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Leaf senescence-like characteristics contribute to cotton's premature photosynthetic decline

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Abstract

Leaf and canopy photosynthesis of cotton (*Gossypium hirsutum* L.) declines as the crop approaches cutout, just as the assimilate needs for reproductive growth are peaking. Our objective with this study was to determine whether this decline is due to remobilization of leaf components to support the reproductive growth or due to some cue from the changing environmental conditions during the growing season. Field studies were conducted in 1995–1996 at Stoneville, Mississippi, using six cotton genotypes and two planting dates (early and late), which produced two distinctly different cotton populations reaching cutout at different times. Among the six genotypes were a photoperiod sensitive line (non-flowering) and its counter part which had photoperiod insensitive genes backcrossed four times to the photoperiod sensitive line (flowering). This pair was used to assess the degree that the photosynthetic decline could be attributed to reproductive sink development. Leaf CO_2-exchange rate (CER) and chlorophyll (Chl) fluorescence measurements were taken in mid-August, a period corresponding to cutout for the early planted plots, and those leaves were collected. Leaf Chl level, soluble protein level, various soluble carbohydrate levels and Rubisco activities were assayed on those leaves. Averaged across years, leaf CER and soluble protein levels were reduced approximately 14% and 18%, respectively, for the early planted compared to the late planted cotton. Neither leaf Chl levels or Chl fluorescence Fv/Fm values for Photosystem II yield were altered by the planting date. In 1996, leaves from the non-flowering line had 12% greater Chl and 20% greater soluble protein levels than the flowering line. However, in 1996, the CER of the early planted non-flowering line was reduced 10% compared to the late planted. Although remobilization of leaf N to reproductive growth appears to be the principle component causing the cutout photosynthetic decline, the data also indicate that environmental factors can play a small role in causing the decline.

Abbreviations: CER – CO_2-exchange rate; Chl – chlorophyll; C_i – internal CO_2 concentration; DAP – days after planting; Fv/Fm – chlorophyll fluorescence variable to maximum ratio; g_s – stomatal conductance to CO_2; PPFD – photosynthetic photon flux density; Rubisco – ribulose 1,5 bisphosphate carboxylase-oxygenase; SLW – specific leaf weight; WUE – water use efficiency

Introduction

Cotton (*Gossypium hirsutum* L.) is a perennial, indeterminate plant that is cultured as an annual in agronomic production systems. Its indeterminate nature provides some flexibility in the production and set of reproductive structures (bolls). This ability to flower over a long period of time allows cotton to withstand short-term unfavourable environmental conditions and still maintain some semblance of reproductive success.

However, this indeterminancy and perennial nature often requires a higher level of in-season management by the producer.

One of the consequences of cotton's growth habit is the occurrence of cutout, a growth stage during which vegetative growth slows or halts due to heavy competition for assimilates from reproductive growth. Following this period of rapid boll loading, there can be a resumption of vegetative growth and initiation of new fruiting sites if conditions are favorable. A perplexing physiological dilemma encountered during cotton's growing season is the decline of leaf and canopy photosynthesis during this period of cutout (Constable and Rawson 1980; Wells et al. 1986; Wells 1988). The development of a large reproductive sink during cutout would seem to necessitate the production of copious amounts of photosynthate, but the opposite actually occurs. Reasons for this decline are unclear; simple canopy aging or some environmental agent could be the cause. Wells (1988) produced data indicating reduced protein and chlorophyll (Chl) concentrations in leaves formed during boll development contributed to this photosynthetic decline. Whether these reductions are the result of an increased N demand by the developing boll load or a down regulation in synthesis of photosynthetic components due to an environmental cue is unclear. Prolonged exposure to low light conditions (Bowes et al. 1972) or high CO_2 concentrations have been known to cause decreased production of photosynthetic components over time in various plant species (Bowes 1991; Van Oosten et al. 1994). Environmental conditions will change considerably throughout the growing season, but there is also a considerable ovule sink for N in the developing bolls (Pettigrew and Meredith 1997).

