Photosynthetic Carbon Production and Use by Developing Cotton Leaves and Bolls

S. D. Wullschleger* and D. M. Oosterhuis

ABSTRACT

Understanding the photosynthetic C contribution of leaves to vegetative and reproductive processes is important in defining yield productivity. However, the morphological complexity of the cotton (*Gossypium hirsutum* L.) canopy has proven a significant barrier to establishing specific yield relationships. Therefore, a 2-yr study examined the developmental sequences of C production and utilization by leaves and bolls within the crop canopy. Photosynthesis of sympodial leaves reached a maximum just prior to anthesis of the subtended flower and thereafter declined throughout the boll-filling period. Carbon budgets for individual sympodial leaves and their subtended bolls at mainstem Nodes 8, 10, and 12 indicated that C production was seldom synchronized with C utilization. Carbon import requirements for the first three fruiting positions at mainstem Node 10 were 50, 37, and 21%, respectively. Bolls at mainstem Node 8 collectively required >60% import of C to sustain growth during the season. Only at mainstem Node 12 were leaves capable of supplying the total C needs of their subtended bolls. Carbon deficiencies at mainstem Nodes 8 and 10 suggested that substantial translocation of photosynthate from adjacent leaves and leaves outside the mainstem node was necessary. This was confirmed through short-term studies of ^{14}C-assimilate movement from leaves to developing cotton bolls. Breeding goals for improved C production by leaves were simulated to evaluate avenues for increased yields through crop genetics. These simulations indicated an advantage of increased leaf longevity in the maintenance of C production.

MAXIMIZING THE YIELD POTENTIAL of any agricultural crop requires an understanding of the photosynthetic C contribution of leaves in the fruiting process (Gifford et al., 1984). Major determinants that govern the efficient utilization of photosynthate for crop growth include net C assimilation, respiratory C losses, and assimilate partitioning to harvestable yield components (Gifford and Evans, 1981; Bunce, 1986; Daie, 1988). While these properties have been used to document assimilate allocation in certain cereals (Biscoe et al., 1975; Scofield et al., 1977), the morphological complexity of a dicotyledonous crop like cotton has proven a significant barrier to establishing crop yield relationships based on observed patterns of C assimilation and allocation.

S.D. Wullschleger, Environmental Sciences Div., Oak Ridge Natl. Lab., Oak Ridge, TN 37831; and D.M. Oosterhuis, Dep. of Agronomy, Altheimer Lab., Univ. of Arkansas, Fayetteville, AR 72701. Published with the approval of the Director, Arkansas Agric. Exp. Stn., Fayetteville, AR. Received 22 January 1990. *Corresponding author.

Cotton is an indeterminate crop in which vegetative and reproductive structures compete for available photosynthates throughout the growing season (Mauney, 1986). Several investigators have quantified this competition by monitoring the movement of ^{14}C-labeled assimilates from cotton leaves to individual fruiting points (Brown, 1968; Ashley, 1972; Benedict et al., 1973; Kerby et al., 1980). Results of these experiments indicated that cotton bolls rely heavily on C allocation from subtending leaves, leaves adjacent to developing bolls, and leaves higher up the mainstem. In addition, Morris (1965), Elmore (1973), and Bhatt (1988) have indicated that bracts and the boll wall may also contribute to the production of photosynthetic C.

Our understanding of C utilization has been improved through the above studies, however, the ^{14}C technique provides only a short-term perspective of a dynamic process which changes both temporally and spatially within the crop canopy. Further insight into the yield productivity of cotton has come from crop simulation models (Baker and Hesketh, 1969; Hesketh et al., 1971; Baker et al., 1972). These studies used simulated data to illustrate how models offer an excellent opportunity whereby relationships between photosynthesis, respiration, and growth can be studied. Landivar et al. (1983) demonstrated via computer simulation that yield could be increased >50% by enhancing the photosynthetic activity of cotton leaves during reproductive development. The successful modeling of crop growth and yield has been highlighted by the introduction of GOSSYM/COMAX software for use in cotton management (Baker et al., 1983).

Despite advancements in modeling yield relationships in cotton, few studies have investigated the possible differences in C utilization by bolls at varying positions within the canopy (Constable and Rawson, 1980). We have previously documented the photosynthetic competency of field-grown cotton leaves during ontogeny (Wullschleger and Oosterhuis, 1990) and observed that C assimilation was seldom synchronized with assimilate utilization by bolls. This suggested that morphological and/or physiological constraints might be limiting yield productivity. Therefore, the objective of the present study was to investigate the daily and seasonal production of photosynthetic C by spatially separate leaves within the canopy in relation to boll growth. Results were used to evaluate several breeding goals for their potential to improve cotton yield.

