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Enhanced Photosynthesis and Stomatal Conductance of Pima Cotton (*Gossypium barbadense* L.) Bred for Increased Yield[1]

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ABSTRACT

Yield of Pima cotton (*Gossypium barbadense* L.) has tripled over the last 40 years with the development of new cultivars. Six genetic lines representing successive stages in the breeding process (one primitive noncultivated accession, four cultivars with release dates from 1949 to 1983, and one unreleased breeding line) were grown in a greenhouse, and their gas exchange properties were compared. Among the cultivated types, genetic advances were closely associated with increasing single-leaf photosynthetic rate (A) and stomatal conductance (g_s), especially in the morning. The A and g_s of the primitive line approached those of the cultivated types early in the morning, but were much lower for the rest of the day. In both morning and afternoon, A was correlated with g_s across genotypes but was not correlated with leaf thickness, concentrations of chlorophyll or starch, or intercellular CO_2 concentration (c_i). In the oldest cultivar, the relationship of A to c_i did not change between morning and afternoon. In the two most recent lines, the slopes of the A:c_i curves at limiting c_i exceeded that of the oldest cultivar by 25 to 50% in the morning, but the differences were much smaller in the afternoon. The maximum A of the newer lines at high c_i exceeded that of the oldest cultivar only in the morning. Breeding for increasing yield has enhanced the photosynthetic capacity and stomatal conductance of Pima cotton and altered the diurnal regulation of photosynthesis.

Leaf gas exchange is a complex, highly regulated process dependent upon interactions between mesophyll cells and stomata (9). Cowan and Farquhar (6) proposed that these interactions "optimize" gas exchange, *i.e.* they maximize WUE[3]. Photosynthesis and transpiration respond differently to environmental factors, and stomata limit the two processes to different degrees. It follows that for a leaf in any specific environment, there is a unique value of g_s producing optimum c_i and maximum WUE. Consistently with the hypothesis of optimization, Wong *et al.* (24) found that stomata tend to maintain c_i at the optimum level for WUE, often 60 to 70% of ambient CO_2 concentration.

The hypothesis of optimized gas exchange is based upon the initial assumption that water availability limits reproductive success, thus assuring strong selection pressure for maintenance of maximum WUE. However, this assumption may not generally apply to agricultural production. Many crop plants are the result of years of breeding in excellent soils, in some cases with supplemental irrigation to relieve water deficits. Under these conditions water is unlikely to limit productivity, and selection pressure to maximize WUE may be slight. Indeed, in upland cotton (*Gossypium hirsutum* L.) in a hot environment, stomatal behavior does not maximize WUE unless the crop becomes water-stressed (5, 14, 16, 19). Rather, midday g_s is so high that it provides a relatively small limitation to gaseous diffusion, and c_i exceeds 80% of ambient CO_2 concentration. Under these conditions, the stomatal limitation to A is minimized, and leaves are cooled considerably by evaporation of large amounts of water. This behavior has been interpreted in terms of heat resistance (15). Radin (16) considered "optimization" to represent acclimation to water stress in this crop.

Pima cotton (*Gossypium barbadense* L.) is grown in hot areas of the southwestern United States. Varieties introduced from elsewhere are seldom productive because they are unadapted, and a major goal of breeders has been to improve the crop's heat resistance (yield in a hot environment). Yield of one advanced breeding line, P-70, is triple that of Pima 32, an obsolete cv released in 1949. We studied gas exchange of Pima cotton lines to test the hypothesis that genetic advances have been accompanied by decreased stomatal limitations to A and to transpiration. The results indicate that selection for high yield has increased both photosynthetic capacity and g_s, and altered diurnal regulation of photosynthesis.

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[3] Abbreviations: WUE, water-use efficiency; A, photosynthetic rate; g_s, stomatal conductance; c_i, intercellular CO_2 concentration; CE, carboxylation efficiency; A_{max}, maximum photosynthetic rate; VPD, vapor pressure deficit; RuBP, ribulose-1,5-bisphosphate; Rubisco, ribulose-1-5-bisphosphate carboxylase-oxygenase.

