Chapter 17

PHOTOSYNTHESIS, DRY MATTER PRODUCTION AND GROWTH IN CO_2—ENRICHED ATMOSPHERES

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INTRODUCTION

The physiological basis of yield in cotton and other crops has been the subject of intense interest (Hesketh, 1963; Eastin *et al.*, 1969; Hesketh and Baker, 1967; Thorne, 1971; Evans, 1975). Despite the obvious importance of carbon dioxide (CO_2) as a limiting factor in photosynthesis (van den Honert, 1930; Moss, 1962; Hesketh, 1963; Wareing *et al.*, 1968; Burris and Black, 1976; Allen, 1979; Wittwer, 1983) most texts on cotton and literature reviews on cotton physiology contain little or no mention of this parameter (Brown, 1927; Hector, 1936; Eaton, 1950, 1955; Brown and Ware, 1958; Dastur, 1959; Dastur and Asana, 1960; Tharp, 1965; Carns and Mauney, 1968; Elliott *et al.*, 1968; Arnon, 1972; Prentice, 1972; McArthur *et al.*, 1975).

The objective of this article will be to review the literature on CO_2 enrichment of cotton and other important species under growth chamber, greenhouse and field conditions, to describe some metabolic effects observed, and to discuss some of the factors influencing CO_2 utilization by the plant.

The benefits of CO_2 enrichment under controlled environments are not confined to greenhouse-grown crops. Results with field crops such as potato, wheat, and sugar beet under controlled environments have been equally striking (Gaastra, 1959, 1963; Wittwer and Robb, 1964; Wittwer, 1970a,b, 1983). Agronomic crops investigated under enhanced CO_2 conditions in controlled environments include: corn (Moss *et al.*, 1961; Moss and Peaslee, 1965; Ford and Thorne, 1967; Sionit and Strain, 1982); soybeans (Brun and Cooper, 1967; Cooper and Brun, 1967; Saminy, 1967; Hardman and Brun, 1971; Clough and Peet, 1981; Clough *et al.*, 1981; Finn and Brun, 1982; Sionit *et al.*, 1982; Jones *et al.*, 1983; Sionit, 1983); barley (Ford and Thorne, 1967); sugar beet (Ford and Thorne, 1967; Wittwer, 1970a,b; Wyse, 1980; Sionit *et al.*, 1982); grain sorghum (Al-Kawas, 1967; Mauney *et al.*, 1978); wheat (Wittwer, 1970a,b; MacDowell, 1972;

Krenzer and Moss, 1975; Fischer and Aguilar, 1976; Gifford, 1977, 1979 a,b; Neales and Nicholls, 1978; Sionit *et al.*, 1980; Sionit *et al.*, 1981 a,c,d); potato (Collins, 1976); tobacco (Thomas *et al.*, 1975); and white clover (Masterson and Sherwood, 1978).

The beneficial effects of CO_2 enrichment on crop productivity can be regarded as a composite effect, with many plant processes contributing to the increase in productivity (Gaastra, 1966; Enoch, 1978b; Enoch and Hurd, 1979). CO_2 enrichment of C_3 plants has been shown to increase the quantum yield (Ehleringer and Bjorkman, 1977), the net photosynthesis rate (Enoch and Hurd, 1977; Ho, 1977; Kramer, 1981), the internal transport of carbon (Ho, 1977), the salt tolerance (Enoch *et al.*, 1973) and the optimum leaf temperature for net photosynthesis (Enoch, 1978a; Enoch and Sachs, 1978).

Relatively few CO_2 enrichment studies have been conducted on cotton plants under controlled environments (Leonard and Pinckard, 1946; Guinn, 1973, 1974a; Hesketh and Hellmers, 1973; Chang, 1975; Mauney *et al.*, 1978, 1979; Wong, 1979, 1980). Most of these studies indicate that cotton is responsive to CO_2 enrichment. Cotton has a relatively high CO_2 compensation point (60-120 μl l^{-1}); it is consistent in its growth response to enhanced CO_2 levels; and it reaches light saturation at levels below those of full sunlight (Hesketh and Baker, 1966; Zelitch, 1971; Harper *et al.*, 1973b; Wittwer, 1978 a). However, Baker *et al.* (1972) observed that the canopy was not light saturated at full sunlight (see also Chapter 16). Harper *et al.* (1973b) measured a 26 percent increase in canopy uptake of CO_2 when carbon dioxide was released into a field-grown crop.

CO_2 ENRICHMENT OF THE ATMOSPHERE

The possibility of using CO_2 enrichment of the atmosphere as a means of increasing crop yield was investigated by numerous researchers during the past century (Brown and Escombe, 1902; Cummings and Jones, 1918; Wittwer and Robb, 1964; Monteith, 1965; Krizek *et al.*, 1968, 1970 a, 1971, 1974; Krizek, 1969, 1970, 1974; Waggoner, 1969; Bailey *et al.*, 1970; Enoch *et al.*, 1970; Wittwer, 1970a,b, 1978a,b, 1980, 1981, 1982a,b, 1983; Madsen, 1971b, 1973, 1974, 1976, 1979; van Bavel, 1972b; Moss 1976; Lemon, 1977; McCoy, 1978; Strain, 1978a,b; Allen *et al.*, 1971; Strain, 1978a,b; Tibbitts and Krizek, 1978; Allen, 1979; Pallas, 1979; Baker *et al.*, 1981; Carlson and Bazzaz, 1980, 1982; Kimball, 1982; Strain and Sionit, 1982). The adverse effects of high CO_2 in the soil atmosphere caused by waterlogging have also been reported by many workers (see review by Krizek, 1982).

CONTROLLED CONDITIONS

Dramatic increases in vegetative growth and flower and fruit development under CO_2-enriched atmospheres in controlled environments were reported for a wide range of species (Kimball, 1982). Vegetables responsive to CO_2 enrichment

include lettuce, tomato, cucumber, (Wittwer and Robb, 1964; Newton, 1966; Hurd, 1968; Wittwer, 1970a,b; Kretchman and Howlett, 1970; Hand and Postlethwaite, 1971; Hand and Soffe, 1971; Madsen, 1973, 1974, 1976; Knecht and O'Leary, 1974; Krizek *et al.*, 1974; Calvert and Slack, 1975; Frydrych, 1976; Hinkleton and Jolliffe, 1978; Kimball and Mitchell, 1978, 1979, 1981; Nilwik *et al.*, 1982; Knecht and O'Leary, 1983; Nilsen *et al.*, 1983); potato (Aoki and Yabuki, 1977); okra (Sionit *et al.*, 1981 b); pepper (Enoch *et al.*, 1970); and radish (Knecht, 1975; Sionit *et al.*, 1982). Ornamental crops accelerated in their growth and development by CO_2 enhancement include petunia, ageratum, marigold, snapdragon, rose, carnation, chrysanthemum, and many others (Krizek *et al.*, 1968; Bailey *et al.*, 1970; Holley, 1970; Purohit and Tregunna, 1974; Enoch and Hurd, 1977, 1979; Mortensen and Moe, 1983a,b).

Carbon dioxide enrichment under controlled environments also increases growth of a number of woody species. These include tea, crabapple (Krizek *et al.*, 1971; Zimmerman *et al.*, 1970; paper birch (Krizek, 1972); guayule (Backhouse *et al.*, 1979) and a number of species of pine and spruce (Funsch *et al.*, 1970; Yeatman, 1971; Tinus, 1972; Green and Wright, 1977; Rogers *et al.*, 1982b). Several investigators also obtained accelerated growth of rooted cuttings under CO_2 enhancement (Laiche, 1978; Lin and Molnar, 1982).

FIELD CONDITIONS

The potential for CO_2 enrichment of crops under field conditions has been examined only to a limited extent (Johansson, 1932; Chapman and Loomis, 1953; Kretchman, 1969, 1970; Enoch *et al.*, 1970; Yoshida, 1972; Moss, 1976; Wittwer, 1978a; Allen, 1979, 1982; Arteca *et al.*, 1979; Rogers *et al.*, 1980, 1981, 1982a,b,c). Plant response to CO_2 enrichment in the field depends on the kind of crop, the meterological conditions, the distribution of CO_2 flux into the vegetation (Anderson, 1975; Wittwer, 1978a; Allen, 1979) and the stage of development (Krenzer and Moss, 1975).

Carbon dioxide enrichment of vegetable crops in the field has increased yields about 12 percent (Kretchman, 1969, 1970; Allen 1979). Enrichment of soybeans, peanuts and peas with CO_2 in open-top enclosures increased yields of these crops presumably by increasing the supply of photosynthate available to symbiotic nitrogen-fixing bacteria (Havelka and Hardy, 1976; Hardy and Havelka, 1973, 1975, 1977; Hardy, 1978; Allen, 1979).

For vegetable crops and most agronomic crops the economic costs of CO_2 enrichment in the field have been considered excessive (Kretchman, 1969, 1970; Anderson, 1975; Wittwer, 1978a; Allen, 1979). Experimental evidence and model predictions led Allen (1979) to conclude that CO_2 enrichment under field conditions is inefficient, since the maximum increase in CO_2 uptake is only about 6.5 percent of the CO_2 enrichment. In his opinion, even turbulent diffusion barriers do not increase the capture of CO_2 sufficiently to make field-scale enrichment feasible. Carbon dioxide enrichment experiments conducted on cot-

ton in the field by Baker (1965), Harper (1971), and Harper *et al.* (1973a,b,c), were viewed by Wittwer (1978a) as economically promising.

A cotton crop in Mississippi enriched with CO_2 at a controlled release rate of 222.6 kg $ha^{-1}hr^{-1}$ (198.6lb $acre^{-1}hr^{-1}$) provided mean CO_2 concentrations of 450 to 500 $\mu l\ l^{-1}$ maintained at three-fourths the plant height (Harper *et al.*, 1973 b). Fluctuations of CO_2 within the canopy varied with meteorological conditions. Photosynthetic assimilation of CO_2 was calculated for crops grown in the open and in a semi-enclosed plexiglass chamber. Seven to 33 percent of the CO_2 applied was calculated to be recovered as photosynthate over a range of solar radiation levels of 205 to 1095 $W \cdot m^{-2}$. Net biomass production on a daily basis was increased by an estimated 35 percent. Based on these tests, Harper (1971) concluded that CO_2 enrichment of cotton and other field crops in Mississippi may be economically feasible. It should be noted, however, that in studies reported by Baker and McKinion (1971), elevated CO_2 levels were not found within the canopy.

Harper *et al.* (1973b) found that CO_2 enhancement was especially beneficial in dense plantings of cotton, particularly in warm bright weather when conditions for minimal restraints on growth and distribution of photosynthate prevailed. They concluded that for maximum recovery of CO_2 in a cotton field the crop should be fully expanded (for maximum interception of photosynthetically active radiation, PAR), and that solar irradiance should be high.

Certain crops (corn) are less responsive to CO_2 enrichment in the field than others (cotton). Even with a 45-fold increase in CO_2 content at the soil level, Lemon *et al.* (1971) obtained little change in CO_2 concentration in the upper part of the canopy. They estimated only a 10-20 percent increase in photosynthesis with the high CO_2 enrichment levels.