MATERIALS AND METHODS

Seeds of 'Stoneville 506' cotton were planted on 22 May 1986 and 8 May 1987 near Fayetteville, AR, in plots with four rows spaced 1 m apart in a Captina silt loam (fine-silty, siliceous, mesic Typic Fragiudult). The 5-m rows, oriented in a north-south direction, were thinned to 10 plants m^{-1} after the stands were established. Fertilizer consisted of 32-14-26 kg ha^{-1} of N-P-K incorporated before planting in 1986 and 1987. Plants in both years received an additional side dressing of 30 kg N ha^{-1} as NH_4NO_3 at 10 wk after planting.

Photosynthetic measurements on individual mainstem and the first three sympodial leaves were made at mainstem Node 10 in 1986 and at mainstem Nodes 8, 10, and 12 in 1987. Net photosynthesis was determined with a model LI-6000 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Ten consecutive measurements at 3-s intervals were taken for CO_2 depletion from the cuvette. During sampling, cuvette CO_2 concentrations declined by 15 to 20 μL L^{-1}, while cuvette temperatures increased <0.4 °C above ambient. All measurements were recorded from four replications, with three subsamples per replicate at each sampling date.

Gas-exchange determinations were made at 3- to 4-d intervals on leaves within the undisturbed canopy between 1230 and 1400 h on days when irradiance exceeded 1700 μmol m^{-2} s^{-1}. No attempt was made to alter or improve leaf orientation with respect to incident irradiance. Dark respiration was monitored 2 h prior to sunrise on leaves at mainstem Node 10 to estimate nighttime C losses during leaf ontogeny. Leaf areas, leaf dry weights, and, when appropriate, boll dry weights were recorded. Leaf areas were determined with an LI-3100 leaf area meter (LI-COR Inc., Lincoln, NE), after which leaves and bolls were dried for 72 h at 60 °C and weighed.

The data set collected during this study comprised >1200 paired measurements of net photosynthesis, leaf area, and leaf and boll dry weight for 12 leaf po-

sitions within the cotton canopy. These data were fitted with curvilinear equations (Table 1) similar to those of Constable and Rawson (1980). Equation coefficients were calculated through an iterative regression program (Proc NLIN, SAS Institute, Inc., Cary, NC). Fitted equations were tested for goodness of fit and all regression coefficients were greater than 0.88.

Daily photosynthetic C production for leaves at stages from unfolding through crop maturity were calculated based on a 7.5 h photosynthetically active period as used by Krieg (1983). Daily net C production was estimated as the integral of photosynthesis less requirements for leaf dry weight accumulation and dark respiration. A constant CO_2 loss was assumed during the dark period (12 h). Growth rate for leaves and bolls (gram dry weight per day) was determined as the derivative of the respective equations in Table 1 and expressed in C equivalents (Radin and Eidenbock, 1986).

Photosynthate translocation between competing C sinks was investigated by monitoring radioactivity in various plant tissues after exposure of source leaves to ^{14}C-labeled CO_2. Labeling was similar to that of Ashley (1972); 5.55 × 10^5 Bq of $^{14}CO_2$ was released into a 4-L polyethylene bag (Ziploc, Dow Chemical, Indianapolis, IN) that had been tightly sealed around the petiole of the source leaf. Evolution of $^{14}CO_2$ was initiated by injecting 4 mL of 2.5 M lactic acid into a scintillation vial (attached to the bag) containing 1.5 mL of $NaH^{14}CO_3$ (specific activity 2.1 × 10^9 Bq $mmol^{-1}$). The mainstem leaf and the first two sympodial leaves at mainstem Node 10 were individually exposed to $^{14}CO_2$ for 15 min and tissues harvested after 5 h. Samples were freeze-dried, a subsample of 50 mg combusted in a sample oxidizer (R.J. Harvey Instrument Corp., Hillsdale, NJ), and the ^{14}C activity counted in a liquid scintillation spectrophotometer (Packard Instrument Co., Downers Grove, IL). Combustion efficiency was 83%. All measurements were recorded from four replications and experiments repeated twice.