Previous research has demonstrated how lint yields of Mid-South cotton crops are limited by the amount of sunlight received during reproductive growth (Pettigrew 1994). Because Pettigrew and Meredith (1994) were able to demonstrate a strong relationship between single leaf photosynthesis averaged over the boll filling period and lint yield for a diverse group of upland cottons, this light limitation of Mid-South cotton yields is probably more correctly a carbon limitation. Nevertheless, this period of reproductive growth is not a stage when you want the plant to experience any sort of limitation to yield or growth.

Intuitively, one might conclude that enhancing photosynthesis during this period of boll development will prove beneficial for yield. However, the first step toward improving the photosynthesis during this period must be to develop a thorough understanding of which factor or factors are presently rate limiting to the photosynthetic process during cutout. Therefore, the objectives of this study were (1) to attempt to separate potential environmental factors from canopy age effects and (2) to identify some of the photosynthetic components that may be rate limiting during this period.

Materials and methods

Field studies were conducted on a Bosket fine sandy loam (fine-loamy, mixed, thermic mollic Hapludalfs) at Stoneville, Mississippi, during 1995 and 1996. Six cotton genotypes were planted on both an early and late planting date during the 2 years of the study. The genotypes used in the study were 'Paymaster H1220', 'DES 119', 'Dixie King', 'MD 51 ne', 'T-78' (a photoperiod sensitive non-flowering line) and 'T-78DN' (a photoperiod insensitive flowering line that had been backcrossed four times to T-78). This flowering and non-flowering pair was used to assess the degree that the photosynthetic decline at cutout could be attributed to the development of a reproductive sink. The plots were planted on 27 April and 19 May in 1995 and on 25 April and 22 May in 1996 to create two distinct cotton populations, reaching cutout and, therefore, developing a strong reproductive sink at different times during the season. The plots, which were comprised of four rows 6.1-m-long and spaced 1 m apart, were originally overseeded and then thinned to one plant per 15 cm of row for a final plant population of 65 000 plants ha^{-1}, when plants from each planting date reached the second or third true leaf stage. Each year, nitrogen was applied preplant incorporated to the experimental area at a rate of 110 kg ha^{-1}. Furrow-irrigation was applied as needed to minimized moisture stress each season. Conventional weed and insect control measures were utilized as needed. None of the plots were treated with mepiquat chloride (N,N-dimethylpiperidinium chloride). This measure ensured that any alterations in physiological activities were due either to planting dates or genotypes, not the application of this growth regulator.

The experiment was laid out as a split plot with the main units consisting of the two planting dates arranged in a randomized complete block design with three blocks. Subunits consisted of the six genotypes. A variation to the standard split plot design had each planting date $\times$ block (main unit plot) divided in

Table 1. Leaf soluble protein and chlorophyll (Chl) levels, Chl fluorescence, variable – maximum ratio (Fv/Fm), and CO_2 exchange rates averaged across genotypes for early July and mid-August measurements in 1995 and 1996 for the early planted plots

Year	Measurement date	CO_2 exchange rate	Chl fluorescence Fv/Fm	Chl	Soluble protein
		μmol m^{-2} s^{-1}		mg m^{-2}	g m^{-2}
1995					
	July	29.2	0.54	373	12.6
	August	24.7	0.69	330	8.8
	$LSD_{0.05}$	3.3	0.09	ns[a]	1.8
1996					
	July	29.7	0.57	392	14.9
	August	23.2	0.68	267	11.1
	$LSD_{0.05}$	1.8	ns	16	2.2

[a] ns = not significantly different at $P \leq 0.05$.

half and the six subunit genotypes randomly assigned within each half.