MATERIALS AND METHODS

Genetic Material

Four released cvs (Pima 32, S-2, S-3, and S-6) and one advanced breeding line (P-70) were selected for study, representing advancing stages of breeding over the last 40 years. They are derived from three separate germplasm pools (Fig. 1). Both pool I and pool III include *Gossypium hirsutum*; thus, of the genotypes tested, Pima 32 (derived from pool II) is the last one to have no introgressed genes from upland cotton. A noncultivated primitive *Gossypium barbadense* originally collected from Peru, B-375, was included for comparison. Lint yields (kg/ha) of the six lines in Arizona were as follows: B-375, zero; Pima 32, 413; S-2, 856; S-3, 707; S-6, 984; and P-70, 1217. B-375 is a short-day plant, and daylengths during the season are too long to induce flowering.

Gas Exchange

Experiments were carried out at two locations. In Phoenix, AZ, plants were grown in pots in a greenhouse under natural lighting and were watered with a modified half-strength Hoagland solution (18). Most days were cloudless, or nearly so, and midday PPFD within the greenhouse exceeded 2000 μmol m^{-2} s^{-1}. CO_2 assimilation rates of leaves were determined throughout the daylight hours on March 6, 1989, using a portable steady-state photosynthesis system (Analytical Development Co., Hoddesdon, England).[4] The minimum and maximum daytime temperatures were 26°C at 7 AM and 35°C at 1 PM, respectively. Relative humidity varied from 24% at 7 AM to 54% at 1 PM (atmospheric VPD of 2.5 and 2.6 kPa, respectively). Diurnal measurements of A were made on leaves of the same four plants per line, in rotation throughout the day. This procedure was feasible because measurements are rapid and nondestructive (19). All measurements were made on the youngest fully expanded leaves on the mainstems of preflowering plants (less than 6 weeks after germination), with the cuvette held normal to the solar radiation. At 9 AM, noon, and 3:30 PM, incident PPFD on the cuvette was approximately 1550, 2100, and 1700 μmol m^{-2} s^{-1}, respectively. Immediately after measurements of A, the same leaves were used to determine g_s with a LiCor LI-1600 steady-state porometer. Polynomial regressions of A or g_s on time of day were fitted to the data and are presented here.

Relationships between A and c_i were delineated as described earlier (19). Air enriched in CO_2 was supplied to the Analytical Development Co. cuvette, and A was determined as soon as the readings stabilized (about 20–30 s). Again, g_s was determined immediately afterward with the LiCor steady-state porometer. In this case, each point on the A:c_i curves is from a different leaf; thus each curve represents a broadly based sampling of the population. Measurements were taken in early February 1989. Polynomial regressions were fitted to the data; slopes and maxima were determined from curves of best fit.

Gas exchange rates were also measured in May 1989 to correlate rates with various leaf properties. Measurements of A and of g_s were taken at 9 AM, 11 AM, 1 PM, and 4 PM, and c_i was calculated for each line at each time of day. Genotypic and diurnal effects were similar to those found in March 1989. Leaf thickness and Chl and starch contents were deter-

[4] 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.

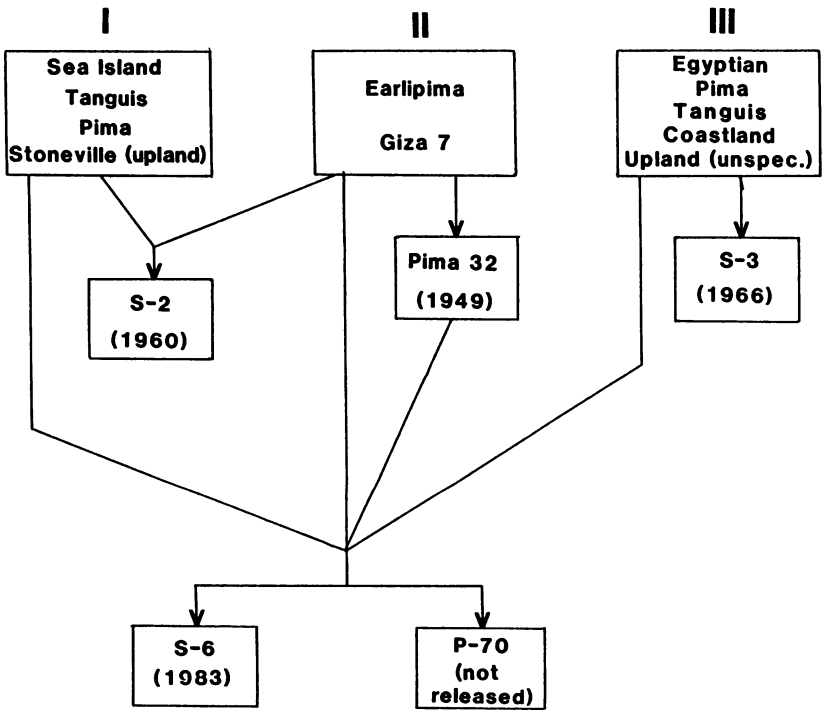

Figure 1. Diagram of genetic relationships among Pima cotton cvs and breeding lines. For cvs, the years of release are indicated. Germplasm pools I and III contain upland cotton (*G. hirsutum*); thus Pima 32 is the last line to have no introgressed genes from this species.

