminate species, *Gossypium hirsutum* L., *Glycine max* L., *Sorghum bicolor* L., *Helianthus annuus* L.

**W**ILL an increase in rate of photosynthesis increase harvestable yield? The question is important to many areas of agricultural research because time involved to establish yield capability in similar genetic stocks is so long. Plant breeders need some assurance that selection for photosynthetic rate is worthwhile before it is attempted. Several reports have questioned the efficiency of breeding for increased photosynthetic rate as a means of increasing yield. Nelson et al. (1975) failed to find a consistent correlation between yield and leaf photosynthesis in field grown tall fescue (*Festuca arundinacea* Schreb.). Heichel and Musgrave (1969) and Musgrave (1974) reported that selection for higher rates of leaf photosynthesis did not increase yield of field grown corn (*Zea mays* L.). Irvine (1975) concluded that differences in photosynthetic rate were not an important determinant for yield differences between cultivars of sugarcane (*Saccharum officinarum* L. and *S. spontaneum* L.).

He stated that "varietal photosynthetic rates and associated leaf characters are unimportant as selection criteria for breeders" of sugarcane.

Hardman and Brun (1971), on the other hand, observed a 43% increase in seed yield of soybean (*Glycine max* L.) due to increased photosynthesis induced by CO<sub>2</sub> enrichment during the entire growing season. Yield was increased 37% when the enrichment was applied only during the pod-filling stage. They concluded that rapid photosynthetic rate is most important to yield during this stage of pod and seed development. Peet et al. (1977) also observed a high correlation between photosynthetic activity during the pod-filling stage of dry beans (*Phaseolus vulgaris* L.) and both biological and economic yield. Similarly, Krenzer and Moss (1975) observed yield increases in wheat (*Triticum aestivum* L.) when CO<sub>2</sub> enrichment was applied during floral initiation and grain development stages. They concluded that a screening procedure for selection of types with higher photosynthetic rates during these stages might be an effective technique for increasing yield of wheat.

Baker et al. (1973) used a mathematical simulation model of cotton (*Gossypium hirsutum* L.) growth and productivity to estimate the effects of increased photosynthetic rate. They predicted that under "clear sky" conditions in Mississippi, cotton yield would be increased 71% if the photosynthetic rate were increased 50%.

This study was undertaken to observe the effect of increased photosynthetic rate, induced by CO<sub>2</sub> enrichment, on the growth and development of cotton, sorghum (*Sorghum bicolor* L.), sunflower (*Helianthus annuus* L.), and soybean. Growth analysis was used to attempt to identify the components of yield most affected by increased photosynthetic rate.

## MATERIALS AND METHODS

Experiments were conducted in Phoenix from May to August 1975 and 1976. During these months, sunlight conditions in Arizona favored maximum photosynthesis. Radian flux reached 2,000  $\mu$ Einsteins m<sup>-2</sup> sec<sup>-1</sup> at noon each day. Total insolation averaged 674 langley days<sup>-1</sup> for May and June 1975, and 681 langley days<sup>-1</sup> in May and June 1976. Only 1 day in 1975 and 6 days in 1976 fell below 600 langley days<sup>-1</sup>.

Plants were grown in 14-liter (30 × 30 cm) containers of nutrient solution in 1975 and in potting mix (1:1:1, sand:peat:vermiculite) with nutrient solution in 1976. Nutrient solution was either normal (Guinn, 1974) or 2× normal concentration. In 1975, concentration of the nutrient solution was monitored daily with a conductivity meter, and the solutions were changed when nutrients were depleted. Thus, nutrient was changed after 14 days when plants were young, but after 5 days when plants were mature. In 1976, the potting mix was watered three times weekly with 2× normal nutrient solution. On days when nutrient solution was not added, the solution cultures were brought to volume and the potting mix was watered with deionized water.

