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Genotypic variance in ^{13}C-photosynthate partitioning and within-plant boll distribution in cotton

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Abstract

Background: Photosynthate partitioning and within-plant boll distribution play an important role in yield formation of cotton; however, if and how they interact to mediate yield remains unclear. The objective of this study was to investigate the genotypic variance in photosynthate partitioning and within-plant boll distribution, with a focus on their interactions with regard to yield and yield components. A field experiment was conducted in the Yellow River region in China in 2017 and 2018 using a randomized complete block design with three replicates. Photosynthate partitioning of three commercial cultivars (DP 99B, Lumianyan 21 and Jimian 169), varying in yield potential, to different organs (including bolls) at early flowering, peak flowering, and peak boll-setting stages, as well as within-plant boll distribution at harvest, and their effects on yield formation were examined.

Results: Lint yield of Jimian 169 was the highest, followed by Lumianyan 21 and DP 99B. Similar differences were observed in the number of inner bolls and boll weight among the three cultivars. J169 partitioned significantly more photosynthate to the fruit and fiber than Lumianyan 21 and DP 99B and allocated over 80% of assimilates to the inner bolls. Additionally, Lumianyan 21 allocated a higher proportion of photosynthate to bolls and fiber, with 12.5%–17.6% more assimilates observed in the inner bolls, than DP 99B.

Conclusions: Genotypic variance in lint yield can be attributed to differences in the number of inner bolls and boll weight, which are affected by photosynthate partitioning. Therefore, the partitioning of photosynthate to fiber and inner bolls can be used as an important reference for cotton breeding and cultivation.

Keywords: Genotypic variance, Within-plant boll distribution, Photosynthate partitioning, Yield, Yield components

Background

Cotton (*Gossypium hirsutum* L.), being one of the main raw material of the textile industry, plays an important role in the stabilization and development of the national economy of China. In recent years, there have been significant advances in the technological processes used by the textile industry. This has been driven by an increased demand by consumers for cotton textile goods, which is causing an increased demand for raw cotton (Dong 2013; Yang 2014). However, the total area planted with cotton and cotton yields have been declining as a result of a continuous rise in production costs. The total area in China cultivated for cotton dropped to 3.2 million hectares in 2017 (from 5.2 million hectares in 2007), the lowest since the establishment of the People's Republic of China in 1949 (National Bureau of Statistics of China). Therefore, the stability and increase of lint yield per unit area is key to the sustainable development of the textile industry.

Cotton yield increased 1.2 times from 790 kg·hm^{-2} during the popularization and application of Bt (*Bacillus thuringiensis*) cotton varieties in the 1990s to 1 720 kg·hm^{-2} in 2017 (National Bureau of Statistics of China). Lint yield is a function of boll number per unit area, boll

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weight, and the percentage of lint. Numerous studies have shown that increases in individual boll weight in the 1970s and 1980s, an increase in the number of bolls per plant and lint percentage in the 1990s (Tang et al. 1993; Kong et al. 2000), and a further increase in boll weight in this century are the main reasons for the current yield levels (Mao 2010; Iqbal et al. 2013; Zhi et al. 2016). Our previous study on the relationship between yield formation and within-plant boll distribution suggested that the main reason for the increase of lint yield of newly bred cultivars was the increase of boll weight and the number of inner bolls (Nie et al. 2019). These findings illustrate that the main factor affecting yield formation has changed as a result of the selection for increased lint yield. However, the mechanism underlying this has received limited attention.

The formation of lint is a process of source-sink interactions. A strong source can provide more photosynthetic products to the sink, regulating the output rate and direction of sucrose transport from the source (Mason and Maskell 1928a, b). As one of the plant species with indeterminate growth habit, cotton has a series of mechanisms to protect itself from yield loss through compensatory growth. Fruit production may take place at different times on different parts of the plant under suitable conditions. Furthermore, the long-term simultaneous growth of vegetative and reproductive organs usually leads to strong competition for assimilates, which induces an imbalance in the source-sink process, changes the direction of the photosynthate partitioning, and thereby results in the abscission of floral buds and bolls (Lee 1984; Constable and Bange 2015). The essence of this source-sink imbalance is that photosynthate produced by the leaves cannot be transported to the reproductive organs in time (Mason and Maskell 1928a, b; Ainsworth and Bush 2011). Numerous studies have revealed the direction of the photosynthate partitioning produced by leaves at different stem positions, the photosynthate distribution to bolls of different ages (days), and the effects of hormones and nutrition on photosynthate partitioning, as early as the twentieth century (Mason and Maskell 1928a; Mason et al. 1936; Ding et al. 1960; Ashley 1972; Brown 1973; Zheng and Chen 1980). Lint yield has increased in the last 30 years of cultivar development. However, the manner in which photosynthate partitioning and yield components interact to mediate yield in a high-yielding cotton cultivar remains unclear.