RESULTS AND DISCUSSION

Previous studies have shown that net photosynthesis during cotton leaf ontogeny is seldom synchronized with the C demands of developing fruiting forms (Constable and Rawson, 1980; Landivar et al., 1987; Wullschleger and Oosterhuis, 1990). Results of our current study indicated that leaf photosynthesis reached a peak of 16.5 μmol m^{-2} s^{-1} just prior to anthesis for those fruiting positions at mainstem Node

Table 1. Mathematical equations used in the modeling of various physiological and morphological parameters vs. leaf age (x) for C allocation studies in cotton.

Parameter	Equation†
Photosynthesis	$y = a + bx[\exp(cx)]$
Dark respiration	$y = a + bx[\exp(cx)]$
Leaf area	$y = a \times \{1-[\exp(-bx)]\}$
Leaf dry weight	$y = a \times \{1-[\exp(-bx)]\}$
Boll dry weight	$y = a \times \{1-[\exp(-bx^c)]\}$

† Coefficients a, b, c were calculated using nonlinear regression techniques.

Table 2. Carbon production by individual mainstem (MS) and the first three sympodial (S1, S2, S3) leaves relative to their position within the cotton canopy in 1987. The C produced by each leaf was partitioned to that required for leaf growth and dark respiration.

	Mainstem node and leaf position											
	Node 8				Node 10				Node 12			
Parameter	MS	S1	S2	S3	MS	S1	S2	S3	MS	S1	S2	S3
Measurement period, d†	75	69	57	51	74	60	50	43	57	46	35	27
Maximum leaf area, cm^2	163	111	88	56	176	119	80	52	103	83	58	50
Carbon produced by leaf, mg	2734	1632	1031	889	3571	2158	1848	1026	2783	1788	770	532
Carbon for leaf growth, mg	497	295	222	134	498	324	198	136	527	281	156	132
Carbon for dark respiration, mg	637	460	338	203	700	425	285	164	545	263	151	96
Net C produced by leaf, mg	1600	877	471	552	2373	1409	1365	726	1711	1244	463	304

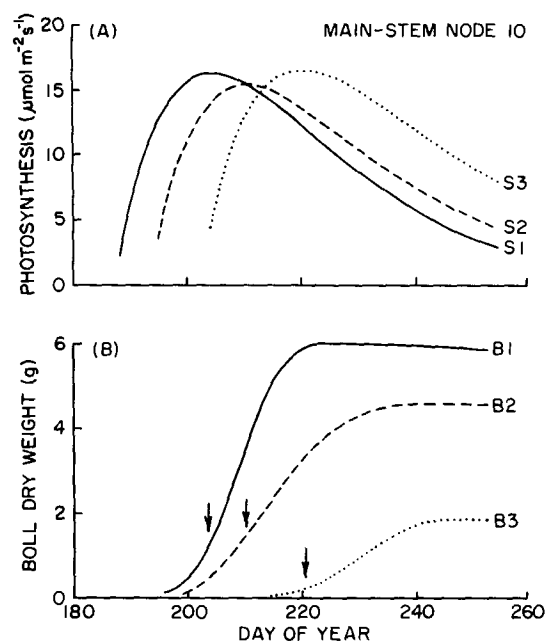† Time from leaf unfolding to crop maturity.

Fig. 1. Patterns of (A) cotton leaf photosynthesis and (B) boll development for the first three sympodial leaves (S1, S2, S3), and their subtended bolls (B1, B2, B3), along the fruiting branch at mainstem Node 10. Curves are best-fit estimates obtained through regression analysis with equations in Table 1. Arrows indicate the time of maximum leaf photosynthesis in relation to boll development.
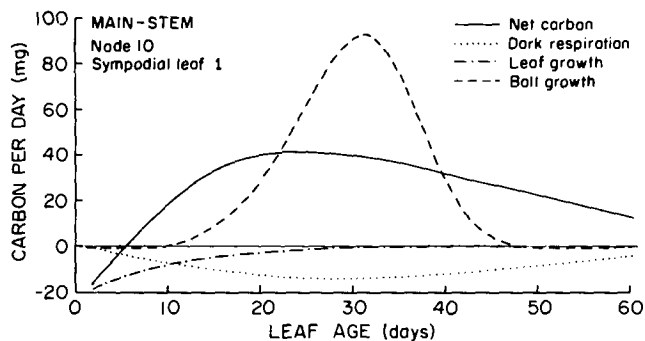

Fig. 2. The allocation of total C produced by the first-position sympodial leaf at mainstem Node 10 to that required for leaf growth and respiration, and for boll growth.