In order to compare the effects of CO<sub>2</sub> enrichment during the entire life of plants with the effects when supplied only during

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later growth, flowering and fruiting, two age groups of plants were used. The plants that received CO<sub>2</sub> enrichment only after they were relatively mature were planted 15 March (cotton) and 1 April (other species). These plants will henceforth be referred to as Group 1. The second group was planted 28 April and the CO<sub>2</sub> treatments were started the same day. These plants were exposed to CO<sub>2</sub> treatments from the time of germination and will henceforth be referred to as Group 2.

Two identical 7 × 9 m glasshouses were programmed by a cam-driven thermostat to produce a daily maximum of 35 °C at 1300 to 1500 hours and a minimum of 21 °C at 0400 to 0600 hours on 28 April. On 28 April, the CO<sub>2</sub> concentration in one glasshouse (designated HiCO<sub>2</sub>) was raised to 630 ppm (v/v). Control was effected by an infrared CO<sub>2</sub> analyzer with limit switches operating the valve of a bottled source of pure CO<sub>2</sub>. The HiCO<sub>2</sub> was maintained during daylight hours for the remainder of the experiment. The other glasshouse (designated LoCO<sub>2</sub>) during the day and both houses during the night were at the natural level of 330 ppm CO<sub>2</sub>. Concentration of CO<sub>2</sub> in both houses was monitored every 2 min.

Plants were arranged in pairs of rows separated by a 40 cm aisle. Within rows the containers were placed lip-to-lip. Thus, each plant had a 30 × 50 cm space for growth. As plants were removed for analysis this minimal spacing was maintained.

Rate of CO<sub>2</sub> uptake (CER) was measured in full sunlight between 1000 and 1400 hours by infrared analysis of CO<sub>2</sub>. Leaves used for analysis were fully expanded and located at the fourth to eighth nodes below the apical bud. Measurements were made daily but usually included only one or two species each day. Twenty to thirty measurements on each species in each CO<sub>2</sub> environment were made from 28 April to 15 July. No statistically significant differences were observed between CER of Group 1 and Group 2 plants of any of the species. Therefore, average CER for each species and environment was based on all measurements.

**Table 1. Effects of LoCO<sub>2</sub> (330 ppm) and HiCO<sub>2</sub> (630 ppm) on CO<sub>2</sub> uptake (CER) of Group 1 and Group 2 plants and leaf area (LA), and dry weight (DW) accumulation after 12 weeks growth of Group 2 plants.**

Species	Year	CER		LA		DW	
		LoCO <sub>2</sub>	HiCO <sub>2</sub>	LoCO <sub>2</sub>	HiCO <sub>2</sub>	LoCO <sub>2</sub>	HiCO <sub>2</sub>
		nmoles/cm <sup>2</sup> /sec		dm <sup>2</sup> /plant		g/plant	
Cotton	1975	2.96	3.34*				
	1976	2.08	2.39*	153	292**	320	670**
Soybean	1975		3.59				
	1976	1.38	1.95**	100	280**	85	410**
Sunflower	1975		3.40				
	1976	2.64	2.83	120	290**	500	800*
Sorghum	1975	3.90	4.28				
	1976	3.78	3.84	20	23	85	100

\*,\*\* Significantly different from LoCO<sub>2</sub> measurement at 5 and 1% levels, respectively.

