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Canopy Photosynthesis and Transpiration of Cotton as Affected by Leaf Type[1]

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ABSTRACT

Cotton (*Gossypium hirsutum* L.) plants with okra or superokra leaves have several agronomic characteristics which could make them better adapted to narrow-row culture than plants with normal leaves. This study was conducted to investigate the effect of these leaf types on canopy photosynthesis and transpiration of narrow-row cotton. A portable, open-chamber system was used in plant communities grown at high and low densities. In 1973 the three leaf types (normal, okra, and superokra) had dissimilar genetic background with the okra and superokra leaf lines being similar in appearance and leaf area. Maximum leaf area index (LAI) of these canopies was approximately 2.8 compared to 4.6 for normal leaf plants. Near-isogenic lines were used in 1974. Although morphologically distinctive, the okra and normal isolines had maximum LAIs of approximately 5.2, compared with 3.5 for the superokra leaf isoline. Apparent photosynthesis was positively associated with LAI, although correlation coefficients were low (0.23 to 0.54). Plant population had little effect on canopy photosynthesis. When data were averaged across populations, normal leaf plants had CO_2 exchange rates 20 and 29% higher than superokra leaf plants in 1973 and 1974, respectively. Okra leaf plants were intermediate. Leaf type effects on transpiration were small and inconsistent during the 2 years. Although differences in photosynthesis to transpiration ratios statistically nonsignificant, the trend was normal>okra>superokra. Thus, the okra leaf types do not appear to be associated with improved efficiency of water use.

Additional index words: Efficiency of water use, Okra leaf, Superokra leaf, Leaf area index, *Gossypium hirsutum* L.

SUPEROKRA leaf cotton plants (*Gosypium hirsutum* L.) are characterized by greatly reduced leaf size with less leaf area per plant than normal leaf cotton. Okra leaf plants usually have a leaf area intermediate to normal and superokra types (15, 16).

Cotton lines with okra type leaves have several desirable characteristics for narrow-row, high-population production: low incidence of boll rot (1, 2, 10, 14), few vegetative branches, little tendency for excessive vegetative growth (10, 16), and earliness (1, 2, 10, 14, 16). These desirable characteristics are partially overshadowed, however, by the high rate of fruiting form abortion reported in such leaf type variants. Kerby and Buxton (11) found that M-8 superokra leaf and 'Stoneville 7A' okra leaf cotton produced 93 and 111% more fruiting positions than 'Deltapine 16' normal leaf but later aborted 180 and 207% more bolls, respectively. When near-isogenic lines of Stoneville 7A were used they obtained similar results. The okra and superokra leaf isolines produced 8 and 26% more fruiting positions, but later aborted 33 and 72% more bolls than did the normal leaf isoline.

Relatively little work has been reported on the association between leaf types and photosynthetic rates (6) and none has been reported for narrow-row canopy photosynthesis of cotton. The danger of extrapolating from single-leaf photosynthetic measurements to canopy photosynthesis has been shown in barley (*Hordeum vulgare* L.) by Berdahl et al. (4). In their study CO_2 exchange rate (CER) per unit leaf area of flag leaf was similar for a wide range of leaf sizes. The potential advantage of plants with large leaves was not realized in field studies.

Buxton and Stapleton (5) described a cotton-leaf model in which the superokra leaf shape is predicted to have a photosynthetic advantage per unit of leaf area over the normal leaf shape, primarily because of reduced boundary layer resistance. Elmore et al. (7), however, found similar rates between superokra leaf plants and several normal leaf lines using single-leaf measurements. Baker and Myhre (3) compared canopy CER per unit ground area of 'Rex' normal and okra leaf cotton communities planted in standard row widths and found no significant difference.

The amount of leaf area present in a canopy should be important in determining the potential for CER of plants regardless of size or shape of individual leaves. Canopy apparent photosynthesis in artificial communities of cotton plants increased with leaf area index (LAI) until a LAI of about 3, after which it either stabilized with additional LAI (at 20 C) or declined (30 and 40 C) (12). CER increased with LAI values up to about 8 with soybeans, *Glycine max* (L.) Merr., (9) and barley (13).

