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Relationship between plant canopy characteristics and photosynthetic productivity in diverse cultivars of cotton (*Gossypium hirsutum* L.)

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ABSTRACT

Genotype and plant type affect photosynthetic production by changing the canopy structure in crops. To analyze the mechanism of action of heterosis and plant type on canopy structure in cotton (*Gossypium hirsutum* L.), we had selected two cotton hybrids (Shiza 2, Xinluzao 43) and two conventional varieties (Xinluzao 13, Xinluzao 33) with different plant types in this experiment. We studied canopy characteristics and their correlation with photosynthesis in populations of different genotypes and plant types during yield formation in Xinjiang, China. Canopy characteristics including leaf area index (LAI), mean foliage tilt angle (MTA), canopy openness (DIFN), and chlorophyll relative content (SPAD). The results showed that LAI and SPAD peak values were higher and their peak values arrived later, and the adjustment capacity of MTA during the flowering and boll-forming stages was stronger in Xinluzao 43, with the normal-leaf, pagoda plant type, than these values in other varieties. DIFN of Xinluzao 43 remained between 0.09 and 0.12 during the flowering and boll-forming stages, but was lower than that in the other varieties during the boll-opening stage. Thus, these characteristics of Xinluzao 43 were helpful for optimizing the light environment and maximizing light interception, thereby increasing photosynthetic capability. The photosynthetic rate and photosynthetic area were thus affected by cotton genotype as changes in the adjustment range of MTA, increases in peak values of LAI and SPAD, and extension of the functional stage of leaves. Available photosynthetic area and canopy light environment were affected by cotton plant type as changes in MTA and DIFN. Heterosis expression and plant type development were coordinated during different growth stages, the key to optimizing the canopy structure and further increasing yield.

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1. Introduction

Optimizing crop canopy structure can improve canopy photosynthetic productivity and thereby crop yield potential [1–8]. The canopy structure of a crop is determined largely by the plant type. The plant type is the pattern of spatial arrangement and the combination of morphological and functional for all organs. The spatial arrangement associated with the yield, and the morphological and functional combination was involved in light-energy utilization in crops [9]. Plant type is important for the interception and use of solar energy and for increasing canopy photosynthetic productivity [10]. Plant type can effectively improve the canopy structure and can also affect canopy light distribution and light interception, increase light-energy absorption [11,12], and increase the yield of crops [13]. Solar energy utilization in the canopy is increased by coordination between heterosis utilization and plant-type modification [14–16].

Cotton has an indeterminate growth habit with a complex shape and living state of leaf, boll and branch [17]. The reproductive growth does not coincide with its apical dominance in cotton, and the reproductive organs are distributed within the cotton canopy, so that cotton plants have many reproductive growth centers distributed throughout the canopy. For this reason, research on its plant structure is more complex than that in gramineous crops [18]. To date, owing to the ecological environment in Xinjiang, China, the canopy photosynthetic capacity of cotton has been considerably increased by the use of heterosis, and its yield in China has markedly increased [6–8]. Thus, improving photosynthetic efficiency is one of the keys to future yield increases in crops [19–21]. It is a research hotspot that the plant type was optimized to improving yield in cotton [22]. Research on optimizing plant type has been focused on the effect of plant type on photosynthate transport [23] and the development [24] and spatial distribution [8] of the boll. However, there has been little research on the relationship between cotton plant type, photosynthetic capacity of the canopy, and yield. In the present study we investigated how heterosis and plant type affect the photosynthetic characteristics of the cotton canopy. We determined the canopy structure and photosynthetic production characteristics of cotton varieties with different genotypes and plant types. The function mechanism of heterosis and plant type on canopy structure was analyzed. The results of this study will provide a reference not only for breeding cultivar combinations with the obvious advantage on yield but also for improving agronomic practices.

2. Materials and methods

2.1. Cultivars and treatments

According to the division method for categorizing cotton plant type [25], four varieties are cultivated over a comparatively large area in the planting area of cotton in Xinjiang (Fig. 1). They include Shiza 2, a hybrid variety with an okra-leaf type and an inverted-cone plant type; Xinluzao 43, a hybrid variety with a normal leaf type and a tower plant type; Xinluzao 13, a

conventional variety with large normal leaf type and compact plant type; and Xinluzao 33, a conventional variety with small normal leaf type, one-flower in each branch, and cylindrical plant type. A type was assigned to the large-leaf type if the leaf area was larger than that of Xinluzao 43 and otherwise to the small-leaf type.

The experiment was conducted at the agricultural experimental station of Shihezi University (45°19' N, 86°03' E), Xinjiang, China in 2009 and 2010. The soil was covered with plastic film (also called soil film), and then small holes were made in the film and seeds were sown by hand. The plastic film was 1 m in width and the distance between two films was 40 cm. Four rows were planted in each film, giving row spacings of 60, 20, 40, and 20 cm (Fig. 2). Each cotton variety had been three replicates, there were twelve plots that each plot had 60.0 m², the plots were randomly established, in this experiment for a total of twelve plots. The planting density was 165,000 plants ha⁻¹ and the same cultivation techniques were used in both years. As basal fertilizer, 1500 kg ha⁻¹ of organic fertilizer, and the fertilizers including 240 kg ha⁻¹ of pure N and 75.3 kg ha⁻¹ of P were mixed into the soil before sowing. Dimethyl piperidinium chloride was applied 6 times throughout the growth period with a cumulative dosage of 300 g ha⁻¹ for regulating cotton plant growth. In 2009, sowing was performed on April 19 and seedlings emerged on April 26. In 2010, sowing was performed on April 24 and seedlings emerged on April 30. Drip irrigation was applied 12 times during the growth period for a total of 6000 m³ ha⁻¹ including 270 kg ha⁻¹ of pure N until the end of August. Topping was performed during July 8–10. Other agronomic practices conformed to local practices for high-yield cotton production.