Because of the inherent limitations of measuring photosynthetic rates in the field, measurements of photosynthesis under CO^2-enriched atmospheres are often difficult to evaluate. Some of these limitations include a cuvette effect, caused by non-standardization of the leaf microenvironment (energy budget), self-shading effects, humidity effects on the infra-red gas analyzer and sampling problems. Since most cuvette systems are air conditioned to prevent overheating, significant differences in photosynthetic activity caused by variations in ambient air and leaf temperature may not be detected (Anderson, 1975). Under field conditions there may also be serious limitations in the time response of CO_2-measuring instruments (Sestak *et al.*, 1971). Bingham *et al.*, (1978) have recently developed a minature, rapid-response CO_2 sensor at the Lawrence Livermore Laboratory which they believe will accurately measure real-time fluctuations in ambient CO_2 concentrations of 0.25 $\mu l\ l^{-1}$. The rapid-response and open cell design promises to have research applicability in aerodynamic transfer investigations and canopy photosynthesis studies.

METABOLIC EFFECTS OF CO_2 ENRICHMENT

PHOTOSYNTHESIS

Species differ greatly in their response to CO_2 enrichment (Tables 1 and 2). In general C_3 plants show a greater increase in photosynthetic rate (P_n) than do C_4 plants (Moss, 1962, 1967; Moss and Rawlins, 1963; El Sharkawy and Hesketh, 1965; El Sharkawy *et al.*, 1965; Jolliffe and Treguna, 1968; Menz *et al.*, 1969;

Table 1. Comparative photosynthesis rates (P_n, mg CO_2 dm^{-2} hr^{-1}) under normal CO_2 and under CO_2-enriched atmospheres. (Data from El-Sharkawy and Hesketh, 1965).

Species	P_n CO_2 μl l^{-1}		
	300	1600	4750
Corn	60	103	71
Sunflower	45	100	90
Cotton	45	70	95
Oats	33	—	66
Tobacco	27	67	—
Hibiscus	27	66	
Soybean	25	56	

Table 2. Influence of CO_2 concentration (330 and 660 μl l^{-1}) on CO_2 uptake (P_n), leaf area (LA), and dry weight (DW) accumulation in cotton, soybean, sunflower, and sorghum grown under greenhouse conditions. LA and DW measurements were taken after 12 weeks of growth. (Data from Mauney *et al.*, 1978).

Species	Year	P_n (nmol cm^{-2} s^{-1})		LA/plant (dm^2) CO_2 μl l^{-1}		DW/plant (g.)	
		330	630	330	630	330	630
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

*,** Value significantly different at the 5% and 1% level, respectively.

Akita and Moss, 1972, 1973; Akita and Tanaka, 1973; Buchanan and Schurmann, 1973; Ito, 1973, 1976; Chollet and Ogren, 1975; Hofstra and Hesketh, 1975; Imai and Murata, 1976, 1977, 1978a,b, 1979a,b; Ho, 1977; Bahr and Jensen, 1978; Enoch, 1978; Enoch and Sachs, 1978; Goudriaan and van Laar, 1978; Powles, 1979; Wong, 1979, 1980; Farquhar *et al.*, 1980; Patterson and Foint, 1980; Downton *et al.*, 1981; Rosenberg, 1981; Strain and Sionit, 1982; Gates *et al.*, 1983; Wittwer, 1983) (Table 2). The current level of CO_2 in the atmosphere is believed to be rate limiting for most C_3 plants (Rogers *et al.*, 1980, 1981, 1982b; Sionit *et al.*, 1981; Wittwer, 1983). Under stress conditions imposed by air pollutants and adverse temperature, moisture and radiation conditions, both C_3 and C_4 plants may benefit from CO_2 enhancement (Allen, 1979; Strain, 1978a,b; Tolbert and Zelitch, 1982; Wittwer, 1982a, 1983). Under N stress, however, the stimulatory effects of CO_2 enrichment on P_n are greatly reduced (Wong, 1979, 1980). This is especially so in a C_3 species such as cotton (Table 3).

Table 3. Influence of CO_2 concentration and nitrogen nutrition on the rate of CO_2 assimilation (P_n, in μmol CO_2 m^{-2} s^{-1}) in cotton, a C_3 plant and in maize, a C_4 plant. (Data from Wong, 1980).

Plant	CO_2	Nitrate	P_n CO_2	
	μl l^{-1}	mM NO_3^-	330 μl l^{-1}	660 μl l^{-1}
Cotton	330	24.0	35.6	52.8
	330	12.0	32.1	49.2
	330	4.0	28.3	42.8
	330	0.6	19.8	24.5
	660	24.0	29.0	51.5
	660	12.0	20.4	34.5
	660	4.0	15.6	25.8
	660	0.6	9.4	15.2
Maize	330	24.0	52.0	65.9
	330	12.0	43.3	54.8
	330	4.0	40.6	50.2
	330	0.6	27.3	32.5
	660	24.0	51.3	66.3
	660	12.0	40.8	54.6
	660	4.0	32.8	40.3
	660	0.6	23.2	26.8

Wong (1980) and other workers (see review by Carns and Mauney, 1968) have reported a linear increase in photosynthesis of leaves of cotton as CO_2 concentration is increased to 600 μl l^{-1} (Figure 1). In short-term experiments on alfalfa, sugar beet, and tomato, Thomas and Hill (1949) obtained a linear increase in P_n

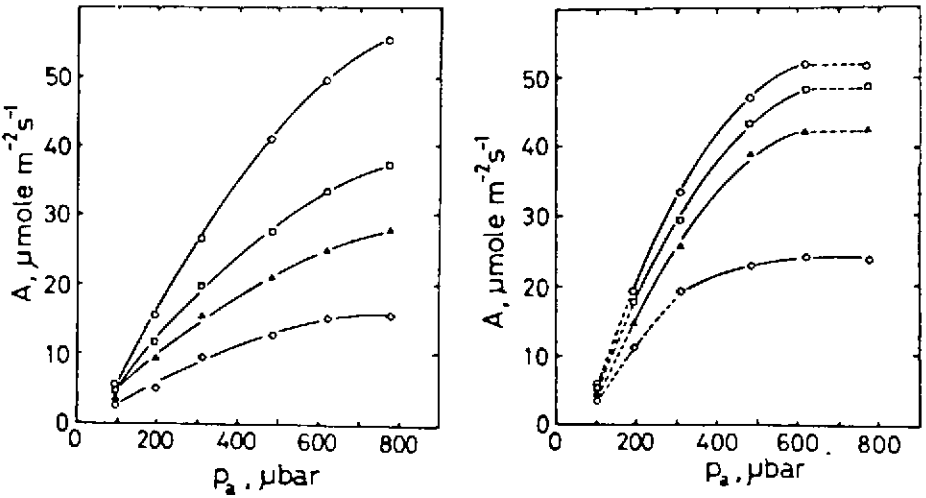

Figure 1. Rate of CO_2 assimilation (A) in cotton as influenced by CO_2 concentration and nitrogen nutrition. Measurements were made at 2000 μmol m^{-2} s^{-1} of PPFD, 30C, and a vapor pressure difference of 20 mbar. The plants were grown at 330 μl l^{-1} (μbar) (left) or 660 μl l^{-1} of CO_2 (right), and under four levels of nitrogen nutrition: ◇, 0.6 mM NO_3^-; ▲, 4 mM NO_3^-; □, 12 mM NO_3^-; and ○, 24 mM NO_3^-. The solid lines are linear or quadratic functions defined by least squares regression. (Data from Wong, 1980).

with increasing CO_2 concentration up to 3500 μl l^{-1} in full sun. Baker (1965) and Bierhuizen and Slatyer (1964, 1965) showed an interaction between photosynthetically active radiation (PAR) and maximum CO_2 concentration. At 10.8 klx (1000 ft-c) net photosynthesis increased with exposures up to 1000 μl l^{-1} CO_2. However, at PAR levels of 64.6 klx (6000 ft-c) little increase in P_n occurred above 600 μl l^{-1} CO_2. These investigators suggested that the higher PAR levels caused the stomates to open wider, decreasing stomatal resistance to CO_2 diffusion. The higher PAR level would also reduce the so-called "mesophyll" resistance to CO_2 uptake (which is infinite in the dark) to several times the mathematical equivalent of the diffusive resistance offered by open stomata to CO_2 exchange at high PAR levels.

Brun and Cooper (1967) reported a four-fold increase in P_n in soybean plants grown in a greenhouse at ambient CO_2 and then exposed to a CO_2 concentration of 1670 μl l^{-1} in the laboratory. Green and Wright (1977) working with branches

of conifers enclosed in cuvettes, obtained an 87 percent increase in P_n at CO_2 concentrations of 450 to 500 μl l^{-1}.

Kramer (1981) pointed out that photosynthetic measurements made over short periods of time do not necessarily provide reliable information concerning what occurs when plants are grown at high CO_2 concentrations for several weeks or longer. Mauney *et al.* (1978) exposed cotton, sorghum, soybean, and sunflower plants to 330 or 630 μl l^{-1} CO_2 during daylight hours in air conditioned greenhouses in Phoenix, Arizona for 12 weeks or more during the period of May to August in 1975 and 1976. They measured the rate of photosynthesis per unit of leaf area at frequent intervals on single leaves during this period and obtained an average increase in P_n of 15 percent for cotton, and 41 percent for soybean, but only 2 percent for sorghum, and 7 percent for sunflower, compared to the P_n of these species at 330 μl l^{-1} CO_2. These differences in P_n were not statistically significant for sorghum and sunflower.

Aoki and Yabuki (1977) grew cucumber plants for up to three weeks in chambers under sunlight conditions at CO_2 concentrations from 300 to 5500 μl l^{-1}. Measurements of photosynthesis were then made at the CO_2 concentrations at which the plants were grown. Although initially the photosynthetic rates at the high CO_2 concentrations (1200, 2400, and 5500 μl l^{-1}) were nearly twice those at the control level (300 μl l^{-1}), they decreased rapidly thereafter. In 5 days the photosynthetic rates at 2400 and 5500 μl l^{-1} had dropped below the control rate; and within 15 days the P_n rate at 1200 μl l^{-1} was below the control rate.

Raper and Peedin (1978) exposed two cultivars of tobacco to 400 and 1000 μl l^{-1} of CO_2 for 35 days after transplanting. At the end of this time, the leaf area of the plants grown under high CO_2 was larger, but the rate of photosynthesis per unit of leaf area of the high CO_2 plants was only 70-80 percent of the P_n of plants maintained at low CO_2. Hicklenton and Jolliffe (1980b) reported that in *Pharbitis nil* the rate of photosynthesis per unit of leaf area of plants kept for 14 days in 1.0 percent CO_2 was lower than the P_n of plants kept at 0.03 percent.

In making P_n measurements at 0.03 percent CO_2, Krizek and Carlson (1968, unpublished results) found that the P_n of petunia plants grown for two weeks at high CO_2 (2000 μl l^{-1}) was lower than that of plants grown at low CO_2 (400 μl l^{-1}). This was true, even though the CO_2-enriched plants had greater dry weights, were better branched,and flowered 2-3 weeks sooner (Krizek *et al.*, 1968). Because of the possible feedback inhibition of P_n caused by CO_2 enrichment, it is important, therefore, to know whether P_n measurements were made at ambient or enhanced CO_2 levels before interpreting data on CO_2 enrichment effects on P_n.

Clough *et al.* (1981) noted that the P_n of high sink soybeans maintained at 1000 μl l^{-1} of CO_2 declined steadily over a 20-day period, while the P_n of high sink plants kept at 350 μl l^{-1} remained constant for 15 days before beginning to decline. In this study, however, the absolute P_n was always greater in plants at 1000 μl l^{-1} than 350 μl l^{-1}.

