Photosynthesis Research 12: 191–203 (1987)

Regular paper

Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field

JOHN W. RADIN,[1] BRUCE A. KIMBALL,[2] DONALD L. HENDRIX[1] & JACK R. MAUNEY[1]

[1] *United States Department of Agriculture, Agricultural Research Service, Western Cotton Research Laboratory, and* [2] *U.S. Water Conservation Laboratory, Phoenix, AZ 85040, USA*

Received 11 June 1986; accepted in revised form 26 November 1986

Key words: photosynthesis, carbon dioxide, water stress, stomatal conductance, mesophyll conductance, *Gossypium*

Abstract. The cotton (*Gossypium hirsutum* L.) plant responds to a doubling of atmospheric CO_2 with almost doubled yield. Gas exchange of leaves was monitored to discover the photosynthetic basis of this large response. Plants were grown in the field in open-top chambers with ambient (nominally 350 μl/l) or enriched (nominally either 500 or 650 μl/l) concentrations of atmospheric CO_2. During most of the season, in fully-irrigated plants the relationship between assimilation (A) and intercellular CO_2 concentration (c_i) was almost linear over an extremely wide range of c_i. CO_2 enrichment did not alter this relationship or diminish photosynthetic capacity (despite accumulation of starch to very high levels) until very late in the season, when temperature was somewhat lower than at midseason. Stomatal conductance at midseason was very high and insensitive to CO_2, leading to estimates of c_i above 85% of atmospheric CO_2 concentration in both ambient and enriched chambers. Water stress caused A to show a saturation response with respect to c_i, and it increased stomatal closure in response to CO_2 enrichment. In fully-irrigated plants CO_2 enrichment to 650 μl/l increased A more than 70%, but in water-stressed plants enrichment increased A only about 52%. The non-saturating response of A to c_i, the failure of CO_2 enrichment to decrease photosynthetic capacity for most of the season, and the ability of the leaves to maintain very high c_i, form in part the basis for the very large response to CO_2 enrichment.

Abbreviations: c_a–atmospheric CO_2 concentration; c_i–intercellular CO_2 concentration; A–rate of assimilation of CO_2; g_s–stomatal conductance to water vapor; g_b–boundary layer conductance to water vapor; g'_m–mesophyll conductance to CO_2; VPD–vapor pressure deficit; ψ_w–leaf water potential; L–stomatal limitation to CO_2 uptake.

Introduction

The cotton plant has a remarkable capacity to respond to CO_2 enrichment. Mauney et al. [15] reported that an approximate doubling of c_a increased lint and seed yields per plant by 179% and 140%, respectively, in a glasshouse. Although the estimated yield increase in the field was about half as great, this estimate stands in marked contrast to the much more modest increases (about 33% on the average) noted with most other crop plants [10]. Field studies have recently confirmed that a doubling of atmospheric CO_2 enhances seedcotton yields up to 92% [11, 12]. The basis for this responsiveness to CO_2 has not been

clearly shown, but it appears to involve enhanced leaf area per plant, enhanced photosynthesis per unit leaf area, and an indeterminate pattern of growth and fruiting [11, 12, 15].

These studies were conducted to compare photosynthetic characteristics of leaves of plants grown at normal and elevated atmospheric CO_2 concentrations. Plants were grown in open-top chambers in the field, and gas-exchange techniques were used to construct curves relating A to c_i.

Materials and methods

Crop culture

Cotton (*Gossypium hirsutum* L., cv. Deltapine 61) was seeded on April 9, 1985 in rows spaced 1 m apart in a clay loam soil. Germination was begun by irrigation on April 11, with most of the seedlings emerging on April 16. After establishment, the stand was thinned to 10 plants/m^2 in mid-May. Insecticides were applied as needed during the season.

Water and fertilizer were applied weekly through a drip irrigation system. The well-watered plots received an amount of water equal to the open-pan evaporation of the previous week with an adjustment for leaf area. Beginning May 24, the water-stressed plots received two-thirds as much water as the well-watered plots. Rainfall was measured in gauges beside the field and was subtracted from the water requirement at the next irrigation. All plots received a total of 183 kg/ha N as urea. There were two replicates of each water level.