**Table 2. Growth analysis of the species at different stages of growth of Group 2 plants in 1976.**

Species	Juvenile				Reproductive				Maturation			
	Stage duration	RGR	NAR	WT	Stage duration	RGR	NAR	WT	Stage duration	RGR	NAR	WT
	Days	g/g/d	mg/dm <sup>2</sup> /d	g/plant	Days	g/g/d	mg/dm <sup>2</sup> /d	g/plant	Days	g/g/d	mg/dm <sup>2</sup> /d	g/plant
Cotton												
HiCO <sub>2</sub>	10-30	0.28	280	29	30-70	0.070	100	480	70-110	0.021	52	1,100
LoCO <sub>2</sub>	10-30	0.23	187	11	30-70	0.072	88	200	70-110	0.025	48	550
Soybean												
HiCO <sub>2</sub>	10-30	0.30	192	41	30-50	0.069	60	180	50-110	0.046	8	1,150
LoCO <sub>2</sub>	10-30	0.22	130	9	30-50	0.081	54	44	50-110	0.031	24	170
Sunflower												
HiCO <sub>2</sub>	10-30	0.31	293	52	30-70	0.062	121	640	70-90	0.017	48	900
LoCO <sub>2</sub>	10-30	0.28	229	25	30-70	0.062	112	300	70-100	0.033	133	800
Sorghum												
HiCO <sub>2</sub>	10-30	0.31	270	19					30-65	0.045	103	95
LoCO <sub>2</sub>	10-30	0.28	190	11					30-70	0.070	129	90

In 1975, the cuvette used to enclose leaves for measurement was 15 × 15 × 2 cm, water-cooled, had an opaque back, and a simple stirring fan for air mixing. In 1976, the 25 × 25 × 4 cm cuvette was electrically cooled with a Peltier device, had both surfaces made of clear plastic and used a series of small fans to circulate air over the cooling device and return it to the leaf chamber. During CER measurement, 30 liters/min of air from the greenhouse were pumped through the cuvette. A fraction of this, 0.6 liter/min, was withdrawn and pumped through a model 865 Beckman Infrared Analyzer<sup>a</sup>.

Data for growth analysis were obtained by harvesting six randomly selected plants twice each week from each species and treatment for the first 6 weeks of growth. Thereafter, two plants were harvested once each week until final harvest. Final harvest included nine plants of each species in each treatment. Leaf area was measured with an electronic area meter and dry weight was determined after drying for 48 hours at 70 °C. The nine cotton plants designated for final harvest in each glasshouse were mapped twice weekly to enable more complete growth analysis. Mapping consisted of notation of date of initiation, abscission, or maturation of each leaf and fruiting position on each plant. Because of mechanical constriction of the stems in the 1975 experiment, the cotton plants did not reach harvest maturity. Therefore, no lint or seed yield could be assigned to the plants for that year.

Calculation of average net assimilation rate ( $\overline{NAR}$ ) and average relative growth rate ( $\overline{RGR}$ ) followed the methods of Radford (1967). Dry weight per plant (DW) and leaf area per plant (LA) for each sampling date were plotted and best-fit curves as a function of time were assigned for each species and treatment. Data from the curves at the beginning and end of each growth stage were used to calculate  $\overline{NAR}$  and  $\overline{RGR}$  by the formulas of Radford (1967). CER was calculated directly from the observed flow of gas through the cuvette and the differential of CO<sub>2</sub> in the supply and exhaust. No corrections were made for photorespiration.

Cultivars of the species examined were as follows: cotton, 'DPL 16'; soybean, 'Bragg'; sunflower, 'Mammoth Russian'; sorghum, Northrup King '285'.

## RESULTS AND DISCUSSION

The average rate of CO<sub>2</sub> uptake by all measured leaves of both groups of plants in direct sunlight is shown in Table 1 with growth indices (LA and DW) of Group 2 plants. No statistically significant difference was found between CER of Group 1 and Group 2. As expected, the CER was not significantly influ-

<sup>a</sup> Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the USDA, and does not imply its approval to the exclusion of other products that may also be suitable.