2.2. Canopy structural and photosynthetic measurements

Indicators of canopy structure including chlorophyll relative content (SPAD value), canopy apparent photosynthesis (CAP), light interception rate (LIR), and accumulation of photosynthate were measured at key stages of cotton growth and development, including peak squaring stage, peak flowering stage, initial boll setting stage, later boll setting stage, and boll opening stage.

2.2.1. Canopy structural measurements

Leaf area index (LAI), mean foliage tilt angle (MTA), and canopy openness (DIFN) were recorded with an LAI-2000 canopy meter (LI-COR, USA) following Malone et al. [26] for 4 replicates in different rows for each plot. First, the probe of the meter was placed at a set level over the canopy, and then the measuring button was pressed once after two alert sounds. Second, the probe was placed at the same level above the ground in a four different row, and then the button was pressed again, with four such readings were taken in different rows after two alert sounds, thrice measure were randomly selected in each plot.

2.2.2. Chlorophyll relative content (SPAD value)

SPAD was measured with a SPAD-502 Plus chlorophyll meter (Minolta, Japan), on a young and fully expanded functional cotton leaf, the fourth below the main stem terminal before plant topping and the second from the top after topping.

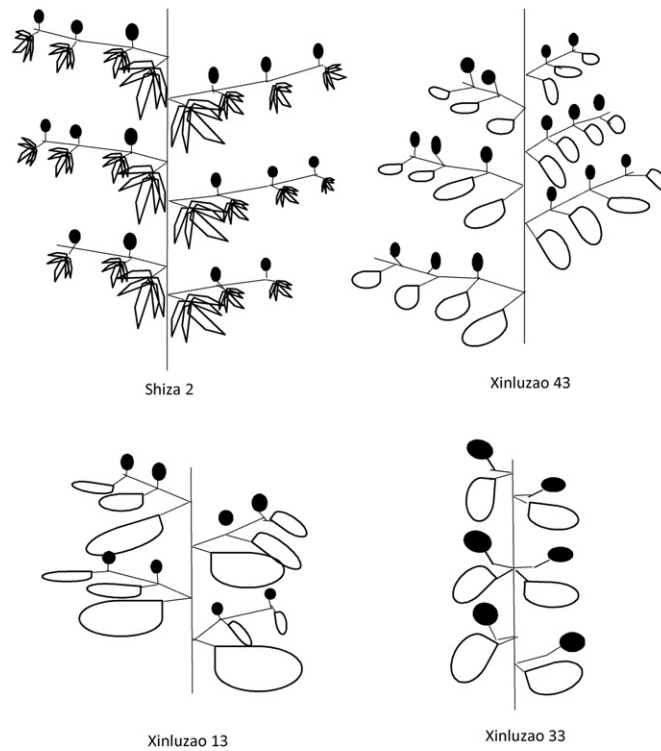


Fig. 1 – Cartoons of the four cotton cultivars used in the experiment.

Fifteen leaves were randomly selected in each plot and two measurements were made per leaf, one on each leaf side at the midrib.

2.2.3. Canopy apparent photosynthesis rate (CAP)

Using the assimilative box method [6], the CAP was measured directly with a GXH-305 infrared gas analyzer (China Agricultural University, China) in the field on clear days under stable light intensity between 1200 and 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (from 11:00 to 14:00, Beijing time). The assimilative box was 0.7 m width and 0.9 m length, with a height determined by plant height changes between different growth stages. Two fans were installed in the box for mixing gases and the frame was covered with transparent Mylar. The infrared gas analyzer was connected with the assimilative box, resulting in a closed-circuit system for measurement. The CAP was measured after the CO_2 concentration in the box decreased steadily for 60 s. Three measuring points were selected for each plot and each point was measured twice. The sequence

of measurement was as follows: three cotton plant samples were chosen for each treatment. Each point was detected twice under forward and reverse sequence. Because the CO_2 of soil respiration could counteract the CAP value, the CO_2 concentration from soil respiration was determined by adjusting the CAP values measured in a selected area, identical to the area of the box, from which the plants had been removed.

2.2.4. Light interception rate (LIR)

Following Du et al. [6], LIR was measured directly with a LI-250A light quantum instrument (LI-COR, USA) in the field on sunny days when light intensity was between 1200 and 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (from 11:00 to 14:00, Beijing time). First, natural light intensity (I_0) was measured 30 cm above the top of the canopy with the instrument's probe surface horizontal and facing the sky, and reflected light intensity (I_n) was measured 30 cm above the top of the canopy with the probe surface facing the ground. Second, incident light intensity (I)

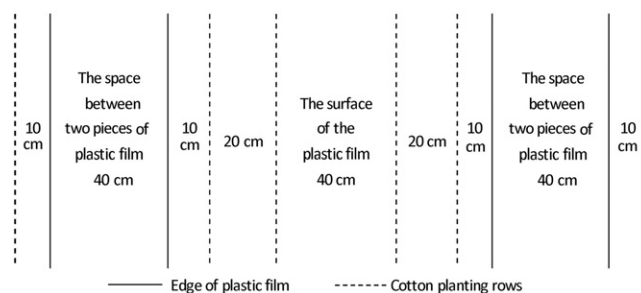


Fig. 2 – Planting row-space configuration used in the experiment.

