MODERN PIMA CULTIVARS HAVE HIGHER PHOTOSYNTHETIC CAPACITY THAN OBSOLETE VARIETIES

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Abstract

Pima cotton (*Gossypium barbadense* L.) yields have tripled since the mid 1940's due to selection for heat tolerance in advanced breeding programs. This study was conducted to investigate intrinsic differences in photosynthetic capacity between modern and obsolete Pima cultivars under field conditions, and to determine the effects of moderate water stress on ambient gas exchange and photosynthetic capacity of these cultivars. The study was conducted at the University of Arizona's Maricopa Agricultural Center, under irrigated field conditions. Four released cultivars (Pima 32, S-1, S-6, and S-7) were selected for study, representing advancing stages of breeding for heat tolerance and yield over 43 years. These findings indicate that breeding for yield has improved photosynthetic capacity and stomatal conductance in advanced cultivars under conditions of water stress. Our results suggest that further improvements in cotton yield may be achieved through enhanced assimilatory processes in modern cultivars, especially as limits to number of fruit supported per unit of leaf area are approached.

Introduction

Most Pima cotton (*Gossypium barbadense* L.) is produced in the arid southwest where air temperatures often exceed 40^o C during the growing season. A major goal of breeders in the USDA-ARS Maricopa Pima Improvement Project has been to improve the crops heat resistance (yield in a hot environment) because introduced varieties are unadapted and seldom productive. This program has improved Pima yields through genetic manipulation of available germplasm variability, selection within segregations, and extensive testing of advanced lines for yield at sites varying in temperature. Yield of one recently released advanced line, Pima S-7, is triple that of Pima 32, an obsolete cultivar released in 1949. Breeders have not attempted to modify physiological or morphological traits of cultivars within this program. Yet a recent comparison of gas exchange properties of obsolete and advanced cultivars showed that extensive breeding has inadvertently improved physiological and morphological properties of advanced cultivars. Cornish et al. (1991) in a greenhouse study, demonstrated that photosynthetic capacity and stomatal conductance has increased in advanced Pima lines in parallel with heat resistance and yield potential. However, they reported little difference between cultivars in assimilation, stomatal conductance, and photosynthetic capacity in afternoon measurements when plant available water may have been less. The present study was conducted to: 1) Investigate intrinsic differences in photosynthetic capacity between modern and obsolete Pima cultivars under field conditions; and 2) Determine effects of moderate water stress on ambient gas exchange and photosynthetic capacity of these cultivars.

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Materials and Methods

Genetic Material

Four released cultivars (Pima 32, S-1, S-6, and S-7) were selected for study, representing opposite extremes in advancing stages of breeding over 43 years. Pima 32, the only cultivar used that has no introgressed genes from upland cotton, was released in 1949. Pima S-1 was released in 1951; S-6 was released in 1983; S-7 was released in 1992.

Experimental Conditions

Field studies were conducted over a two year period at the University of Arizona's Maricopa Agricultural Center, Maricopa. The four cultivars were planted in beds on 40 inch spacings with conventional plant density. The experiment was designed as a randomized complete block with four replicates per cultivar. Plot size was 6 rows by 36 feet. All plots were well fertilized and irrigated throughout the season, with irrigation applications every 10 days to 2 weeks.

Gas Exchange Measurements

Gas exchange measurements were initiated immediately after an irrigation cycle when field entry was possible, and were continued through to the next irrigation application. This sampling method allowed for monitoring changes in gas exchange parameters of each cultivar with the onset of mild water stress. Measurements of net assimilation rate of CO_2 (A), stomatal conductance to CO_2 (g), and intercellular CO_2 (c_i) were made with a Li-Cor 6200 portable photosynthesis system with a 1.0-L leaf chamber (Li-Cor Inc., Lincoln, NE). For measurement of the relationship between A and c_i (A:c_i), the chamber was mounted to a portable tripod, and was externally ventilated with a small portable 210 cfm fan to maintain leaf temperature at pre-measurement levels. Gas exchange at ambient CO_2 and A:c_i measurements were made on the upper-most, fully expanded, sunlit main stem leaves (i.e., located on the fourth of fifth main stem node from the terminal), oriented perpendicular to the sun. Measurements of A:c_i responses were made using techniques outlined by McDermitt et al. (1989). Immediately following an ambient or A:c_i measurement, leaves were excised and placed in a pressure chamber (model 3005, Soil Moisture Equipment Corp., Santa Barbara, CA) to determine leaf water potential (Ψ_L).