Genotypic variance in lint yield is mainly caused by the different competitive abilities of reproductive organs in obtaining assimilates, rather than photosynthetic performance (Hearn 1969; Wells and Meredith 1984a, b). High-yielding cotton cultivars often exhibit fewer fruiting nodes, earlier boll development, larger boll weight, and more highly coordinated vegetative and reproductive organs (Bhardwaj et al. 1971; Verhalen et al. 1975; Guinn 1982; Bange and Milroy 2004). Differences in within-plant boll distribution affect the direction and distance of photosynthate partitioning between the source and the sink (Sadras 1995). Dai et al. (2015) reported that cotton yield was stable in a density range of 3.3–10.5 plants per square meter, mainly due to the optimized regulation of photosynthate on boll number and boll weight.

However, previous studies on the genotypic variance of the source-sink relationship primarily focused on the accumulation and distribution of dry matter, rather than the application of the carbon isotope tracer technique (Hu et al. 2008; Dai et al. 2015; Mao et al. 2015). Information on the partitioning of ^{13}C-photosynthate to spatial bolls within the canopies is also limited. In this study, three commercially available Bt cotton cultivars (DP 99B, Lumianyan 21, and Jimian 169) were selected to investigate genotypic variance in photosynthate partitioning and plant boll distribution with a focus on their interaction in relation to yield and yield components.

Materials and methods

Experimental materials

Three commercial Bt cotton cultivars, which are local to and prevalent in the Yellow River region in China, were selected: (1) DP 99B (99B), a mid-season conventional cultivar introduced from the United States, with a growth period of approximately 130 days, boll weight of 4.9–5.5 g, and lint percentage of 36.0%–38.8%; (2) Lumianyan 21 (L21), the first era mid-season conventional cultivar bred by Chinese breeders, with a growth period of approximately 133 days, boll weight of 5.8 g, and lint percentage of 41.6%; and (3) Jimian 169 (J169), the second era mid-season conventional cultivar bred by Chinese breeders, with a growth period of 123 days, boll weight of 6.3 g, and lint percentage of 39.4%.

Experimental design

Field experiments were conducted in 2017 and 2018 at the State Key Laboratory of Crop Biology and an experimental farm in the Shandong Agricultural University (36°10′N, 117°09′E, 158 m a.s.l.), Shandong, China. The climate is temperate and monsoonal with an average annual temperature of 13 °C, rainfall of 697 mm, sunshine duration of 2 627 h, and a frost-free period of 195 d. The experimental soil type was a brown loam with 17.54 $g{\cdot}kg^{-1}$ of organic matter, 1.08 $g{\cdot}kg^{-1}$ of total N, 40.78 $mg{\cdot}kg^{-1}$ of rapidly available phosphate, and 126.47 $mg{\cdot}kg^{-1}$ of rapidly available potassium in the upper 20 cm. The cumulative temperature (≥ 10 °C) and rainfall during the cotton growing season (May 1 to October 31) was 4 375.2 °C and 452.0 mm in 2017 and 4 271.7 °C and 602.0 mm in 2018. Daily average temperature and rainfall are shown in Fig. 1. Cotton seeds were planted using