at the bottom and 1/3, and 2/3-height positions of the canopy was measured with the probe surface again facing upward. All of the above measures were made six times per plot. Light reflectivity rate (LRR), light transmittance rate (LLR), and light interception rate (LIR) was calculated as follows:

$$\begin{aligned} \text{LRR}(\%) &= I_n/I_o \times 100, \text{LLR}(\%) = I/I_o \times 100, \text{and LIR}(\%) \\ &= 100 - \text{LRR} - \text{LLR}. \end{aligned}$$

2.2.5. Yield and yield components

Ten plants were selected randomly from each plot at harvest, which occurred on September 9 in 2009 and September 15 in 2010. Boll weights on all fruiting branches were recorded for each plant to calculate average boll weight. Three areas of 3.4 m² were randomly chosen in each plot and the plants and bolls were counted in each area to calculate the number of bolls per plant and per ha. Finally, seed cotton yield was harvested from each area to estimate crop yield.

2.2.6. Statistical analysis

The experimental data were analyzed with Microsoft Excel 2003 and SPSS 11.0. Differences between treatment means were tested for significance using least significant difference (LSD) after ANOVA indicated a significant treatment effect (genotype and genotype \times season interaction) by F-test at the probability level of 0.05.

3. Results

3.1. Yield and its components

The lint yields of the hybrids Xinluzao 43 and Shiza 2 exceeded 3000 kg ha⁻¹ (Table 1). The yield of Xinluzao 43 was the highest among all varieties, 13.8%–16.6% higher than that of Shiza 2, 41.8%–42.2% higher than that of Xinluzao 33, and 52.3%–55.4% higher than that of Xinluzao 13. Analysis of yield components indicated that the higher increase in the output of Xinluzao 43 than in that of Shiza 2 was due to the increases in single-plant boll number, boll weight, and lint percentage. These factors were also responsible for the yield above 3500 kg ha⁻¹. The single-plant boll number and boll weight of Xinluzao 13 were 10.6%–15.1% and 17.5%–22.9%,

respectively, lower than those of Xinluzao 43. These factors were responsible for the yield below 2500 kg ha⁻¹. The decrease in boll weight limited further increases in yield.

3.2. Leaf area index (LAI)

LAI change of the different cotton varieties described a unimodal curve with growth stage (Fig. 3). Varietal differences were small at the squaring and peak flowering stages, but larger at subsequent stages. LAI of the conventional cotton varieties reached peak values at the full-flowering stage and declined thereafter. LAI peak values ranged from 3.1 to 3.6. LAI peak values of the hybrids were reached at the full bolling stage. These values were higher and were sustained over more days than those of the conventional cotton varieties. The LAI peak value of Xinluzao 43 was 4.9, the highest among the 4 varieties. It was 2.4%–5.4% higher than that of Shiza 2 and 23.2%–36.7% higher than that of the conventional varieties. Until the boll opening stage, the LAI values of the hybrids ranged from 2.5 to 4.0, whereas those of the conventional varieties ranged from 1.2 to 2.5. The LAI values of the hybrids were generally higher than those of the conventional varieties. From the later boll setting stage to the boll opening stage, the LAI decrease rate of the hybrids was 2.4×10^{-2} to 5.1×10^{-2} day⁻¹, and that of the conventional varieties was 4.0×10^{-2} to 5.8×10^{-2} day⁻¹ (Fig. 2). The leaf source capacity of different cotton varieties differed in different growth stages. The LAI peak value, its occurrence time, and its rate of decline were significantly different between the hybrids and conventional varieties. The abundant leaf source capacity was beneficial for capturing high amounts of light energy and establishing a material basis for reaching high yield.

3.3. Chlorophyll content (SPAD)

SPAD changes in the different cotton genotypes and plant types described a unimodal curve during the growth period (Fig. 4). The peak value and time of peak occurrence of SPAD both differed. As the yield of a cotton variety increased with SPAD peak value, the SPAD peak values of hybrids were generally higher than those of the conventional varieties. The SPAD peak value of Xinluzao 43, occurring at the initial boll setting stage, ranged from 66.4 to 67.1 and was higher than those of the other 3 varieties. The SPAD peak values of Shiza 2,

Table 1 – Yield and its components in four cotton cultivar plant types in 2009 and 2010.