10 (Fig. 1A). Thereafter, photosynthesis declined throughout the boll-filling period, with assimilation rates decreasing by 50% during maximum dry-weight accumulation by the bolls (Fig. 1B). This suggested that yield development at individual fruiting sites was supported by a senescent photosynthetic system and that these leaves were limited in their potential to produce sufficient photosynthates for boll growth.

Total C production by the mainstem and first three sympodial leaves at mainstem Nodes 8, 10, and 12 was dependent on seasonal net photosynthesis, leaf area development, and the photosynthetic longevity of each leaf within the canopy (Table 2). Mainstem leaves produced the greatest amount of C at each mainstem node due to their large leaf area and longer leaf duration compared to sympodial leaves. Averaged across leaf position, C production was $\approx$0.25, 0.32, and 0.43 mg C cm^{-2} d^{-1} for leaves at mainstem Nodes 8, 10, and 12, respectively. These seasonal averages

are lower than that calculated by Krieg (1983), although his value of 0.62 mg C cm^{-2} d^{-1} was an estimate of peak C production. In our study, peak C production for the first sympodial leaf at mainstem Nodes 8, 10, and 12 was 0.50, 0.54, and 0.68 mg C cm^{-2} d^{-1}, respectively. Partitioning of total C to accommodate leaf growth (11–25%) and dark respiration (15–33%) resulted in an estimation of the net C available to support reproductive development (Table 2). The pattern of total C utilization for leaf growth and respiration, and for boll growth, during development of the first fruiting position at mainstem Node 10 is illustrated in Fig. 2.

Net C production by individual leaves along a sympodial branch was, in almost all cases, insufficient to support the C requirements for observed boll growth (Table 3). This was evident at mainstem Node 8, where <40% of the required C for boll growth was supplied by the subtending leaf. Sympodial leaves higher in the canopy were capable of increased C assimilation, due to better light exposure and, hence, supplied a greater percentage of the growth requirement of subtended bolls. The photosynthetic longevity of leaves at mainstem Node 8 has been shown to be less (58 vs. 70 d) than that of leaves at mainstem Nodes 10 and 12, due to shading by upper-canopy leaves (Wullschleger and Oosterhuis, 1990).

The inability of individual leaves to provide sufficient C for boll growth was related not only to deficiencies in net C production, but also to the poor synchronization of C production with C utilization by developing bolls (Fig. 3). Maximum C production by sympodial leaves occurred prior to peak photosyn-

Table 3. Net C production by individual mainstem (MS) and the first three sympodial (S1, S2, S3) leaves of cotton relative to their position within the canopy in 1987. The C production by the subtending leaf that coincided with a boll requirement at a given fruiting position was assumed available for boll growth. The boll requirement not met by C produced by the leaf must be imported from other sources.

| | Mainstem node and leaf position | | | | | | | | | | | |
| | Node 8 | | | | Node 10 | | | | Node 12 | | | |
Parameter	MS	S1	S2	S3	MS	S1	S2	S3	MS	S1	S2	S3
Net C produced by leaf, mg	1600	877	471	552	2373	1409	1365	726	1711	1244	463	304
Carbon required for boll growth, mg	—	2801	2167	1056	—	2224	1727	734	—	945	447	—
Carbon supplied by subtending leaf, mg†	—	759	460	389	—	1123	1091	583	—	927	417	—
Carbon supplied by import, %	—	72.9	78.8	63.2	—	49.5	36.8	20.6	—	1.9	6.7	—

† Carbon supplied by subtending leaf to developing boll is less than net C produced by leaf due to the lack of temporal synchrony between the two processes.
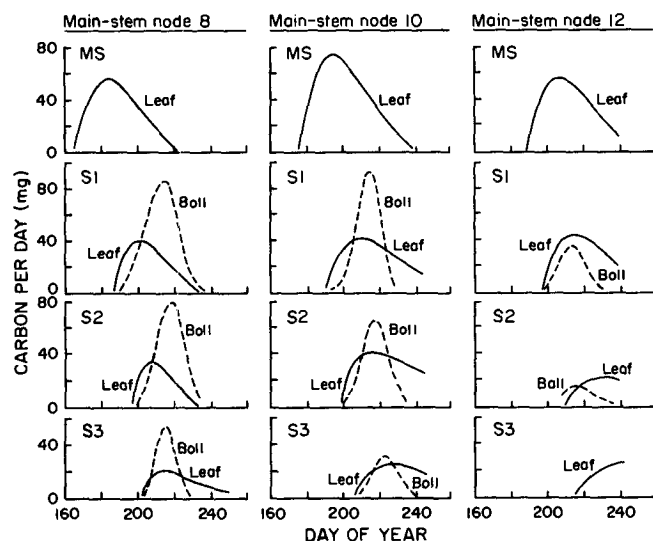
Fig. 3. Carbon production by individual mainstem (MS) and sympodial leaves (SI, S2, S3), and utilization by bolls during the season at mainstem Nodes 8, 10, and 12.