Design and operation of open-top CO_2 enrichment chambers

The chambers and the CO_2 enrichment system have been described in detail [11, 12]. Briefly, the chambers covered a square 3 m × 3 m and were 2 m tall with walls of clear polyethylene film. Chambers within each plot were separated by two external border rows. CO_2 (purchased locally from a commercial source and stored on site in a tank) was injected into a blower that drew in outside air and discharged the enriched air into 4 lengths of perforated polyethylene tubes 200 mm in diameter. The tubes ran the length of the chamber in the 4 furrows surrounding the 3 rows of plants enclosed by the chamber. Air flow rate was about 4 chamber volumes per minute, with an average upward velocity in the chamber of 0.13 m/s. A sampling pump within each chamber pumped air from the top of the canopy to an infrared CO_2 analyzer in a nearby cabin. A computer-controlled system compared the actual CO_2 concentration within the chamber to the desired concentration and adjusted the CO_2 injection rate accordingly. The automated system sequentially sampled all chambers over about a 30-min cycle. Despite the relatively slow net upward flow of air, considerable turbulence existed inside the chambers leading to random variation in CO_2 level. Across all water levels and replicates the CO_2 concentration

(mean ± SD) was 363 ± 48 μl/l in the open field, 367 ± 51 μl/l in the ambient chambers, 507 ± 66 μl/l in the chambers nominally at 500 μl/l, and 646 ± 79 μl/l in the chambers nominally at 650 μl/l. Concentrations during daylight hours were 2 to 5% lower than these values, and at night they were slightly higher.

Air dry- and wet-bulb temperatures were measured with aspirated psychrometers inside the chambers and recorded on an automatic data-acquisition system. Pan evaporation was measured from small pans (225 mm diameter, 110 mm high) of water near the top of the crop canopy in each of the chambers and in the open-field plots. Solar radiation was monitored with a Spectran model 4048 pyranometer.

Photosynthetic gas exchange

Photosynthesis rate was monitored on seven clear days in June, July, and August with a LiCor LI-6000 portable photosynthesis system (LiCor Instruments, Lincoln, NE)[1]. Measurements were made at midday on sunlit, fully expanded leaves at the top of the canopy. Treatment effects on A were assessed by a split-plot analysis of variance, with irrigation as the main plot and CO_2 level as the subplot. Individual means were separated by a Student-Newman-Keuls *t*-test.

Curves relating A to c_i were constructed by a different method. The ADC portable photosynthesis system (Analytical Development Co. Hoddesdon, England)[1] is a compact, open gas-exchange system which lends itself to rapid determination of gas exchange rates. Air containing about 2000 μl/l CO_2 was passed from a high-pressure cylinder into the air pump of the system. The air stream was split into two parts at the pump, with the ratio between the two controlled by an adjustable valve. One part was passed through two tubes of soda lime to remove all CO_2. The two parts of the stream were then recombined and passed through the cuvette and into the analyzer. Control of c_a was easily achieved within the range 0 to 1000 μl/l by adjustment of the valve. Flow rate was monitored with the rotameter on the air pump and maintained near 500 ml/min. The analyzer was set in the absolute mode, rather than differential mode, to register the exiting absolute concentration of CO_2. Photosynthetic rates were determined by comparison of readings without a leaf in the cuvette to readings with a leaf in place. Following Gaastra [7], the effective c_a was assumed to be the mean of the incoming and exiting concentrations. Readings typically were stable 15 s after the cuvette was closed on a leaf, before stomata could react to the altered environment. The protocol involved numerous measurements of A in rapid sequence, using a different leaf and a different CO_2 concentration each time. All readings were made between 0930 and 1200 h on

[1] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture, and does not imply its approval to the exclusion of other products that may also be suitable.

cloudless days, using fully-expanded sunlit leaves near the top of the canopy. Despite the air temperature approaching or exceeding the nominal maximum temperature for operation of the ADC system, its performance was unimpaired as long as the IR analyzer was kept shaded.