Cultivar or line	Plant density ($\times 10^4$ ha ⁻¹)	Boll no. per plant	Total boll no. ($\times 10^4$ ha ⁻¹)	Boll weight (g)	Lint percentage (%)	Seed cotton yield (kg ha ⁻¹)	Lint yield (kg ha ⁻¹)
2009							
Shiza 2	16.2 \pm 0.41	8.40 \pm 0.40 b	136.2 \pm 5.63 b	5.59 \pm 0.35 b	43.5 \pm 1.57 b	7345 \pm 350.2 b	3195 \pm 135.0 b
Xinluzao 43	16.1 \pm 0.35	8.91 \pm 0.34 a	143.6 \pm 6.78 a	5.86 \pm 0.29 a	44.6 \pm 1.03 a	8010 \pm 289.4 a	3724 \pm 147.5 a
Xinluzao 13	16.4 \pm 0.71	7.74 \pm 0.16 c	126.5 \pm 4.87 c	4.77 \pm 0.23 c	40.7 \pm 0.93 c	5887 \pm 293.4 d	2397 \pm 104.4 d
Xinluzao 33	16.3 \pm 0.31	7.10 \pm 0.31 d	115.6 \pm 5.02 d	5.63 \pm 0.33 b	41.3 \pm 1.35 c	6339 \pm 281.7 c	2619 \pm 101.9 c
2010							
Shiza 2	15.9 \pm 0.67	8.55 \pm 0.43 b	135.9 \pm 6.34 b	5.71 \pm 0.29b	43.4 \pm 2.02 b	7571 \pm 354.8 b	3285 \pm 137.5 b
Xinluzao 43	16.0 \pm 0.70	9.04 \pm 0.44 a	144.6 \pm 7.12 a	5.84 \pm 0.29a	44.0 \pm 2.05 a	8494 \pm 401.7 a	3737 \pm 157.3 a
Xinluzao 13	16.2 \pm 0.71	8.17 \pm 0.40 bc	132.3 \pm 6.24 b	4.97 \pm 0.24c	38.2 \pm 1.82 c	6425 \pm 311.3 d	2454 \pm 112.7 d
Xinluzao 33	16.2 \pm 0.81	7.54 \pm 0.37 d	122.0 \pm 6.02 c	5.73 \pm 0.26b	38.8 \pm 1.75 c	6793 \pm 302.0 c	2636 \pm 107.2 c

Values followed by different letters are significantly different at the 0.05 probability level for different cultivars in the same year.

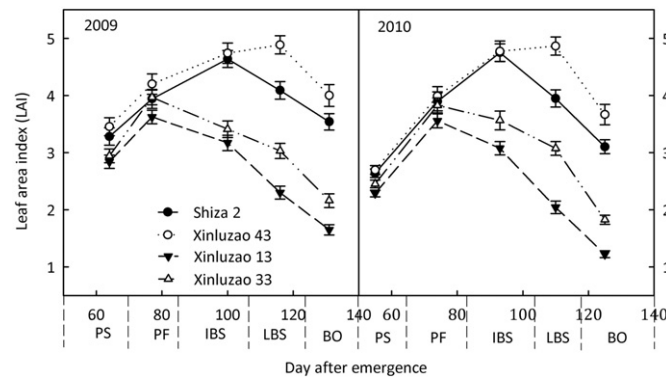


Fig. 3 – Leaf area index (LAI) of four cotton cultivars with different plant types during plant growth and development stages in 2009 and 2010 experiments, respectively. PS, peak squaring stage; PF, peak flowering stage; IBS, initial boll setting stage; LBS, later boll setting stage; BO, boll opening stage.

Xinluzao 13, and Xinluzao 33 occurred at the peak flowering stage, and that of Xinluzao 13 was the lowest among the 4 varieties. Until the boll opening stage, the SPAD of Xinluzao 43 ranged from 56.6 to 57.8 and was 8.4%–9.5% higher than that of Shiza 2, 11.6%–12.2% higher than that of Xinluzao 33, and 21.3%–22.2% higher than that of Xinluzao 13. With higher SPAD peak value and longer duration of SPAD value, utilization of light energy was more efficient.

3.4. Mean foliage tilt angle (MTA)

The living fashion and adaptability of leaves are reflected by the mean foliage tilt angle (MTA). MTA is a major characteristic indicator of canopy structure and its value strongly affects the effective photosynthetic area of leaves. MTA of the genotypes and plant types increased initially and then decreased over the cotton growth period. MTA was significantly different among the varieties, as reflected in the peak value occurrence time and the adjustment capacity of MTA (Table 2). The MTA peak value of Xinluzao 33 was reached at the peak flowering stage, whereas those of the other 3 varieties were reached at the initial boll setting stage. The MTA of Shiza 2 was the lowest among the 4 varieties, that of Xinluzao 33 was the second lowest, and that of Xinluzao 43

was the highest among the 4 varieties. The ranges of increase for the 2 hybrids were wider than those of the 2 conventional varieties between the peak squaring stage and the initial boll setting stage, whereas the ranges of their decrease were wider than those of the 2 conventional varieties between the initial boll setting stage and the boll opening stage. It is noteworthy that MTA was effectively adjusted for adaptation to ever-changing light environments, increasing effective photosynthetic area and capturing more light energy in cotton.

3.5. Canopy openness (DIFN)

Canopy openness (DIFN) of the cotton genotypes and plant types increased initially and then decreased during the growth period. Differences in DIFN were reflected in minimum value occurrence time and adjustment range (Fig. 5). The DIFN values of the 2 conventional varieties reached their minimum values at the peak flowering stage in cotton. The DIFN value of Xinluzao 13 was the lowest among the 4 varieties, and its LAI ranging from 3.2 to 3.6 was also the lowest among the 4 varieties. This result was associated with lower MTA and a larger leaf, so that the middle and lower canopy were more closed. The DIFN values of the 2 hybrids were higher than those of the 2 conventional varieties from