With limited moisture supply in many areas and high cost of irrigation, especially where pumping is involved, it is important to know the effect of leaf type on transpiration rates and efficiency of water use. The cotton-leaf model of Buxton and Stapleton (5) predicts similar transpiration rates for single normal or superokra leaves. Baker and Myhre (3) found that canopies of normal leaf plants had somewhat higher transpiration rates than okra leaf cotton. Ludwig et al. (12) reported that transpiration in-

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creased with leaf area until a LAI of approximately 4 was reached.

This study was conducted to determine the influence of leaf type on canopy CER and transpiration rate in narrow-row cotton.

MATERIALS AND METHODS

Experiments were conducted at the Univ. of Arizona Campbell Ave. Farm in Tucson during two summers. Seed of Deltapine 16 (normal leaf), Stoneville 7A (okra leaf), and M-8 (superokra leaf) were planted in four row plots with 51 cm between rows in irrigated basins on 23 Apr., 1973. Seed of three near-isogenic lines of Stoneville 7A (obtained from J. E. Jones of Louisiana State Univ.) were planted on 22 Apr., 1974. The near-isogenic lines of okra and superokra leaf resulted from six backcrosses of commercial Stoneville 7A (the recurrent parent) to La Okra 2 and La Superokra Leaf 2, respectively. Plant populations of 11.2 and 18.5 plants/m² and 10.0 and 20.0 plants/m² were established in 1973 and 1974, respectively, by hand-thinning. The experimental design in each year was a randomized block in a split-plot arrangement with four replicates. The whole plot was leaf type and the subplot was plant population. All observations were taken from the center two rows within each 18 m-long subplot.

Pre-emergence herbicides plus some additional hand-weeding were used to control weeds. Nitrogen at the rate of 84 kg/ha was applied pre-plant in both years. No insecticides were applied and slight insect damage resulted. Irrigations were applied a few days before photosynthesis and transpiration measurements to reduce moisture stress. The irrigation schedule in 1974 was more satisfactory than the 1973 schedule in terms of avoidance of visual evidence of plant water stress during the afternoons measurements were made.

The open chamber system, of similar design to that used by Jeffers and Shibles (9), included a transparent field chamber, a portable air-conditioned mixing chamber, flexible, high-pressure, insulated ducting between the two chambers, and an air-conditioned instrument trailer. The field chamber was built in a modular fashion of square aluminum tubing and plexiglas sheets. The assembled chamber had dimensions of 102 cm W × 160 cm L × 112 cm H. The width allowed simultaneous sampling of two rows. A flanged 28 cm-high transparent dome (heat-formed from 0.48 cm-thick plexiglass) and a wooden floor made the chamber reasonably rigid and air tight. The north end of the field chamber contained both inlet and outlet ports for air exchange to minimize shading effects. Two small blowers on the inside of the transparent field chamber served to circulate air throughout the enclosed plant canopy.

The mixing chamber was an air-conditioned plywood box on wheels with a detachable plywood air stack (2.7m high) at one end and an air blower at the other. Air was pushed out of the mixing chamber by a high pressure "squirrel cage" blower through a 10-m length of cylindrical (17.8-cm diameter) insulated duct and into the field chamber. The rate of air flow through the field chamber could be regulated within the range of 1.0 to 1.5 air volume changes per minute.

The final 2.4 m of the ducting from the mixing chamber to the field chamber was rigid in order to smooth the air flow profile for air flow measurements with a hot-wire anemometer (Hastings Model B22 with an S22A directional probe).

CER of plants within the field chamber was monitored by comparing the CO_2 content of incoming and outgoing air streams. Samples were pumped through 64-m lengths of nylon tubing to the differential infrared gas analyzer (IRGA, Beckman Model 865-25) located in the instrument trailer. Air samples were dried with Drierite and passed sequentially through a cotton filter, a rotameter, and one of the cells of the IRGA. Standard mixtures of CO_2 in N_2 (approximately 300 and 350 μl/liter) were used to calibrate the IRGA. In 1974 different "standards" were used and were periodically checked against primary-standard-grade gas mixtures (obtained from Liquid Carbonics, Los Angeles, Calif.). This resulted in more accurate absolute CER measurements in 1974.