mined at 9 AM and 4 PM (see below). Only the results of the correlation analyses from this experiment are presented here, relating A and g_s at 9 AM and at 4 PM to the other factors.

The same lines were also grown and studied in Los Angeles, CA. Plants were grown in pots in a greenhouse and transferred to a laboratory for steady-state gas exchange measurements in an open system (26). Measurements were made in late morning or midday at an air temperature of 30°C, PAR of 1300 μmol m^{-2} s^{-1}, and VPD of 0.5 kPa. Data presented are the means of four leaves per line.

Chl

Six discs, each having 0.42-cm^2 area, were cut in midafternoon from the youngest fully expanded leaf of four replicate plants of each line, avoiding vascular tissue. The cuts were uniformly distributed across the leaf. Discs from each leaf were placed into tubes containing 80% acetone and stored at −19°C. After all color had been extracted from the discs, the solution was diluted, and Chl was assayed spectrophotometrically (1). Chl contents were expressed per unit leaf area.

Starch

Starch was assayed by the method of Hendrix (11), using an intact-tissue digestion procedure with an enzymatic assay of glucose modified from Hendrix and Peelen (12). The bleached discs remaining after the Chl analysis described above were suspended in 1.0 mL of 0.2 M KOH. Samples were placed in a bath of boiling water for 30 min, then allowed to cool to room temperature. The cooled solutions were neutralized with 0.2 mL of 1 M acetic acid. Starch in the discs was then hydrolyzed by adding 1.0 mL amyloglucosidase (3, 13) to each tube and incubating them at 55°C for 30 min. The reactions were halted by heating at 100°C for 1 min in boiling water. The volume in each tube was brought to 6 mL with H_2O and the mixture thoroughly vortexed. Aliquots were stored at −80°C in 1.5-mL microfuge tubes until analyzed. After centrifugation, 20 μL of each preparation was pipetted into four wells of a microtitration plate. Deionized water blanks and a range of glucose standards (0.1–5.0 μg/mL) were used for comparison. To each well was added 100 μL of enzyme reagent (Sigma 115-A kit) under low light. The plates were then incubated in the dark at 37°C for 15 min. A_{492} was determined using an ELISA plate reader (4). Starch content of the leaf discs was expressed per unit leaf area.

Leaf Thickness

The thickness of leaves of six replicate plants of each line was determined using a micrometer gauge.

RESULTS

Diurnal Patterns of Gas Exchange

A preliminary experiment (not shown) indicated diurnal differences in A and g_s among lines. This was followed by a more complete experiment including all six lines. Genetic effects on diurnal cycling of A and g_s were substantial (Fig. 2). In the advanced lines, A was increased most noticeably in the morning, and to a lesser degree at midday, but not late in the afternoon (Fig. 2A). The differences between Pima 32 (released in 1949) and P-70 (the most advanced line) were pronounced, with P-70 maintaining the highest A of all the lines throughout the day. In the primitive accession, B-375, A was similar to the modern lines early in the morning, but was much lower than in the modern lines throughout the rest of the day (Fig. 2A). S-2 and S-3 had intermediate diurnal photosynthetic rates (data not shown).

