

Carbon Source-Sink Relationships within Narrow-Row Cotton Canopies¹

T. A. Kerby, D. R. Buxton, and K. Matsuda²

ABSTRACT

Cotton (*Gossypium hirsutum* L.) is an indeterminate crop in which vegetative and reproductive sinks compete for photosynthetic assimilates. The objective of this study was to evaluate the carbon source sink relationship in cotton canopies with differing leaf types grown under narrow-row culture and to determine if measurement of specific leaf weight (SLW) can be used as a simplified evaluation of photosynthetic rate within cotton canopies. Three near-isogenic lines of 'Stoneville 7A' (normal, okra, and superokra) cotton which differed in blade area/leaf were grown in narrow-row culture at a plant density of 10 plants m⁻². During the 3rd (29 July) and 5th (13 August) weeks of flowering, whole plants were exposed to ¹⁴CO₂ and evaluated at three height intervals (0 to 30 cm, 30 to 55 cm, and above 55 cm) for leaf area index (LAI), ¹⁴CO₂ uptake, and biomass distribution. Okra and superokra leaf types generally had higher ¹⁴CO₂ uptake within the canopy on a leaf area basis, but lower LAI than normal leaf plants. Uptake of ¹⁴CO₂ among leaf types on a land area basis was different only on 13 August in the top interval where the ranking was normal > okra > superokra. By 13 August, the top interval accounted for 81, 77, and 69% of the canopy ¹⁴C-assimilate production, but contained only 29, 28, and 32% of the fruit dry weight for normal, okra, and superokra leaf plants, respectively. Mutant leaf types had a larger percentage of dry weight as fruit and less as leaves and petioles compared to normal leaf plants. This study suggests that vegetative growth is favored at the expense of reproductive growth due to high LAI at the top of normal leaf canopies when grown in narrow-row culture. However, the mutant leaf types tend to have less biomass resulting in only equivalent yields to normal leaf plants when grown under full-season culture. Significant correlation coefficients between C uptake and SLW ranged between 0.72 and 0.89 depending upon time of SLW measurement and sampling date, but were not altered by leaf type. Use of SLW is a simple method for estimating photosynthetic activity of leaves within cotton canopies.

Additional index words: *Gossypium hirsutum* L., Leaf type, Okra leaf, Superokra leaf, Radioactive C, Specific leaf weight.

DEVELOPMENT of cotton (*Gossypium hirsutum* L.) bolls depend primarily on assimilates provided by subtending leaves and leaves which are near-

est to the fruits. In a qualitative radioautographic study, Brown (6) found that bolls received assimilates from bracts, subtending leaves, and leaves higher up on the same side of the main stem. Bracts and leaves, however, varied widely in their photosynthetic rates and in their assimilate contribution to fruit development. Elmore (12) found that bracts and boll walls were only 28 and 1% as efficient as leaves in ¹⁴CO₂ uptake on a dry weight basis. Benedict and Kohel (3) observed that bracts were only 5 to 10% as important as subtending leaves in supplying assimilates to bolls.

These data support earlier work by Ashley (2) who demonstrated that about 90% of the ¹⁴C-assimilate produced within a fruiting branch remained within the branch and that the subtending leaf was the most important assimilate source for boll development. More recently, Horrocks et al. (14) found that at least three leaves were important in nourishing bolls located at the first position on a sympodial branch of cotton grown under narrow-row culture. The leaf subtending the boll, the subtending leaf one position further along the sympodial (where no subtending boll was present), and the leaf subtending the sympodial branch supplied 41, 37, and 22%, respectively, of the ¹⁴C-assimilates received by 10-day-old bolls. These results are similar to those obtained with soybeans [*Glycine max* (L.) Merr.] (22) which showed that sink strength was inversely proportional to the distance from the source.

Since cotton is an indeterminate crop where vegetative growth continues above active developing fruiting branches, shading due to extensive upper growth may increase boll abscission (13) by limiting photosynthesis of leaves that supply assimilates to developing bolls. This is probably intensified under narrow-row culture where shading of lower leaves would be greater than under normal row spacings. Conceivably, higher photosynthetic rates of leaves adjacent to developing fruit and reduced boll abscission could be obtained if radiation penetration into the canopy is increased. Recently, near-isogenic lines of cotton that have leaves with modified amounts of lobing have been developed. These plants (okra and superokra) are characterized by reduced leaf area index (LAI), reduced blade area per leaf, and have a more open canopy than normal leaf plants (19).