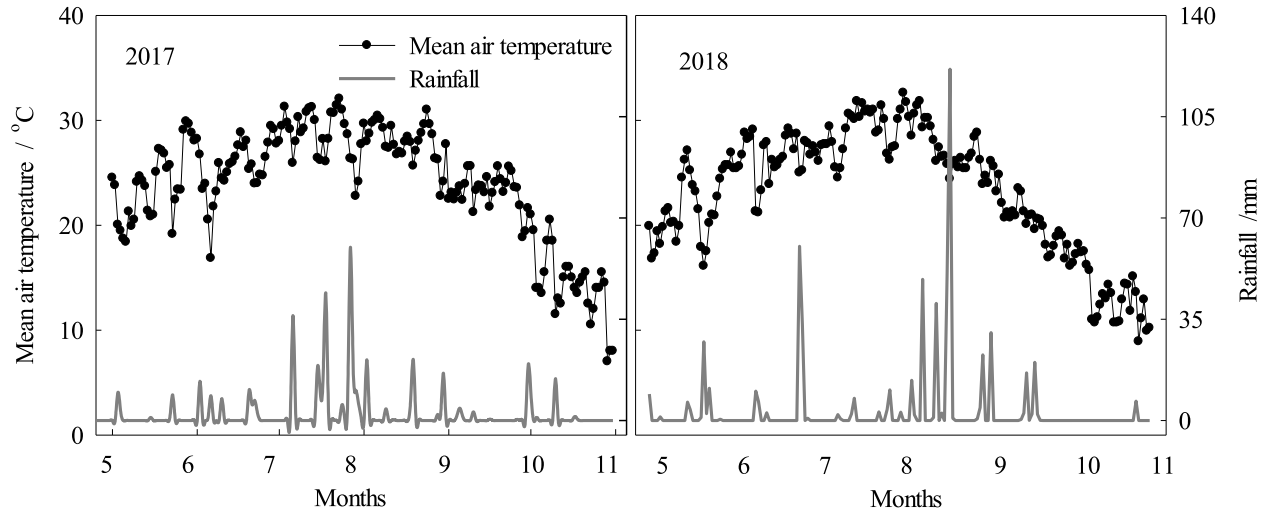

Fig. 1 Daily mean air temperature and rainfall recorded during the cotton growing seasons

manual hill-drop planting methods in late April in a randomized complete block design with three replications. Each plot contained eight rows of cotton, 8 m long with inter-row spacings of 1.0 m and 0.6 m, and a plant-to-plant distance of 0.25 m.

Seedlings were freed from mulching by cutting film above hills at full emergence and thinning to the desired planting density by retaining one vigorous plant per hill at the two-leaf stage. Vegetative branches and growth terminals on the main stems of cotton plants in each plot were completely removed at squaring in mid-June and at peak boll setting in mid-July. Basal fertilizer was applied at the rate of 110 kg·hm^{-2} of pure nitrogen, 120 kg·hm^{-2} of P_2O_5, and 120 kg·hm^{-2} of K_2O with urea (46%, N), superphosphate (12%, P_2O_5), and potassium sulfate (50%, K_2O). In addition, 110 kg·hm^{-2} of pure nitrogen was top-dressed in the flowering and boll-setting stages. Other management practices, such as, insect and weed control and plant growth regulator applications, were conducted according to local agronomic practices.

$^{13}CO_2$ labeling and measurement

A $^{13}CO_2$ feeding experiment was conducted to determine export and partitioning of labeled assimilates in various plant parts for a short (72 h) and a long (from the day of feeding to the end of harvest) time period. Two groups of three consecutive and representative cotton plants were selected separately in each plot for $^{13}CO_2$ labeling on a clear and windless day, from 9 to 11 a.m., during each of the three key stages of boll-formation (the early flowering stage, the peak flowering stage, and the peak boll-setting stage). $^{13}CO_2$ was generated by a reaction between $Ba^{13}CO_3$ (provided by Shanghai Research Institute of Chemical Industry with a purity of > 98%) and 1 mol·L^{-1} hydrochloric acid. Following the method described by Bie et al. (1998), we controlled the concentration of CO_2 in the sealed photosynthetic chamber at 0.5%. Three cotton plants were enclosed in a photosynthetic chamber (the volume was 0.9 m^3, the length was 0.75 m, the width was 0.8 m, and the height was 1.5 m) into which a 2-L beaker of $Ba^{13}CO_3$ was placed in the middle between the three plants. Excess hydrochloric acid was injected using a 50-mL syringe to produced $^{13}CO_2$. The plants assimilated the $^{13}CO_2$ under natural light conditions for 1 h.

One group of the three consecutive labeled plants was harvested at 72 h after the end of the $^{13}CO_2$ assimilation. Harvested plants were immediately divided into roots, main stem, branches, leaves, and fruits. The fruits were further separated according to within-plant position: lower bolls at the position of 1–4 fruiting branches, middle bolls at the position of 5–8 fruiting branches, upper bolls at the position of greater than nine fruiting branches, inner bolls at the fruiting node of 1–2 near the main stem, and distal bolls at the fruiting node of three and greater at the main stem. All the separated plant parts were dried at 65 °C to a constant weight. The plant parts were then weighed and ground to a fine powder with a micro grinding-machine (Model FZ 102 Taisite Co. Ltd., Tianjin, China; Type MM400 Retsch GmbH, Haan, Germany). Sub samples (4 mg) were used to determine the ^{13}C abundance with an Isoprime 100 instrument (Isoprime 100 Isoprime Ltd., Cheadle, UK).