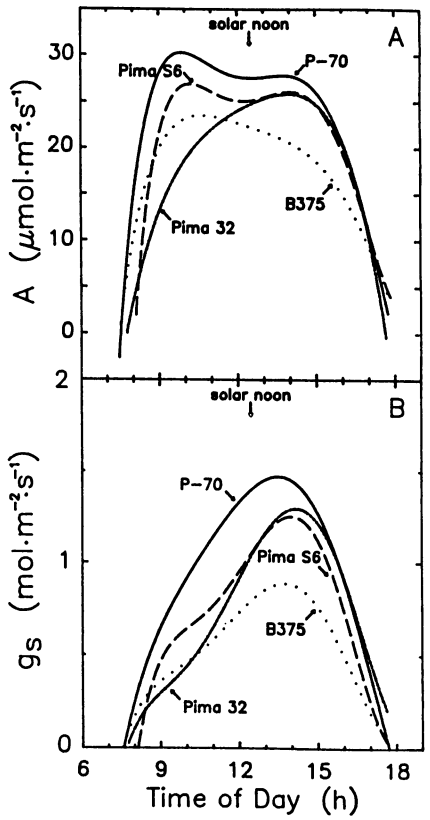

Figure 2. Photosynthetic rates (A) and stomatal conductances (g_s) of Pima cotton leaves on March 6, 1989. Diurnal changes are represented by fifth-order polynomial regressions. Each curve is based upon measurements from four plants. Panel A, photosynthesis. Correlation coefficients are as follows: B-375: $r = 0.912$, $n = 27$; Pima 32: $r = 0.911$, $n = 20$; S-6: $r = 0.925$, $n = 17$; P-70: $r = 0.934$, $n = 26$. Panel B: stomatal conductance from the same leaves as in panel A. Correlation coefficients are as follows: B-375: $r = 0.791$, $n = 27$; Pima 32: $r = 0.896$, $n = 20$; S-6: $r = 0.861$, $n = 17$; P-70: $r = 0.904$, $n = 26$. All correlation coefficients are significantly different from zero ($P < 0.05$).

The g_s also differed markedly among lines. P-70 maintained a substantially higher g_s than the other lines until midafternoon, whereas B-375 had the lowest g_s for most of the day (Fig. 2B). Again, S-2 and S-3 exhibited intermediate behavior (data not shown). However, diurnal patterns of A and g_s were not synchronized in all lines (Fig. 2, A and B). During the morning, A increased much faster than g_s in all lines except Pima 32, reaching a maximum several hours before solar noon and then leveling off or declining slightly. Conductances increased more slowly but continued to increase beyond solar noon, indicating that A and g_s were not simply following the

Table I. *Steady-State A and g_s of Pima Cotton Genotypes*

Plants were grown in a greenhouse in Los Angeles, CA. Data are means of four leaves. Means within a column followed by the same letter are not significantly different ($P > 0.05$ by t test).

Genotype	A	g_s
	$\mu mol\ m^{-2}\ s^{-1}$	
Pima 32	20.8ab	0.58a
S-2	18.8a	0.54a
S-3	22.4b	0.67b
S-6	26.4c	0.70bc
P-70	25.3c	0.74c

daily irradiance (which is maximum at solar noon). In midafternoon, both A and g_s began a rapid synchronous decline (Fig. 2, A and B). The c_i fell during the first part of the morning and rose again at the end of the day in all lines, but differences among them were not consistent (data not shown).

Gas Exchange under Steady-State Conditions

Steady-state gas exchange rates of plants grown in a greenhouse in Los Angeles confirmed the strong genotypic differences in A and g_s found in Phoenix. (The primitive accession, B-375, was excluded from this study.) Again, A and g_s were lowest in Pima 32 and S-2, the oldest lines, and were highest in S-6 and P-70, the most recent lines (Table I). Within either of these groupings, differences were not significant ($P > 0.05$); however, all comparisons of lines across these two groupings were significant, and many comparisons with the intermediate line, S-3, were also significant (Table I). The results from this location clearly show the same genetic trend toward increased A and g_s as found earlier.

A:c_i Relationships

The relationship between A and c_i was determined for Pima 32, S-6, and P-70 (Fig. 3). In Pima 32, the slope of the curve at limiting c_i (CE) was within 5% of 0.1 mol m^{-2} s^{-1} in both the morning and the afternoon (Fig. 3A). The highest A observed within the range of CO_2 concentrations applied (A_{max}) was approximately 50 μmol m^{-2} s^{-1}. In S-6, the CE exceeded that of Pima 32 by approximately 25% in the morning and 20% in the afternoon (Fig. 3B). A_{max} of S-6 was >60 μmol m^{-2} s^{-1} in the morning, 20% greater than that of Pima 32, but in the afternoon A_{max} declined to match that of Pima 32. In P-70, the CE exceeded that of Pima 32 by approximately 50% in the morning and 20% in the afternoon (Fig. 3C). As in S-6, though, A_{max} exceeded that of Pima 32 only in the morning. These results are consistent with the rankings of lines for A at the two times of day (Fig. 2). The differences in A:c_i curves indicate that differences in photosynthesis arise from altered properties of the mesophyll (9).

