Physiological and Yield Responses of Field-grown Cotton to Shade

D. Zhao and D. Oosterhuis
Department of Agronomy, University of Arkansas, Fayetteville, AR 72701, USA

ABSTRACT

Field studies were conducted to determine the effects of an 8-day period of shade (63% light reduction) at pinhead square (PHS), first flower (FF), peak flower (PF) or boll development (BD) stage on cotton (Gossypium hirsutum L.) carbohydrate composition, mineral nutrient status, lint yield and fiber quality. Shading for 8 days at the early square stage did not affect cotton growth and yield. Shade during flowering and fruiting significantly increased fruit abscission, and decreased lint yield and fiber quality. The detrimental effect of shade on yield increased with later growth stages. At all four stages, shade significantly decreased leaf net photosynthetic rate (43-55%) and nonstructural carbohydrate concentration (47-71%) and increased the concentration of mineral nutrients. Effects of shade on carbohydrates and mineral nutrients of bracts and floral buds were also recorded. Shade during plant reproductive growth significantly reduced leaf net photosynthetic rate and total nonstructural carbohydrate (TNC) concentrations and affected mineral nutrient status and TNC/N ratio of field-grown cotton, resulting in increased fruit abscission, decreased lint yield and poor fiber quality.

Introduction

Cloudy, overcast weather frequently occurs during the growing season and it is speculated that overcast periods have a detrimental effect on cotton yield. Although the effect of shade on cotton yield has been documented in earlier studies, little is known about the physiological and yield responses of field-grown cotton to the timing of shade during the season. Effects of low photosynthetically active radiation (PAR) stress at different growth stages on cotton growth and yield may be quite different because of the indeterminate growth habit and changing nutritional requirements of plants during the season. An understanding of growth, physiological and yield responses to shade at different growth stages may help improve management efficiency by explaining yield variability. The objectives were: a) to determine the effects of shade at four growth stages on yield, yield components and fiber quality; b) quantify these effects on leaf photosynthesis and nonstructural carbohydrates in leaves, bracts and floral buds of field-grown cotton; and c) investigate changes in mineral nutrient status of plants under low PAR.

Material and Methods

Plant Culture

The field experiments were conducted at the Arkansas Agricultural Research and Extension Centre, University of Arkansas in Fayetteville, Arkansas, USA in 1993-1995. Cotton (cv. Deltapine 20) was planted on May 26, 1993, May 17, 1994 and May 15, 1995. Plots consisted of five rows spaced 1-m apart, oriented in a south-north direction and hand thinned to nine plants m^{-1} row at the three true leaf stage. Control of insects and weeds, fertilizer and furrow irrigation were given as needed during the seasons according to Arkansas cotton production recommendations. The shade shelters (5 X 5 m and 1.9 m tall) had PVC pipe frames, covered with black shade cloth that provided approximately 63% reduction in PAR.

Experimental Treatments

The 1993 treatments consisted of a no-shade control and three shade treatments where one 8-day period of shade was imposed at the beginning of the first flower (FF), peak flower (PF) or boll development (BD) growth stages. FF was defined as the date when 50% of plants had a white flower and the PF and BD stages were at 12 and 24 days after FF, respectively. Based on the 1993 study, an additional treatment of shade beginning at the pinhead square (PHS) stage when 50% of plants had the first visible, 3-cm floral buds, was added in 1994.

In the first of two experiments in 1995, treatments consisted of (1) no-shade control, (2) shade applied for 8 consecutive days beginning at PHS, (3) shade applied for 8 consecutive days beginning at 8 days after PHS, and (4) shade applied for 8 consecutive days beginning at 16 days after PHS. The second experiment investigated the effect of the duration of the shade interval at BD (91 days after planting) on cotton yield and quality. The treatments were: (1) an unshaded control, (2) alternating 1-day shade intervals over a 16-day period, (3) alternating 2-day shade intervals over a 16-day period, and (4) alternating 4-day shade intervals over a 16-day period, each treatment receiving a total of 8 days of shade.