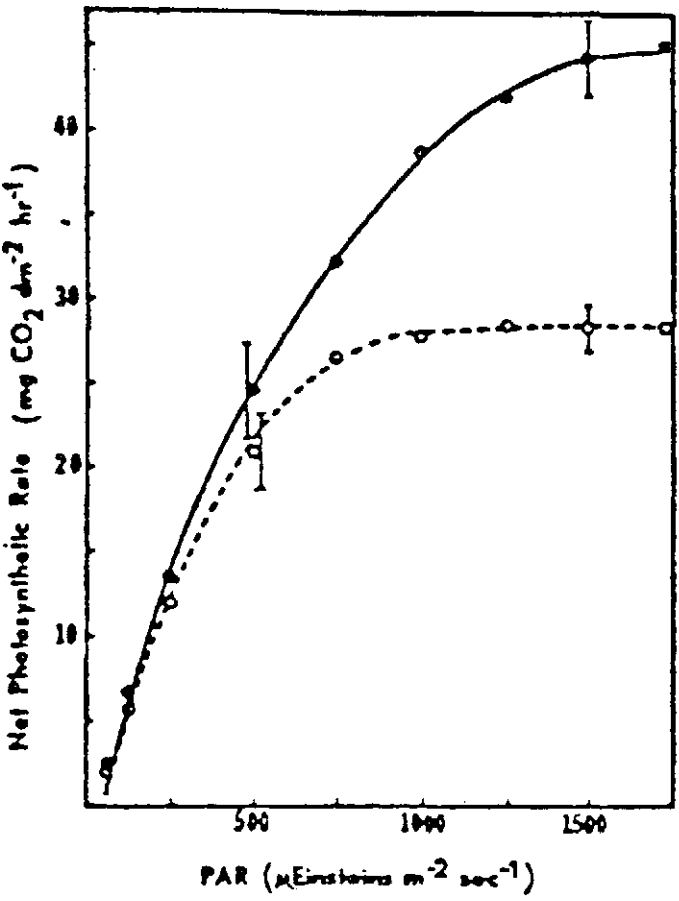

Figure 2. Relation between net photosynthetic rate per unit leaf area and photosynthetically active radiation (PAR, 400-700 nm) in cotton plants grown in the growth chamber (dotted line) and in the field (solid line). Vertical bars indicate the SE of the mean. Each point is an average of four observations. (From Patterson *et al.*, 1977).

Previous studies have shown that maximum P_n in cotton are often greater in field-grown plants than in those grown in the greenhouse (El-Sharkawy *et al.*, 1965; Elmore *et al.*, 1967; Bazzaz, 1973). However, comparisons of P_n between field-grown and growth chamber-grown plants have seldom been made (Hesketh, 1968; Patterson *et al.*, 1977). Hesketh (1968) found that cotton plants grown in a growth chamber under 32.3 klx (3000 ft-c) of fluorescent light had P_n similar to winter-grown greenhouse plants. When the chamber-grown plants were given

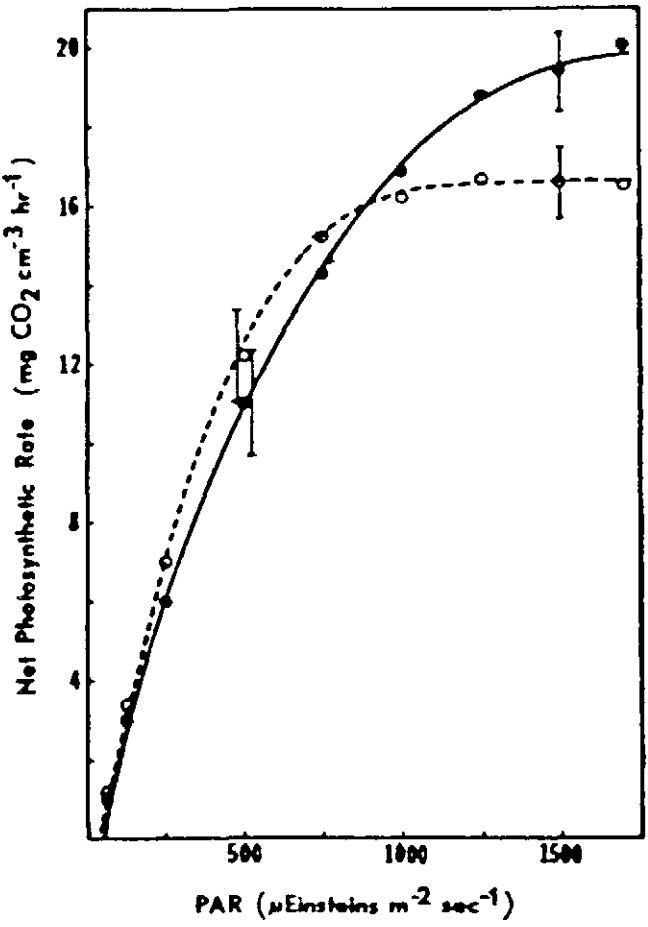

Figure 3. Relation between net photosynthetic rate per unit mesophyll volume and photosynthetically active radiation (PAR, 400-700 nm) in cotton plants grown in the growth chamber (dotted line) and in the field (solid line). Vertical bars indicate the SE of the mean. Each point is an average of four leaves. (From Patterson *et al.*, 1977).

supplemental higher intensity incadescent light during their growth, the P_n was increased to the level of summer-grown greenhouse plants. These studies illustrate the importance that differences in photosynthetically active radiation (PAR) level and spectral quality during growth may have on measurements of P_n and indicate the difficulty of using photosynthetic data obtained from plants grown in different environments in making a comparison of the photosynthetic efficiencies of different species and cultivars.

Patterson *et al.* (1977) found differences in *in situ* P_n between cotton plants grown under ambient conditions in the field and those grown in a growth chamber in the Duke University Phytotron. Measurements of the response of P_n to changes in PAR level were made under standard conditions in the laboratory to determine whether the differences observed *in situ* were related to the plant material itself or to differences in the ambient PAR conditions. Exposed canopy leaves on field-grown cotton plants had *in situ* P_n per unit leaf area nearly two times greater than rates determined *in situ* for similar leaves on chamber-grown plants. Average PAR levels measured in the field (2000-2200 μmol m^{-2} s^{-1}) during the period of vegetative growth (May through early August) were approximately three times greater than in the growth chamber (600-700 μmol m^{-2} s^{-1}) (Figures 2 and 3).

Stomatal diffusive resistance, leaf anatomy and chloroplast lamellar characteristics were studied as possible explanations for the differences observed in P_n. Light saturated stomatal resistances did not differ in cotton leaves of similar age and exposure on field-grown and chamber-grown plants. Lower P_n in leaves of chamber-grown plants was associated with greater mesophyll resistance. Differences in P_n were related to differences in leaf thickness. When the P_n was expressed per unit of mesophyll volume or per unit of chlorophyll (Figure 3), differences between field-grown and chamber-grown plants were much less than when rates were expressed per unit leaf area (Figure 2). Thus, total chlorophyll content may be a better indicator of photosynthetic potential than leaf area. Characterization of the chloroplast lamellar proteins indicated that the leaves of plants grown in the field had smaller photosynthetic units that those from chamber-grown plants. Since the field leaves also contained more chlorophyll per unit area, this resulted in a much larger number of photosynthetic units per area than in the chamber leaves. Thus, the basis chosen to express photosynthetic rates is important in extrapolating the results from growth chamber studies to the field (Patterson *et al.*, 1977) and in constructing and applying photosynthetic models (Shawcroft *et al.*, 1974).

CARBOHYDRATE METABOLISM AND FEEDBACK CONTROL OF PHOTOSYNTHESIS

Several investigators suggest that the decrease in P_n following prolonged CO_2 enhancement is caused by an accumulation of starch in the leaves (Brown and Escombe, 1902; Smith, 1944; Madsen, 1968; 1971a, 1976; Ito, 1973; Downs and Hellmers, 1976; Hoffstra and Hesketh, 1975; Thomas *et al.*, 1975; Apel, 1976; Mauney *et al.*, 1979; Cave *et al.*, 1981; Wulff and Strain, 1982). Brown and Escombe (1902) were among the first to note an increase in starch content in CO_2 enriched plants of *Fuchsia* spp., *Cucurbita pepo,* and *Impatiens platypetala.*

Madsen (1976) reported that the starch content in tomato leaves from plants grown at 2200 μl l^{-1} CO_2 increased nearly seven-fold; there was no further increase when the CO_2 content in the atmosphere was increased up to 5000 μl l^{-1}. So much starch accumulated at 1000 μl l^{-1} or more of CO_2 that the chloroplasts

and leaves became severely deformed and leaves began to wither. The starch content showed a pronounced variation between day and night. The content was greatest during the last part of the afternoon (1.9 percent in control leaves and 12.5 percent in leaves from plants grown at 2200 μl l^{-1} CO_2) and lowest from midnight until sunrise (1.0 percent in control leaves and 7.3 percent in leaves from CO_2-enriched plants). The starch content also increased with age of the plants. Leaves from 19-day-old tomato plants in 2200 μl l^{-1} CO_2 contained 9.1 percent starch while those from 23-day-old plants contained 10.3 percent starch.

The content of glucose and sucrose increased with an increase in CO_2 concentration up to 1000 μl l^{-1}, above which no further increase was observed (Madsen, 1976). In comparison to control plants, CO_2-enriched tomato plants contained a 50 percent increase in glucose and sucrose. The content of glucose did not vary during a 24-hour period but the sucrose content varied greatly. The content was higher in daylight when photosynthesis was active and lower at night. This variation was particularly noticeable in plants given CO_2 enhancement. Bishop and Whittingham *et al.* (1968) also found an increase in the content of soluble carbohydrates when CO_2 was added to the atmosphere. Ito (1973) obtained an increase in the reducing, as well as in the non-reducing carbohydrates, and in the starch content in leaves, stems and roots of several vegetable species grown under CO_2 enhancement. Starch accumulation in the leaves of tomato plants was particularly high in the afternoon in a CO_2-enriched atmosphere. Starch content showed a high negative correlation with P_n. Removal of fruits decreased P_n more at 1065 μl l^{-1} than at 300 μl l^{-1} CO_2.

Several workers have reported a characteristic chlorosis and increase in thickness and brittleness of leaves taken from CO_2-enriched plants (Madsen, 1968, 1976; Downs and Hellmers, 1975; Cave *et al.*, 1981). These changes have been accompanied by a decrease in chlorophyll content and changes in starch grain structure (Cave *et al.*, 1981). Immature leaves of clover plants grown in the growth chamber under 1000 μl l^{-1} of CO_2 contained significantly less total chlorophyll content per unit dry weight and a significantly lower chlorophyll a:b ratio than plants grown at 350 μl l^{-1} CO_2. Fully expanded mature clover leaves partially overcame the deficit in chlorophyll content; however, the chlorophyll a:b ratio still remained much lower in these high CO_2-enriched plants (Cave *et al.*, 1981). Electron micrographs of CO_2-enriched clover plants taken by these investigators revealed a large amount of starch accumulated as irregularly shaped grains. This accumulation of starch was thought to disrupt the normal chloroplast structure of these plants. This in turn was reflected in a large decrease in chlorophyll content per dry weight contributing to chlorosis of the leaves.

Mauney *et al.* (1979) conducted CO_2 enrichment studies in sealed, air-conditioned greenhouses in Phoenix, Arizona in cloudless weather in May to August, 1975 and 1976 to determine the correlation between photosynthetic rate and carbohydrate accumulation. Species were chosen that varied in their tendency to accumulate starch in the leaves: sorghum (low starch, high P_n); cotton (high

Table 4. Influence of CO_2 enrichment on photosynthetic CO_2 uptake (P_n) and sugar and starch content of 14 to 18 day old leaves of four species grown under high CO_2 (630 μl l^{-1}) or low CO_2 (330 μl l^{-1}) and measured as grown or 2 to 4 hours after transfer to the other environment. Correlation coefficients (r) for starch and P_n were calculated for all leaves measured in high or low environment. Plants were 55 to 125 days old at time of measurement. (Data from Mauney *et al.*, 1979).