Gas exchange measurements were taken from 14 to 16 August in 1995 and 13 to 15 August in 1996. These periods corresponded to approximate cutout for the April (early) planting in each year. Gas exchange measurements in the early planted plots were also collected on 7 July in 1995 and from 1 to 2 July in 1996. These gas exchange measurements were taken on the youngest, fully expanded, healthy, fully sunlit leaves in each plot using a LI-COR 6200 portable photosynthesis unit (Li-Cor, Lincoln, NE[1], with the leaves oriented perpendicular to the sun. All measurements were taken in the morning prior to solar noon with the light intensity during the measurement always equal to or exceeding 1600 μmol photons m^{-2} s^{-1} photosynthetic photon flux density (PPFD). Measurements were collected from two leaves per plot with the average of the two used in later statistical analysis.

Chlorophyll (Chl) fluorescence measurements were collected from the same leaves and at the same time as the CO_2-exchange rates (CER) using a CF-1000 Chl fluorescence measurement system (P.K. Morgan, Inc., Andover, Massachusetts). A dark adaption cuvette was placed on the leaf following the CER measurement and the leaf was allowed to dark adapt for at least 15 min prior to the fluorescence measurement. Similar to the gas exchange measurements, the average of the two leaves measured per plot was used in later statistical analysis of the Chl fluorescence measurements.

After completion of the Chl fluorescence measurements, two 0.7 cm diameter leaf disks were collected for Chl concentration determinations from the first of the two leaves used in the gas exchange and Chl fluorescence measurements for each plot. Two additional 0.7 cm diameter leaf disks were collected from this same leaf for soluble protein determinations. The remainder of the leaf was instantly frozen with liquid N_2 and transported to the laboratory. Once in the laboratory, the frozen leaves were ground in liquid N_2 and stored at –80 °C for later enzymatic assays. The second leaf was transported on ice to the laboratory where ten 1.2 cm diameter leaf disks were collected for starch, glucose, fructose and sucrose assays. These ten leaf disks were stored at –80 °C for later carbohydrate assays. Leaf area and dry weight were determined on the remainder of this leaf. These numbers were then used to calculate specific leaf weights (SLW).

Chlorophyll was extracted from the two leaf disks collected using 5 mL of 950 ml l^{-1} ethanol for a 24 h period in darkness. The extracted Chl was then quantified spectrophotometrically according the methods of Holden (1976). Soluble protein was extracted by grinding the two leaf disks in 1 mL of a grinding buffer containing 0.1 M Tris (pH 7.6, HCl), 0.1 M $Na_2B_4O_7$, 5 mM $MgCl_2$, 10 mM ascorbate, 0.1% (w/v) β-mercaptoethanol, 1% (w/v) polyvinylpyrrolidone, and 2 M urea. The resulting brei was then centrifuged at

[1] Trade names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product or service, and the use of the name by USDA implies no approval of the product or service to the exclusion of others that may be suitable.

Table 2. Monthly weather summary for 1995 and 1996 at Stoneville, Mississippi

	Precipitation		Thermal[a] units		Solar[b] radiation	
	1995	1996	1995	1996	1995	1996
	mm				MJ m^{-2}	
May	79	62	262	299	–	732
June	102	133	305	323	–	655
July	148	84	379	380	–	672
August	36	110	415	327	–	601
September	41	112	224	226	–	525

[a] [(max. temp. + min. temp.)/2] – 15.5 °C.
[b] Solar radiation sensor was not functioning properly in 1995.

Table 3. Effects of planting date on CO_2 exchange rates for various cotton genotypes when measured in mid-August in 1995

Genotype	Planting date	
	Early	Late
	μmol m^{-2} s^{-1}	
MD51ne	26.4	31.8
Paymaster H1220	25.6	30.3
T-78 DN (flowering)	23.7	30.2
T-78 (non-flowering)	25.8	28.0
Dixie King	24.1	29.2
DES 119	22.8	30.0

The $LSD_{0.05}$ to compare planting date means in the same row is 4.33.
The $LSD_{0.05}$ to compare genotype means in the same column is 1.92.

5000 *g* for 10 min. The soluble protein in the resulting supernatant was quantified by the methods of Bradford (1976). Ribulose 1,5 bisphosphate carboxylase-oxygenase (Rubisco, EC 4.1.1.39) was extracted from the ground, frozen leaf material and assayed for activity by previously described methods (Pettigrew and Turley 1998).