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Measurements

At 2, 4, 6 and 8 days after shade initiation in 1993 and 1994, net photosynthetic rate and dark respiration of the uppermost fully expanded main-stem leaves were measured between 1100 and 1300 h using a LiCor 6200 photosynthesis system (LICOR Inc, Lincoln, NL). The petioles and blades of 6 leaves were sampled for photosynthesis measurement. Ten 20-day-old squares from the first sympodial fruiting position from each plot were collected 8 days after shade initiation of treatments to determine the concentrations of nonstructural carbohydrates and mineral nutrients in different plant tissues. The nonstructural carbohydrates in plant tissues were extracted and determined (Hendrix, 1993; Zhao and Oosterhuis, 1998). The sum of hexose (glucose + fructose), sucrose and starch was defined as total nonstructural carbohydrate (TNC). Petiole NO_3-N, P, K and S and total mineral nutrient concentrations in leaves, bracts and floral buds, were determined by the University of Arkansas Soil Testing and Research Laboratory, Marianna, Arkansas, USA. Seedcotton samples were hand harvested from 2 m of the centre row of each plot. Boll numbers, seedcotton and lint weight were determined. Average boll weight, lint percentage and lint yield were calculated to analyze effects of the timing of shade on boll retention, lint yield and yield components. Fiber quality (HVI) was determined in 1994 and 1995.

Experimental Design and Data Analysis

The experiments were arranged in randomized complete blocks with two (1993) or three (1994 and 1995) replications. Data were statistically analyzed using analysis of variance and the least significant difference (LSD) tests according to the general linear model (GLM) procedure of the Statistical Analysis System (SAS Inc). The differences between treatment means were considered significant when $P > 0.05$.

Results and Discussion

Lint Yield and Yield Components

Lint yield did not differ statistically between unshaded control and plants shaded at PHS (1994 and 1995) and FF (1993) stages (Table 1), whereas yield was significantly decreased by shade at the PF and BD stages. The reduction in lint yield from shaded cotton increased progressively with later growth stages. The decrease in lint yield for shaded cotton was mainly associated with a decrease in harvestable bolls. Shade at PHS, FF or PF stage did not decrease average boll weight. Both boll numbers and boll weight were significantly decreased by shade at the BD stage. No significant differences in lint percentage were found among shade treatments. In 1995 (Experiment 1), shade prior to flowering did not affect lint yield or yield components (data not shown).

In the 1995 study of the duration of shade intervals (Experiment 2), all three shade treatments of 1-, 2- and 4-day intervals during boll development decreased lint yield significantly by 19, 41 and 34%, respectively (Table 2).

Fiber Quality. In the 1994 study, all shade treatments significantly decreased fiber micronaire values by 8-16% ($P > 0.05$) (Table 3). Shade at the PF and BD stages exhibited the greatest effect on micronaire value. In the 1995 (Experiment 1), none of the fiber quality parameters were affected by shade during the squaring period (data not shown). In the 1995 experiment with shade intervals during boll development (Experiment 2), micronaire value was significantly decreased by all three shade-treatment intervals ($P > 0.05$) compared to unshaded control. Results of micronaire value response to low light in our study agreed with the observations of Pettigrew (1995). Of the five fiber quality parameters measured, micronaire was the most sensitive to low PAR during boll development but shade also affected uniformity index and strength. The responses of fiber length and elongation to shade during boll development were relatively small compared to other fiber properties.

Photosynthetic and Respiration Rates

Leaf net photosynthetic rate (Pn) was significantly decreased by shade ($P \leq 0.001$). At 2, 4 and 8 days after initiation of shade at the FF stage, the Pn of shaded plants declined by 52, 43 and 42%, respectively, compared to unshaded control plants. Shade had similar effects on the Pn at all growth stages. The Pn of unshaded control plants at the PHS, FF, PF, and BD stages was 21.2, 28.7, 26.8, and 28.8 μmol CO_2 m^{-2} s^{-1}, respectively; whereas the Pn of shaded plants was 9.9, 16.0, 12.7, and 14.9 μmol CO_2 m^{-2} s^{-1}, respectively. The leaf dark respiration rate did not statistically differ between the no-shade control and shaded plants (data not shown). However, leaves of shaded plants exhibited a higher stomatal conductance, lower transpiration rates and higher intercellular CO_2 concentrations than the unshaded control plants at most growth stages (Table 4). This indicated that the conductance and CO_2 concentration were not the major factors causing the decrease in leaf net photosynthetic rate of shaded plants in our studies.

Nonstructural Carbohydrates

In general, nonstructural carbohydrate concentrations in leaves, bracts and floral buds were affected significantly by shade and growth stage, but less affected by year. No interaction was found between year and shade. Sucrose appeared to be the most sensitive to both shade and growth stage among the three nonstructural carbohydrates of hexose, sucrose and starch.