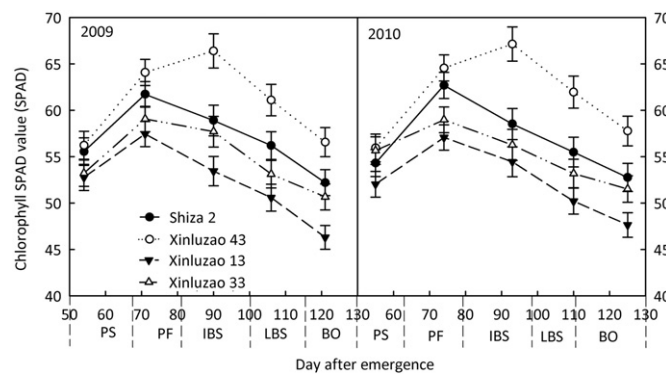


Fig. 4 – Change in chlorophyll content (SPAD) in different genotypes and plant types at different growth stages in cotton during 2009 and 2010. PS, peak squaring stage; PF, peak flowering stage; IBS, initial boll setting stage; LBS, later boll setting stage; BO, boll opening stage.

Table 2 – Change in mean foliage tilt angle (MTA) in four cotton cultivars of different plant types with crop growth and development during 2009 and 2010.

Year	Cultivar	Peak squaring stage	Peak flowering stage	Initial boll setting stage	Later boll setting stage	Boll opening stage
2009	Shiza 2	40.2 ± 1.7 c	42.3 ± 1.8 c	43.0 ± 1.8 c	40.0 ± 1.7 c	36.0 ± 1.4 c
	Xinluzao 43	43.7 ± 1.8 a	46.4 ± 1.9 a	49.3 ± 1.8 a	47.3 ± 2.0 a	40.2 ± 1.7 a
	Xinluzao 13	41.5 ± 1.7 b	43.7 ± 1.8 b	44.2 ± 1.9 b	42.4 ± 1.7 b	39.3 ± 1.6 a
	Xinluzao 33	40.9 ± 1.6 bc	43.1 ± 1.8 b	42.7 ± 1.8 c	40.7 ± 1.6 c	37.0 ± 1.6 b
2010	Shiza 2	41.7 ± 1.8 b	42.2 ± 1.8 c	45.0 ± 1.9 b	42.0 ± 1.8 c	36.6 ± 1.5 c
	Xinluzao 43	43.3 ± 1.9 a	47.7 ± 2.0 a	51.7 ± 2.1 a	49.7 ± 2.1 a	42.3 ± 1.8 a
	Xinluzao 13	42.1 ± 1.7 b	44.3 ± 1.9 b	45.7 ± 2.0 b	44.7 ± 1.8 b	41.2 ± 1.7 a
	Xinluzao 33	40.3 ± 1.6 c	43.7 ± 1.8 b	42.6 ± 1.8 c	40.1 ± 2.0 d	38.1 ± 1.6 b

Within a column, values followed by different letters in the same year are significantly different at the 0.05 probability level.

the peak squaring to peak flowering stages. The light transmission of the canopy was higher than those of the others. The DIFN values of the 2 hybrids reached their minimum values at the initial boll setting stage in cotton. Thus, the DIFN minimum values of hybrids appeared about 20 days later than those of the conventional varieties. The DIFN value of Xinluzao 43 was shifted least and that of Xinluzao 13 was shifted most among the 4 varieties. Thus, if an optimum DIFN value is realized in the early growth stage and the value remains relatively stable in later growth stages, not only the light transmission of the canopy is increased but also the waste of light energy is lower, contributing to light energy capture and photosynthate accumulation.

3.6. Light interception rate (LIR)

The light interception rate (LIR) of a crop canopy is closely related to photosynthesis and dry matter production [27]. In this study, the LIR values of different genotypes and plant types increased initially, reached their peak values at the initial boll setting stage, and then decreased over the growth period. The higher the yield of a variety, the higher was the value of LIR (Fig. 6). LIR did not differ significantly among varieties at the flowering and full bolling stage, but did differ at the peak squaring and boll opening stages. The LIR values of the 2 hybrids were higher than those of the conventional varieties from the peak squaring stage to the later boll setting stage. LIR of that of Xinluzao 43 was 80.6%–87.0% at the boll-opening stage. Thus, the rapid decline in LIR was the

limiting factor in further increasing yield of Shiza 2, Xinluzao 13, and Xinluzao 33 during the later growth stages.

LIR values of different genotype and plant type varieties differed significantly in different layers of the canopy (Fig. 7). The LIR values of the 2 hybrids were 50.0% lower and no significantly different in the upper layer of the canopy, but the LIR of Xinluzao 43 was higher than that of Shiza 2 in the lowest layer of the canopy. The LIR values of the 2 conventional varieties increased in the upper layer of the canopy from the peak squaring stage to the later boll setting stage, and their maximum values were 50.0% higher at full bolling stage, significantly higher than that of the 2 hybrids. The LIR values of Xinluzao 43, Shiza 2, and Xinluzao 33 decreased from the peak flowering stage in the middle layer of the canopy. The LIR values of the 2 hybrids exceeded 30.0% from the full-budding stage to the later boll setting stage and ranged from 22.7% to 27.8% at the boll opening stage. The LIR values of the 2 conventional varieties were lower than those of the 2 hybrids, which remained below 30% from the peak squaring stage to the later boll setting stage. The LIR of Xinluzao 13 was the lowest among the 4 cotton varieties, decreasing continuously from the peak squaring stage to the boll opening stage and remaining below 20% at the peak flowering stage and 8.0%–11.7% at the boll opening stage. LIR values in the lowest layer of the canopy increased with yield. LIR of Xinluzao 43 was the highest and that of the conventional variety Xinluzao 13 was the lowest among the 4 varieties in the lowest layer of the canopy.