Estimates of g_s were made with a LiCor LI-1600 steady-state porometer. Both the ADC and LiCor humidity sensors were calibrated against an ADC WG-600 water vapor generator to ensure comparability of readings. Total leaf g_s was taken to be the sum of the g_s of both sides of the leaf. Before beginning a series of photosynthesis measurements, three fully sunlit leaves were selected randomly near the top of the canopy, and g_s was measured on each. Similar measurements were made at the end of each series, using leaves which had not been perturbed by a previous measurement of either g_s or A. Within the time required for a series of 10 to 12 determinations of A over the entire range of c_a (about 30 min), initial and final g_s did not differ beyond the coefficient of variation ($< 10\%$). Leaf g_s was taken to be the mean of the initial and final values.

The c_i was calculated from the relationship

$$c_i = c_a - 1.6\, A/g_s. \tag{1}$$

This equation neglects the effect of mass flow of water vapor through the stomata [6] and the effect of boundary layer. Because of the former, estimates of c_i are slightly ($< 2\%$) too high. The effect of the latter error is similarly small when $g_b \gg g_s$, as is the case within the well-stirred cuvette. $A(c_i)$ relationships were approximated as quadratic regressions of A versus c_i because there was a pronounced tendency for A to decrease at very high c_i (see [25]). For any given c_a, the degree of stomatal limitation to A was calculated from the relationship

$$L = 100\left(1 - \frac{A_{c_i}}{A_{c_i = c_a}}\right). \tag{2}$$

Starch determinations

Leaf samples were taken at 0630 (dawn) and 1900 (sunset) by removing six discs 1 cm in diameter from three mature leaves at the top of the canopy. The same leaves were used for both samplings. The discs were immediately placed in 4 ml ice-cold 80% ethanol and taken to the laboratory, where they were stored at $-85°$ until analysis. Samples, still in the 80% ethanol, were transferred to a water bath at 80° for 25 min and then ground with a Brinkmann Polytron equipped with a PT-10 generator. After centrifugation, the insoluble matter was re-extracted three times with 80% ethanol at 80° for 15 min. Starch in the residue was digested with amyloglucosidase (Sigma Chemical Co., St. Louis, MO) and the glucose released was determined enzymatically [2]. Standard curves were run with amylopectin.

Leaf water potentials and soil water content

Water potentials were estimated by an indirect method, necessitated by the limited amount of plant material for destructive sampling. The youngest fully-expanded mainstem leaves were shaded, covered with plastic bags, excised, and quickly placed in a moist storage container for transport to the laboratory. Leaves were weighed, then rehydrated and subjected to pressure-volume procedures similar to those described earlier [20]. Water potentials at the time of excision were later read from the pressure-volume curves by interpolation to the original leaf weight. All reported water potentials are from harvests about 1400 h, near the time of minimum daily water potential.

Plant water potentials were not determined late in the season but soil moisture content was measured to a depth of 1 m throughout the season using neutron attenuation [20].

Results

Midday photosynthesis was monitored with the LiCor LI6000 from June through August. On average, enrichment to 650 μl/l stimulated photosynthesis of unstressed plants 77% (Table 1). Photosynthesis of stressed plants, measured 3 to 4 days after irrigation, was 10 to 15% less than that of the unstressed plants at all CO_2 levels. The effects of irrigation and CO_2 were significant ($P < 0.05$) but the interaction of irrigation and CO_2 was not. Photosynthesis of plants in the ambient chamber was not significantly different from that of plants in the open field.

Measurements for calculating $A(c_i)$ curves were also taken on selected dates during the season. The July and August dates exhibited very high temperatures and VPD, whereas the September date was somewhat cooler (Table 2). Maximum solar radiation was slightly less in September. The July measurements were initiated 4 days after an irrigation, whereas the August measurements were

Table 1. Photosynthesis rates of leaves of plants at 3 levels of CO_2 and two irrigation rates. Results are means of rates on 7 clear days during the season. Means within a row or column followed by the same letter are not significantly different ($P = 0.05$). Numbers in parentheses are the percentage changes with respect to the ambient chambers.