Leaves. The major nonstructural carbohydrate found in the upper most fully-expanded main-stem leaves was starch, accounting for 85 to 91% of leaf TNC,

compared to hexose and sucrose concentrations which only accounted for 4 to 10% (Table 5). Leaf starch and TNC concentrations gradually declined with increased plant age. This was mainly due to the increase in plant boll load, in which more assimilate was translocated to developing fruits because leaf net photosynthetic rate did not decrease with progressive growth stage. Shade significantly decreased the concentrations of sucrose and starch in the leaves at all growth stages except for sucrose at the PF stage in 1993, whereas no consistent effects of shade on leaf hexose concentration were observed in this study. Of the three nonstructural carbohydrates, averaged over the four stages for both years, under the shade conditions leaf starch exhibited the greatest decrease (61%), followed by sucrose (45%) and hexose (6%) compared with no-shade control plants (Table 5).

Bracts. The TNC concentration in bracts was only 25-40% of that in leaves (Table 5) but the proportions of hexose and sucrose in bracts were much higher than in leaves. Low bract TNC may be associated with a lower photosynthetic rate of bracts than leaves (Wullschleger *et al.*, 1990). High fractions of soluble sugar in bracts are probably beneficial for carbohydrate translocation from bracts to fruits (Benedict and Kohel, 1975). In a pattern similar to that in the leaves, shade significantly decreased hexose, sucrose, starch and TNC concentrations in bracts. Shade at the BD stage caused the greatest decrease (52%) in bract TNC among the FF, PF and BD stages.

Floral Buds. Shade at the FF and PF stages did not affect TNC concentration of floral buds (Table 5). The floral buds of shaded plants at the BD stage, however, exhibited significantly lower TNC (20%) than that of unshaded control plants. This was probably due to the strong competition of the developing bolls with the squares for available carbohydrates, reflected in the greater partitioning of photosynthate to older bolls. These results indicated that the effect of shade on the carbohydrate compositions differed among the leaves, bracts and floral buds. During boll development, insufficient carbohydrate supply under low PAR conditions was a major factor that increased fruit abscission and decreased yield.

Plant Mineral nutrient Status

Petioles. Petiole NO_3-N, P, K and S concentrations declined sharply with plant age under normal growing conditions (Table 6). Shade at any growth stage significantly increased petiole NO_3-N, P and K Shade at all growth stages significantly decreased leaf photosynthetic rate and nonstructural carbohydrate concentration of leaves and bracts of field-grown cotton. Shade also affected mineral nutrient status of plants. Insufficient carbohydrate supply and a decreased TNC/N ratio are probably major factors correlated with increased fruit abscission and decreased lint yield and quality of shaded cotton. concentrations except petiole K at the FF. Petiole S concentration of plants shaded at FF increased 43%, while shading at the PF stage had no effect on S. Plants shaded at the BD stage showed a significant decline in petiole S compared to unshaded control plants.

Leaves. Under normal (unshaded) growing conditions, leaf total N, P and K concentrations showed a similar trend to petiole NO_3-N, P and K concentrations with a gradual decrease as plants aged. However, changes in leaf N, P and K with increased plant age were much less than in petiole nutrients. Leaf S concentration remained almost constant during flowering and fruiting (Table 7). The response of leaf total N, P and K concentrations to shade was similar to that of petiole NO_3-N, P and K. Shade at any growth stage increased leaf total N (17-21%), P (18-39%) and Mg (11-24%) concentrations. Leaf K concentration in shaded cotton was significantly higher than in unshaded plants except for the shading treatment at the FF stage. Shading at PHS, FF and PF stages increased the leaf S, Ca and Mg concentrations but shading at the BD stage did not significantly affect the concentrations of these elements in leaves.

Floral Buds and Bracts. Floral buds had higher total N, P K, Mg and Zn, and lower S, Ca, Na, Fe, Mn and B concentrations than the subtending bracts under unshaded conditions (Table 8). The floral buds of shaded plants had significantly higher K and Ca concentrations than those of the no-shade control plants. Ca in the bracts of shaded cotton was higher than that in the bracts of unshaded control plants. There were no statistical differences between the two shading treatments for other mineral nutrients in the buds and bracts. In contrast, the total N concentrations in floral buds and bracts of shaded plants were decreased numerically (6%). The increased leaf N and decreased floral bud N of shaded cotton illustrated that shade affected N partitioning in plants, and under low light, more N was allocated to the vegetative tissues (especially leaves).