Transpiration rates were measured by determining moisture contents of the air streams using matched aspirated thermistor-type psychrometers. The psychrometer which monitored incoming air was housed within the mixing chamber while a second psychrometer, located in the field chamber outlet port, measured the outgoing air. The dry-bulb air temperature at the point of entry into the field chamber was monitored by a thermistor within the inlet port. A third psychrometer, which measured ambient temperatures, was situated in the field near the instrument trailer. All thermistors were connected by low impedance, twisted-pair wire to a Wheatstone bridge in the instrument trailer.

Table 1. LAI determinations for cotton plant communities with contrasting leaf shapes.

Date	Population	Leaf type: Normal	Okra	Superokra	Mean
	Plants/m²	—— 1973 ——			
10 July	11.2	2.95 a*	2.18 a	1.74 a	2.29 m
	18.5	3.50 a	2.16 a	2.10 a	2.59 m
	Mean	3.22 x	2.17 y	1.92 y	
26 July	11.2	5.21 ab	2.68 c	2.94 c	3.61 n
	18.5	5.98 a	2.96 c	4.08 bc	4.34 m
	Mean	5.60 x	2.82 y	3.51 y	
24 August	11.2	5.07 x	3.24 y	3.03 y	3.78
		—— 1974 ——			
25 July	10.0	3.94 ab	4.04 ab	2.75 c	3.58 m
	20.0	4.66 a	4.31 a	3.00 bc	3.99 m
	Mean	4.30 x	4.18 x	2.88 y	
13 August	10.0	5.62 a	5.86 a	4.28 a	5.25 m
	20.0	6.98 a	6.75 a	3.96 a	5.90 m
	Mean	6.30 x	6.30 x	4.12 y	

* Means followed by the same letter within a series and date were not significantly different at the 0.05 probability level in the Student-Newman-Keuls Range Test.

Measurements of canopy photosynthesis and transpiration were made during a 10-min period when solar irradiance remained in the range of 1.0 to 1.4 cal/cm²/min (measured by an Eppley pyranometer on the roof of the instrument trailer). One replication per day was measured in each of three experiments: 1) 30 July to 2 Aug. 1973, 2) 30 July to 2 Aug. 1974 and 3) 6 Aug. to 9 Aug. 1974.

LAI determinations were made during each summer on at least two dates, one of which was within a few days of the period of photosynthesis and transpiration measurements. Four adjacent plants, near the plants sampled for gaseous exchange, were cut at ground level and all leaves removed. The leaf area of 10 to 15 leaves from each plant was determined with a photosensitive automatic area meter (Type AAM-5, Hayashi Denko Co., Ltd., Tokyo, Japan). These leaves were dried and weighed and leaf area to leaf weight ratio was determined, which was used to derive the total leaf area from total leaf weight. Heights and above-ground biomass of these plants were also measured.

RESULTS AND DISCUSSION

Characteristics of Plants

The three cotton lines were used to obtain a gradient in LAI with normal > okra > superokra. As seen in Table 1, however, the LAI values for okra- and superokra-leaf plants were similar in 1973, while normal and okra leaf plants had similar LAI's in 1974. It was difficult to visually distinguish M-8 superokra leaf plants from Stoneville 7A okra leaf plants in 1973, with both resembling the superokra type. In 1974, okra leaf plants were intermediate in appearance between normal and superokra leaf plants but LAIs of the normal and okra leaf isolines were similar (Table 1). No significant differences in plant height among genotypes were noted in either year (Table 2). There also was no consistent trend detected in above-ground biomass. Number of leaves, determined only in 1973, indicated that okra and superokra leaf plants tended to have more leaves per unit ground area than did plants with normal leaves. These data, in conjunction

Table 2. Plant height, above-ground biomass, and number of leaves in cotton plant communities with contrasting leaf shapes.

Plant characteristic	Leaf type		
	Normal	Okra	Superokra
	10 July 1973		
Plant height (cm)	48 a*	49 a	51 a
Above-ground biomass (g/m^2)	319 a	298 a	303 a
No. of leaves/m^2	886 a	1,127 a	1,031 a
	26 July 1973		
Plant height (cm)	75 a	73 a	78 a
Above-ground biomass (g/m^2)	709 a	545 c	645 b
No. of leaves/m^2	1,009 b	1,482 a	1,683 b
	25 July 1974		
Plant height (cm)	65 a	76 a	72 b
Above-ground biomass (g/m^2)	562 a	624 a	539 a
	13 Aug. 1974		
Plant height (cm)	84 a	87 a	78 a
Above-ground biomass (g/m^2)	1,079 a	1,250 a	998 a

* Means followed by the same letter within a series were not significantly different at the 0.05 probability level in the Student-Newman-Keuls Range Test.

with the LAI values in Table 1, confirm the visual observation of smaller, but more numerous leaves in the canopies of okra and superokra leaf plants.