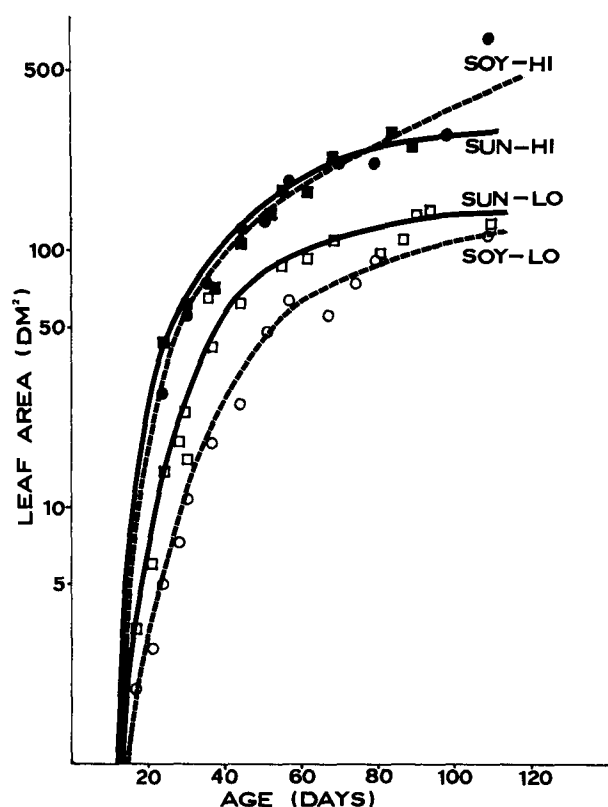


Fig. 1. Leaf area per plant development of sunflower (SUN) and soybean (SOY) grown in 330 ppm CO<sub>2</sub> (LoCO<sub>2</sub>) or 630 ppm CO<sub>2</sub> (HiCO<sub>2</sub>) from germination (Group 2 — 1976).

enced by the concentration of CO<sub>2</sub> in the air surrounding sorghum, a C<sub>4</sub> plant. The CER increased 15, 7, and 41% for cotton, sunflower, and soybean, respectively. It is apparent, however, that the growth rates of the species and the increase in growth produced by greater CO<sub>2</sub> uptake bear no consistent relationship to the CER. Sunflower produced 500 g of plant material in 12 weeks in LoCO<sub>2</sub> with a CER of 2.64 nmoles·cm<sup>-2</sup>·sec<sup>-1</sup> (42 mg CO<sub>2</sub>·dm<sup>-2</sup>·hour<sup>-1</sup>), whereas sorghum accumulated only 85 g dry weight during the same period in LoCO<sub>2</sub> with an average CER of 3.78 nmoles·cm<sup>-2</sup>·sec<sup>-1</sup> (60 mg·dm<sup>-2</sup>·hour<sup>-1</sup>). Cotton and soybean accumulated 110 and 380%, respectively, more dry matter in HiCO<sub>2</sub> than in LoCO<sub>2</sub> in association with 15 and 41% increases in CER.

In an attempt to explain these differences in response to photosynthetic rate, we analyzed the growth pattern of the plants. Figures 1 and 2 show leaf area increases with time for the Group 2 plants. Because the growth analysis formulae give appreciable error when calculated for long periods of time if LA and DW are not linearly related (Radford, 1967), the calculations were made for three stages of growth. Though the stages were not precisely delineated, an arbitrary dividing point was assigned (Table 2) based upon changes in LA/DW relationships. The juvenile stage was characterized by exponential increase in both LA and DW and a very nearly constant LA/DW. In all species, the juvenile stage extended from germination to about day 30.