Soluble carbohydrates were extracted from the ten leaf disks using three successive 12 mL washes of boiling 800 ml l^{-1} ethanol, followed by incubation in a 60 °C water bath, and finally centrifugation at 9400 *g* for 10 min. The resulting pellet was saved for starch analysis, while the three supernatants were pooled and evaporated to dryness using a Zymark TurboVap LV evaporator (Zymark Corp., Hopkinton, Massachusetts). The dried supernatant residue was resuspended in 10 ml of 800 ml l^{-1} ethanol for 15 min in a 60 °C water bath. Glucose, fructose, and sucrose were assayed on the resuspended supernatant according to previously described protocols (Hendrix 1993). The starch in the remaining pellets were digested with amyloglucosidase for 100 min at 55 °C and quantified according to procedures described by Hendrix (1993) and Pettigrew (1999).

In 1996, leaf tissue samples of MD 51 ne from each replicate of each planting date were fixed for electron microscopy. These tissue samples were collected on 19 August 1996, approximately 1 week after the gas exchange measurements were taken. Samples for electron microscopy were prepared according to the protocal for Spurr's-epon resin embedding as described by Pettigrew and Vaughn (1998).

Statistical analyses were performed using analysis of variance for the split plot design. Planting date, genotype and planting date × genotype were the fixed effects of interest. Block, block × planting date, rep(block planting date), block × genotype (planting date) and the residual error: rep × genotype (block planting date) were the random sources of error. Treatment and genotype means were separated by use of a protected LSD (0.05). Because the non-flowering vs. flowering comparison was the only genotype comparison of interest, significant genotype effects will not be mentioned unless the means of the non-flowering and flowering lines were also significantly different.

Results and discussion

Photosynthetic measurements taken on the April planted cotton (early) in August, after the crop had reached cutout, were lower than those taken during July in the same plots for both years of the study (Table 1). This approximate 19% reduction in CER for the leaves in this older canopy confirms the observations made by Wells (1988). There was a significantly larger Chl fluorescence variable – maximum ratio (Fv/Fm) during the August measurement in 1995, but Fv/Fm was not significantly different between measurement dates in 1996. Both, Chl (in 1996) and soluble protein levels (both years) were significantly lower during the August measurement period, which matches the results reported by Wells (1988).

At first glance, these data would seem to indicate that leaves from these plants may have remobilized the leaf N reserves to feed the N needs of a strong developing boll load, resulting in the reduction in CER. However, environmental contributions to the CER decline cannot be ruled out entirely due to the

Table 4. Effects of planting date on stomatal conductance to CO_2, internal CO_2 concentration, and water use efficiency when measured in mid-August 1995 averaged across genotypes

Planting date	Stomatal conductance	Internal CO_2 concentration	Water use efficiency
	mol m^{-2} s^{-2}	μl l^{-1}	mol CO_2 mol H_2O^{-1}
Late	0.690	284	1.95
Early	0.491	278	1.85
$LSD_{0.05}$	0.173	ns[a]	ns

[a] ns = not significantly different at $P \leq 0.05$.

Table 5. Effects of planting date on CO_2 exchange rates, stomatal conductance to CO_2, internal CO_2 concentration and water use efficiency when measured in mid-August 1996 averaged across genotypes

Planting date	CO_2 exchange rate	Stomatal conductance	Internal CO_2 concentration	Water use efficiency
	μmol m^{-2} s^{-1}	mol $m^{-2}s^{-1}$	μl l^{-1}	mol CO_2 mol H_2O^{-1}
Late	25.6	0.552	271	2.19
Early	22.8	0.562	278	1.95
$LSD_{0.05}$	2.3	ns[a]	3	ns

[a] ns = not significantly different at $P \leq 0.05$.