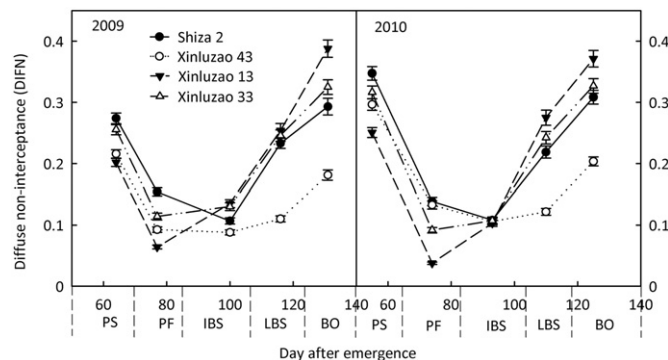


Fig. 5 – Change in canopy openness (DIFN) in different cotton genotypes and plant types at different growth stages during 2009 and 2010. PS, peak squaring stage; PF, peak flowering stage; IBS, initial boll setting stage; LBS, later boll setting stage; BO, boll opening stage.

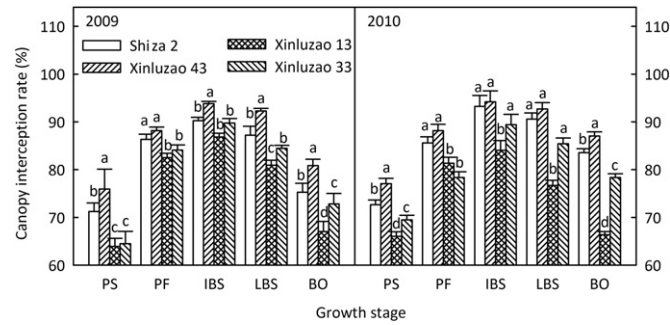


Fig. 6 – Change in total light interception rate (LIR) in different cotton genotypes and plant types at different growth stages during 2009 and 2010. PS, peak squaring stage; PF, peak flowering stage; IBS, initial boll setting stage; LBS, later boll setting stage; BO, boll opening stage. Values followed by different letters in the same year are significantly different at the 0.05 probability level.

3.7. Canopy apparent photosynthesis (CAP)

Canopy apparent photosynthesis (CAP) accurately describes the photosynthetic capacity per unit land area of a crop and integrates genotype effects and canopy structure characteristics [28]. CAP values of all genotypes and plant types increased initially, reached their peaks at the initial boll setting stage, and then decreased through the growth period. The higher the yield, the higher was the CAP at each growth stage and the CAP peak value (Fig. 8). CAP values differed significantly among the varieties and their speeds of increase and decline also differed through the growth period. The CAP values of the 2 hybrids were not significantly different at the peak squaring stage, ranging from 41.1 to 48.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the initial boll setting stage. The CAP values of the 2 conventional cottons

were not significantly different at the peak squaring stage, and they reached peak values at the initial boll setting stage, with peak values 59.8%–63.7% and 64.6%–87.7%, respectively, higher than those at the peak squaring stage but 15.0–40.8% lower than those of the 2 hybrids. The CAP of Xinluzao 43 varied from 20.2 to 20.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The CAP values of the 2 hybrids decreased respectively from 63.1% to 64.0% and 55.4% to 57.2% at the boll opening stage and were 19.8%–166.5% higher than those of the 2 conventional cottons. Increasing CAP at each growth stage and high CAP peak value are keys to high yield, and a rapidly declining CAP is a yield constraint.

A correlation analysis of CAP with canopy structure index indicated that the CAP values of the 4 cotton varieties showed significant or highly significant positive correlations with SPAD and MTA (Table 3). The CAP of Xinluzao 43 and Shiza 2

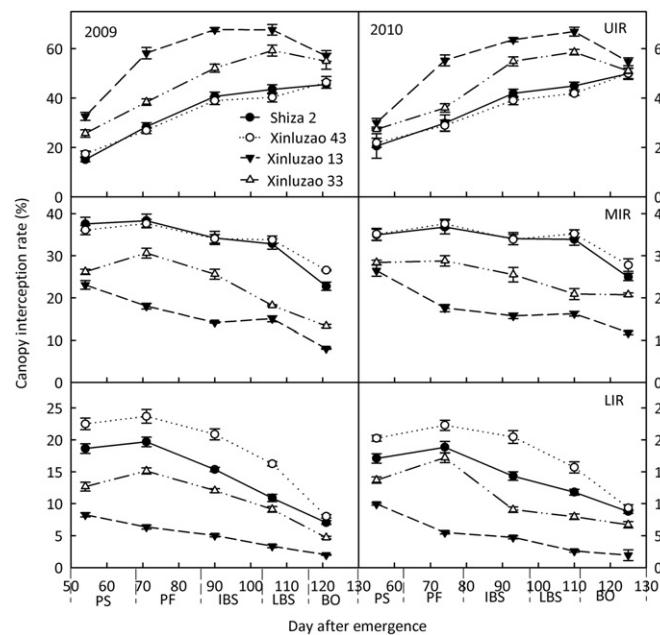


Fig. 7 – Change in light interception rate (LIR) in different cotton genotypes and plant types at different growth stages during 2009 and 2010. PS, peak squaring stage; PF, peak flowering stage; IBS, initial boll setting stage; LBS, later boll setting stage; BO, boll opening stage. UIR, upper canopy interception rate; MIR, middle canopy interception rate; LIR, lower canopy interception rate.