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² Former graduate associate in research, (now assistant professor, New Mexico State Coop. Ext., Box 3AE, Las Cruces, NM 88003), former professor, (now professor, Malheur Exp. Stn., Oregon State Univ., Ontario, OR 97914), and associate professor, Dep. of Plant Sciences, Univ. of Arizona, Tucson, AZ 85721.

Determination of C exchange rates (CER) under field conditions is expensive and time consuming. Some workers have noted a close relationship between CER and specific leaf weight (SLW) which is much easier to measure. Positive correlations between CER and SLW have been reported in alfalfa (*Medicago sativa* L.) (9) and soybeans (11). Older shaded soybean (5) and alfalfa (24) leaves had lower CER and SLW than fully expanded leaves in the upper canopy. Conversely, differences in SLW were not closely related to differences in CER of soybean leaves grown under various irradiation environments (5). Also, genotypic differences in CER of soybeans could not be accurately predicted by SLW (4). If there is a close relationship between SLW and CER of leaves at various cotton canopy heights, SLW may be a useful means for selecting plant types with leaves within the plant canopy with a high CER.

This study was conducted to evaluate photosynthetic activity of normal, okra, and superokra leaf types at different height intervals within narrow-row, field-grown cotton in relation to location of developing bolls. Additionally, experiments were performed to determine if SLW can be used as an accurate index of CER of leaves within plant canopies.

MATERIALS AND METHODS

Three near-isogenic lines (17) of 'Stoneville 7A' which differed in leaf type (normal, okra, and superokra) were planted 3 May 1975 at the University of Arizona Campbell Avenue Farm in Tucson. Nitrogen was applied preplant at a rate of 84 kg/ha. Plants were grown in irrigated basins in rows 51 cm apart and hand thinned in June to 10 plants m⁻². Plant observations were taken from the center two rows of plots that were four rows wide and 20 m long. The experimental design was a randomized block with six replications in a split-plot arrangement with leaf type as the whole plot. Plant height intervals were imposed as subplots and consisted of three intervals (0 to 30 cm, 30 to 55 cm, and above 55 cm from the soil surface). Data were collected during two sampling periods which corresponded to the 3rd and 5th weeks of flowering.

Plants were harvested at the soil line within 2 days of C uptake measurements and biomass partitioned into leaves, stems, petioles, and fruit and dried at 70 °C. Leaf area index was determined prior to drying with a photosensitive automatic area meter (Type AAM-5, Hayashi Denko Co., Ltd., Tokyo, Japan). Specific leaf weight determinations were made from fully expanded upper leaves, leaves near 45 cm, and leaves near 25 cm above the ground. These leaves were representative of top, middle and bottom height intervals, respectively. Two replications were sampled at 0600 (AM SLW) and 1800 hours (PM SLW) on each of 3 days for each sampling period. Fifty 0.305-cm² leaf discs were collected with a paper punch from four leaves within each plant height interval of each plot and dried at 70 °C. Main leaf veins were avoided.

Photosynthetic irradiation (PI) above the canopy at solar noon on clear days ranged between 540 to 560 W m⁻². Percentage PI reaching the soil surface on 21 August was obtained by comparing two sensors at five locations within each plot.

Measurements of ¹⁴CO₂ uptake were made using a plexiglass chamber with a removable dome. The chamber dimensions were 55 × 61 × 107 cm which enclosed three plants within one row. Design of the chamber, plywood floors, mixing fans, air seals, and other features were similar to those described by Pegelow et al. (19), except that the chamber was a closed system and smaller in size. All ¹⁴CO₂ labeling experiments were conducted between 1000 and 1400 hours when total solar radiation (measured by an Eppley pyranometer) was greater than 700 W m⁻².

Source of radioactivity was NaH ¹⁴CO₃ (sp. act. of 0.15 mCi mg⁻¹) dissolved in 0.02 N NaOH. One hundred microcuries of radioactivity were introduced into a vial at the air intake of the mixing fan with a hypodermic syringe. After the chamber

dome was attached, ¹⁴CO₂ was generated by injecting an excess of 0.1 N HClO₄. A short pulse-labeling period of 2.5 min was used to minimize heat buildup inside the chamber. The temperature increase was less than 2 °C. After pulse-labeling, four leaves were harvested from each of the same heights used for SLW determinations and stored in dry ice. To determine rate of ¹⁴C-assimilate disappearance from leaves, a second set of leaf samples was harvested 5 hours after labeling. Frozen samples were lyophilized, ground with mortar and pestle, and stored at room temperature for assay.