Table 6. Effects of planting date on leaf chlorophyll (Chl) levels, Chl *a* to *b* ratio, soluble protein levels and specific leaf weight (SLW) when measured in mid-August in 1995 and 1996 averaged across genotypes

Year	Planting date	Chl	Chl *a*:*b*	Soluble protein	Specific leaf weight
		mg m^{-2}		g m^{-2}	
1995					
	Late	327	5.5	11.0	60.4
	Early	330	5.1	8.7	68.3
	$LSD_{0.05}$	ns[a]	ns	2.0	ns
1996					
	Late	298	3.68	13.0	59.0
	Early	267	3.70	11.1	47.1
	$LSD_{0.05}$	ns	ns	1.8	3.5

[a] ns = not significantly different at $P \leq 0.05$.

Table 7. Effects of planting date on the variable to maximum Chl fluorescence ratio (Fv/Fm) and Rubisco[a] activities when measured in mid-August in 1995 and 1996 averaged across genotypes

Year	Planting date	Chl fluorescence Fv/Fm	Rubisco activity Initial	Rubisco activity Total
			μmol m^{-2} s^{-1}	
1995				
	Late	0.65	44.0	78.3
	Early	0.69	36.2	60.6
	$LSD_{0.05}$	ns[b]	5.5	ns
	P>F	0.37	0.03	0.06
1996				
	Late	0.67	49.2	93.0
	Early	0.68	35.0	65.2
	$LSD_{0.05}$	ns	ns	21.4
	P>F	0.91	0.09	0.03

[a] Rubisco = Ribulose 1,5 biphosphate carboxylase-oxygenase.
[b] ns = not significantly different at $P \leq 0.05$.

substantial differences in climatic conditions between the July and August measurements (Table 2). Two aspects of our experimental design addressed the question of whether environmental conditions or boll load influenced the photosynthetic decline. First, our two planting dates resulted in the crops reaching cutout at different times. The other approach involved was using two genetically similar cotton lines (one of which was insensitive to photoperiodic changes and, therefore, flowered normally while the other line was sensitive to photoperiodic changes and did not flower during a normal growing season).

Measuring CER of the different planting dates in mid-August (when the 'early planted' plots had

Table 8. Effects of planting date on leaf starch, glucose, fructose and sucrose levels when measured in mid-August in 1995 and 1996 averaged across genotypes

Year	Planting date	Starch	Glucose	Fructose	Sucrose
		g m^{-2}			
1995					
	Late	3.29	0.48	0.24	1.03
	Early	4.85	0.25	0.20	1.29
	$LSD_{0.05}$	ns[a]	ns	ns	0.25
	P>F	0.19	0.11	0.14	0.05
1996					
	Late	8.88	0.82	0.24	1.76
	Early	8.76	0.52	0.22	1.74
	$LSD_{0.05}$	ns	ns	ns	ns
	P>F	0.89	0.13	0.52	0.89

[a] ns = not significantly different at $P \leq 0.05$.

reached cutout but the 'late planted' plots had not) detected a significant planting date by genotype interaction in 1995 (Table 3). All genotypes had significantly lower CER for plots planted on the early planting date compared to plots planted on the late planting date, except for the non-flowering line. The CER values of the non-flowering line were statistically similar between the planting dates, although the early planted was numerically lower than the late planted. Comparison of the flowering vs. non-flowering lines showed that the non-flowering line had a greater CER in the early planting but lower CER in the late planting compared to the flowering line. There was no genotype by planting date interaction for the other gas exchange components measured in 1995. The only significant effect detected for planting dates showed the late planting to have a 40% greater stomatal conductance to CO_2 (g_s) than the early planting (Table 4).

In 1996, a genotype by planting date interaction was not detected for CER as all genotypes behaved similarly across planting dates for the gas exchange parameters measured. Averaged across genotypes, the CER was 11% lower in the early planted plots than the late (Table 5). This reduced CER allowed the early planted plants to maintain a slightly higher internal CO_2 concentration (C_i) than that of the late planted plants. Neither g_s or water use efficiency (WUE) was affected by planting date. Although there was a significant genotype effect for CER averaged across planting dates, the flowering (23.3) and non-flowering (23.6) genetically similar pair did not exhibit statistically different CER.