Conclusions

These studies indicate that shade during flowering and fruiting significantly increase cotton fruit abscission and decrease lint yield and fiber quality. The reduction in lint yield of shaded cotton increased when the shade was imposed at progressively later growth stages. The decreased lint yield of shaded cotton was mainly attributed to low boll retention.

Results indicate that weather conditions and time of sampling are critical when taking tissue samples for plant nutrient diagnoses.

References

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Table 1. Effects of an 8-day shading (63% of light reduction) period at four different growth stages on lint yield and yield components of field-grown cotton in 1993 and 1994.

Treatment	Lint yield		Boll number		Boll weight		Lint fraction	
	kg ha^{-1}		no. m^{-2}		g boll^{-1}		%	
	1993	1994	1993	1994	1993	1994	1993	1994
Control	810	1103	61	70	3.4	4.0	40	39
Shade at PHS[H]	---	1025	---	61	---	4.3	---	40
Shade at FF	661	903	50	60	3.4	4.0	39	38
Shade at PF	534	878	40	54	3.5	4.1	38	40
Shade at BD	384	779	36	53	2.6	3.8	41	40
LSD(0.05)	216	163	12	8	0.4	0.4	NS[I]	NS

[H] PHS, FF, PF and BD are the pinhead square, first flower, peak flower and boll development stages, respectively.
[I] NS = not significant (P>0.05).

Table 2. Effects of length of shade intervals during boll development on lint yield and yield components of field-grown cotton in 1995.

Treatment[H]	Lint yield	Boll number	Boll weight	Lint fraction
	kg ha^{-1}	no. m^{-2}	g boll^{-1}	%
Control	977	62	4.7	34
1-d shade intervals	791	59	3.9	35
2-d shade intervals	576	44	3.8	35
4-d shade intervals	645	45	3.9	37
LSD(0.05)	133	8	0.3	2

[H] Total shade of eight days for three shade treatments

Table 3. Fiber micronaire values, length, uniformity index, strength and elongation of cotton in the different shade treatments in 1994 and 1995.

Treatment	Micronaire value	Length (cm)	Uniformity (%)	Strength (kN m kg^{-1})	Elongation (%)
			(1994)		
Control	3.8	28.4	83.2	259	8.8
Shade at PHS	3.5	28.7	83.3	259	8.7
Shade at FF	3.5	29.2	83.4	261	8.5
Shade at PF	3.2	28.7	82.6	250	9.1
Shade at BD	3.2	29.5	84.8	263	8.7
LSD(0.05)	0.3	NS[H]	1.4	NS	NS
			(1995 interval shade during the BD period)		
Control	3.3	28.4	82.8	254	9.3
1-d shade interval	2.4	29.0	81.8	246	9.5
2-d shade interval	2.3	28.2	81.1	224	9.2
4-d shade interval	2.5	27.9	80.2	239	9.4
LSD(0.05)	0.7	NS	1.2	23	NS

[H] NS = not significant ($P > 0.05$).

Table 4. Effects of an 8-day shade period at different growth stages on leaf transpiration rate, intercellular CO_2 concentration and stomatal conductance.

Stage	Transpiration rate --- mmol $_{C2}$ s^{-1} ---		Intercellular CO_2 --- µl CO_2 L^{-1} air ---		Stomatal conductance --- cm s^{-1} ---	
	Control	Shade	Control	Shade	Control	Shade
PHS	14.6	11.6 *	267	302*	3.22	4.19 *
FF	10.2	7.6 **	232	277*	2.69	2.84 *
PF	15.4	13.4 *	264	335**	3.40	3.70 *
BD	12.0	10.8 ns	243	298*	3.26	3.20 ns

Each value is the mean of 1993 and 1994.

The * and ** indicate that differences between control and shade treatments are significant at P # 0.05 and 0.01 probability level, respectively, and ns = not significant ($P > 0.05$).

Table 5. Effects of shade at different growth stages on nonstructural carbohydrate concentrations of leaves, bracts and floral buds.