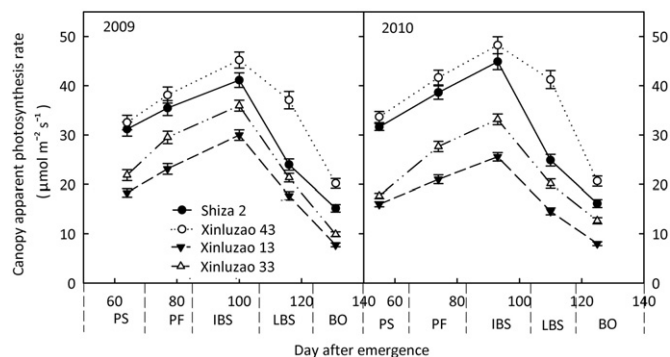


Fig. 8 – Change in canopy apparent photosynthesis rate (CAP) in different cotton genotypes and plant types at different growth stages during 2009 and 2010. PS, peak squaring stage; PF, peak flowering stage; IBS, initial boll setting stage; LBS, later boll setting stage; BO, boll opening stage.

showed a significant positive correlation with LAI and LIR, but significant negative or no significant correlation, respectively, with DIFN. The CAP of Xinluzao 33 showed significant or highly significant positive correlations with LAI and LIR, but no significant correlation with DIFN. The CAP of Xinluzao 13 showed significant positive correlation with DIFN but not with LAI or LIR. Although DIFN is an important indicator of canopy structure optimization, it did not show a simple correlation with photosynthetic performance. The chlorophyll content (SPAD) and leaf angle (MTA) adjustments were correlated with the photosynthetic potential of different varieties and with adaptability to light environmental change. SPAD and the MTA adjustment capability of the cotton hybrids were higher than those of the conventional varieties. The hybrids can conduct normal photosynthesis under low-light conditions, so that CAP was not highly correlated with DIFN. SPAD and MTA adjustment capabilities of conventional varieties were lower than those of the hybrids. The conventional varieties conduct normal photosynthesis under high-light conditions. The light environment in the canopy was strongly affected by plant type. Thus, CAP of the conventional varieties was not highly correlated with DIFN, LAI, or LIR.

3.8. Accumulation of photosynthate

Total photosynthate accumulation of different cotton genotypes and plant types increased initially with the growth

period (Table 4). The accumulation of total photosynthate of Xinluzao 43 at the boll opening stage ranged from 27,792.4 to 28,087.8 kg ha⁻¹ and was higher than those of the other 3 varieties, and that of Xinluzao 13 was the lowest among the 4 varieties. The rate of total photosynthate accumulation of Xinluzao 43 was 20.5%–70.2% higher than that of Shiza 2, 21.5%–92.7% higher than that of Xinluzao 33, and 37.0%–154.1% higher than that of Xinluzao 13 from the initial boll setting stage to the boll opening stage. Thus, the cotton genotype and plant type affected the rate of total photosynthate accumulation during the key stages of yield formation. Total photosynthate accumulation during the key stages of yield formation decides the magnitude of yield.

4. Discussion

4.1. The relationship between change in canopy structure index and light interception in different cotton types

Light interception and the efficiency of light energy utilization are affected directly by canopy structure. Optimum canopy structure is the basis of improving photosynthetic efficiency and achieving high crop yields [1–8]. The light interception and transmittance of the canopy are decided by the leaf area, MTA, and their distribution in the canopy [29,30]. MTA characteristics are affected strongly by genotype [31]. Our results showed that there was a complementary effect of MTA and DIFN on LIR in different cotton genotypes and plant types. The canopy of the hybrid variety Shiza 2 with inverted-cone plant type and okra-leaf type showed higher light transmittance [6], larger DIFN, smaller MTA, and larger effective photosynthetic area and LIR under the same LAI in the early growth stage, but the leakage of light was severe during the later growth stage. The canopy of the hybrid variety Xinluzao 43, with normal leaf type and tower plant type, showed smaller DIFN, larger MTA, and more upright leaves, allowing more light penetration to the middle and lower layers of the canopy. The MTA adjustment ability of Xinluzao 43 was stronger than other cultivars during the later growth stage. DIFN remained relatively stable by changing MTA and LIR was increased by changing MTA. Thus, Xinluzao 43 has a longer stage for the efficient utilization of light energy. The canopy of conventional variety Xinluzao 13, with tower plant type and

Table 3 – Correlation coefficients of lint yield with canopy structure characters and apparent photosynthesis rates for four cotton cultivars with different plant types based on two-year means.

Cultivar	LAI	SPAD	MTA	DIFN	LIR
Xinluzao 43	0.743**	0.918**	0.943**	-0.915**	0.907**
Shiza 2	0.876**	0.847**	0.764**	0.369	0.888**
Xinluzao 33	0.845**	0.737*	0.874**	0.487	0.706*
Xinluzao 13	0.583	0.687*	0.768**	0.662*	0.465

LAI, leaf area index; MTA, leaf angle; DIFN, canopy openness; SPAD, chlorophyll SPAD value; CAP, canopy apparent photosynthesis rate; LIR, light interception rate.

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

Table 4 – Change in accumulation of photosynthates in four cotton cultivars of different plant types during crop growth and development during 2009 and 2010 ($\times 10^3$ kg ha $^{-1}$).