Neither the leaf Chl level or Chl *a* to *b* ratio were altered by planting date in either year of the study (Table 6). In contrast, the leaf soluble protein level in the early planted plots was 21% lower in 1995 and 15% lower in 1996 compared to the late planted plots. Specific leaf weight (SLW) was 20% lower in the early planted plots in 1996, but did not differ between planting dates in 1995. Genotypic differences were detected in leaf Chl levels and SLW in 1995, but the flowering and non-flowering lines did not differ significantly for those traits (data not shown). Genotypic differences were detected in leaf Chl and soluble protein levels in 1996 as well. The non-flowering line's leaf Chl (290 mg m^{-2}) and soluble protein (12.8 g m^{-2}) were significantly greater than the Chl (258 mg m^{-2}) and soluble protein (10.7 g m^{-2}) levels from leaves of the flowering line.

Chlorophyll fluorescence Fv/Fm ratio when measured in mid-August was not altered by planting date for either year of the study (Table 7). Genotypic differences were detected in Fv/Fm for both years of the study. In 1995, Fv/Fm of the flowering line (0.69) was significantly greater than the non-flowering line (0.61). The same significant differences between these lines was detected in 1996. The Fv/Fm of the flowering line for that year was 0.66 compared to 0.60 for the nonflowering line. Both the initial and total rubisco activities from the early planted plots were significantly lower at the 0.10 level of significance for both years of the study compared to the late planted. Focusing only on differences in rubisco activity that were significantly different at the $P \leq 0.05$, the initial rubisco activity in 1995 was reduced about 18% in the early planted plants, while the total rubisco activity for the early planting in 1996 was reduced 30% compared to the late planting. Only for the initial rubisco activity in 1995 were genotypic differences detected in either of the rubisco activities. For 1995, the initial rubisco activity of the flowering line (41.5 μmol m^{-2} s^{-1}) was significantly greater than that of the non-flowering line (28.8 μmol m^{-2} s^{-1}).

For the most part, leaf carbohydrate levels at the mid-August sampling were not affected by planting date (Table 8). The lone exception to that generalization found the sucrose levels from the early planted plots to be 25% greater than those from the late planted plots. Genotypic differences were found in all the leaf carbohydrates assayed for both years. The only consistent difference detected between the flowering and non-flowering line was in leaf glucose levels which were 55% greater in 1995 and 34% greater in 1996