The reproductive stage was characterized by a less

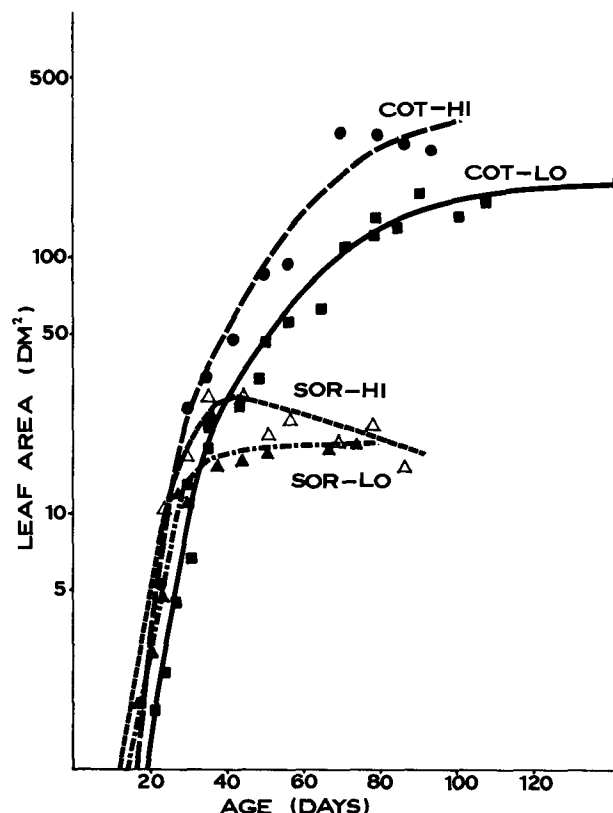


Fig. 2. Leaf area per plant development of cotton (COT) and sorghum (SOR) grown in 330 ppm CO<sub>2</sub> (LoCO<sub>2</sub>) or 630 ppm CO<sub>2</sub> (HiCO<sub>2</sub>) from germination (Group 2 — 1976).

rapid increase in both LA and DW. DW accumulated more rapidly during this period than LA. The length of this stage varied with species (Table 2) and was so short for sorghum that no analysis was possible. The maturation stage was characterized by a very slow increase or actual decrease in LA while DW continued to increase.

Most of the increase in LA in response to the high CO<sub>2</sub> treatment occurred during the juvenile phase of the Group 2 plants and during the first 20 days after treatment began in the Group 1 plants. Thereafter, the rates of expansion in the two treatments were similar. However, relative area differences were maintained as the plants matured.

Growth analysis of dry weight accumulation in these three stages of Group 2 plants is shown in Table 2. It is obvious that not only the rate of growth, but the duration of that rate influences the weight at the end of a stage. Though all species had a higher growth rate in HiCO<sub>2</sub> than in LoCO<sub>2</sub> in the juvenile stage, only the indeterminate species cotton and soybean maintained this size difference through maturity. In the determinate species, sunflower and sorghum, the maturation stage was 5 to 10 days longer in LoCO<sub>2</sub> than in HiCO<sub>2</sub>, and therefore plants from both treatments were virtually the same size at maturity.

Without growth analysis, it would be difficult to establish the effects of HiCO<sub>2</sub> and LoCO<sub>2</sub> on the determinate species. Because duration of growth compensated for difference in NAR, final area and weight of these species did not reflect the growth character-

**Table 3.** Components of yield of Group 1 cotton plants as influenced by  $\text{LoCO}_2$  (330 ppm),  $\text{HiCO}_2$  (630 ppm), and nutrient concentration.