Results and Discussion

Our data indicates that modern Pima cotton cultivars selected for increased yield (heat tolerance) also have improved gas exchange properties (Table 1), and are able to maintain greater A and g with mild water stress that periodically exists in irrigated cultivation. Because data for Pima S-1 and S-6 were not different from Pima 32 and S-7, respectively, we will only discuss gas exchange data for Pima 32, the oldest line, and Pima S-7, the most advanced line studied.

Gas exchange measurements under non-stressed conditions when Ψ_L averaged approximately -0.99 MPa, revealed 18% greater average A in Pima S-7 compared to Pima 32 (Fig. 1; Table 1). Assimilation declined in both cultivars as water stress intensified, but the effects of declining Ψ_L on A were more pronounced in Pima 32 than in S-7 (Fig. 1; Table 1). For a comparative range of Ψ_L's between -0.95 and -1.7 MPa, the average decline in A in S-7 was 6% compared to 17% in Pima 32 (Fig 1). This marked effect of water stress on A in Pima 32 was tightly coupled to effects on g, contrasting with little synchronization between A and g in S-7 (Fig. 2). Stomatal conductance was similar in both cultivars when leaves were under little stress. But as Ψ_L declined in Pima 32, g was reduced by approximately 40% (Fig. 2). There was little change in g of S-7 with declining Ψ_L (Fig. 2). Correspondingly, c_i in S-7 was also not affected by water stress, but declined significantly in Pima 32 as a result of concomitant reductions in A and g (Figs. 1-3). In a recent study comparing diurnal cycling of gas exchange parameters of obsolete and modern Pima cultivars, Cornish et al. (1991) also reported the highest rates of A and g in the modern cultivars in the morning, but rates were similar in the afternoon. Their study was conducted under greenhouse conditions with plants in well watered pots. Our results indicate that under field conditions, modern Pima cultivars are quite tolerant to levels of water stress that typically exist in irrigated cultivation, and are able to minimize the stomatal limitation to A. Intercellular CO_2 is thereby maintained in excess of 80% of ambient, and the leaves are cooled considerably by evaporation of large amounts of water. Thus in selecting for heat tolerance and yield, breeders have developed cultivars that acclimate to mild water stress and maximize assimilation.

One striking result of our ambient gas exchange measurements under well-watered conditions was significantly higher A in S-7 when stomatal conductance was similar in both cultivars (Figs. 1-2; Table 1). This indicates significantly greater photosynthetic capacity in S-7 compared to Pima 32 under non-stressed conditions. Cornish et al. (1991) in a diurnal greenhouse study, also reported higher photosynthetic capacity in modern compared to obsolete Pima cultivars in the morning. However, differences in photosynthetic capacity were minimized in the afternoon when plant available water within pots may have been reduced. Do modern Pima cultivars maintain higher photosynthetic capacity under irrigated field conditions with mild water stress? Or was higher A observed in modern cultivars under water stress in this study simply due to higher g (Figs 1-2)?

The relationship between A and c_i (A:c_i) was determined for the cultivars under conditions of slowly developing water stress (Table 2). Figures 4 and 5 display average response curves for the two cultivars under the opposite extremes of Ψ_L's measured. Our data show that the initial slope of the A:c_i response curve at limiting c_i (S_i) was not different between advanced and obsolete Pima cultivars under non-stressed conditions (Fig. 4; Table 2). Also, the average maximum A observed within the range of CO_2 concentrations applied (A_{max}), was not different between Pima 32 and S-7 when plants were not stressed (Fig 4; Table 2). As water stress intensified, A:c_i relationships were not changed in S-7, but indicated a significant reduction in photosynthetic capacity in Pima 32 due to both lower S_i and A_{max}. Cornish et al. (1991) reported higher S_i and A_{max} in modern Pima cultivars when there was a lack of water stress, but they did not investigate the genetic improvement in photosynthetic capacity under stress. In a study of two upland cotton cultivars that had one common parent in their breeding history, Faver et al. (1996) reported genetic improvement in photosynthetic capacity under water stress as implied by higher S_i of the A:c_i response. We are unaware of other reports investigating the genetic improvement of water stress tollerance in cotton from a photosynthetic capacity perspective.