CO_2 treatment	Photosynthesis rate (μmol m^{-2} s^{-1})		
	Unstressed	Stressed	Mean
Open field	21.6	20.6	21.1a
Ambient chamber	24.3	21.3	22.8a
500 μl/l	38.3 (+58)	34.8 (+63)	36.6b (+61)
650 μl/l	42.8 (+76)	38.0 (+78)	40.4c (+77)
Mean	31.8A	28.6B	

Table 2. Climatic parameters for 3 days in 1985 when gas exchange characteristics were determined. These parameters were monitored within the chambers. Values represent means of all chambers in which photosynthetic data were recorded on that day. The data for 1000–1200 hours are the average values for that interval (which encompassed most of the gas exchange measurements).

Parameter	Date		
	3 July	28 August	17 September
Air temperature (°C)			
Maximum	45.5	43.8	38.5
Minimum	28.9	26.5	21.4
1000–1200 hours	40.5	38.9	33.6
VPD (kPa)			
Maximum	8.34	6.66	5.06
Minimum	2.87	1.17	0.84
1000–1200 hours	6.20	4.50	3.61
Solar radiation (Wm^{-2})			
Maximum	1060	960	917
1000–1200 hours	953	863	742

made 5 days after an irrigation. On 3 July the midday ψ_w was -2.1 and -2.5 MPa in the fully-irrigated plots at ambient and 650 μl/l CO_2, respectively. In the stressed plots the corresponding values were -2.5 and -2.7 MPa, respectively. No data on ψ_w were collected on the two later dates; however, soil moisture content in the stressed plots was 90% and 83% of the fully-irrigated plots on 28 August and 17 September, respectively (compared to 111% of the fully-irrigated plots on 3 July). Clearly the stress was more severe later in the season.

In July and August, CO_2 enrichment had no effect on $A(c_i)$ curves for unstressed plants, so the data were combined for analysis. A increased with increasing c_i to very high rates before it began to saturate (Fig. 1, Fig. 2). At high c_i, A decreased somewhat, especially in the water-stressed plants (Fig. 1, Fig. 2). This phenomenon has been reported and discussed before [25]. The slope of the curve at low c_i defines g'_m; at 100 μl/l g'_m was 0.12 mol $m^{-2} s^{-1}$ in July and 0.14 mol $m^{-2} s^{-1}$ in August. Water stress only slightly changed the g'_m in July but greatly decreased it in August (Fig. 1, Fig. 2). In July, the major difference between stressed and unstressed plants was at high c_i (Fig. 1). The $A(c_i)$ curves of stressed plants saturated at a lower c_i and A_{max} was substantially decreased. As a result, even though water stress decreased g_s somewhat, the c_i was only slightly altered (Table 3). At either ambient or 650 μl/l CO_2, the degree of stomatal limitation to A was small because the c_i was very high (Table 3). In August, on the other hand, the plant stress was apparently more severe, affecting both g'_m and A_{max}, and causing greater stomatal closure than in July (Fig. 2, Table 3). On this date water stress noticeably decreased the c_i and increased the stomatal limitation to photosynthesis (Table 3).

On 17 September, the $A(c_i)$ curves were quite different from those in July or August, and they were also affected by CO_2 enrichment (Fig. 3). In plants grown in ambient CO_2, A_{max} was similar to the earlier values for unstressed plants. The g'_m, however, was substantially greater than on the earlier date. In contrast, the

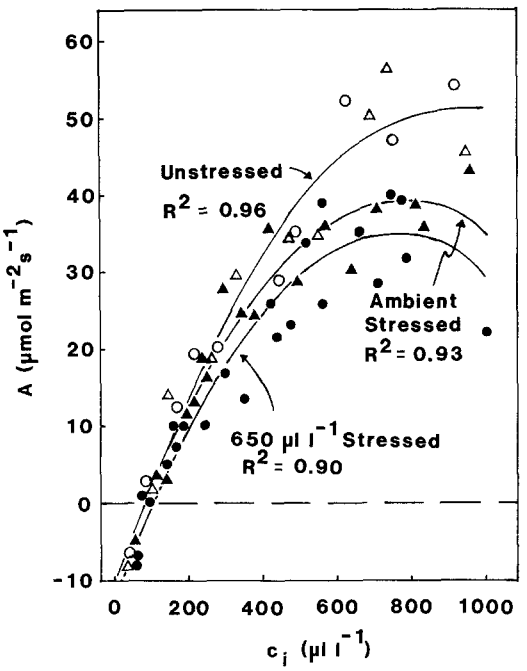

Fig. 1. Regressions of A against c_i from data collected on 3 and 4 July, 1985. △, Ambient unstressed; ○, Enriched unstressed; ▲, Ambient stressed; ●, Enriched stressed.