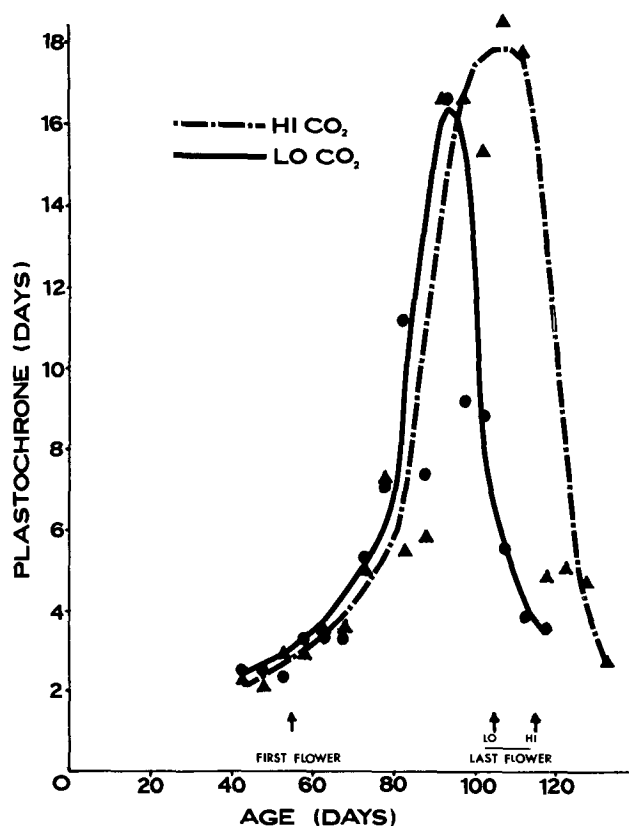
Yield component	Year and nutrients					
	1975, normal		1975, 2×		1976, 2×	
	$\text{LoCO}_2$	$\text{HiCO}_2$	$\text{LoCO}_2$	$\text{HiCO}_2$	$\text{LoCO}_2$	$\text{HiCO}_2$
Leaf area ( $\text{dm}^2/\text{plant}$ )					195	260
Dry weight ( $\text{g}/\text{plant}$ )					650	950
Blooms/plant (No.)	67	86	69	105	69	110
Bolls/plant (No.)	39	59	42	75	37	80
% retention	66	78	61	71	54	74
Boll weight ( $\text{g}/\text{boll}$ )					4.7	5.5
Lint yield ( $\text{g}/\text{plant}$ )					61	170
Seed yield ( $\text{g}/\text{plant}$ )					114	274
Fraction of yield increase due to:						
Increase bloom/plant		0.60		0.77		0.47
Increase retention		0.40		0.23		0.29
Increase lint/boll						0.24

istics of the productive season. The sunflowers had large seed heads but all seed were without embryos. Seed head weights of sunflower averaged 280 and 272 g and heads of sorghum averaged 32 and 30 g in  $\text{HiCO}_2$  and  $\text{LoCO}_2$ , respectively.

The indeterminate species, on the other hand, showed a dramatic response of final area and weight to the increased photosynthetic rate induced by high  $\text{CO}_2$ . In cotton, the harvested yield fraction was increased more than was total plant weight (Table 3). For this analysis, the "Mature" group of plants was used. Though the indeterminate habit of cotton allows a long flowering period, the plant typically has a hiatus of flowering while the initially set fruit matures. This hiatus occurred about day 105 in  $\text{LoCO}_2$  and day 115 in  $\text{HiCO}_2$ . All fruit which set before those dates were allowed to mature and were included in the yield analysis for Table 3. Soybeans in this experiment did not set many fruit and frequently had empty pods due, presumably, to incomplete fertilization. Therefore, no similar analysis was made for soybean.

The analysis in Table 3 shows that for cotton to achieve the full benefit of the increased photosynthetic fixation of  $\text{CO}_2$ , the nutrient levels had to be increased. In 1975,  $\text{CO}_2$  enrichment increased boll set 51% with normal nutrients and 79% with 2× nutrients, but the experiment had to be terminated before all the bolls matured. In 1976, with 2× nutrients,  $\text{CO}_2$  enrichment increased the number of bolls set by 116%. An additional yield increase due to greater weight per boll and higher lint-percent (lint wt/seed cotton wt) caused the harvestable lint weight to increase by 180%. This increase was obtained from an average increase in CER of 15% and an increase in leaf area of 49% (Table 3).