Approximately 50 mg of leaf tissue were accurately weighed and homogenized in 1 ml of water for radioactive assay. Triplicate 0.1-ml aliquots were placed in separate polypropylene scintillation vials, dried at 60 °C, and bleached with 0.3 ml of 30% H₂O₂ at 60 °C for approximately 4 hours to reduce quenching. After cooling to room temperature, 10 ml of scintillation liquid (2 liters toluene, 16.5 g PPO, 0.3 g POPOP, and 1 liter of Triton X-100) were added, and the samples were counted in a Packard Tricarb Model 3320 Liquid Scintillation Spectrometer. Counting efficiencies for each replicate were determined after adding ¹⁴C-labelled standards of known radioactivity to sample aliquots. The results are reported as disintegrations/min (dpm).

Data were analyzed statistically. Significance was determined by analysis of variance at the 0.05 level. When the AOV was significant, means were separated with the L.S.D. at the 0.05 level.

RESULTS AND DISCUSSION

Source Sink Relationships. Okra leaf plants were taller than normal or superokra leaf plants (85, 74, and 79 cm, respectively) on 28 July. Two weeks later the corresponding heights were 100, 96, and 90 cm. Averaged over leaf type, the middle interval (30 to 55 cm) contained more LAI than the bottom or top intervals at both sampling periods (Table 1). The top interval contained more LAI than the bottom by the last sampling except in superokra leaf plants. Normal and okra leaf plants had greater LAI than superokra leaf plants by 11 August. The leaf type × height interaction was significant on 11 August. This is reflected in the normal > okra > superokra ranking in the middle and top canopy intervals while differences among the leaf types were not significant in the bottom interval.

There were no significant differences among leaf types in total above-ground dry weight during either sampling date (Table 1). Biomass distribution was characterized by superokra leaf plants partitioning a larger percentage of total dry weight into fruit and a smaller percentage into leaves and petioles compared to normal leaf plants. The okra leaf plants were intermediate between normal and superokra leaf plants, but not always statistically different from either.

The canopy intervals varied in ¹⁴CO₂ uptake per unit leaf area with top > middle > bottom on both sampling dates (Table 2). Averaged over leaf types, rates of the middle and bottom were 34 and 24% of the top on 29 July. These values were reduced to 21 and 13% by 13 August.

Mean CER per unit leaf area did not differ significantly among the three leaf types (Table 2). However, there was a trend during both dates for mean CER of normal-leaf plants to be lower than that of the two mutant leaf types. Additionally, CER of normal-leaf plants was consistently lower than that of okra and superokra leaves in the bottom two intervals.

De Oliveira (10) measured greater solar radiation penetration into superokra plant canopies than into

Table 1. Leaf area index and above ground biomass distribution within three near-isogenic lines of cotton sampled on 2 days.

Height interval	Leaf type	LAI	Dry wt.	Dry wt.			
				Stems	Petioles	Leaf blades	Fruit
cm			g/m ²	%			
<u>28 July</u>							
Above 55	Normal	1.18	94	17.5	10.0	68.3	4.3
	Okra	1.26	127	24.3	7.9	58.1	9.8
	Superokra	0.85	90	23.1	6.4	54.1	16.4
30-55	Normal	1.67	151	31.9	10.1	53.2	4.8
	Okra	1.80	193	35.7	8.8	45.9	9.7
	Superokra	1.27	153	36.2	7.3	41.4	15.1
0-30	Normal	1.41	166	54.8	7.3	36.2	1.8
	Okra	1.41	213	56.0	6.9	32.2	5.1
	Superokra	0.96	182	51.3	6.5	31.9	10.4
L.S.D. (0.05)	Interaction	0.38	28	4.8	1.4	5.0	3.3
	Height interval	0.22	16	2.8	0.8	2.9	1.9
	Leaf type	N.S.	N.S.	2.9	0.5	2.3	2.2
<u>11 Aug.</u>							
Above 55	Normal	2.09	263	22.5	10.1	55.5	12.0
	Okra	1.73	249	25.6	9.8	49.6	15.4
	Superokra	1.26	209	25.4	6.9	43.4	24.4
30-55	Normal	2.60	316	33.9	9.2	41.9	15.0
	Okra	1.84	282	36.7	7.8	35.6	19.3
	Superokra	1.46	258	35.9	5.8	33.1	25.3
0-30	Normal	1.33	264	66.0	4.4	19.2	10.5
	Okra	1.12	255	60.8	4.6	19.0	15.6
	Superokra	1.22	258	57.7	4.3	20.3	17.7
L.S.D. (0.05)	Interaction	0.36	57	5.2	1.5	4.5	6.4
	Height interval	0.21	33	3.0	0.8	2.6	3.7
	Leaf type	0.43	N.S.	N.S.	1.1	3.1	4.3