Maintenance of higher Si under water stress in S-7 may reflect significant improvement in the ability of mesophyll cells to carboxylate ribulose-1,5-bisphosphate (RuBP) in cultivars selected for improved yield (Von Caemmerer and Farquhar 1981; Woodrow and Berry 1988). Greater A_{max} in S-7 compared to Pima 32 when plants were stressed implies genetic increases in the capacity to regenerate RuBP (Von Caemmerer and Farquhar 1981) which involves electron transport and photophosphorylation reactions (Woodrow and Berry 1988). Therefore, advanced Pima cultivars apparently maintain higher photosynthetic capacity under water stress due to improved metabolic regulation of the carboxylation step of photosynthesis, and enhanced electron transport and photophosphorylation reactions.

Our results confirm previously published observations that advanced Pima cultivars bred for increased yield have increased photosynthetic capacity and stomatal conductance. Further, these modern cultivars maintain higher photosynthetic capacity under conditions of water stress that typically exists in field cultivation. These findings suggest that further improvement in photosynthetic capacity, water stress tolerance, and ultimately yield may be possible through breeding, especially as the limits to harvest index are approached.

Summary

Photosynthetic capacity of modern and obsolete Pima cultivars was similar under non-stressed conditions. As water stress intensified, modern cultivars maintained higher photosynthetic capacity. Stomatal conductance was less in obsolete cultivars for any level of water stress measured. As a result, the modern Pima cultivars studied maintained higher A for any level of water stress due to greater g and photosynthetic capacity.

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Table 1. Comparison of assimilation and stomatal conductance rates, and intercellular CO_2 concentrations of two Pima cotton cultivars during four measurement periods at Maricopa, AZ.

Days after irrigation	Cultivar 32 A	32 g	32 c_i	Cultivar 7 A	7 g	7 c_i	Mean Ψ_L
2	25.8 b	0.74	280.24	31.3 a	1.14	287.38	-0.99
4	25.9 b	0.93	286.96	31.8 a	1.00	282.14	-1.16
5	25.3 b	0.73 b	279.17	28.2 a	1.22 a	291.82	-1.21
7	21.6 b	0.49 b	270.03	29.5 a	0.94 a	283.19	-1.51

† For each sampling date, means followed by the same letter are not significantly different a P>0.95.

Table 2. Comparison of initial slopes and maximum assimilation rates the response of assimilation to intercellular CO_2 concentrations for four Pima cotton cultivars during five measurement periods at Maricopa, AZ.

Days after irrigation	Cultivar 32 Initial Slope	32 Maximum Assimilation	Cultivar 7 Initial Slope	7 Maximum Assimilation	Mean Ψ_L
2 †	0.172	60.6	0.183	62.5	-1.05
3	0.154 b	52.0 b	0.176 a	59.3 a	-1.07
4	0.146 b	45.0 b	0.169 a	56.0 a	-1.2
5	0.126 b	47.0 b	0.166 a	58.0 a	-1.3
7	0.138 b	40.5 b	0.184 a	59.5 a	-1.6

† For each sampling date, means followed by the same letter are not significantly different a P>0.95.

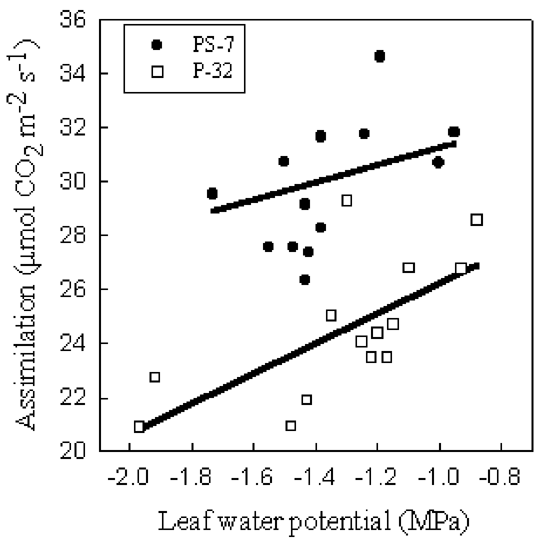

Figure 1.Relationship between assimilation and leaf water potential for two Pima cultivars. Data were collected over an 8 day period at Maricopa, AZ.