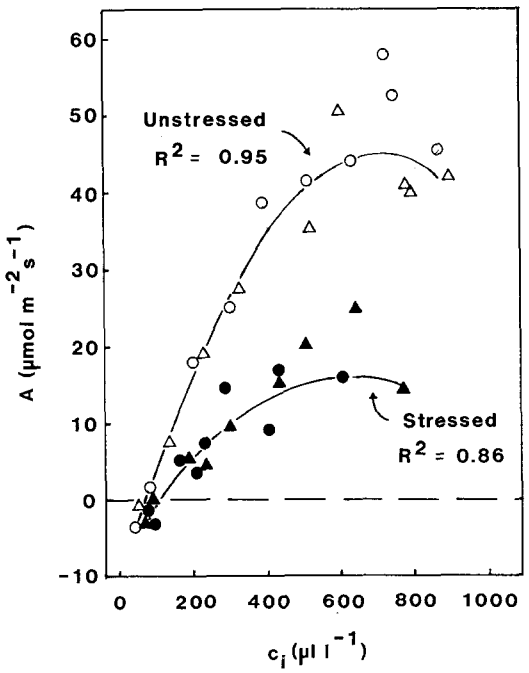

Fig. 2. Regressions of A against c_i from data collected on 28 August, 1985. △, Ambient unstressed, ○, Enriched unstressed; ▲, Ambient stressed; ●, Enriched stressed.

Table 3. Photosynthetic characteristics of cotton leaves on 3 days in 1985. Values of A, c_i, and L were calculated from the curves shown in Figs 1–3. The nominal c_a for the ambient treatment was 350 $\mu l\,l^{-1}$ and for the enriched treatment was 650 $\mu l\,l^{-1}$. Numbers in parentheses are the percentage changes with respect to the ambient chambers.

Treatment	A $\mu mol\,m^{-2}\,s^{-1}$	g_s $mol\,m^{-2}\,s^{-1}$	c_i $\mu l\,l^{-1}$	L %
3–4 July 1985				
Ambient				
Unstressed	24	0.84	304	14
Stressed	21	0.58	292	16
Enriched				
Unstressed	42 (+75%)	0.78	564	9
Stressed	30 (+42%)	0.34	509	7
28 August 1985				
Ambient				
Unstressed	26	0.80	298	15
Stressed	8	0.14	259	29
Enriched				
Unstressed	43 (+65%)	0.83	567	4
Stressed	13 (+62%)	0.08	390	19
17 September 1985				
Ambient	21	0.23	204	45
Enriched	26 (+24%)	0.17	405	33

g'_m of CO_2-enriched plants was decreased from the earlier values (Fig. 3). Within the range of c_i's tested, the regression did not indicate saturation of A in the CO_2-enriched plants. On this date, unlike the earlier ones, A was substantially limited by g_s (Table 3). The c_i was very low in comparison to the earlier dates, at about 60% of c_a (Table 3).

No data are presented for water-stressed plants in September because the g_s was so low that calculations of c_i were deemed unreliable.

Diurnal starch levels were measured on 29 August, a day very similar to the preceding day when $A(c_i)$ curves were determined. In unstressed plants, CO_2 enrichment greatly increased starch levels both at dawn and at the end of the day (Table 4). The net increase during daylight hours was much less affected. The same pattern was evident in stressed plants, but the amount accumulated during the day was much reduced (Table 4). The large effect of CO_2 enrichment on starch level was not accompanied by any effects on gas exchange properties (Fig. 2). In the unstressed plants at 650 $\mu l/l$, the maximum starch level corresponds to a concentration of about 40% of leaf dry mass.