okra or normal-leaf canopies. In our study, photosynthetic irradiation beneath the three canopies was 14.0, 9.7, and 8.7% of that above the plants on 21 August for superokra, okra, and normal leaf plants, respectively. Photosynthesis of lower leaves of soybeans (15), beans (*Phaseolus vulgaris* L.) (8), and alfalfa (7) were all increased as a result of increased irradiation.

An estimate of CER per unit land area was obtained by multiplying the photosynthetic rate of the intervals by the leaf area per intervals by the leaf area per interval (Table 2). Although these data contain a high degree of variability, total CER of superokra was significantly lower than that of okra on 29 July. On 13 August superokra tended to be lower in CER than normal-leaf plants. These results are in general agreement with those of Pegelow et al. (19) who measured CER of plant canopies of these leaf types with infrared gas analyses.

The leaf type \times height interaction was significant during both sampling dates. Leaf types had similar CER on a land area basis in the bottom portion of the canopy (Table 2). However, in the upper level, the okra-leaf plants had the highest CER on 29 July while the normal-leaf plants were highest on 13 August. The reversal was consistent across replications and a similar reversal occurred in plant height, LAI, and dry weight.

In order to obtain some understanding of the export of absorbed $^{14}\text{CO}_2$, representative leaves in each height interval were sampled 5 hours after labelling. Okra and superokra-leaf plants tended to have less label remaining in source leaves than normal-leaf plants (Table 2). Also, leaves in the bottom canopy level generally retained a higher percentage of the

^{14}C -assimilates than leaves in the middle or top canopy levels on both sampling dates (Table 2). This suggests that the lower leaves had relatively lower respiration and/or translocation than leaves located higher on the plant. Wolf and Blaser (23) reported much lower respiration rates in lower than in upper alfalfa leaves, but our data do not exclude either of the above possibilities.

Total fruit weight was 16, 42, and 58 g/m² land area on 28 July and 112, 136, and 166 g/m² on 11 August, for normal okra, and superokra plants, respectively. Averaged over leaf types, the top height interval contained only 27.6% of the fruit dry weight but produced 55.5% of the ^{14}C -assimilate during the first sampling period (Table 3). By the second period, the top accounted for 29.6% of the fruit while ^{14}C -assimilate production was increased to 75.6% of the total. All height intervals contained active, growing reproductive sinks since the fruit growth rate between the two periods for top, middle, and bottom averaged 2.1, 2.8, and 2.2 g day⁻¹m⁻² land area, respectively (Table 4).

Cotton is an indeterminate crop where vegetative and reproductive sinks compete for assimilates (20). The relative strength of the reproductive sink can be expressed as the ratio of fruit growth rate to total growth rate (partitioning coefficient) between the two sampling dates. A larger portion of assimilates were utilized for fruit development in the bottom and middle intervals than in the top interval (Table 4). Also, superokra leaf plants utilized a larger portion of assimilates for reproductive growth than did normal-leaf plants.

Yield data were not taken in this study. A yield advantage could exist for mutant leaf plants in a short

Table 2. Uptake of $^{14}\text{CO}_2$, percent of labelled assimilates remaining 5 hours after exposure to $^{14}\text{CO}_2$, and specific leaf weight (SLW) within three canopy intervals of three near-isogenic lines of cotton.