		Measured at high CO_2							Measured at low CO_2						
		Grown at low CO_2			Grown at high CO_2				Grown at low CO_2			Grown at high CO_2			
Species	Year	P_n nmol $cm^2 s$	Sugar $mg \cdot g^{-1}$	Starch $mg \cdot g^{-1}$	P_n nmol $cm^2 s$	Sugar $mg \cdot g^{-1}$	Starch $mg \cdot g^{-1}$	r	P_n nmol $cm^2 s$	Sugar $mg \cdot g^{-1}$	Starch $mg \cdot g^{-1}$	P_n nmol $cm^2 s$	Sugar $mg \cdot g^{-1}$	Starch $mg \cdot g^{-1}$	r
Cotton	1975	5.2	43	74	3.3	30	256	-0.34	3.0	43	99	2.0	43	302	-0.73**
	1976	2.6	57	137	2.4	61	314	-0.32	2.1	57	87	1.6	56	251	-0.68**
Soybean	1975	3.8	42	40	3.6	49	136	-0.41	-		-	-		-	
	1976	1.7	47	133	2.0	55	229	0.37	1.3	50	112	1.3	51	187	0.01
Sunflower	1975	4.7	75	185	3.4	86	181	-0.12	2.2	62	-	-		-	
	1976	3.1	66	90	2.9	74	117	0.55**	2.6	58	90	2.0	81	75	0.35
Sorghum	1975	4.2	78	8	3.9	88	12	0.61	4.3	46	11	3.5	49	15	-0.63
	1976	3.7	66	57	3.8	69	74	0.30	3.8	58	36	3.5	91	39	0.36

*,** Value for r statistically significant at the 0.05 and 0.01 level, respectively.

starch, intermediate P_n); soybean (intermediate starch, intermediate P_n); and sunflower (intermediate starch, high P_n). Measurements were made of average CO_2 uptake (P_n), and average sugar and starch content of 14-to 18-day-old leaves of the four species grown in high CO_2 (630 μl l^{-1}) or low CO_2 (330 μl l^{-1}) and measured as grown or 2 to 4 hours after transfer to the other environment (Table 4). High CO_2 increased the starch concentration in all species, but neither CO_2 level significantly altered the amount of soluble sugars. In no case was there a significant correlation between sugar concentration and P_n. Carbon dioxide enrichment caused large increases in starch content of cotton and soybean leaves but relatively small increases in sunflower and sorghum leaves (Table 4). The P_n of sorghum, a C_4 plant, was relatively insensitive to CO_2 enrichment, and its leaves always contained low concentrations of starch. Starch content of cotton leaves, on the other hand, increased to levels as high as 50 percent of their dry weight after a few days in high CO_2 (Guinn and Mauney, 1980; Mauney *et al.*, 1979). When cotton plants were moved from normal to high CO_2, the P_n increased 45 percent in the first 2 hours after transfer and then declined as starch accumulated, until the

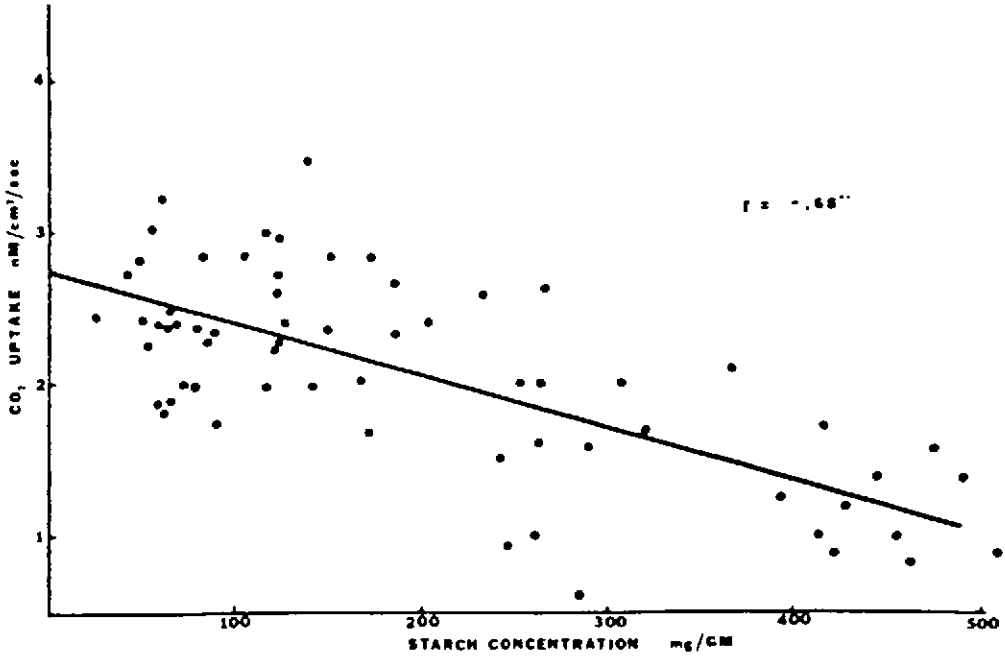

Figure 4. Correlation of leaf starch concentration and CO_2 uptake (P_n) in leaves of greenhouse-grown cotton. Plants were grown and and measured at 330 μl l^{-1} CO_2 or grown at 630 μl l^{-1} CO_2 and and measured at 330 μl l^{-1} CO_2. (From Mauney *et al.*, 1979 and Guinn and Mauney, 1980).

P_n was only 15 percent greater for leaves in high CO_2 than in normal CO_2. When these plants, high in starch, were returned to 330 μl l^{-1} CO_2, the P_n fell below that of plants kept in normal air.

Significant negative correlations were obtained between starch content and photosynthetic rates measured in ambient CO_2 (Figure 4). The poorer negative correlation between P_n and starch in cotton leaves measured in high CO_2 was not anticipated by these workers since a higher starch content generally was expected to cause a greater inhibition of P_n (Mauney *et al.*, 1970; Guinn and Mauney, 1980). They proposed that starch inhibits P_n by interfering with diffusion of CO_2 to fixation sites (Mauney *et al.*, 1979) in line with an earlier hypothesis developed by Kriedemann *et al.* (1976) and Nafziger and Koller (1976). Guinn and Mauney (1980) suggested that the CO_2-induced buildup of starch may affect photosynthesis via stomatal effects since it is known that CO_2 enhancement causes partial closure of stomata. Nafziger and Koller (1976) and Mauney *et al.* (1979) attempted to circumvent this effect by allowing 30 minutes and 2 hours respectively, for stomatal adjustment after transferring plants to different CO_2 concentrations before determining P_n. Hofstra and Hesketh (1975) exposed two soybean cultivars to 800-1000 μl l^{-1} CO_2 and found that the P_n was negatively correlated with mesophyll resistance, starch content of the leaves and specific leaf weight. However, they found no correlation between apparent photosynthesis and stomatal resistance, indicating that the inhibition of apparent photosynthesis at high starch levels was not a stomatal effect.

Nafziger and Koller (1976) treated soybean plants with 50, 300, and 2000 μl l^{-1} CO_2 for 12.5 hours and then measured P_n at 300 μl l^{-1} CO_2. Carbon dioxide enrichment had no effect on sugar content, but increased the starch level. The P_n decreased with increasing amounts of starch. The difference in P_n was largely attributed to increased mesophyll resistance which increased more than stomatal resistance with increase in starch content of the leaves. This effect was observed only at starch levels greater than 1 mg cm^{-2} (about 200 mg g^{-1}) which, as they point out, may explain why some workers fail to observe an inhibition of P_n by starch.

Evidence for end-product inhibition of photosynthesis has been presented (Neales and Incoll, 1968; Guinn and Mauney, 1980). At the time of Neales and Incoll's review in 1968, the evidence for feedback control of photosynthesis was largely circumstantial and primary emphasis was on sugars. There was little evidence or concern for the role of starch in end-product inhibition of photosynthesis. Since that time most of the evidence for feedback regulation of photosynthesis has involved starch rather than sugars. Results with sugars have been largely negative (Guinn and Mauney, 1980).

Demonstration of end-product inhibition of photosynthesis is difficult to obtain. In a number of studies on CO_2 enrichment (Clough and Peet, 1981; Hicklenton and Jolliffe, 1980 a) there was no evidence obtained for feedback inhibition of either photosynthesis or net assimilation rate (NAR) in high CO_2 grown plants.

Demonstration of a negative correlation between photosynthesis and assimilate supply is complicated by the fact that assimilates are themselves products of photosynthesis. Thus, as pointed out by Guinn and Mauney (1980), higher photosynthetic rates should cause the production of more assimilates and result in a positive, rather than in a negative correlation. Failure to demonstrate a negative correlation does not prove the absence of end-product inhibition when accumulation of assimilates and measurement of P_n are not separated in time.

In addition to CO_2 enrichment, other approaches have been used to investigate the question of feedback control of photosynthesis. These include alteration of temperature, photoperiod and source-sink relations; exogenous application of sugars and plant growth regulators; and examination of diurnal, seasonal or ontogenic changes in carbohydrates, P_n, specific leaf weight and other growth parameters (Mason, 1928a,b; Maskell and Mason, 1930; Wardlaw, 1968; Wareing *et al.*, 1968; Gifford, 1980; Guinn and Mauney, 1981; Gifford and Evans, 1981).

Attempts to demonstrate end-product inhibition of photosynthesis with various experimental approaches vary in their success rate depending upon the species. Some species, such as sugarbeet, sugarcane and sorghum do not accumulate much starch, and therefore show no evidence of end-product inhibition. On the other hand, species such as alfalfa, cotton, pangolagrass, soybean and tomato accumulate starch and thus exhibit end-product inhibition. Alfalfa and pangolagrass are able to accumulate inhibitory amounts of starch under natural conditions, while cotton, soybean and tomato require CO_2 enrichment to show statistically significant evidence of end-product inhibition. Approximately 200 mg of starch per gram dry weight of leaves is required before any end-product inhibition of P_n is observed in soybean and cotton (Nafziger and Koller, 1976; Mauney *et al.*, 1979; Guinn and Mauney, 1980).

According to Guinn and Mauney (1980), the starch content of cotton leaves in full sunlight and normal CO_2 increases from a low of about 50 mg to a high of about 150 mg per gram dry weight of leaves during each day. Carbon dioxide enrichment increases the rate of starch synthesis but not its breakdown; consequently starch accumulates. The starch content of older, shaded leaves on field-grown leaves is much lower (Guinn, unpublished results as cited by Guinn and Mauney, 1980). Thus, only young leaves in full sunlight are likely to accumulate enough starch to inhibit P_n, and then only for a portion of each day. However, if the predicted increases in CO_2 content of the atmosphere occur, starch would be expected to accumulate to supraoptimal levels in several species (Guinn and Mauney, 1980). Outlaw and Manchester (1979) quantitatively related starch content of the guard cells to stomatal aperture. Changes in organic acids also are implicated in stomatal movement (Pallas and Wright, 1973).

Several investigators have observed that chlorosis of plants under CO_2 enhanced atmospheres can be avoided by increasing the nutrient supply (Krizek, 1966, unpublished results; Wittwer, 1967; Downs and Hellmers, 1975). Hesketh

(personal communication, 1972, as cited by Downs and Hellmers, 1975) reported that increasing the day temperature from 31 to 35C was effective in preventing high starch accumulation and chlorosis in cotton.