Discussion

Our data show substantial differences in photosynthetic response to c_i between midsummer and late summer. In July and August, CO_2 enrichment did not

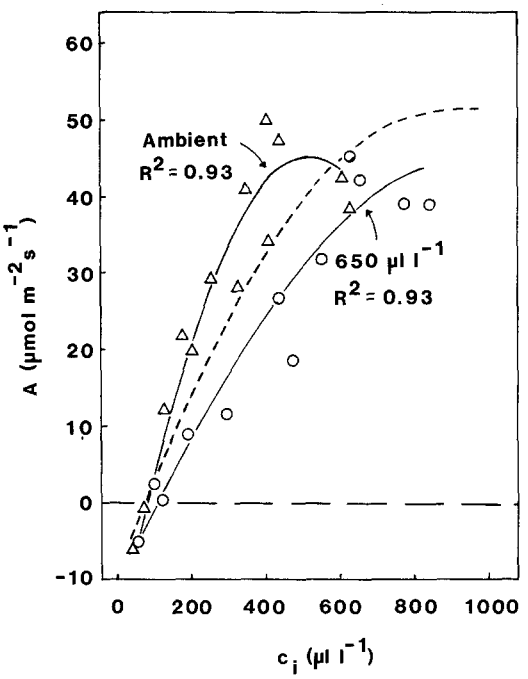

Fig. 3. Regressions of A against c_i from data collected on 17 September, 1985. △, Ambient unstressed; ○, Enriched unstressed. For comparison, the regression for unstressed plants on 3–4 July is shown as a dashed line.

affect the A(c_i) curves. In September, though, the plants grown at ambient CO_2 had a greater g'_m than earlier; in contrast, the CO_2-enriched plants had a lower g'_m (Fig. 3). Decreasing temperature increases the solubility of CO_2 relative to O_2 [13] and increases the affiniity of RuBP carboxylase-oxygenase for CO_2 [14]. Both these changes suppress photorespiration, which is known to decrease with decreasing temperature in this species [18]. The increased g'_m of ambient CO_2-

Table 4. Starch contents of leaves of plants at 3 levels of CO_2 and two irrigation rates. Samples were taken at dawn or dusk on 29 August, 1985. Results are means ± SE of 3 leaves, expressed per unit leaf urea.

Treatment	Starch content of leaves ($g\,m^{-2}$)	
	Dawn	Dusk
Unstressed		
Ambient CO_2	2.2 ± 0.3	9.6 ± 1.2
500 µl/l	4.3 ± 0.5	11.4 ± 1.5
650 µl/l	11.6 ± 1.1	16.2 ± 1.8
Stressed		
Ambient CO_2	0.8 ± 0.4	3.2 ± 0.4
500 µl/l	5.0 ± 0.3	8.8 ± 1.1
650 µl/l	6.9 ± 0.5	9.9 ± 0.9

grown plants in September is consistent with this interpretation. However, the decreased g'_m of CO_2-enriched plants in September cannot be similarly explained.

In common with many C_3 plants [17], cotton is known to 'acclimate' to increased CO_2 with a decreased photosynthetic capacity [5, 16, 22, 24]. In experiments carried out in controlled environments, this decrease has been correlated with increasing starch concentration [5, 16, 22]. Mauney et al. [16], however, noted without presenting data the absence of any such correlation in field-grown plants in Arizona. Our results show that accumulation of large amounts of starch need not decrease photosynthetic efficiency. In fact, in August the correlation was in the opposite direction: across both CO_2 and water treatments, high A was accompanied by high starch levels. In September, though, there was some 'acclimation'.

Why did 'acclimation' to CO_2 enrichment in field-grown plants occur only at the end of the season? One important seasonal change is the fruit load on the plants. Most fruits mature before 17 September, leaving the plant in a 'sink-limited' condition [20]. However, the ratio of leaf area to fruit number was near 600 cm^2 per fruit as early as 28 August (data not shown). This high value implies some degree of sink limitation even at that time [21]. The failure to use all the starch present at high CO_2 also points strongly to a sink limitation (Table 4). Despite this possibility, CO_2 enrichment did not cause 'acclimation' in late August.

Another factor to consider is the ambient temperature. A postulated temperature dependence of feedback effects could explain the seasonal change in photosynthetic response to CO_2 enrichment Indeed, feedback effects in wheat occur only at cool temperatures [1]. Because September temperatures resembled those typically maintained in controlled environments, such a postulate could also explain the divergence of glasshouse-grown and field-grown cotton plants [16]. A mechanism for this effect remains unclear, although Sharkey's [23] concept of limitation by triose-P utilization might be applicable. Even without identifying the cause, the data show that 'acclimation' requires very specific circumstances.