Height interval	Leaf type	Leaf area basis	Land area basis	Label remaining 5 hours after exposure	SLW	
					0600 hours	1800 hours
					mg/dm ²	
cm		dpm, in thousands/dm ²		%	29-31 July	
29 July						
Above 55	Normal	73.9	84.1	46.7	527	594
	Okra	90.1	110.4	40.8	484	581
	Superokra	85.7	57.5	42.3	489	565
30-55	Normal	22.9	36.4	51.5	379	360
	Okra	32.3	56.6	32.7	418	417
	Superokra	31.1	35.1	42.2	407	421
0-30	Normal	14.5	20.3	59.7	369	388
	Okra	19.8	25.6	56.8	419	400
	Superokra	25.2	23.8	53.5	402	425
L.S.D. (0.05)	Interaction	13.7	19.6	16.3	48	54
	Height interval	13.7	11.3	9.4	28	31
	Leaf type	N.S.	53.5	N.S.	N.S.	N.S.
13 Aug.						
13-15 Aug.						
Above 55	Normal	124.7	262.8	43.7	635	746
	Okra	120.8	212.9	42.2	634	713
	Superokra	124.0	155.1	41.8	613	695
30-55	Normal	16.1	44.1	54.2	353	372
	Okra	29.9	51.5	44.5	398	430
	Superokra	31.2	45.3	46.7	418	457
0-30	Normal	12.7	19.9	77.3	302	297
	Okra	16.1	18.7	48.3	322	356
	Superokra	19.1	23.1	59.0	394	373
L.S.D. (0.05)	Interaction	16.6	41.6	20.6	45	46
	Height interval	9.6	24.0	11.9	26	26
	Leaf type	N.S.	N.S.	N.S.	30	N.S.

Table 3. Percentage distribution of fruit dry weight and $^{14}\text{CO}_2$ uptake on a land area basis. Percentage dmp was calculated from the data in Table 2.

Height interval	Leaf type							
	Normal		Okra		Superokra		Mean	
	% fruit	% dmp	% fruit	% dmp	% fruit	% dmp	% fruit	% dmp
cm	28-31 July							
Above 55	27.3	59.8	29.5	57.3	26.1	49.4	27.6	55.5
30-55	53.3	25.9	44.4	29.4	40.0	30.2	45.9	28.5
0-30	19.4	14.4	26.0	13.3	34.0	20.5	26.5	16.1
11-15 Aug.								
Above 55	28.7	81.2	28.4	77.2	31.8	68.7	29.6	75.6
30-55	42.3	13.0	40.2	16.2	39.5	20.8	40.7	16.7
0-30	28.9	5.7	31.4	6.3	28.7	10.7	29.7	7.6

growing season due to earliness, but are not achieved under normal growing seasons (1, 16, 21). The potential advantage of greater partitioning of biomass to reproductive structures by mutant leaf plants is partially offset by a tendency for less total biomass compared to normal leaf plants. An average of 10 comparisons from three locations in each of 4 years has shown superokra leaf plants to yield 99.8% of normal leaf plants (18).

Sink strength is inversely proportional to distance from source (22). Efficient use of assimilates would result in cotton if photosynthates were produced in zones of the plant canopy where reproductive growth is favored. We expressed source to reproductive sink index (SRSI) as the product of the partitioning coefficient (fruit/total growth rate) and the percent of

Table 4. Absolute fruit growth rate (FGR), absolute total above ground biomass growth rate (TGR), partitioning coefficient (FGR/TGR), and source to reproductive sink index (SRSI) within three canopy intervals of three near-isogenic lines of cotton.

Height interval	Leaf type	FGR	TGR	Partitioning coefficient	SRSI
cm		— g day ⁻¹ m ⁻² —			
		28 July–13 Aug.			
Above 55	Normal	2.0	12.1	0.16	11.2
	Okra	1.9	8.7	0.22	15.0
	Superokra	2.7	8.5	0.35	20.2
30–55	Normal	2.8	11.8	0.22	4.6
	Okra	2.6	6.4	0.33	9.5
	Superokra	3.0	7.5	0.43	10.7
0–55	Normal	2.1	7.0	0.30	3.0
	Okra	2.3	3.0	0.39	4.2
	Superokra	2.0	5.5	0.30	4.8
L.S.D. (0.05)	Interaction	N.S.	4.5	0.16	3.4
	Height interval	N.S.	3.2	0.09	2.8
	Leaf type	N.S.	N.S.	0.10	2.4

total canopy ^{14}C uptake on a land area basis within each height interval. The order for SRSI is top > middle > bottom (Table 4). This results entirely from the large source in the top interval since the partitioning coefficient is in the opposite direction. Superokra leaf plants had improved SRSI compared to normal leaf plants especially in the middle and top interval. The improvement in SRSI by mutant leaf plants resulted primarily because they had less LAI (Table 1) and $^{14}\text{CO}_2$ uptake (Table 2) in the top interval but had similar uptake per unit land area in the bottom and middle levels of the canopy compared to normal leaf plants. This probably decreases available

Table 5. Correlations between $^{14}\text{CO}_2$ uptake on a leaf area basis and specific leaf weight (SLW) (d.f. = 52).