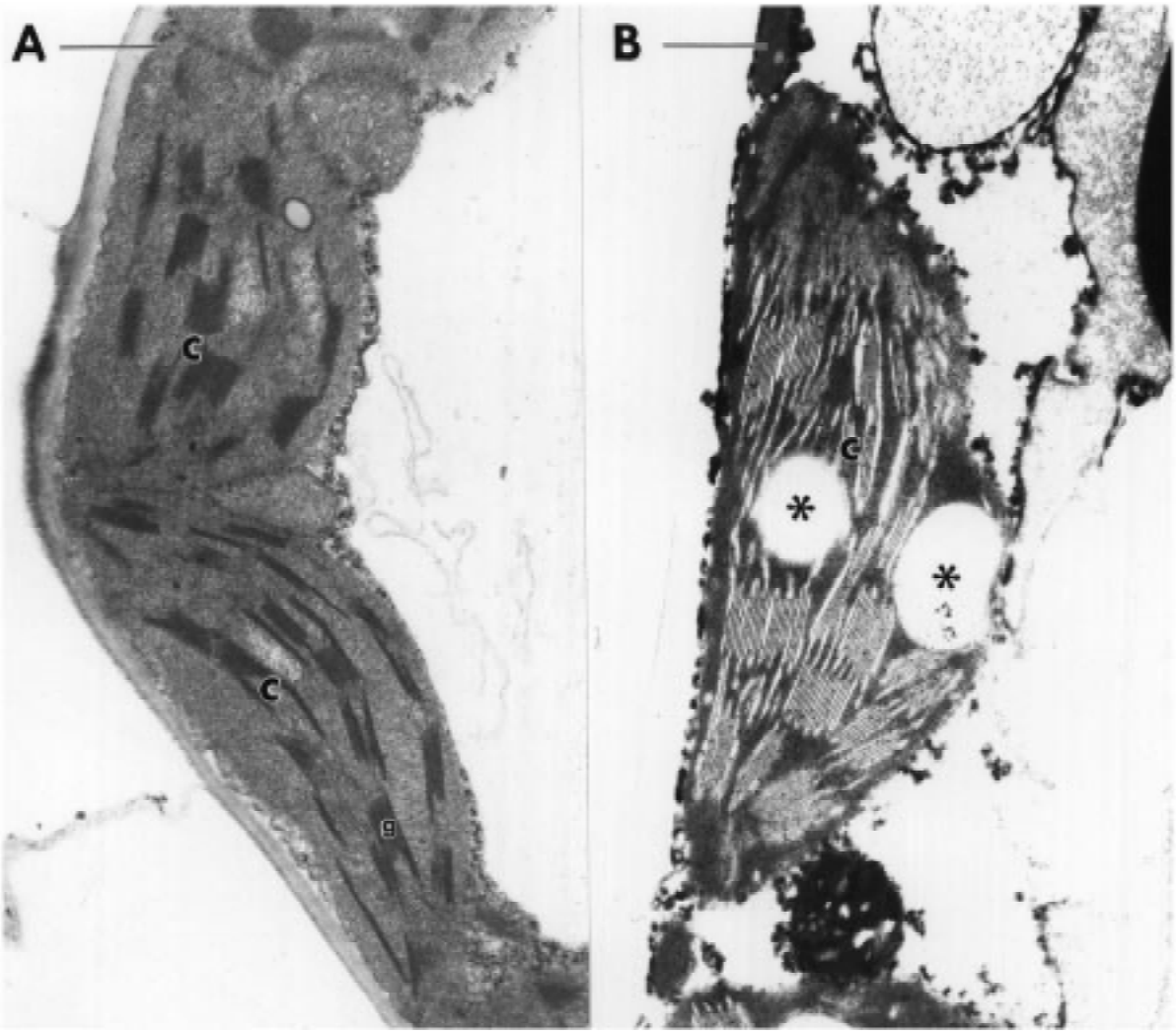

Figure 1. Ultrastructure of chloroplasts of cotton planted either late (A) or early (B). The late-planted leaves contain chloroplasts (c) with a normal-appearing thylakoid system arranged into stroma and grana (g) lamellae. The stroma is full of ribosomes and is less electron opaque than the thylakoids. In the leaves of the plants from early planting, the chloroplasts show signs of senescence. The stroma is electron opaque and ribosomes are indistinct. The thylakoid membranes are of less opacity than the stroma. Large electron-translucent plastoglobuli a (*) are now prominent components of the stroma. Bars = 0.50 μm.

for the non-flowering line compared to the flowering line (data not shown).

Leaf structure traits exhibited by the early planted leaves in mid-August were symptomatic of senescing leaves. The late planted leaves, on the other hand, exhibited traits that are typical of a healthy functional leaf (Figure 1). Chloroplasts between the planting dates were distinctly different structure. The chloroplasts of leaves from the late planting date resembled those of fully expanded leaves as described by Pettigrew and Vaughn (1998): Well defined grana and stroma lamellae, an abundance of plastid ribosomes, electron opaque plastoglobuli and abundant starch grains. In contrast, the chloroplasts in the leaves of the early-planted material showed signs reminiscent of early senescence. The thylakoids were less electron opaque and the stroma displayed fewer distinct ribosomes and an overall increase in electron opacity. The plastoglobuli were gathered into large and very electron translucent areas.