In July and August, enrichment to 650 μl/l enhanced A of unstressed plants by an average of 70% (Table 3). In September, the enhancement was only 24% (Table 3). This shift was exclusively from the change in the $A(c_i)$ curve; stomatal limitations did not play a role. In fact, CO_2 enrichment decreased stomatal limitation to A under all conditions (Table 3). Water stress also slightly decreased the effect of CO_2 enrichment, to an average of 52% enhancement in July and August (Table 3).

The two methods for determining A in midseason agree fairly well (Tables 1, 3), with the exception that $A(c_i)$ curves show a more severe effect of water stress. We assign this discrepancy to the acquisition of $A(c_i)$ data fairly late in the irrigation cycle, when stress was more severe than for the other photosynthesis measurements. The agreement provides validation for the $A(c_i)$ procedure. Even

though measurements were made before the stomata could react to the CO_2 level in the cuvette, the error introduced into the estimates of steady-state A seems to be small.

Another important point concerns the c_i of the leaves. In ambient CO_2-grown plants, the c_i was near 300 μl/l in July and August and 200 μl/l in September (Table 3). These values reflect the very large effect of temperature on g_s. The g_s and c_i of plants on the cool September day resemble values reported elsewhere [19, 24] for cotton grown in glasshouses (i.e. at temperatures resembling a cool day in the field). Hutmacher and Krieg [9] also reported very high c_i's in field-grown cotton. Stomatal opening in response to increasing temperature has been demonstrated in numerous species, especially when VPD is held constant [3, 4, 8]. Although VPD was uncontrolled in our experiments and varied with temperature (Table 2), the increase in g_s with high temperature is opposite to any direct effect expected from increasing VPD. Under these circumstances, any stomatal response to VPD would seem to be overshadowed by a larger response to temperature itself.

The very high c_i's (near 300 μl/l) must be viewed in the context of system behavior. The $A(c_i)$ curves for these plants are essentially linear to a c_i near 600 μl/l. Without saturation in that portion of the curve, there is no c_i that is clearly optimum for water-use efficiency. In field plantings of irrigated cotton in Arizona, g_s of upper sunlit leaves frequently reaches 1.5 mol $m^{-2} s^{-1}$ in mid-summer [20], a value so high that transpiration rate may be co-limited by g_b. In this situation, stomatal behavior may not determine water-use efficiency. It is interesting that under these conditions, there is virtually no stomatal response to CO_2, and thus no feedback system to limit the degree of stomatal opening (Table 3). Detailed quantitative interpretation of our results is inappropriate, though, because our calculations of c_i did not include g_b. We have no accurate estimates of g_b in the chambers; however, seasonal pan evaporation was only 9% less in the chambers than in the open field, so that chamber g_b presumably approached that of the open field.

In conclusion, these experiments have defined the photosynthetic factors that contribute to the great response of cotton to CO_2 enrichment. The very high g_s, and small response of g_s to CO_2, ensure that c_i is maximal in enriched plants. The nearly linear $A(c_i)$ curves of unstressed plants, and the lack of an 'acclimation' response for most of the season, provide the photosynthetic capacity to use that increased CO_2 supply efficiently.

Acknowledgements

We thank P. Nixon, T. Zarembinski, and K. Peelen for technical assistance, and Dr T.D. Sharkey for helpful comments. This work supported in part by grant DE AI01-81ER60001 from the U.S. Department of Energy, Carbon Dioxide Research Division.