From studies to date, it is clear, that in some species, photosynthetic rates can be controlled by the balance between supply of, and demand for, photosynthates. Some results suggest primary control by end-product inhibition (chiefly by starch), while others indicate hormonal control. Sinks such as developing fruits can stimulate photosynthesis by either type of control mechanism (Guinn and Mauney, 1980). In some cases, both types of regulation may occur in the same plant, either independently or as primary and secondary events (Guinn and Mauney, 1980). Although elaborate models of cotton growth have been developed (Hesketh *et al.*, 1972; Guinn *et al.*, 1976; Gifford and Jenkins, 1981; Jones *et al.*, 1980), it is clear that much more research is needed to elucidate the mechanism of feed-back control of photosynthesis and the role of CO_2 in this process. The influence of plant growth regulators, *e.g.*, abscisic acid (ABA), auxins, gibberellins, cytokinins and brassinosteroids (Tognoni *et al.*, 1967; Zhur *et al.*, 1970, 1972; Thomas, 1975; Raven and Rubery, 1982; Krizek and Mandava, 1983a,b) in photosynthetic partitioning, stomatal regulation, reproduction, senescence, abscission and other physiological processes must also be investigated in greater detail. In view of the possible and complex effects and interactions of these substances and assimilates such as sugars and starch, it is understandable that findings to date appear contradictory and confusing (Guinn and Mauney, 1980).

Recent techniques using ^{14}C-labeled CO_2 provide a rapid and convenient method for studying carbon allocation in plants (Manuson *et al.*, 1982; Fares *et al*, 1983; Strain and Nelson, 1983). The role of sucrose phosphate synthetase in partitioning of carbon in leaves has also attracted considerable interest (Huber 1981a,b, 1983). This enzyme provides a biochemical basis for partitioning of carbon between starch and sucrose in soybean (Huber and Israel, 1982). Studies are in progress to determine the activity of this enzyme under CO_2-enriched atmospheres (Huber *et al.*, 1982).

GROWTH AND DRY MATTER PRODUCTION

The effects of CO_2 enrichment on vegetative growth and dry matter production are summarized in various publications (Wittwer and Robb, 1964; Bailey *et al.*, 1970; Kretchman and Howlett, 1970; Krizek *et al.*, 1970; Pettibone *et al.*, 1970; Wittwer, 1970, 1983; Strain, 1978; Allen 1979; National Academy of Sciences, 1979; Wong, 1979; Kramer, 1981). Wittwer and Robb (1964) reported large increases in fresh weight of cucumber, lettuce and tomato plants grown in CO_2 enriched greenhouses. Similar results were obtained by Krizek (1969, 1970, 1974) and Krizek *et al.* (1968, 1970a,b, 1974) for a wide range of vegetable, woody and ornamental species under controlled-environment conditions. Ten to fifty-fold increases in fresh and dry weights of young seedlings were obtained

under CO_2-enriched atmospheres in the growth chamber when the PAR level and temperature were elevated as well as the CO_2 concentration and high relative humidity and nutrient levels were maintained.

In general, the best time to begin CO_2 enrichment is at the seedling stage. In some cases, even greater acceleration in growth can be obtained by direct seeding under CO_2 enhanced-atmospheres (Krizek *et al.*, 1970b). The growth habit of the plant also appears to be an important determinant of CO_2 sensitivity. Indeterminate plants such as cotton and soybean are more responsive to CO_2 enrichment

Table 5. Influence of CO_2 enrichment in the greenhouse on growth and development of DPL 16 cotton plants. Plants were grown in nutrient solution and were harvested shortly after they started blooming. (Data from Guinn, 1972a).

Parameter	CO_2 conc. 350 μl l^{-1}	1000 μl l^{-1}
Node number of:		
First fruiting position	5.2	5.1
First square	6.5	5.8
Squares/plant, no.	9.7	14.0
Blooms/plant, no.	0.8	0.2
Squares shed, %	29.7	15.4
Fresh wt., g/plant	105.0	115.0

Table 6. Components of yield of cotton plants as influenced by CO_2 and nutrient concentration. (Data from Mauney *et al.*, 1978).

Yield component	Year and nutrient conc.					
	1975, normal		1975, 2x,		1976,2x	
			CO_2 conc. μl l^{-1}			
	330	630	330	630	330	630
LA, dm^2/plant					195	260
Dry wt, g/plant					650	950
Blooms/plant, no.	67	86	69	105	69	110
Bolls/plants, no.	39	59	42	75	37	80
Percent boll retention	66	78	61	71	54	74
Boll wt, g/boll					4.7	5.5
Lint yield, g/plant					61	170
Seed yield, g/plant					114	274
Percent yield increase due to:						
Increase in blooms/plant		60		77		47
Increase in retention		40		23		29
Increase in lint/boll						24

Table 7. Influence of CO_2 concentration on growth analysis of cotton plants at different stages of growth and development. RGR, relative growth rate; NAR, net assimilation rate; DW, dry weight. (Data from Mauney *et al.*, 1978).

Stage growth	Duration days	CO_2 $\mu l\ l^{-1}$	RGR g/g/day	NAR mg/dm²/day	DW g/plant
Juvenile	10-30	630	0.28	280	29
	10-30	330	0.23	187	11
Reproductive	30-70	630	0.07	100	480
	30-70	330	0.07	88	200
Maturation	70-110	630	0.02	52	1100
	70-110	330	0.03	48	550

than are determinate plants such as corn, sorghum, sunflower, tobacco and Alaska pea (Kramer, 1981).

Typical effects of CO_2 enrichment on vegetative growth in cotton are shown in Tables 5, 6, and 7. Mauney *et al.* (1978) obtained significant increases in the rate of leaf initiation and in leaf area development in cotton grown under CO_2-enriched atmospheres (Figures 5 and 6). In 40-day-old cotton plants grown in a greenhouse at 630 $\mu l\ l^{-1}$ CO_2, there was a 2-fold increase in dry weight and a 1.6-fold increase in leaf area as compared with plants grown under ambient CO_2. A decrease in nitrogen level in the nutrient solution gave a proportional decrease in the dry weight and leaf area. The assimilation rate increased 1.5-fold when the plants were grown with high nitrogen and high CO_2. This increase was less at lower levels of nitrate in the nutrient solution (Wong, 1979). Cotton plants grown in high CO_2 had a lower assimilation rate in ambient CO_2 than plants grown at ambient air. The difference was due to the reduction in RuBPcase activity (Wong, 1979).

Studies to date indicate that the relationship between P_n and responsiveness to CO_2 enhancement is rather poor. Consequently high photosynthetic rates alone under CO_2 enriched atmospheres may not be the crucial factor in determining yield. In many plants, there is a poor correlation between P_n per unit leaf area and growth rate, total dry matter production or seed yield (Baker *et al.*, 1973; Evans, 1975; Peet *et al.*, 1977; Elmore, 1980; Wong, 1979).

The relationship between P_n and yield depends on the developmental stage and many other factors (Muramoto *et al.*, 1965; Nagarajah, 1975a; Guinn *et al.*, 1977; Mauney, 1978; Elmore, 1980, see also Chapters 2 and 16). In dry bean (*Phaseolus vulgaris* L.), only at pod set, when P_n was highest, were significant correlations found between P_n and biological and seed yield in eight of nine field-grown cultivars (Peet *et al.*, 1977). In wheat, Krenzer and Moss (1975) found that CO_2 enhancement during floral initiation or grain development increased yield but had no effect if applied prior to flowering. In soybean, Hardman and Brun (1971) obtained no effect of CO_2 enrichment (1200 $\mu l\ l^{-1}$) on either total

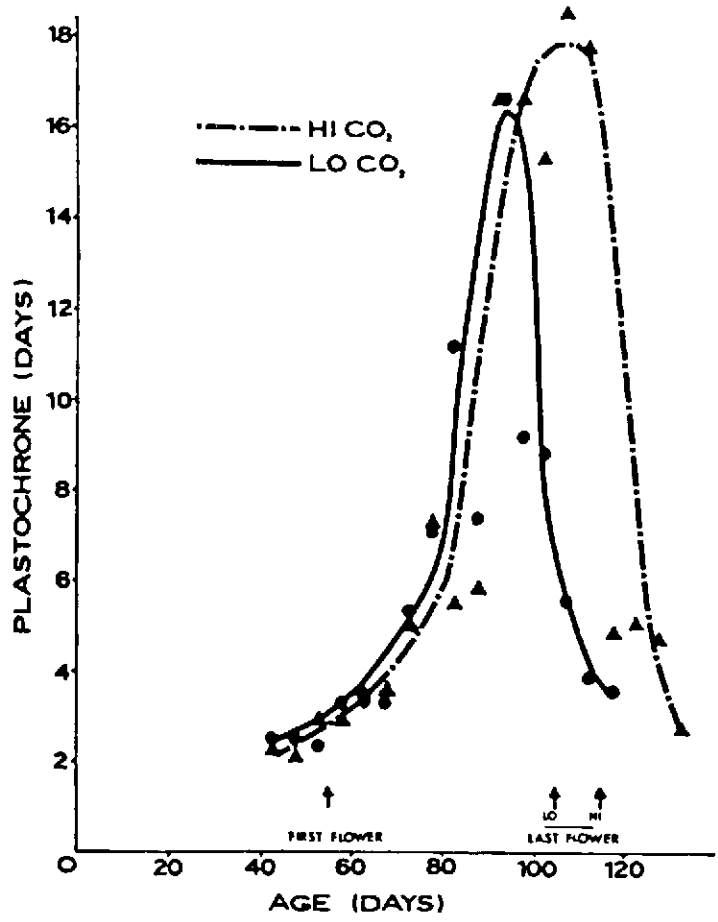

Figure 5. Rate of initiation of primary leaves of cotton as measured by plastochron (days between leaves) for plants grown at 330 μl l^{-1} CO_2 (Lo) or 630 μl l^{-1} CO_2 (Hi) from 45 days of age. (Data from Mauney *et al.*, 1978).

dry matter or yield, if given for a 5-week period during the vegetative stage prior to flowering. Carbon dioxide enrichment given for a 5-week period during flowering increased node number, leaf and stem dry weight, and pod number, but had no effect on seed yield. However, CO_2 enhancement given for a 5-week period during pod filling caused a marked increase in pod weight and seed yield at maturity but had no effect on vegetative growth.

Time of CO_2 enrichment in the field, may, therefore, be of considerable importance in cotton culture. Carbon dioxide enrichment during the juvenile state resulted in the maximum increase in cotton growth based on measurements of relative growth rate (RGR) and net assimilation rate (NAR) (Mauney *et al.*,

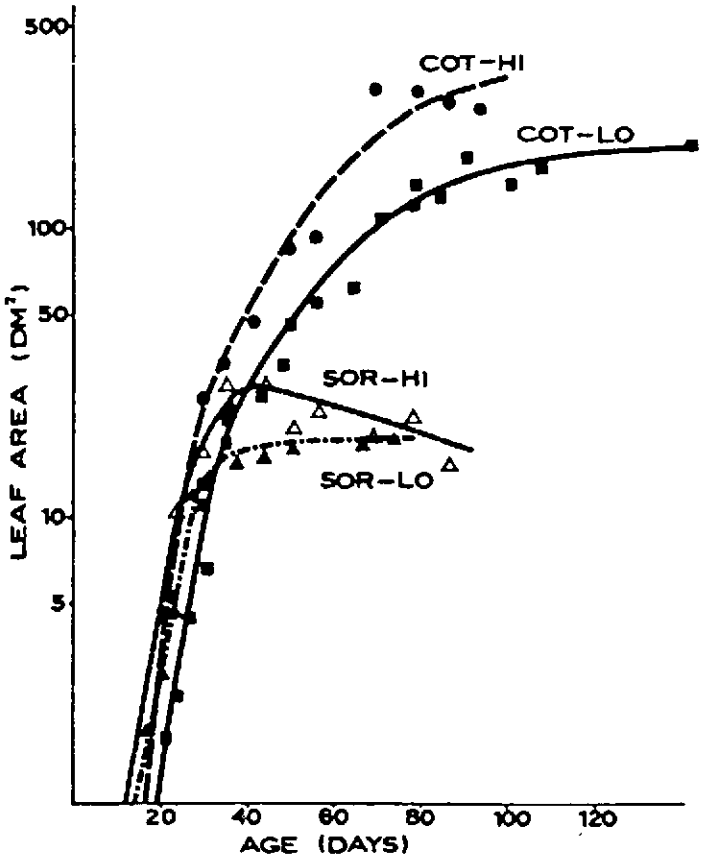

Figure 6. Leaf area development of cotton (COT) and sorghum (SOR) plants grown from germination in the greenhouse under 330 μl l^{-1} CO_2 (Lo) or 630 μl l^{-1} CO_2 (Hi). (Data from Mauney *et al.*, 1978).