The other labeled group was enclosed in a 5 cm mesh nylon protective net and the shedding organs and opening bolls were regularly collected. The plants were uprooted at harvest time. The vegetative organs were separated into roots, main stems, branches, leaves, and redundant buds. The reproductive organs were harvested according to fruiting position (lower, middle, upper, inner, and distal),

and subdivided into boll shell, fiber, and seed. The shedding organs were divided into leaves, buds, and bolls. Plant parts were individually bagged, dried, weighed, ground as above, and then the ^{13}C abundance was determined according to the method of Liu et al. (2015).

Within-plant boll distribution and lint yield

Two central rows of cotton plants were manually harvested to determine yield and yield components. Opening bolls were hand-harvested according to fruiting position and numbers of bolls were recorded separately. Seed cotton was weighed after sun-drying, and then the individual boll masses were determined. The cotton seeds and fibers were separated using a roller ginning machine (Jianghe SY-20A, Henan Jianghe Machinery Factory, China), and the lint percentage was then determined. The overall yield was calculated by multiplying the following three yield components: the number of bolls, average boll weight, and lint percentage.

Statistical analysis

The mean and standard error were calculated using the three replicates from each treatment with Microsoft Excel 2010. Lint yield and yield component data shown in this paper represents the averages of 2017 and 2018. Analysis of variance was conducted using the General Linear Models procedure in SPSS 20 (IBM, Armonk, NY, USA). Least significant differences were used to compare treatment means at $P < 0.05$. In the two-year data analysis, cultivar and year were entered as fixed effects, and block (replicate) was entered as a random factor and nested within year. All graphs were drawn using Sigma Plot 12.5 software (Systat Software Inc., San Jose, CA, USA).

Results

Yield and yield components

Cotton yield was significantly affected by year and cultivar (Table 1). Boll number and lint percentage were only affected by year while boll weight was only affected by cultivar. This indicates that boll weight is genetically determined. No interaction effect between year and cultivar was observed in relation to yield and its components except boll weight. The lint yield of J169 was the highest, followed by L21 and 99B. The variation in boll weight of the three cultivars was consistent with its yield: J169 had the largest boll weight, 13.2% and 38.8% higher than L21 and 99B, respectively. However, the other two yield components were inconsistent with the yield. There was no significant difference in lint percentage between any of the treatments. Although the boll number of 99B was significantly higher than that of J169, it could not compensate for the yield gap caused by the smallest boll weight. Furthermore, path analysis of yield components and lint yield among the three cultivars showed that boll number and weight contributed almost equally to the yield, yet lint percentage was negatively correlated.

Genotypic variance in within-plant boll distribution

A significant difference among the three cultivars was detected when comparing boll distribution, boll weight, and the percentage of total plant yield, but not the lint percentages of any fruiting position or node (Table 2). In the vertical fruiting position, the proportion of middle bolls was significantly higher than that of the upper bolls, but was much lower than that of the bottom bolls (within-plant). No genotypic variation was observed in the proportion of lower bolls. However, there were significant genotypic differences in the middle and upper bolls. The proportion of upper bolls in J169 was much higher than that of other cultivars, but the opposite result was observed for middle bolls. The only significant difference between L21 and 99B was in terms of the proportion of upper bolls. In the horizontal fruiting node, the proportion of inner bolls was 2–4 times higher than that of the distal bolls within individual plant. J169 and L21 had 19.6% and 17.3% higher proportions of inner bolls than 99B, respectively. However, in terms of distal bolls, 99B had a much higher percentage compared with J169 and L21. Significant genotypic differences in boll

Table 1 Genotypic variance in yield and yield components

Cultivar		Boll number /($\times 10^4$ hm^{-2})	Boll weight /g	Lint percentage /%	Lint yield /(kg·hm^{-2})
J169		71.58 b	7.05 a	40.91	2059.17 a
L21		69.17 b	6.23 b	40.56	1 733.59 b
99B		77.27 a	5.08 c	40.32	1 583.92 c
P-value	Year (Y)	0.000 9	ns	0.000 6	0.006 4
	Cultivar (C)	ns	< 0.000 1	ns	0.013 5
	Y × C	ns	0.000 6	ns	ns
Path coefficient		0.646 0**	0.633 8**	−0.194 9	–

1) J169, Jimian 169; L21, Lumianyan 21; 99B, DP 99B. Means within a column followed by different letters are not significantly different at $P < 0.05$
2) "ns" means non significance
3) "**" means significantly correlation