Relationships among Gas Exchange Parameters

Changes in leaf thickness, or other leaf characteristics not directly related to metabolism, could account in part for the observed genetic differences in A (Fig. 2). To test that possibility, various leaf characteristics, including A, g_s, and c_i, were correlated across genotypes at two times of day (9 AM and 4 PM). At each time, A was significantly correlated only with g_s and not with c_i, Chl or starch contents, or leaf thickness (Table II). Correlations between A at 9 AM and A at 4 PM were significant, as were correlations between g_s at 9 AM and g_s at 4 PM, indicating that rankings for these characteristics remained similar at the two times of day. The c_i was correlated with g_s (Table II). The poor correlation between A and c_i implies that genetic differences in photosynthetic rates did not result from altered stomatal limitations to CO_2 supply, despite the correlations between A and g_s.

DISCUSSION

Our data show that breeding Pima cotton for improved yield has increased single-leaf photosynthetic rates (Fig. 2). In the advanced lines S-6 and P-70, CE and A_{max} are both higher, especially in the morning, than in the early cv Pima 32 (Fig. 3). In the afternoon, some differences in CE persist (among the three lines for which A:c_i curves were determined) but they are smaller. No genetic differences in A_{max} persist in the afternoon (Fig. 3). We are unaware of other reports showing similar apparent genetic control of the diurnal regulation of photosynthesis.

The CE may reflect the ability of mesophyll cells to carbox-

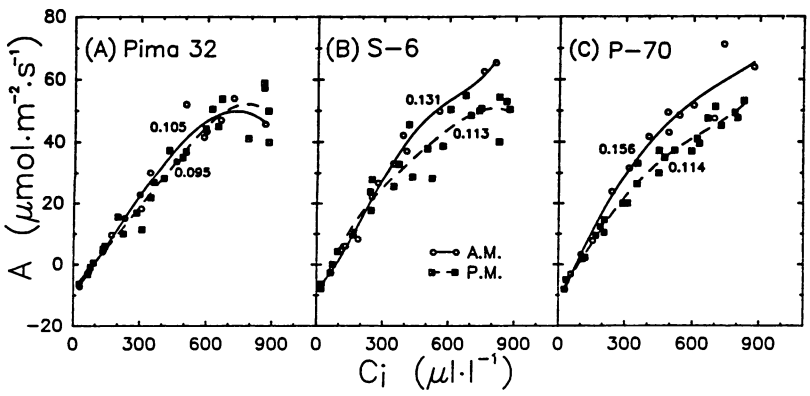

Figure 3. Relationships between A and c_i for Pima cotton leaves in the morning (all measurements made between 9:12 and 11:12 AM) and the afternoon (all measurements made between 2:49 and 4:19 PM). Each point in these curves represents a measurement on a separate leaf. A:c_i relationships are represented by fourth-order polynomial regressions. For each genetic line and time of day, the CE (units of mol m^{-2} s^{-1}) was determined as the slope between c_i = 100 and c_i = 300 and is shown adjacent to the A:c_i curve. Correlation coefficients are as follows: Pima 32 (AM) r = 0.980, n = 15; (PM) r = 0.973, n = 25; S-6 (AM) r = 0.996, n = 13; (PM) r = 0.968, n = 26; P-70 (AM) r = 0.985, n = 15; (PM) r = 0.989, n = 25. All correlation coefficients are significantly different from zero ($P < 0.05$).

Table II. *Linear Correlation Matrix for Relationships among Various Leaf Characteristics of Six Genetic Lines*

Plants were grown in a greenhouse in Phoenix, AZ. Correlation coefficients significantly different from zero ($P < 0.05$) are designated by an asterisk.

	Correlation Coefficient							
	A (9 AM)	A (4 PM)	g_s (9 AM)	g_s (4 PM)	c_i (9 AM)	c_i (4 PM)	Chl	Starch
A (4 PM)	0.89*	—						
g_s (9 AM)	0.91*	0.83	—					
g_s (4 PM)	0.79	0.91*	0.99*	—				
c_i (9 AM)	0.71	0.83	0.97*	0.97*	—			
c_i (4 PM)	0.79	0.77	0.95*	0.99*	0.94*	—		
Chl	0.79	0.60	0.26	0.35	0.30	0.17	—	
Starch	0.53	0.28	0.60	0.66	0.59	0.80	0.26	—
Thickness	0.35	0.02	0.26	0.33	0.22	0.48	0.37	0.26

ylate RuBP (22, 25). In other species, the total amount of Rubisco does not change diurnally to a significant extent (25). Rather, activity of Rubisco is diurnally regulated by mechanisms involving either activation by carbamylation, or inhibition by binding of carboxyarabinitol-1-P (25). Therefore, the increases in CE associated with genetic yield gains may result from altered metabolic regulation of the carboxylation step of photosynthesis.