1979). The frequency of CO_2 application may also be important (Clough and Peet, 1981).

Compared to leaves of other species, the cotton leaf is able to photosynthesize quite rapidly (Table 2) and compares well with other efficient species in the rate of CO_2 fixation based on the amount of leaf surface exposed to PAR (El Sharkawy *et al.*, 1965; El Sharkawy and Hesketh, 1965; Carns and Mauney, 1968; Zelitch, 1971; Wittwer, 1978a,b). However, cotton does not translocate as much photosynthate into new leaf surfaces as do other species with comparable P_n. As a result, it does not accumulate plant dry weight as rapidly as sunflower, corn, and

soybean (Carns and Mauney, 1968). Carns and Mauney (1968) have pointed out that in view of the rapid photosynthetic rate in cotton, increased dry weight accumulation could be achieved best through changes in the transport of photosynthate to the leaf surface and partitioning of the photosynthate. Because of the compound interest accretion of leaf growth, a high proportion of photosynthate translocated to new leaf development early in the growing season would be especially important, since the increased foliar surface forms the basis for additional CO_2 fixation.

Whether source or sink is the more critical factor in controlling abscission of flowers, squares and bolls in cotton is difficult to establish since the demand for assimilates for fiber and seed production can have a marked feedback effect on the rate of photsynthesis (Hawkins *et al.*, 1933; Brown, 1968; Evans, 1975; Wareing and Patrick, 1975; Saleem and Buxton, 1976; Ho, 1978; Harrocks *et al.*, 1978; Treharne, 1982). Photosynthetic rates in individual leaves may differ strikingly with ontogenetic changes in the plant. Photosynthetic rates in soybean leaves are much higher during filling of the pods than during flowering, even under water stress, presumably due to increased demand at a later stage (Evans, 1975). Studies by Cock and Yoshida (1973) and Yoshida *et al.* (1971) showed that CO_2 enrichment in the field can change source and sink relationships in rice. Evans (1975) pointed out that in cotton, leaves supporting large bolls may have relatively low rates of photosynthesis due to the withdrawal of nitrogen from them by the boll.

The allocation of photosynthate is the result of complex interactions between competitive sinks for available assimilate (Yoshida, 1973). In sugarbeet, increasing the concentration of CO_2 to 1000 μl l^{-1} increased P_n by as much as 50 to 100 percent in one study (Ford and Thorne, 1967). In another study (Wyse, 1980), CO_2 enrichment for 10 days increased total dry weight production of sugarbeet seedlings by 180 percent. However, decreasing the oxygen concentration from 21 to 5 percent to reduce the rate of photorespiration had no significant effect on biomass production. The primary effect of low O_2 was to enhance root diameter and leaf number but had little effect on other growth parameters.

One of the most striking effects of CO_2 enrichment in plants is an increased branching response (Krizek *et al.*, 1968, 1971, 1974). Axillary branches of cotton plants can be greatly stimulated at 30C under CO_2 enriched atmospheres or other conditions conducive to a rapid supply of photosynthate (*e.g.*, intense solar radiation) (Evans, 1975). Other investigators have also reported marked effects of CO_2 enrichment on apical dominance (Poez *et al.*, 1980).

TRANSPIRATION AND STOMATAL ACTIVITY

One of the primary benefits of CO_2 enhancement is to increase the water-use efficiency (Figure 7) of plants by partial closure of stomates and a concomitant decrease in transpiration (Figure 8 and Table 8) (Heath, 1948, 1949, 1950, 1959; Heath and Milthorpe, 1950; Heath and Russell, 1954; Stalfelt, 1959; de Wit,

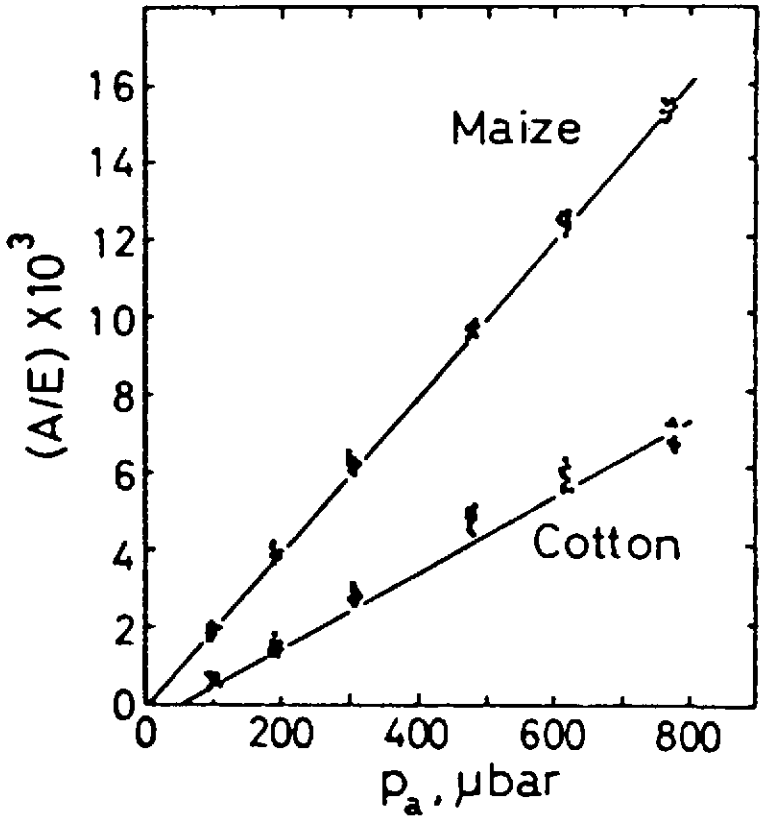

Figure 7. Water use efficiency (A/E) (mol CO_2/mol H_2O) of cotton and maize plants as influenced by CO_2 concentration (μl l^{-1} or μbar). The straight lines were theoretical relationships as described by Wong, 1980, assuming a vapor pressure difference of 20 mbar. The dots are actual experimental values.

1958; Pallas, 1965; Jarvis, 1971; Raschke, 1972, 1974, 1975a,b, 1976, 1979; van Bavel, 1972a, 1974, van Bavel *et al.*, 1973; Farquhar and Cowan, 1974; Tinus, 1974; Takami and van Bavel, 1975; Raschke *et al.*, 1976; Goudrian and van Lear, 1978; Enoch and Hurd, 1977, 1979; Farquhar *et al.*, 1978; Gifford, 1979a,b; Carlson and Bazzaz, 1980; Louwerse, 1980; Sionit *et al.*, 1980, 1981d; Wong, 1979, 1980; Heath and Meidner, 1981; Rosenberg, 1981; Farquhar and Sharkey, 1982; Björkman and Pearcy, 1982; Wittwer, 1983). The ratio of CO_2 taken up in photosynthesis to the water lost in transpiration is termed photosynthetic water-use-efficiency (Bjorkman and Pearcy, 1982). Water-use-efficiency may also be expressed in terms of the amount of biomass gain for the amount of water lost in a given period of time. One of the direct effects of CO_2 enhancement on photosyn-

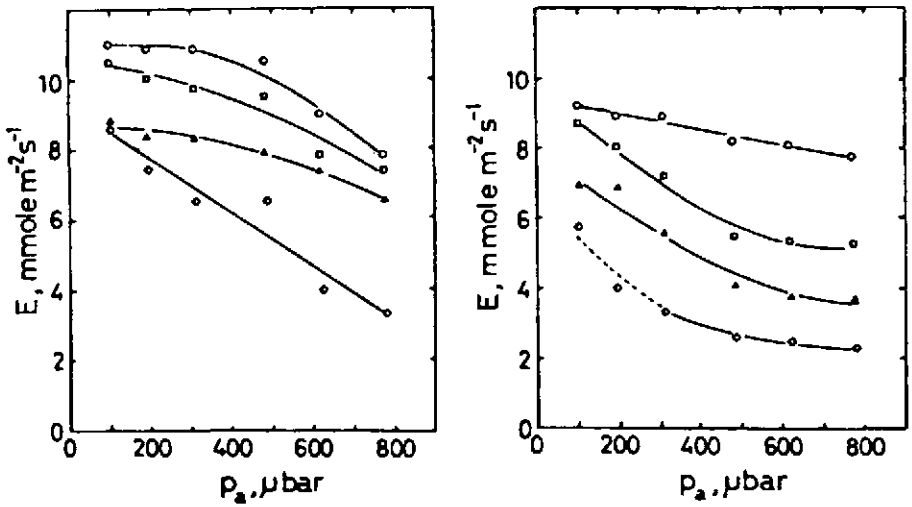

Figure 8. Rate of tranpiration (E) in cotton as influenced by CO_2 concentration. The plants were grown at 330 μl l^{-1} (μbar) (left) or 660 μl l^{-1} CO_2 (right) and under four levels of nitrogen nutrition. Details as in Figure 1. (Data from Wong, 1980).

Table 8. Transpiration rate of 40-day old cotton plants and 30-day old maize plants as influenced by CO_2 concentration and nitrogen nutrition. (Data from Wong, 1980).

	Transpiration rate (mmol m^{-2} s^{-1})			
	Cotton		Maize	
Nitrogen	CO_2 (μl l^{-1})			
mM NO_3^-	330	660	330	660
24.0	1.79	2.12	1.52	0.99
12.0	1.33	2.25	1.08	0.89
4.0	1.05	0.97	1.64	0.24
0.6	0.29	0.21	0.26	0.11

thesis in C_3 plants is increased photosynthetic water-use-efficiency. Water-use-efficiency was doubled in both cotton and maize plants grown at high CO_2 irrespective of the nitrate level in the solution. This increase in water-use-efficiency was due primarily to reduced transpiration in some treatments and to increased assimilation in others (Wong, 1979). According to Björkman and Pearcy (1982) photosynthetic water-use-efficiency in C_3 plants would be expected to double with a doubling of CO_2 in the atmosphere. In a C_4 species this effect would likely be smaller but still significant. In a mixture of C_3 and C_4 species, the C_3

crops would likely benefit to a greater extent from an increase in atmospheric CO_2 concentration (Wittwer, 1983). From a model of CO_2 uptake of carnation plants, Enoch and Hurd (1979) estimated that the water-use-efficiency (net photosynthesis rate/transpiration rate) would increase by 40-50 percent during the next 50 years assuming a global increase in atmospheric CO_2 level to 600 $\mu l\ l^{-1}$.