Evidence collected in this research supports the theory that both the remobilization of leaf N to support the N demand of the developing reproductive sinks and environmental factors contribute to the decline in

CER occurring around cutout. Much, but not all of the data, suggest that the plant cannibalizes its leaf N to supply the high N demand of the bolls. The lower mid-August CER, soluble protein levels and rubisco activities for the early planted plots compared to the late planted plots support the large reproductive sink demand for N as a contributing factor. Similarities in CER between planting dates for the non-flowering line in 1995 reinforce this reproductive sink as a negative influence concept, although the early planted CER of all genotypes was statistically lower than the late planting in 1996. The non-flowering line's greater leaf Chl and soluble protein levels in 1996 compared to the flowering line also provides evidence in support of this concept. The near self-destruction of the leaves in plants that produce high protein seeds via remobilization of leaf N has been put forth in an elegant theory by Sinclair and De Wit (1975). The reduction of leaf soluble protein for cotton as its reproductive sink increases in size is similar to the leaf senescence observed in annual dicot species (Sadras et al. 2000)

The reduced CER of the early planted non-flowering plots compared to the late planted non-flowering plots during the mid-August measurements in 1996 provides evidence of factors other than a developing reproductive sink (possibly environmental) also being responsible for the photosynthetic decline at cutout. The instances where the non-flowering line and flowering line did not differ in CER, Chl levels, soluble protein levels or rubisco activities also offer support of an environmental component to the cutout photosynthetic decline. The greater Photosystem II capacity as shown by Chl Fv/Fm of the flowering line compared to the non-flowering line and the lack of significant differences between planting dates for Fv/Fm indicate Photosystem II capacity is not diminished by the development of a large boll load. A number of factors related to the environment could come into play at this time. Most notably, the shorter daylength around cutout maybe inducing some sort of photoperiodic effect on some physiological process. In addition, cooler night temperatures, which sometimes occur during the period around cutout, have been shown to reduce CER (Pettigrew et al. 1993) and Fv/Fm (Warner and Burke 1993) in cotton. There could also be a situation where the leaf constituents are being remobilized to support other vegetative sinks instead of reproductive sinks.

It appears that the remobilization of leaf N is an underlying cause for much of the reproductive sink development component to the photosynthetic decline, although other nutrient elements are certainly also remobilized to the bolls. This leaf N remobilization up to this stage appears to come primarily at the expense of the soluble protein levels in as much as the Chl levels did not differ between planting dates for either year. In addition, this research indicates that the loss of rubisco is a primary contributor to the soluble protein reduction, which is not surprising considering that rubisco constitutes about 50% of the leaf's soluble protein level. The lack of significant differences in Chl levels or Chl fluorescence Fv/Fm values between planting dates during this stage of growth indicate that neither the light harvesting system nor the photosynthetic electron transport system have been dismantled for remobilization to the bolls yet. That conclusion does not preclude remobilization of these components at a later date.

This apparent contribution of leaf N remobilization as an underlying cause of the cutout photosynthetic decline puts forth the question of whether additional N fertilization (possibly applied as a late season foliar treatment) could prevent or delay this photosynthetic decline. Bondada et al. (1996) showed that increased N fertilization of cotton, increased canopy photosynthesis, delayed cutout, extended the duration of the cotton canopy and resulted in increased seed cotton yield. However, this extended period of canopy function could have negative implications for crop defoliation. Because the cotton canopy needs to be fully defoliated prior to harvesting or the producer will receive fiber quality penalties when marketing the crop, a fine line must be walked with cotton N fertilization (late season foliar or otherwise).

In conclusion, the photosynthetic decline that occurs around cutout appears to be associated primarily with a simultaneous reduction in leaf N along with an increasing size of the reproductive sink, reminiscent of the leaf senescence process for an annual plant. However, there are other aspects of the data set where the photosynthesis is reduced without the concurrent development of reproductive growth. These data indicate that either some environmental cue or competition from other vegetative sinks also contributes to this photosynthetic decline. A carefully managed late season N fertility program might help alleviate the problem, but this plan runs the risk of promoting vegetative regrowth and complicating crop management and the defoliation process. In addition, any late season N fertility program would not address the environmental component.

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