Stage	---------- g kg^{-1} DW ----------					
	Leaves		Bracts		Floral buds	
	Control	Shade	Control	Shade	Control	Shade
			(Hexose)			
PHS	23	16*	---[H]	---	---	---
FF	12	17 ns	7	5 ns	4	4 ns
PF	13	11 ns	7	4 ***	6	7 *
BD	9	5 *	11	3 ****	4	4 ns
			(Sucrose)			
PHS	15	7 ****	---	---	---	---
FF	22	14 ***	23	15 *	11	8 *
PF	15	9 **	27	12 ****	8	5 ***
BD	10	4 **	5	4 ns	4	3 *
			(Starch)			
PHS	259	131 ****	---	---	---	---
FF	209	92 ****	39	25 ***	77	68 ns
PF	178	59 ****	49	31 ****	71	70 ns
BD	167	52 ****	51	24 ****	77	63 **
			(TNC)			
PHS	297	154 ****	---	---	---	---
FF	243	123 ****	70	45 ***	91	80 ns
PF	206	79 ****	83	47 ****	85	82 ns
BD	185	61 ****	66	32 ****	85	70 **

Data are the means of 1993 and 1994, except for data (only1994) of PHS.

[H] Not available.

The *, **, *** and **** indicate that differences are significant at P # 0.05, 0.01, 0.001 and 0.0001 probability level, respectively, and ns = not significant ($P > 0.05$).

Table 6. Changes in petiole NO_3-N, P, K and S concentrations of unshaded control and shaded cotton plant with an 8-day period of shade at three growth stages of first flower (FF), peak flower (PF) and boll development (BD).

Stage	g kg^{-1} DW							
	NO_3-N		P		K		S	
	Control	Shade	Control	Shade	Control	Shade	Control	Shade
FF	6.8	13.2***	2.3	2.5 **	42	46 ns	1.3	1.9 ***
PF	1.6	3.6 *	1.8	2.2 ***	22	30 ***	0.9	1.0 ns
BD	0.1	0.2 **	1.1	1.2 *	11	15 **	0.8	0.7 *

Each value is the mean of 1993 and 1994 over 4 sampling times (2, 4, 6 and 8 days) in three replications.

The *, ** and *** indicate that differences are significant at $P < 0.05$, 0.01 and 0.001 probability level, respectively, and ns = not significant ($P > 0.05$).

Table 7. Effects of shade at different growth stages on leaf total N, P, K, S, Ca and Mg concentrations of field-grown cotton. Data are means of 1993 and 1994 over 4 sampling times (2, 4, 6 and 8 days after initiation of shading).

Nutrient	Treatment	g kg^{-1}DW			
		Growth stage[1]			
		PHS	FF	PF	BD
N	Control	41.1	39.3	30.7	27.0
	Shade	49.0**	46.2****	37.3****	31.5***
P	Control	3.5	3.8	3.2	2.6
	Shade	4.4***	4.9****	4.5****	3.1**
K	Control	11.2	8.6	7.4	5.5
	Shade	13.5*	8.3 ns	9.6**	7.0**
S	Control	5.1	5.5	5.2	5.5
	Shade	6.7**	7.4****	6.2****	5.6 ns
Ca	Control	24.4	23.7	22.2	25.4
	Shade	30.2*	27.2**	24.6*	25.5
Mg	Control	3.7	3.7	4.2	5.2
	Shade	4.6***	4.1*	4.7*	5.7 ns

[1] PHS, FF, PF and BD are the pinhead square, first flower, peak flower and boll development stages, respectively.

The * , ** , *** and **** indicate that the differences are significant at the 0.05, 0.01, 0.001 and 0.0001 probability level, respectively, and ns = not significant ($P > 0.05$).

Table 8. Mineral nutrient concentrations in floral buds and bracts of 20-day old squares for no-shade control and 8-day shaded cotton plants.

Treatment	g kg^{-1} DW						mg kg^{-1} DW				
	N	P	K	S	Ca	Mg	Na	Fe	Mn	Zn	B
	Buds										
Control	36.8	6.3	18.6	3.8	11.7	3.7	35	60	55	125	40
Shade	34.5	7.2	21.3	4.7	12.9	4.7	45	65	70	100	50
LSD(0.05)	NS[H]	NS	2.0	NS	0.8	NS	NS	NS	NS	17	6
	Bracts										
Control	24.4	4.8	14.3	6.1	23.5	3.1	135	125	170	55	55
Shade	23.0	6.2	16.3	7.1	26.4	3.9	135	110	210	115	60
LSD(0.05)	NS	NS	NS	NS	2.5	NS	NS	NS	NS	35	NS

Data are means of measurements at the FF, PF and BD growth stages in 1993 and 1994.

[H] NS= not significant ($P > 0.05$).