Table 2 Within-plant genotypic variance in boll distribution

	Cultivar	Vertical distribution			Horizontal distribution	
		Lower	Middle	Upper	Inner	Distal
Boll fraction/%	J169	51.53 a	28.41 b	20.06 a	80.27 a	19.73 b
	L21	53.98 a	33.09 a	12.93 c	78.71 a	21.29 b
	99B	49.60 a	35.36 a	15.04 b	67.10 b	32.90 a
Boll weight/g	J169	7.38 a	7.15 a	6.61 a	7.46 a	6.64 a
	L21	6.32 b	6.24 b	6.13 b	6.73 b	5.73 b
	99B	5.14 c	5.23 c	4.88 c	5.33 c	4.83 c
Lint percentage/%	J169	40.88 a	41.63 a	40.20 a	41.22 a	40.59 a
	L21	41.18 a	41.10 a	39.39 a	41.09 a	40.02 a
	99B	40.78 a	40.96 a	39.23 a	41.00 a	39.65 a
Percentage of total plant yield/%	J169	52.99 ab	28.76 c	18.25 a	82.24 a	17.76 b
	L21	54.63 a	33.14 b	12.22 c	81.72 a	18.28 b
	99B	49.81 b	36.39 a	13.80 b	69.86 b	30.14 a

[a, b,] and [c] Values are mean±standard deviation. Values followed by a different small letter within same row are significantly different in a column at 0.05 probability level

weight by node and position per plant were detected between all three cultivars with J169 the largest, followed by L21 and 99B. This was likely due to the high number of inner bolls observed. The variation in the percentage of total plant yield produced by each zone among the three cultivars was in line with the observations of boll proportions.

Genotypic variance in ^{13}C-photosynthate partitioning at different growth stages

^{13}C- photosynthate partitioning to different organs

No significant difference was observed in ^{13}C-photosynthate partitioning to vegetative organs among the three cultivars, except for 99B which contained a higher amount of assimilate than L21 at the peak boll-setting stage (caused by the high transportation in root and branch) (Table 3). In contrast to the vegetative organs, the export of carbohydrate from photosynthesizing organs to reproductive organs was found to be related to genotypic differences in this study. L21 partitioned the highest ratio of photosynthate to bolls at the three labeled stages, which was 19.6%, 21.2%, and 3.6% higher than that of J169, and 25.9%, 28.5%, and 12.6% higher than that of 99B, respectively. Furthermore, photosynthate transported to fruit in J169 was significantly higher than 99B in the peak flowering and boll-setting stages.

^{13}C-photosynthate partitioning to bolls at varying within-plant position and fruiting node

The same within-plant pattern of photosynthate partitioning was observed in bolls in relation to position and node among the three cultivars at any of the labeled stage (the early flowering stage, the peak flowering stage, and the peak boll-setting stage) (Table 4). Vertically, the

Table 3 Within-plant genotypic variance in distribution of ^{13}C- photosynthate to different organs after 72 h of ^{13}C-labeling at the early flowering, peak flowering, and peak boll-setting stages /%

Growth stage	Cultivar	Vegetative organ					Reproductive organ
		Root	Stem	Branch	Leaf	Total	
Early flowering stage	J169	8.35 b	25.41 a	10.35 b	48.73 a	92.84 a	7.16 b
	L21	8.30 b	26.46 a	11.12 a	45.56 b	91.44 a	8.56 a
	99B	9.04 a	25.35 a	8.96 c	49.86 a	93.20 a	6.80 b
Peak flowering stage	J169	6.69 b	26.62 b	13.27 a	43.40 a	89.98 a	10.02 b
	L21	7.13 ab	29.17 a	11.96 b	39.59 b	87.86 a	12.14 a
	99B	7.59 a	27.91 ab	13.02 a	42.03 a	90.55 a	9.45 c
Peak boll-setting stage	J169	4.41 c	19.15 a	9.81 b	28.24 a	61.61 ab	38.39 a
	L21	5.17 b	18.41 a	8.55 c	28.11 a	60.24 b	39.76 a
	99B	5.62 a	18.89 a	10.70 a	29.48 a	64.70 a	35.30 b

[a, b,] and [c] Values are mean±standard deviation. Values followed by a different small letter within same row are significantly different in a column at 0.05 probability level

Table 4 Within-plant genotypic variance in ^{13}C-photosynthate partitioning in bolls depending on position and node after 72 h ^{13}C-labeling at the early flowering, peak flowering, and peak boll-setting stages /(%)