References

1. Azcon-Bieto J (1983) Inhibition of photosynthesis by carbohydrates in wheat leaves. Plant Physiol 73:681–686
2. Bergmeyer HU, Bernt E, Schmid F and Stork H (1970) Glucose. In: Bergmeyer HU (ed.) Methoden der Enzymatische Analyse, pp 1163–1168. Weinheim/Bergstrasse: Verlag Chemie
3. Berry J and Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol 31:491–543
4. Carter PR and Sheaffer CC (1983) Alfalfa response to soil water deficits. II. Plant water potential, leaf conductance, and canopy temperature relationships. Crop Sci 23:676–680
5. DeLucia EH, Sasek TW and Strain BW (1985) Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. Photosyn Res 7:175–184
6. Farquhar GD and Sharkey TD (1982) Stomatal conductance and photosynthesis. Annu Rev Plant Physiol 33:317–345
7. Gaastra P (1959) Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. Meded Landbouwhogesch. Wageningen 59:1–68
8. Hall AE, Schulze ED and Lange OL (1976) Current perspectives of steady-state stomatal responses to environment. In: Lange OL, Kappen L and Schulze ED (eds) Water and Plant Life: Problems and Modern Approaches, pp. 169–188. Berlin: Springer-Verlag
9. Hutmacher RB and Krieg DR (1983) Photosynthetic rate control in cotton: stomatal and nonstomatal factors. Plant Physiol 73:658–661
10. Kimball BA (1983) Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. Agron J 75:779–788
11. Kimball BA, Mauney JR, Guinn G, Nakayama FS, Pinter PJ Jr, Clawson KL, Reginato RJ and Idso SB (1983) Effects of increasing atmospheric CO_2 concentration on the yield and water use of crops. Number 021, Response of Vegetation to Carbon Dioxide. US Department of Energy, Carbon Dioxide Research Division and the US Department of Agriculture, Agricultural Research Service, Washington, DC
12. Kimball BA, Mauney JR, Guinn G, Nakayama FS, Pinter PJ Jr, Clawson KL, Idso SB, Butler GD Jr and Radin JW (1984) Effects of increasing atmospheric CO_2 concentration on the yield and water use of crops. Number 023, Response of Vegetation to Carbon Dioxide. US Department of Energy, Carbon Dioxide Research Division and the US Department of Agriculture, Agricultural Research Service, Washington, DC
13. Ku SB and Edwards GE (1977) Oxygen inhibition of photosynthesis. I. Temperature dependence and relation to O_2/CO_2 solubility ratio. Plant Physiol 59:986–990
14. Laing WA, Ogren WL and Hageman RH (1974) Regulation of soybean net photosynthetic CO_2 fixation by the interaction of CO_2, O_2, and ribulose 1, 5-diphosphate carboxylase. Plant Physiol 54:678–685
15. Mauney JR, Fry KE and Guinn G (1978) Relationship of photosynthetic rate to growth and fruiting of cotton, soybean, sorghum, and sunflower. Crop Sci 18:259–263
16. Mauney JR, Guinn G, Fry KE and Hesketh JD (1979) Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sorghum, and sunflower. Photosynthetica 13:260–266
17. Pearcy RW and Bjorkman O (1983) Physiological effects. In: Lemon ER (ed.) CO_2 and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide, pp. 65–105. Boulder, Colorado: Westview Press
18. Perry SW, Krieg DR and Hutmacher RB (1983) Photosynthetic rate control in cotton: Photorespiration. Plant Physiol 73:662–665
19. Radin JW and Ackerson RC (1981) Water relations of cotton plants under nitrogen deficiency. III. Stomatal conductance, photosynthesis, and abscisic acid accumulation during drought. Plant Physiol 67:115–119
20. Radin JW, Mauney JR and Guinn G (1985) Effects of N fertility on plant water relations and stomatal responses to water stress in irrigated cotton. Crop Sci 25:110–115

21. Radin JW, Mauney JR and Guinn G (1986) Diurnal osmotic cycling in cotton leaves as an indicator of source-sink balance. Plant Cell Environ 9:349–352
22. Sasek TW, DeLucia EH and Strain BR (1985) Reversibility of photosynthetic inhibition in cotton after long-term exposure to elevated CO_2 concentrations. Plant Physiol 78:619–622
23. Sharkey TD (1985) O_2-insensitive photosynthesis in C_3 plants, its occurrence and a possible explanation. Plant Physiol 78:71–75
24. Wong SC (1979) Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44:68–74
25. Woo KC and Wong SC (1983) Inhibition of CO_2 assimilation by supraoptimal CO_2: Effect of light and temperature. Aust J Plant Physiol 10:75–85