Canopy Photosynthesis

CER of the different leaf types in 1973 were lower than those in 1974, although similar trends are noted in each year (Table 3). The higher CER observed in 1974 could be due to a number of reasons, some of which have already been mentioned (differences in genetic background of the plants, improved CO_2 standards, and a lower degree of water stress in 1974). The data for 1974 are averaged for the two experiments since in a combined ANOV there were no significant experimental interactions.

Normal leaf plants tended to have the highest LAI (Table 1) and CER per unit ground area (Table 3), while superokra leaf cotton generally had the lowest values. There was little consistent effect of plant population on CER nor was there a significant leaf type $\times$ population interaction. Averaged across populations, normal leaf plants had 20 and 29% higher CER than superokra leaf plants in 1973 and 1974, respectively. LAI and CER were positively correlated in all experiments, with $r = 0.36$, 0.54^{**}, and 0.23 for 1973 and the two 1974 experiments, respectively. These correlations were obtained by using individual LAI and CER of the 24 experimental plots in each case.

In 1974 okra and normal leaf cotton were similar both in terms of LAI and CER per unit ground area. Baker and Myhre (3) reported similar canopy CER between Rex normal and okra leaf lines at a population of 19.3 plants/m^2 (approximately 80 mg CO_2/dm^2 ground area/hour at a solar irradiance of 1.2 to 1.4 cal/cm^2/min), which is in agreement with our 1974 results.

When CER is expressed on a unit leaf area basis using the respective values of LAI and apparent photosynthesis for each plot and then averaged over population, mean values of 15.2, 15.1, and 17.9 mg CO_2/dm^2 leaf area/hour are obtained for normal, okra, and superokra leaf plants, respectively, for the 1974 data.

Table 3. CER of cotton plant communities with contrasting leaf shapes.

Population	Leaf type			Mean
	Normal	Okra	Superokra	
Plants/m^2	mg CO_2/dm^2 ground area/hour			
		1973		
11.2	44.5 a*	44.3 a	41.5 a	43.4 m
18.5	55.2 a	46.9 a	41.8 a	48.0 m
Mean	49.8 x	45.6 x	41.6 x	
		1974		
10.0	76.0 a	74.6 a	57.8 b	69.4 m
20.0	74.0 a	71.8 a	58.6 b	68.1 m
Mean	75.0 x	73.2 x	58.2 y	

* Means followed by the same letter within a series and a year were not significantly different at the 0.05 probability level in the Student-Newman-Keuls Range Test.

Although these means are not significantly different, there is a trend for superokra leaf plants to have higher rates per unit leaf area than normal leaf types. This trend agrees with the 1973 study, when the okra leaf plants closely resembled the superokra type, where rates of 8.9, 16.6, and 12.5 mg CO_2/dm^2 leaf/hour were obtained for normal, okra, and superokra leaf plants, respectively. These differences in CER per unit leaf area are probably due mainly to greater penetration of sunlight to lower leaves within a relatively open canopy (when LAIs are low). To a lesser extent, leaf boundary layer differences (as affected by leaf size and shape), the amount of air movement in the canopy, and differences in leaf temperature may have also affected the rate of photosynthesis.

Kerby and Buxton (11), in a companion study to the one presented here, found an association between rate of fruiting form abortion and reduction in LAI, which was presumed to result in reduced carbohydrate production per fruiting position. Although the central role of carbohydrates in the fruiting of cotton is widely recognized, additional explanations have been proposed. For example, a reduction in leaf area could result in inadequate available N pools within the plant, which could prove limiting to fruiting form retention. Studies such as that of Guinn (8), however, in which elevated CER was seen to reduce boll shedding in cotton, indicate that fruiting form retention can be limited by photosynthesis. Processes underlying fruiting in cotton are complex and incompletely understood. No unified hypothesis is now available to explain the varied observations concerning fruiting in cotton.