Fig. 4. Collective C production and utilization by all leaves and bolls along the sympodial fruiting branch at mainstem Nodes 8, 10, and 12.

thate demand by bolls for all fruiting positions at mainstem Nodes 8 and 10. Only at mainstem Node 12 were individual leaves capable of supplying the total C needs of their subtended bolls. The C requirements of those bolls at mainstem Node 12 were minor, however, compared to the higher yielding positions at mainstem Nodes 8 and 10 (Table 3).

The lack of synchronization between C production and utilization by leaves and bolls necessitated that observed rates of boll growth rely on C import from sources other than the subtending leaf. In this regard, C could be shared within a mainstem node by the collective contribution of the mainstem leaf and the first three sympodial leaves to boll development (Fig. 4). Estimations of C production indicated that the contribution of C from all four leaves over the season could eliminate some C deficiencies and lessen the need for imported photosynthate. However, even with this combined C production, bolls at mainstem Node 8 and 10 required additional import of C to support boll growth. Results indicated that >60% of the total C required to sustain boll development at mainstem Node 8 must be imported, while at mainstem Node 10 the import requirement was <10%.

Carbon utilization in this study was calculated assuming a boll at each of the three fruiting positions along a sympodial branch. This is somewhat atypical, considering that boll abscission can frequently exceed 35% under field conditions (Lieth et al., 1986). Therefore, our estimates of C utilization and import needs are possibly overestimated. However, since boll shedding at one fruiting position is often compensated for by a larger boll at an adjacent fruiting site (Kerby and Buxton, 1981), we are confident that our values are realistic estimates.

Earlier investigations with ^{14}C-labeled photosynthates showed that within 24 h of application, radiolabeled assimilates could be found throughout the cotton canopy (Brown, 1968; Benedict et al., 1973), and confirmed that extensive translocation is neces-
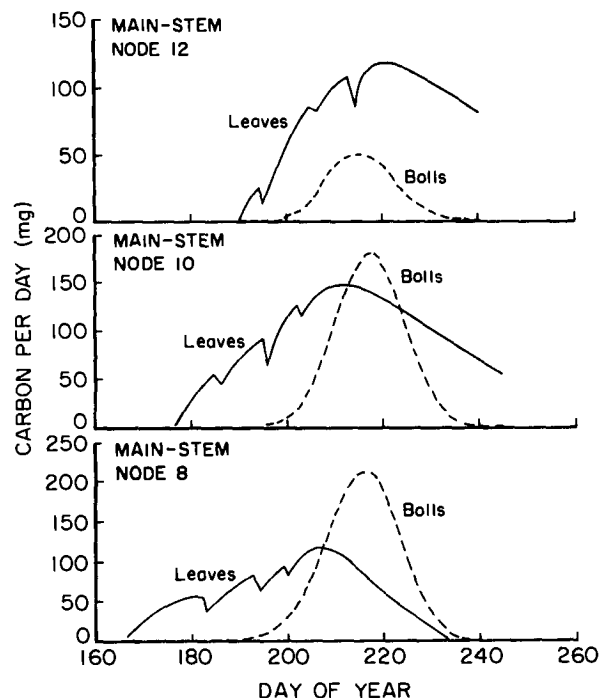
sary to supply assimilate for reproductive growth. Similar results were observed in our study when the short-term export of ^{14}C-labeled photosynthate was monitored from selected source leaves (Table 4). Mainstem leaves contributed significantly to the C requirements of the first fruiting position but very little to that of the second position boll. In contrast, sympodial leaves were capable of supplying ^{14}C-assimilate to both fruiting positions, with ^{14}C activity also observed in the sympodial branch. Sympodial leaves exported a greater percentage of their assimilate to bolls within the fruiting branch (75% of total export), while the mainstem leaf exported more to other structures within the plant. Obviously, photosynthates produced by leaves within the canopy form a dynamic pool of available assimilates that function to sustain crop dry weight increases and respirational C losses throughout the season.