Stomatal conductance decreases with increasing CO_2 concentration in both C_3 and C_4 species (Wittwer, 1983). Increasing the CO_2 content of the atmosphere in controlled-environment chambers to 400 $\mu l\ l^{-1}$ reduced the transpiration rate of corn and sorghum and to a lesser extent, that of cotton, soybean and tomato plants by causing the stomata to close. Stomata of the two monocots, corn and sorghum, closed when the CO_2 concentration was at 2000 and 3000 $\mu l\ l^{-1}$ respectively. Cotton, soybean and tomato stomata, on the other hand, did not close completely even at CO_2 concentrations up to 4000 $\mu l\ l^{-1}$ (Pallas, 1965).

On the basis of natural fluctuations in CO_2 level in crop stands (about 5 percent) one might conclude that the antitranspirant action of CO_2 in open field culture might be insignificant. However, if one accepts the premise that it is the internal concentration of CO_2 rather than the external concentration that regulates stomatal behavior, the role of CO_2 as an antitranspirant may have greater significance than is generally appreciated (van Bavel, 1974).

Because of the close connection between CO_2, abscisic acid (ABA), ethylene and water stress, their role in stomatal regulation needs to be considered when conducting CO_2 studies on cotton and when developing models of cotton productivity (Zelitch, 1963, 1965; Whiteman and Koller, 1967; Meidner and Mansfield, 1965, 1968; Meidner, 1969; Horton, 1971; Kriedemann *et al.*, 1972; Hirand Kriedemann, 1974; Beardsell and Cohen, 1975; Davenport *et al.*, 1977; Loveys, 1977; Dorffling *et al.*, 1977, 1980; Dubbe *et al.*, 1978; Mansfield *et al.*, 1978; Korner *et al.*, 1079; Malloch and Fenton, 1979; Schulte and Dorffling, 1981; Fenton *et al.*, 1982; Ackerson and Radin, 1983; Paez *et al.*, 1983). The role of water stress and ABA in inducing stomatal closure is well known (Milthorpe and Spencer, 1957; Dale, 1961; Slatyer and Bierhuizen, 1964a,b; Allaway and Mansfield, 1967; Slatyer, 1967; Cowan and Milthorpe, 1968; Milthorpe, 1969; Mittelheuser and Van Steveninck, 1969, 1971; Jordan, 1970; Cowan and Troughton, 1971; Cummins *et al*, 1971; Jordan and Ritchie, 1971; Hsiao, 1973; Sharpe, 1973; Milborrow, 1974a,b, 1979, 1980; Turner, 1974; Raschke, 1975a,b; Mansfield, 1976; Ackerson *et al.*, 1977; Cowan and Farquhar, 1977; Walton *et al.*, 1977; Ackerson and Hebert, 1981; Henson, 1981; Sionit *et al.*, 1981d; Ackerson, 1980, 1982; Cowan *et al.*, 1982).

Slatyer and Bierhuizen (1964b) and Holmgren *et al.* (1965) reported that the stomatal resistance of leaves of cotton grown under controlled conditions increased with age. Jordan *et al.*, (1975) obtained evidence to suggest that stomatal closure on lower leaves of cotton plants subjected to water stress was associated with leaf age as well as with PAR effects. The nature of the age-related changes is unknown. The effect of age on stress-induced stomatal closure was not associated

with a loss of potassium from the older leaves. Increases in both the free and bound forms of ABA were observed in water-stressed plants, but the largest accumulation of ABA was found in the youngest leaves. Thus, the pattern of ABA accumulation in response to water stress did not parallel the pattern of stomatal closure induced by water stress.

Goudriaan and van Laar (1978) observed that the stomatal conductance of corn and bean, but not sunflower, was reduced by an increase in CO_2. They attributed this to a greater efficiency in utilization of water in corn than in sunflower. Reports of increased water-use-efficiency under CO_2 enriched atmospheres have also been published for cotton (Ehrler *et al.*, 1966), wheat (Gifford, 1979a,b) and carnation (Enoch and Hurd, 1979).

REPRODUCTIVE DEVELOPMENT

Typical effects of CO_2 enrichment on flower initiation, boll production, lint and seed yield, and other parameters of reproductive development are summarized in Tables 5, 6 and 9. In experiments reported by Mauney *et al.* (1978), cotton plants grown under CO_2 enriched atmospheres of 630 $\mu l\ l^{-1}$ set twice as many bolls as plants exposed to 330 $\mu l\ l^{-1}$ CO_2. Similar increases in yield were obtained by Guinn (1972a, 1974) at 1000 $\mu l\ l^{-1}$ CO_2. In addition to increasing the number of squares, Guinn (1972a) also observed that increasing the CO_2 level in the greenhouse from about 350 $\mu l\ l^{-1}$ to 1000 $\mu l\ l^{-1}$ lowered the node number of the first boll (Table 5). In contrast, warm nights (30C) and short photoperiods raised the node number of the first boll (Guinn, 1973).

Table 9. Influence of atmospheric CO_2 level in the greenhouse on total number of fruiting positions (FP), percentage of the total fruiting positions that abscised their fruiting forms (Percent FP abscised), and on number of squares, blooms, and bolls remaining on DPL 16 cotton plants at time of harvest (No. FP retained). Means and their standard errors are based on 40 plants per treatment. (Data from Guinn, 1974a).

CO_2 conc. $\mu l\ l^{-1}$	Total No. fruiting positions	Percent FP abscised	No. FP retained
First test:[1]			
350	14.3 ± 0.5	30.9 ± 2.3	9.9 ± 0.6
1000	16.8 ± 0.6	16.4 ± 2.2	14.2 ± 0.7
Second test:[2]			
350	37.2 ± 1.5	25.6 ± 1.6	28.4 ± 1.5
1000	36.9 ± 1.3	17.1 ± 1.4	30.8 ± 1.4

[1]Plants were harvested as soon as the first squares reached the bloom stage.
[2]Plants were permitted to set some bolls before they were harvested.

SENESCENCE AND ABSCISSION

Numerous studies concerning the influence of CO_2 and O_2 on abscission or senescence in intact plants are available (Hall, 1958; Abeles and Gahagan, 1968; Widholm and Ogren, 1969; Davis and Addicott, 1972; Addicott and Lyon, 1973; Hesketh and Hellmers, 1973; Guinn, 1973, 1974a; Osborne, 1974; Chatterjee, 1977; Chatterjee and Chatterjee, 1972; Chang, 1975; Warma, 1976a,b,c,d; Vaughan and Bate, 1977; Nooden, 1980; Satler and Thimann, 1983; Thimann, 1978; Thimann and Satler, 1979; St. Omer and Horvath, 1983a,b). In general, CO_2 retards abscission while O_2 promotes it (Carns, 1951; Yamaguchi, 1954; Abeles and Gahagan, 1968; Addicott and Lyon, 1973; Kozlowski, 1973). Abeles and Gahagan (1968) reported that a few percent of CO_2 in air reduced the rate of explant abscission appreciably. However, in mixtures of CO_2 and O_2 Yamaguchi (1954) found that more than 15 percent CO_2 was needed to reduce abscission rates to half those observed in pure O_2.

There is increasing evidence that ethylene is involved in the shedding of various plant parts (McAfee and Morgan, 1971; Lipe and Morgan, 1972a,b, 1973; Abeles, 1973; Kozlowski, 1973). Ethylene promotes abscission in at least two ways. It decreases the auxin content of the abscission zone, and it stimulates the synthesis of lytic enzymes (*viz.*, pectinase and cellulase in the abscission zone) that weaken the middle lamella and cell wall (Guinn, Chapter 12). Virtually any environmental stress can induce ethylene production in cotton plants (Guinn, 1974b, 1976a,b, 1979, 1982). These include water stress (McMichael *et al.*, 1972; Jordan *et al.*, 1972), chilling injury (Abeles, 1973; Guinn, 1979) and other stresses.

Ethylene has been shown to interact strongly with both O_2 and CO_2 (Yamaguchi, 1954; Abeles and Gahagan, 1968; Lipe and Morgan, 1972b; Abeles, 1973; Marynick, 1977). Depending on the tissue, CO_2 can inhibit, promote, or have no effect on ethylene (Abeles, 1973). Except for rice, low concentrations of oxygen typically inhibit ethylene production. The inhibition of ethylene production under anaerobic conditions has been observed by many investigators for a wide range of tissues.

A literature review of CO_2 action on various ethylene-mediated processes indicates that in most cases CO_2 blocks or retards ethylene action (Dhawan *et al.*, 1981). A few exceptions include growth promotion of respiration in lemon, and removal of astringency from persimmons. In these cases, CO_2 had the same effect as ethylene (Abeles, 1973). Cracker and Abeles (1969) reported that ABA stimulated ethylene production by cotton and bean explants, but the stimulation was small and evident for cotton only at the highest concentration (0.5 nM) of ABA tested.

Lipe and Morgan (1972a,b) found that fumigation of detached cotton fruits with 10 percent CO_2 readily delayed dehiscence. The CO_2 effect was duplicated by placing the fruits under reduced pressure (200 mm mercury) to promote the escape of ethylene from the tissues. Dehiscence was delayed in both detached and

attached fruits. By varying the mixture of CO_2 and ethylene, they were able to vary the rate of dehiscence in cotton fruits. A combination of 13 percent CO_2 and 1.0 μl l^{-1} of ethylene resulted in a competitive balance in which fruits dehisced at the same rate as control fruits.

The influence of hormonal and environmental factors on boll shedding in cotton has been reported by various investigators (Lloyd, 1920; Mason, 1922; Dunlap, 1943, 1945; Saad, 1951; Eaton and Ergle, 1953, 1954; Goodman, 1955; King *et al.*, 1956; Dale, 1959; Johnson and Addicott, 1967; Heilman *et al.*, 1971; Jordan *et al.*, 1972; Abeles, 1973; Kozlowski, 1973; Guinn, 1972a,b, 1973, 1974a,b, 1976a,b; McMichael *et al.*, 1973; Osborne, 1974; Guinn and Fry, 1981). Hearn (1972) postulated that bolls are retained only if the demand for carbohydrates does not exceed the supply and that boll abscission is regulated by the balance between supply and demand. Cloudy weather (Mason, 1922; Goodman, 1955; Ehlig and Le Mert, 1973), low photosynthetically active radiation (PAR) levels (Dunlap, 1943, 1945), artificial shading with muslin (Sorour and Rassoul, 1974), close spacing (Brown, 1971) and partial (Eaton and Ergle, 1954a) or complete (Mason, 1922) leaf removal can also cause shedding of flowers, squares and bolls, presumably by reducing the amount of photosynthesis and carbohydrate supply (Guinn, 1978), but also by reducing the supply of growth regulators (Eaton and Ergle, 1953).

By increasing the CO_2 concentration of the atmosphere in a greenhouse from 350 μl l^{-1} to 1000 μl l^{-1}, Guinn (1973, 1974) was able to decrease shedding in DPL 16 cotton plants (Table 9) and increase the concentration of sugars (Table 10) in the leaves. Increasing the daily photoperiod from 8 to about 14 hours produced effects similar to those of CO_2 enrichment.

Table 10. Influence of CO_2 level and photoperiod on sugar content of leaves from DPL 16 cotton plants grown in the greenhouse. Means and their standard errors are based on 40 plants per treatment. (Data from Guinn, 1974a).

Treatment	Fructose	Glucose	Sucrose
		mg/g dry weight	
CO_2 Conc.			
1000 μl l^{-1}	6.7 ± 0.4	17.4 ± 1.0	10.9 ± 0.4
350 μl l^{-1}	3.9 ± 0.4	9.3 ± 0.7	12.6 ± 0.6
Photoperiod			
long-day[1]	3.6 ± 0.4	16.3 ± 1.3	7.8 ± 0.4
8-hour day	1.9 ± 0.4	10.2 ± 0.6	6.8 ± 0.4

[1]Long-day conditions ranged from 14.4 hours at the beginning of the experiment to 12.5 hours at the end.