Year	Cultivar	Peak squaring stage	Peak flowering stage	Initial boll setting stage	Later boll setting stage	Boll opening stage
2009	Shiza 2	10.2 ± 0.5 a	16.6 ± 0.7 a	21.6 ± 0.7 b	22.8 ± 1.0 b	24.7 ± 0.9 b
	Xinluzao 43	10.6 ± 0.5 a	17.5 ± 0.8 a	23.6 ± 1.1 a	25.6 ± 1.0 a	28.1 ± 1.1 a
	Xinluzao 13	7.4 ± 0.4 b	11.9 ± 0.5 c	14.9 ± 0.6 d	16.3 ± 0.7 d	17.3 ± 0.7 d
	Xinluzao 33	7.9 ± 0.3 b	13.0 ± 0.6 b	16.9 ± 0.7 c	17.6 ± 0.7 c	19.1 ± 0.7 c
2010	Shiza 2	1.0 ± 0.4 a	16.2 ± 0.7 a	19.7 ± 0.8 b	22.5 ± 0.7 b	23.9 ± 0.8 b
	Xinluzao 43	1.0 ± 0.5 a	16.7 ± 0.7 a	22.0 ± 1.0 a	25.4 ± 1.1 a	27.8 ± 1.2 a
	Xinluzao 13	7.0 ± 0.2 b	9.2 ± 0.3 b	13.0 ± 0.5 d	14.4 ± 0.6 d	15.5 ± 0.6 d
	Xinluzao 33	6.7 ± 0.3 b	10.2 ± 0.5 b	13.9 ± 0.6 c	16.8 ± 0.6 c	18.0 ± 0.7 c

Within a column, values followed by different letters in the same year are significantly different at the 0.05 probability level.

normal leaf type, showed a slightly lower MTA than that of Xinluzao 43, with lower DIFN, so that its canopy was closed and leaves could capture less light in the lower layer of the canopy. Its DIFN increased rapidly and its MTA adjustment ability was lower, so that the effective photosynthetic area was insufficient and leakage of light was severe during the later growth stage. The canopy of the conventional variety Xinluzao 33 with normal leaf type, short fruiting branches with only one boll each, and cylindrical plant type showed higher light transmittance and lower MTA and MTA adjustment ability, but its leaves tended to the horizontal and light leakage was not severe during the later growth stage.

A previous study [32] showed that the effect of canopy light distribution on photosynthesis was greater than that of other factors. The MTA adjustment ability of hybrids was greater than those of the conventional varieties, and their DIFNs remained relatively stable during the flowering and full bolling stages. Consequently, not only the deterioration of the light environment was prevented in the middle and lower canopy layer under higher LAI, but the higher LIR was retained for a longer period. The lower LIR of the conventional varieties was due to their lower LIR in the middle and lower canopy layers. The lower LIR of Xinluzao 13 was attributed to the lower LIR in the upper canopy layer during the later growth stage. Increasing LIR in the upper canopy was the key to the higher LIR of the canopy during yield formation stage, and higher LIR in the middle and lower canopy layers was the key to improving the LIR of the canopy. Light energy absorption can be increased in different canopy layers through increasing MTA and improving the light conditions of leaves under lower DIFN and transmittance during the flowering and full bolling stages. During the later growth stage, the LAI declined, the canopy structure changed, the MTA was smaller, and the leaves tended to the horizontal, so that the LIR of the canopy increased.

4.2. Relationship between plant type, heterosis, and canopy photosynthetic production in cotton

Increasing the light-energy utilization rate of a crop will increase light interception and the light-energy transformation efficiency [33]. Chlorophyll plays a vital role in the absorption and transformation of light in photosynthesis. Cotton hybrids have a distinct advantage in vegetative growth, higher LAI and chlorophyll content, and a clear advantage in photosynthesis compared with conventional varieties [8,34]. In this study, the

chlorophyll content of the hybrids was significantly higher than that of the conventional varieties. During the early growth stage, the DIFN, SPAD, LIR, and CAP of Shiza 2 were higher than those of the other varieties. During the later growth stage, the DIFN of Shiza 2 increased rapidly, whereas its effective photosynthetic area, MTA adjustment ability, LIR, and SPAD decreased rapidly. These phenomena led to the rapid decrease in CAP of Shiza 2 and the shorter duration of efficient production in the Shiza 2 canopy, with all of these processes limiting yield. Each leaf of Xinluzao 43 was a larger leaf area than other cultivars; thus, the photosynthetic potential of Xinluzao 43 leaves can be maximized in the middle and lower canopy layer by further increasing the transmittance by increasing the MTA during the growing period with higher LAI and smaller DIFN. Furthermore, the SPAD of Xinluzao 43 was higher than those of the other varieties and decreased slowly, while its light-energy utilization improved during the later growth stage. All of these phenomena served as the material basis of yield formation. The SPAD of the conventional varieties was lower in the early growth stage and decreased rapidly in the later growth stage. Moreover, the light leakage of the 2 conventional varieties was exacerbated by their weaker MTA adjustment ability. Thus, during the later growth stage, light energy could not be intercepted or captured by leaves, increasing the reduction in CAP. Thus, the heterosis of hybrids influences canopy photosynthetic production characteristics by changing LAI and chlorophyll content, whereas the plant type affects the effective photosynthetic area by changing DIFN and MTA.

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