Canopy Transpiration

The loss of water by transpiration per unit ground area was not consistently influenced by leaf shape (Table 4). The 1974 data are averaged for the two experiments since there were no significant experimental interactions. The data suggest that the lowest LAIs were sufficient for near-maximal rates of transpiration and that the additional LAI of normal leaf plants added little to water loss by transpiration. These results are consistent with those of Ludwig et al. (12).

When transpiration was expressed per unit leaf area and averaged over plant populations in 1974, values

Table 4. Net water vapor exchange rates of cotton plant communities with contrasting leaf shapes.

Population	Leaf type			Mean
	Normal	Okra	Superokra	
Plants/m^2	g H_2O/dm^2 ground area/hour			
		1973		
11.2	12.59 a*	11.87 a	14.72 a	13.06 m
18.5	11.75 a	14.16 a	13.15 a	13.02 m
Mean	12.17 x	13.02 x	13.94 x	
		1974		
10.0	9.23 a	10.82 a	7.27 a	9.11 m
20.0	8.75 a	7.94 a	7.85 a	8.18 m
Mean	8.99 x	9.38 x	7.56 x	

* Means followed by the same letter within a series and a year were not significantly different at the 0.05 probability level in the Student-Newman-Keuls Range Test.

Table 5. Ratio of apparent photosynthesis to transpiration rates of cotton plant communities with contrasting leaf shapes.

Population	Leaf type			Mean
	Normal	Okra	Superokra	
Plants/m^2	mg CO_2/g H_2O			
		1973		
11.2	3.53 ab*	3.73 ab	2.82 b	3.36 m
18.5	4.70 a	3.31 ab	3.18 ab	3.73 m
Mean	4.12 x	3.52 x	3.00 x	
		1974		
10.0	8.48 a	7.31 a	8.46 a	8.08 m
20.0	9.46 a	9.40 a	7.78 a	8.88 m
Mean	8.97 x	8.35 x	8.12 x	

* Means followed by the same letter within a series and a year were not significantly different at the 0.05 probability level in the Student-Newman-Keuls Range Test.

of 1.83, 1.90, and 2.25 g H_2O/dm^2 leaf area/hour were obtained for normal, okra, and superokra leaf plants, respectively. These means were not significantly different, but indicate a trend toward higher transpiration rates per unit leaf area in the superokra leaf plants. In 1973 corresponding transpiration rates of 2.26, 4.72, and 4.14 g H_2O/dm^2 leaf area/hour were obtained for Deltapine 16 normal leaf, Stoneville 7A okra leaf, and M-8 superokra leaf, respectively. The transpiration rate per unit leaf area of normal leaf plants in 1973 was significantly lower than rates of the other two leaf types, both of which morphologically resembled the "typical" superokra leaf type.

The ratio of apparent photosynthetic to transpiration rates (P/T) is an index of efficiency of water use. The three canopy types did not differ significantly in P/T ratio as seen in Table 5. There is a trend, however, for high P/T ratio with high LAI values. The 1974 data are the average of the two experiments which had no significant experimental interactions.

The similarity in transpiration rates and P/T do not indicate a pronounced advantage of any leaf type in canopy water use, although the normal leaf plants tended to be more efficient in this regard. Apparently, any potential advantage gained as a result of reduction in leaf size of the okra leaf types is offset by other considerations such as a greater opportunity for solar heating of lower leaves and greater air movement within a more-open canopy.

This study shows that the approximate 35% reduction in LAI of cotton plants, represented by the superokra leaf type in narrow-row culture, is associated with an average reduction of 25% in canopy CER relative to normal leaf plants. It appears that LAI, rather than leaf type per se, is the major determinant of CER per ground area and that any potential advantage of a reduced leaf size, such as those discussed by Buxton and Stapleton (5) for single cotton leaves, are not recognized in a canopy situation. This is in agreement with the findings of Baker and Myhre (3), who did not find a pronounced advantage in CER in either Rex normal or okra leaf genotypes, both with an LAI of approximately 5. The superokra leaf type represents such a high degree of reduction in leaf size and LAI that canopy CER is distinctly lowered, but with no concomitant lessening of canopy transpiration rates relative to normal leaf plants. Thus an increase in efficiency of water use by the okra types relative to normal leaf plants would not be expected.

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