Warm nights (30C) and/or short photoperiods increased shedding and decreased starch content of the leaves (Guinn, 1973, 1974a). These results suggest

that fruiting and shedding in cotton are influenced by a balance between photosynthesis and respiration. Factors that decrease photosynthesis or increase respiration (low PAR, short photoperiod, low CO_2 and warm nights) tend to delay fruiting and increase abscission of squares and bolls while those conditions that increase photosynthesis or decrease respiration (high PAR, long photoperiods, high CO_2 and cool nights) tend to enhance fruiting and decrease abscission of reproductive structures (Guinn, 1974a).

The influence of brief periods of low PAR on shedding of cotton bolls was reported by Guinn (1973). He found a gradual depletion of sugars, starch and lipid-soluble phosphate in 6-day-old bolls when plants were transferred from the greenhouse to low PAR conditions. This shedding was preceded by a decreased rate of growth and lower protein and RNA contents.

Levels of PAR reaching the lower part of the plant canopy in high density populations (more than 100,000 plants per hectare) of cotton may, therefore, be severely limiting to photosynthesis (Guinn, 1974a). Since developing bolls obtain most of their photosynthate from subtending leaves, bracts and leaves one node removed (Ashley, 1972), low PAR levels in this position would probably limit boll retention there (Guinn, 1974a). Close spacing could also result in increased root competition or ethylene accumulation in the plant canopy (Heilman *et al.*, 1971).

The mutually compensating effect of PAR and CO_2 under field conditions for wheat (Imazu *et al.*, 1965) and in the greenhouse for horticultural crops (Hopen and Ries, 1962) suggests that CO_2 enrichment in the field under cloudy conditions might be beneficial in reducing abscission in cotton by increasing the amount of assimilate and by reducing the substrate for photorespiration.

Guinn (1976a) pointed out that the nutritional and hormonal theories for the control of boll shedding in cotton are not necessarily contradictory or exclusive. His results indicate that nutritional stress increases the rate of ethylene evolution by young cotton bolls. The additional ethylene may be a causal factor in increasing boll abscission when cotton plants are subjected to nutrient stress.

Carbon dioxide and ethylene are generally antagonistic in their effects on abscission. Certain nutritional and other environmental stresses are known to promote ethylene production. Jordan *et al.* (1972) reported that 15 percent CO_2 could reverse the abscission-promoting effects of ethylene on cotyledonary leaves of Stoneville 213 cotton plants when given in combination with water stress at plant water potentials above -1.2 mPa but had no reversal effect at lower water potentials.

In many industrial areas (*e.g.*, the Los Angeles basin), ambient CO_2 levels can increase to 500 μl l^{-1} and higher (Pallas, 1970). Since ethylene levels are also generally high in these same locations, it is hard to say whether any salutory effect of CO_2 enrichment on the yield of nearby cotton crops might result.

The potential use of CO_2 enrichment to increase cotton production will depend upon many environmental and morphological factors. Environmental factors include plant and soil water status, relative humidity, nutrient supply, tempera-

ture, light spectral quality and composition of other gases such as O_2, ethylene and pollutants. Morphological factors include canopy structure, leaf shape and anatomy, boundary layer thickness, stomatal diffusive resistance, chloroplast lamellar characteristics, root development and endogenous rhythms.

INTERACTION OF CO_2 AND OTHER ENVIRONMENTAL AND MORPHOLOGICAL FACTORS

The age of the plants and stage of development are also likely to be important factors based on results obtained with other crops (Krizek *et al.*, 1968, 1971; Zimmerman *et al.*, 1970; Yoshida, 1973; Krenzer and Moss, 1975; Wittwer, 1978a). Mauney *et al.* (1978) found that the greatest effect of CO_2 on net assimilation rate (NAR) in cotton was during the juvenile stage (Table 7). Careful studies—both under controlled-environment and field conditons—are needed to determine the optimum age, time, and duration of CO_2 enrichment. The type of substrate and irrigation system also are important in CO_2 enrichment studies (Plaut *et al.*, 1975; Lawson *et al.*, 1978; Nakayama and Bucks, 1980; Tarter, 1983).

Because of the vagaries of the field environment, it is often difficult to extrapolate findings from studies on CO_2 enrichment under controlled-environment conditions to those in the field. Temperature and moisture are perhaps the two most limiting environmental parameters in the field. Temperature effects on cotton production are discussed in Chapter 5, so they will not be discussed here. The role of water stress on the utilization of CO_2 and carbohydrate accumulation will only be covered briefly since this topic is addressed in Chapters 7, 8 and 10.

WATER STRESS

The time of application and severity of water stress appear to be the main factors influencing yield in cotton. Severe moisture stress applied for 9 days during the peak flowering period reduced yield of Acala SJ-1 cotton in the San Joaquin Valley more than water stress periods of comparable duration applied either early or late in the flowering period (Grimes *et al.*, 1970). Severe water stress occurring early in the flowering period reduced yield by increasing shedding of squares before they flowered. Water stress late in the flowering period reduced flowering rate and retention of bolls. In some cultivars of cotton, soil moisture stress during the pre-flowering period was found to stimulate flower initiation and hence increase the number of bolls, while in other cultivars, boll size was increased (deBruyn, 1964; Singh, 1975).

The growth and development of the cotton plant is sharply curtailed during periods of water stress (Ergle, 1936, 1938; Eaton and Ergle, 1948; Jordan, 1970; Marin and da Silva, 1972; Marani and Levi, 1973). In cotton leaves, drought causes an increase in hexose sugars, variable effects on sucrose and large reductions in starch concentration. In stems and roots, however, there were always

moderate to large increases in the concentrations of hexoses, sucrose and starch (Eaton and Ergle, 1948). On the basis of averages of leaves, stems and large roots, these carbohydrates, for the plant as a whole, were doubled by protracted drought. Thus, drought appears to depress carbohydrate utilization to a greater extent than it does photosynthesis (Eaton and Ergle, 1948, see also Chapter 10).

In wheat, water stress during CO_2 enrichment under controlled environments was found to enhance the effects of CO_2 on grain yield (Gifford, 1979b). While similar effects are possible in cotton, one can only speculate at this time as to the comparative effects of CO_2 enrichment under water stress conditions.

AIR POLLUTION

Air pollution has a significant effect on cotton yield (Ting and Dugger, 1968; Brewer and Ferry, 1974; Millican, 1976; Heggestad *et al.*, 1977; Heggestad and Christiansen, 1982). Most field studies have been conducted in open top chambers described by Heagle *et al.* (1973). Elevated levels of CO_2 in the atmosphere ameliorate the effects of SO_2 and other pollutants in both C_3 and C_4 plants (Mansfield and Majernik, 1970; Majernik and Mansfield, 1972; Hou *et al.*, 1977; Mansfield *et al.*, 1981; Carlson and Bazzaz, 1982; Carlson, 1983; Strain and Bazzaz, 1983). Since stomata provide the main routes for the entry of sulfur dioxide (SO_2), ozone (O_3) and other air pollutants into the leaves of higher plants, and CO_2 is known to reduce stomatal conductance, it is not surprising that increased CO_2 concentration should afford some protection against these pollutants (Mansfield, 1973; Unsworth *et al.*, 1973; Unsworth, 1981).

IMPLICATIONS OF PROJECTED GLOBAL INCREASES IN ATMOSPHERIC CO_2

Estimates as to the magnitude of increase in P_n that might be expected in C_3 and C_4 plants with increased ambient levels of CO_2 vary widely (Bassham, 1977; Kramer, 1981; Baker and Enoch, 1982; Bjorkman and Pearcy, 1982; Kimball, 1982; Tolbert and Zelitch, 1982; Wittwer, 1983). Some reports suggest that a doubling in atmospheric CO_2 level may increase photosynthesis in C_3 plants by 50 percent, increase yield and dry weight by 20-45 percent and increase primary productivity by 40 percent (Baker and Enoch, 1982; Bjorkman and Pearcy, 1982; Bassham, 1977; Tolbert and Zelitch, 1982; Wittwer, 1983). Kimball (1982) tabulated and analyzed the results of more than 430 observations on the yields of 37 species grown under CO_2-enriched atmospheres. These results were extracted from more than 70 reports published during a 64-year period. CO_2 enrichment increased the economic yield of all studied agricultural crops by an average of 28 percent (with a 99.9 percent confidence interval from 22 to 35 percent). Based on his analysis, a doubling in atmospheric CO_2 level was projected to increase yields by 33 percent (with a 99.9 percent confidence interval from 24 to 43 percent).

Kramer (1981), however, indicates that over the long term, exposure to high

CO_2 concentration often results in only a temporary increase in P_n. The high P_n observed in the seedling stage disappears, and the P_n often falls below that of plants kept at ambient CO_2. Kramer (1981) concludes that it is doubtful if a global doubling in CO_2 concentration will result in a large sustained increase in P_n per unit of leaf surface, even though it may result in an increase in dry matter production of some species.

At the present rate of fossil fuel consumption, CO_2 concentration in the atmosphere is increasing on a global basis approximately 0.8 μl l^{-1} per year. Background level of CO_2 concentration before the industrial revolution was about 258 μl l^{-1} (Allen, 1979). If CO_2 concentration rises to 400 μl l^{-1} by the year 2080 as some predict (Baes *et al.*, 1976), we might expect a 20 percent increase in photosynthesis rates of C_3 plants such as cotton, assuming no other factors are limiting (Allen, 1979).

Thus far, we have concerned ourselves only with the direct effects of CO_2 increases that are expected. However, because of the well-known greenhouse effect associated with CO_2, any increase in global CO_2 concentration is also expected to result in an increase in surface temperature of the Earth (Kerr, 1977; Hoyt, 1979; NAS, 1979; Pearmon, 1980; Lockwood, 1982; Strain, 1982; Strain and Armentano, 1982). Such indirect climatic effects of CO_2 enhancement would be expected to have a significant impact on crop production under field conditions. Since this topic is beyond the scope of this chapter the reader is referred to the following references for further information on the long-term climatic effects of projected increases in CO_2 concentration: Keeling, 1970, 1977; Attiwill, 1971; Keeling *et al.*, 1976; Woodwell, 1978; Idso, 1980, 1983a,b; Gribbin, 1981; Hansen *et al.*, 1981; Kellogg and Schware, 1981; Clark, 1982; Kimball and Idso, 1982.

SUMMARY

Most studies on CO_2 enrichment under greenhouse and growth chamber conditions have demonstrated the stimulatory effects of elevated CO_2 levels on the growth and development of cotton and other economically important plants. Recent tests involving CO_2 enrichment of cotton and other crops in the field are encouraging, but further studies are needed to determine whether or not the practice is economically feasible.

One of the most pronounced effects of CO_2 enrichment in cotton, tomato and other species is a large build-up in sugars and starches stored in the leaves. Increasing the CO_2 level from 330 μl l^{-1} to 630-1000 μl l^{-1} under controlled environments lowered the node number of the first flower, doubled boll production and delayed abscission of squares and bolls.

The metabolic consequences of CO_2 enrichment of cotton plants need to be examined in greater detail. Since CO_2 utilization can be influenced by a myriad of genetic, physiological, biochemical and morphological factors, careful studies are

required to determine the interaction of CO_2 with these factors. Because of the marked influence of CO_2 enrichment on water-use-efficiency through its effect on CO_2 assimilation, transpiration and stomatal regulation, special attention should be given to this area of research.

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