It is clear that the major portion of the additional carbohydrate in cotton in  $\text{HiCO}_2$  was partitioned first into leaf area expansion and then into support for additional fruit load. To emphasize the increased productivity per unit of leaf area of the cotton plants in the  $\text{HiCO}_2$  environment, we calculated the expected yield of these plants on a land surface basis. If we assume a leaf area index (LAI) of 5.0, a figure common in productive cotton plantings, there would have been 28,500 plants/ha in  $\text{LoCO}_2$  which would have produced 1,740 kg/ha (3.1 bales/Ac) of lint. This is a high, but frequently achieved, yield in commercial

**Fig. 3.** Rate of addition of primary leaves as measured by plastochrone (days between leaves) for cotton plants grown in 630 ppm  $\text{CO}_2$  ( $\text{HiCO}_2$ ) or 330 ppm  $\text{CO}_2$  ( $\text{LoCO}_2$ ) from age 45 days (Group 1 — 1976).

plantings. On the same basis, there would have been 19,250 plants/ha in the  $\text{HiCO}_2$  environment that would have produced 3,250 kg/ha (5.8 bales/Ac)—an increase of 88%.

The fact that increases with  $\text{HiCO}_2$  in all components of yield shown in Table 3 were similar supports the conclusion that carbohydrate supply in cotton is a critical limiting factor in growth, fruit set, and fiber development. The growth rate of plants with age is also consistent with the conclusion (Fig. 3). The time between primary leaves (plastochrone) began to increase immediately after the first fruit was set. This occurred in both environments, but was delayed slightly in  $\text{HiCO}_2$ . After the hiatus in flowering, the time between leaves decreased to values similar to those observed during juvenile growth.

These experiments allow several conclusions regarding the place of measurements of photosynthetic activity in selecting varieties or management techniques for increased yield.

1. Growth of the juvenile stage was directly related to photosynthetic rate within treatments of each species. However, there was little relationship of growth rate and photosynthetic rate across species. That is, cotton and soybean accumulated greater weight than sorghum even though their CER was less than 70% of the rate of sorghum. This observation is similar to that of Wallace et al. (1976) who emphasized that in dry bean growth and seed yield are determined by

complex interacting of CO<sub>2</sub> fixation and partitioning and that it is unlikely that "one component process such as CO<sub>2</sub> uptake or ribulose diphosphate carboxylase activity will be rate limiting under all conditions". Though Peet et al. (1977) observed positive correlation of yield and CER during pod filling for eight dry bean cultivars, they had to exclude Pinto from the calculations because growth and partitioning of Pinto did not bear the same relationship to CER. Thus, selection for increased CER is likely to be effective in increasing yield only if the genetic pool is made up of strains with similar partitioning and growth characteristics.

2. While increased CO<sub>2</sub> uptake resulted in greater plant weight and leaf area during the juvenile stage in the four species, it would not be expected to increase yield of the determinate species unless earliness were an important factor in production. Final weights of the indeterminate species, cotton and soybean, were increased many times more than CO<sub>2</sub> uptake per unit leaf area or NAR. This resulted from the feedback or "compound interest" effect of the increase in leaf area. A further enhancement of economic yield of cotton resulted from the higher proportion of plant weight in seed and lint in the HiCO<sub>2</sub> environment. No conclusions can be reached regarding economic yield of soybeans in these experiments.

3. The conclusion of Muramoto et al. (1965) that direct measurement of CER of individual leaves gives highly variable results was confirmed. More than 60 measurements on cotton leaves were required to establish statistical significance at the 5% level for a difference of 0.3 nmoles<sub>cm</sub><sup>-2</sup> sec<sup>-1</sup> (5 mg CO<sub>2</sub><sub>dm</sub><sup>-2</sup> hour<sup>-1</sup>).

4. This 0.3 nmoles<sub>cm</sub><sup>-2</sup> sec<sup>-1</sup> increase in CER resulted in approximately 90% increase in economic yield (yield per ha) of cotton. Thus, the technique of direct measurement of individual leaves appears inappropriate for screening breeding material because most varietal improvement is in steps of 10% increase or less. If

this range of yield increase is to be correlated with photosynthetic activity, a highly sensitive and reliable measurement of photosynthetic activity must be found. From these experiments, the accumulation of leaf area and dry weight during the juvenile stage appears to be the most reliable measurement for correlation with final yield.

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