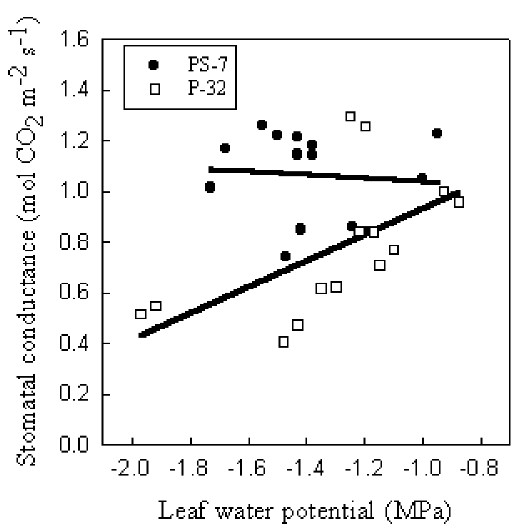

Figure 2. Relationship between stomatal conductance and leaf water potential for two Pima cultivars. Data were collected over an 8 day period at Maricopa, AZ.

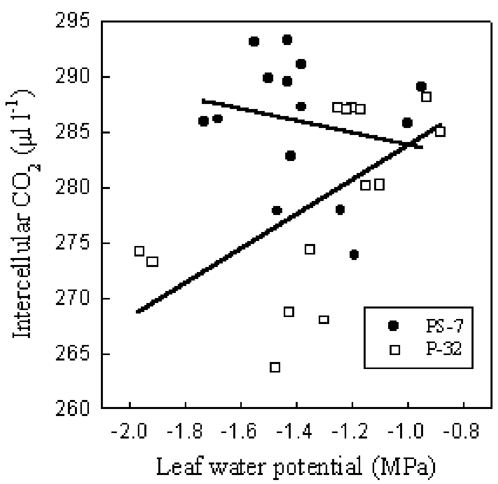

Figure 3. Relationship between intercellular CO_2 and leaf water potential for two Pima culivars. Data were collected over an 8 period at Maricopa, AZ.

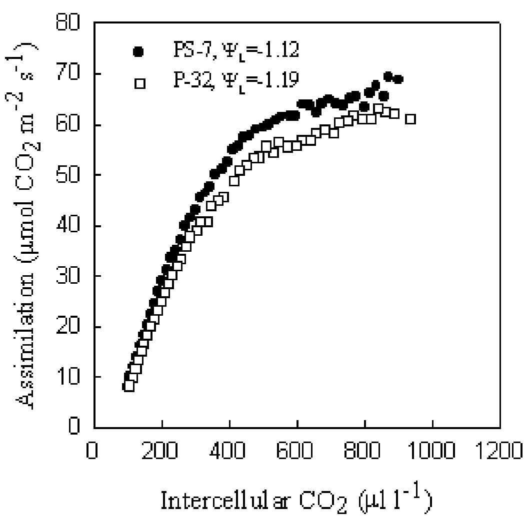

Figure 4. Relationship between assimilation and intercellular CO_2 for two Pima cultivars under non-stressed conditions. Data are averages of four response curves for each cultivar collected at Maricopa, AZ.

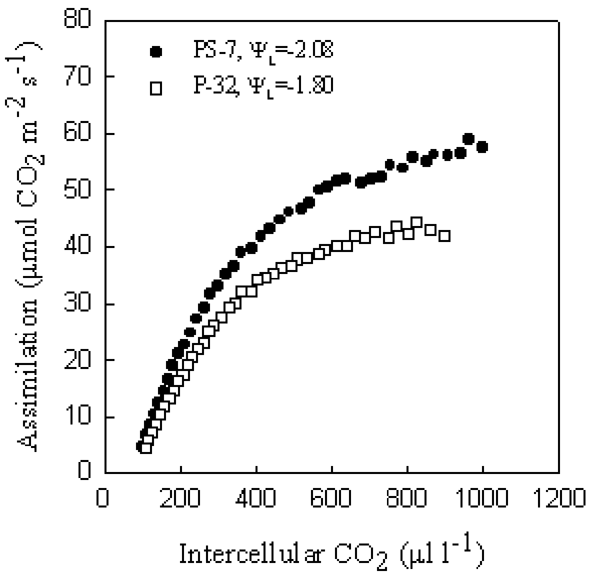

Figure 5. Relationship between assimilation and intercellular CO_2 for two Pima cultivars under non-stressed conditions. Data are averages of four response curves for each cultivar collected at Maricopa, AZ.