Sampling period	SLW factor correlated with $^{14}\text{CO}_2$ uptake		
	PM-AM SLW†	AM SLW	PM SLW
29-31 July	0.29*	0.73**	0.74**
13-15 Aug.	0.48**	0.83**	0.83**

*,** Significant at the 0.05 and 0.01 levels, respectively.

† Difference between SLW taken at 0600 and 1800 hours.

assimilates for vegetative sinks at the top of the mutant leaf plants and allows proportionately greater utilization of ^{14}C -assimilates by reproductive sinks. This observation is supported by the fact that a larger percentage of dry weight occurs as fruit, and a lesser percentage as leaves and petioles in mutant leaf types compared to normal leaf plants (Table 1). Furthermore, normal, okra, and superokra leaf plants increased in above-ground dry weight by 30.8, 18.1, and 21.5 g day⁻¹m⁻² land area, respectively, between the two dates. However, fruit growth rates were very similar at 6.9, 6.8, and 7.7 g day⁻¹m⁻² land area for the three leaf types (Table 4).

Relationship of $^{14}\text{CO}_2$ Uptake to Specific Leaf Weight. Workers in alfalfa (9) and soybeans (11) have reported positive correlations between CER and specific leaf weight. Accordingly, SLW values were obtained using plants adjacent to those used for $^{14}\text{CO}_2$ absorption studies. Measurements were made at 0600 and 1800 hours to account for possible diurnal effects.

Diurnal changes in SLW in the bottom and middle of the canopies were smaller than those in the top interval (Table 2). Older, shaded leaves in the bottom of the canopy had lower SLW (AM or PM) than younger, irradiated leaves at the top of the canopy. This agrees with reported effects of age and irradiation environment on SLW for soybeans (5) and alfalfa (24).

Small, non-significant differences in AM and PM SLW existed among leaf types in the top canopy interval with normal leaf plants frequently having greater SLW than okra or superokra-leaf plants. This trend was reversed in the middle and low intervals with okra and superokra-leaf plants generally having greater SLW than normal leaf plants. This was reflected in a significant leaf type \times height interval interaction at the second sampling period for both AM and PM SLW.

Significant correlations between C uptake and SLW were obtained during both sampling periods (Table 5). The data in Table 5 include observations for the three canopy heights and the three leaf types. Similar correlation coefficients were obtained when the leaf types were examined individually. The high positive coefficients result because top leaves have both high photosynthetic activity and high SLW while bottom leaves have low photosynthetic activity and low SLW. The correlations improved as the range of values for C uptake and SLW increased. It should be emphasized, the correlations exist due to changing irradiation environment by height. No correlation was observed when genotypes were evaluated within a height interval. The range of values for C uptake and SLW are small within a height interval (Table 2), resulting in a lack of correlation.

Diurnal changes in SLW did not show the same degree of correlation with C uptake as either AM or PM SLW. This was probably due to the high coefficient of variation of 173% for diurnal changes in SLW compared to 10% for AM or PM SLW. It is apparent that SLW is a good index of photosynthetic activity of leaves within cotton canopies where photosynthetic activity is controlled primarily by radiation environment.

CONCLUSIONS

Our studies demonstrate a spatial separation between assimilate production and fruit development in cotton under narrow-row production. Adjacent leaves are most important in supplying photosynthates to developing bolls. Normal leaf cotton plants have low ^{14}C -uptake by adjacent leaves due to heavy shading by upper leaves. Mutant leaf types have improved ^{14}C -uptake, on a leaf area basis, but insufficient adjacent leaf area.

This suggests that efficient use of assimilates in cotton plants grown in narrow rows could be encouraged by selection for plants with normal-type leaves near developing bolls and erect mutant-type leaves at the top of the canopy. The selection process can be greatly simplified by measuring SLW since it is an accurate index of CER of leaves within the plant canopy.

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