The observed inability of subtending leaves to produce sufficient C to support boll growth prompts the question as to how might the cotton plant be manipulated to increase C availability for yield productivity. Landivar et al. (1983), based on simulation studies using the GOSSYM model, suggested that 15% higher photosynthetic rates could result in a 50% yield increase, provided N and water were adequate. Increased leaf longevity and prolonged photosynthetic activity during reproductive development were also proposed as potential means to increase yield. Constable and Rawson (1980) indicated that increased leaf size on fruiting branches to provide a larger photosynthetic surface might also enable increased yield, but cautioned that this could be counterproductive if extensive leaf shading occurred, particularly for those leaves at the bottom of the canopy.

Table 4. Percent of exported ¹⁴C recovered from the cotton mainstem (MS) leaf and the first three sympodial (S1, S2, S3) leaves of cotton, and the first two boll positions (B1, B2), at mainstem Node 10.

Source leaf	¹⁴C recovered							
	MS	S1	S2	S3	B1	B2	Branch	Total
	%							
Mainstem	NA†	0.9a	0.9a	0.8a	27.5a	1.1b	4.5c	35.8b
Sympodial 1	0.7a‡	NA	0.3a	0.2a	17.5a	32.4a	21.0a	72.2a
Sympodial 2	0.4a	0.2a	NA	0.2a	22.3a	37.9a	13.9b	75.0a

† The radioactivity of the source leaf was not considered in the estimates of recovery.
‡ Within columns, values followed by the same letter are not significantly different at the 0.05 level of probability.

Table 5. Evaluation of five different leaf trait combinations for improved net C production by individual cotton leaves.

Leaf trait†	Assumed leaf attributes			Predicted leaf C budget			
	Photosynthesis	Longevity	Area	Growth	Respiration	Net	Increase‡
	μmol m⁻² s⁻¹	d	cm²	mg C			%
1	15	70	95	−133	−469	1328	—
2	15	85	95	−133	−491	1623	22
3	18	70	95	−133	−469	1717	29
4	18	85	95	−133	−503	2091	57
5	15	70	115	−192	−542	1476	11

† Trait 1 = no change; 2 = 20% increase in leaf longevity; 3 = 20% increase in net photosynthesis; 4 = increase in both photosynthesis and leaf longevity; 5 = 20% increase in leaf area.
‡ Percent increase in net C production relative to leaf Trait 1 (control).

The potential for increased cotton yields was evaluated by estimating C production for leaves exhibiting different physiological and morphological traits (Table 5). The traits considered were (i) no change from that observed in this study, (ii) a 20% increase in leaf longevity (70 to 85 d), (iii) a 20% increase in net photosynthesis (15 to 18 μmol m⁻² s⁻¹), (iv) a combination of increased photosynthesis and leaf longevity, and (v) a 20% increase in leaf area. Results indicated that net C production could be improved by selecting for any of the above traits, although breeding for improved photosynthesis, increased leaf longevity or, preferably, a combination of the two would be most advantageous (Table 5). Surprisingly, increased leaf area resulted in only a minor increase in C production, due to the added expense of C to support growth and dark respiration of a larger leaf.

Recent reports have addressed the genetic association between photosynthesis and yield (Ford et al., 1983; Nelson, 1988). Results of these investigations indicated that although selection programs can increase leaf photosynthesis, seldom are these improvements reflected in seed yield or harvest index (Ford et al., 1983). Day and Chalabi (1988) reconciled these observations by reporting that <25 to 40% of genetic gains in leaf photosynthesis are ultimately expressed in canopy photosynthesis, due to leaf shading and low irradiance for the majority of the photoperiod. Apparently, success in manipulating the physiological behavior of single leaves will not ensure benefits at the whole-canopy level.

In conclusion, C production and utilization by leaves and bolls in this study illustrate the complexity of yield productivity within a field-grown cotton canopy. Individual leaves, once thought to supply the ma-

jority of C for subtended boll development (Brown, 1968; Ashley, 1972) were shown to differ dramatically in their ability to supply C for boll growth. Synchronization of C production and allocation to developing bolls varied with individual fruiting positions, which necessitated the import of C from adjacent leaves and other leaves away from the sympodial branch. The extent to which this constitutes a yield limitation is unknown, but our data suggest that alterations in photosynthesis and/or leaf longevity could contribute to increased yield. Although past studies have shown little or no benefit of increased photosynthesis to yield productivity (Bunce, 1986), the possibility exists that better synchronization of leaf and boll development in early maturing cultivars would be a useful feature (Wells and Meredith, 1984). These improvement strategies await verification.

ACKNOWLEDGMENTS

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