The genetic increases in A_{max} in the morning (Fig. 3) imply enhanced capacity to regenerate RuBP at that time of day (22, 25). Diurnal regulation of RuBP regeneration could involve reactions of electron transport and photophosphorylation or reactions of the photosynthetic carbon reduction cycle (25).

It is also possible that differences between A:c_i curves may be associated with stomatal patchiness rather than photosynthetic metabolism. The calculation of c_i depends upon some assumptions, one of which is uniformity of g_s across the leaf. This assumption is not always fulfilled (20), although Radin *et al.* (17) discounted any role for patchiness in field-grown upland cotton. Beyschlag and Pfanz (2) recently suggested that patchiness may be a transient phenomenon, occurring only at certain times of day. Genetic effects on photosynthesis of Pima cotton can be detected, to a greater or lesser degree, throughout the day (Fig. 2, Fig. 3, Table II). It is emphasized that genetic differences in A occur regardless of the uniformity of g_s; patchiness influences only the interpretation of the A:c_i curves.

The ambient temperature regime may also play a role in the diurnal fluctuations reported here. In steady-state gas exchange, increasing the temperature (at constant VPD) enhances A of Pima 32 slightly more than A of advanced lines (Z Lu, E Zeiger, unpublished data). As a result, differences between lines become smaller with increasing temperature, although the shift is small. These temperature effects on A most likely are derived from altered mesophyll properties (CE and A_{max}), as stomatal limitations to A are small in all lines. The rate of RuBP oxygenation (photorespiration) relative to carboxylation may account for the effects, as this ratio is temperature sensitive (25). If diurnal fluctuations result from temperature responses, it is clear that breeding has altered the magnitude of those responses. In the case of RuBP oxygenation, at least, such an event seems unlikely because the two reactions are catalyzed at the same reaction site on Rubisco, and previous efforts to find differential regulation of the two activities have been unsuccessful (21).

A and g_s are strongly correlated across genotypes at each time of day (Table II). Nonetheless, A is poorly correlated with c_i. This result is an independent confirmation that genetic differences in A do not arise from altered stomatal limitations to photosynthesis. Considering the results at only one time of day (to remove temperature as an environmental variable), it seems possible that g_s is coupled in some manner to A. One result of this coupling is a relatively constant c_i across lines. Cowan *et al.* (7) proposed, on theoretical grounds, that ABA originating in the mesophyll regulates stomatal opening. In upland cotton in controlled environments, stomata are apparently coupled to mesophyll photosynthetic properties, but this coupling is altered or lost in the field (14, 16, 17, 19). Field behavior can be ascribed to high temperatures that promote extensive net degradation of ABA, thereby diminishing its influence on guard cells in the intact leaf (5, 16, 17). Presuming that Pima cotton behaves like upland cotton, the relationships between A and g_s in the greenhouse (Table II) may not be valid in the field. The possibility of coupling between A and g_s in this species in the field has not been tested.

Finally, although both A and yield are higher in modern Pima cotton lines, these two observations may not be directly related. The relationship between single-leaf A and canopy A is complex, depending upon canopy structure as well as photosynthetic characteristics of single leaves (8). The relationship of single-leaf A to yield is even more tenuous; in most crops (8, 10), including upland cotton (23), genetic yield gains result from enhanced partitioning of assimilates to harvested organs. Pima cotton apparently conforms to this model, inasmuch as modern lines are shorter at harvest and more heavily fruited than old lines. The agronomic importance of the increase in A remains to be established in this little-studied species.

In conclusion, we report that increased g_s, CE, and A_{max} for at least part of the diurnal cycle accompany genetic yield gains in Pima cotton. The data indicate a genetic change in the diurnal regulation of RuBP carboxylation and RuBP regeneration. Factors linking increases in A and g_s to increases in yield are not yet clear. Studies of the comparative physiology of gas exchange in these lines are continuing, with emphasis on the stomata.

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