Growth stage	Cultivar	Vertical distribution			Horizontal distribution	
		Lower	Middle	Upper	Inner	Distal
Early flowering stage	J169	66.83 b	28.82 a	4.35 a	80.68 ab	19.32 b
	L21	76.36 a	21.28 c	2.36 c	82.65 a	17.35 c
	99B	70.10 b	26.39 b	3.51 b	76.85 b	23.15 a
Peak flowering stage	J169	60.16 b	26.08 a	13.76 a	86.99 a	13.01 c
	L21	66.46 a	23.45 b	10.09 b	83.88 a	16.12 b
	99B	62.35 b	26.81 a	10.84 b	79.17 b	20.83 a
Peak boll-setting stage	J169	56.91 b	32.41 b	10.69 a	96.45 a	3.55 b
	L21	57.38 b	37.42 a	5.20 b	97.32 a	2.68 c
	99B	77.03 a	20.30 c	2.67 c	87.04 b	12.96 a

[a, b,] and [c] Values are mean±standard deviation. Values followed by a different small letter within same row are significantly different in a column at 0.05 probability level

middle bolls contained higher levels of photosynthate than the upper bolls but lower levels than the lower bolls. Horizontally, the inner fruits contained much higher photosynthate levels than the distal parts. The transportation of photosynthate to the lower bolls in L21 was much higher than that of J169 and 99B at the early and peak flowering stages, whereas 99B partitioned a much higher amount of carbohydrate to the lower parts than the other two cultivars at the peak boll-setting stage. These results suggest that 99B distributes more assimilate to the distal nodes of bottom fruiting branches. J169 and 99B transported 11.2%–35.4% and 14.3%–24.0% higher amounts of assimilate, respectively, to middle bolls than L21 at the early and peak flowering stages, but the opposite was observed at the peak boll-setting in which L21 transported the highest amount. The partitioning of photosynthate to the upper bolls in J169 was the highest among the measured cultivars, which was 84.3%, 36.4%, and 105.6% higher than that of L21, and 23.9, 26.9, and 300.4% higher than that of 99B at the three labeled stage (the early flowering stage, the peak flowering stage, and the peak boll-setting stage), respectively. J169 and L21 partitioned 5.0%–10.8% and 5.9%–11.8% more carbohydrate to inner bolls than 99B, respectively. Significant genotypic differences were detected in the carbohydrate partitioning of the distal bolls, which was 99B the highest, L21 the second, and J169 the lowest.

Genotypic variance in ^{13}C-photosynthate partitioning at different growth periods

Within-plant ^{13}C-photosynthate partitioning in different organs Significant genotypic differences were observed in the partitioning of ^{13}C-photosynthate to various organs during boll setting (Table 5). In the growth period of early flowering to boll-opening, the partitioning of photosynthate to the vegetative organs in 99B was significantly higher than that of J169 and L21, due to a high proportion of photosynthate to the transported and redundant organs. Photosynthate partitioning to the reproductive organs of J169 was 14.1% and 14.8% higher than that of L21 and 99B, respectively. Photosynthate partitioning to fiber was also 41.9% higher in J169 than 99B. Although there was no significant difference between cultivars in terms of total photosynthate distributed to cotton bolls, L21 did partition much higher amounts of photosynthate to fiber than 99B. Furthermore, the shedding organs (squares, flowers and young bolls) of L21 wasted 30.3% and 47.3% more carbohydrate than J169 and 99B, respectively.

From peak flowering to boll-opening stage, J169 partitioned 9.2% and 12.1% more photosynthate to vegetative organs than L21 and 99B, respectively, with a high proportion of carbohydrate observed in fruiting branches and leaves. There were no genotypic differences in photosynthate partitioning to the overall reproductive organs, but the ratio of photosynthate transported to boll shells in L21 and 99B were 22.4% and 23.3% higher than in J169, respectively. Additionally, the photosynthate consumed by the shedding organs in L21 and 99B were approximately 1.2 times that of J169.

In the period between peak boll-setting and harvest, L21 partitioned 11.5% and 7.9% higher amounts of photosynthate to the overall vegetative organs than J169 and 99B, respectively, resulting by the high ratio of assimilate to root and stem. The distribution ratio of photosynthate to bolls in J169 was comparable to that of 99B but 12.6% higher than that of L21. J169 partitioned the highest amount of photosynthate to the shedding organs, being 22.0% and 13.1% higher than that of L21 and 99B, respectively.

Table 5 Within-plant genotypic variance in distribution of ^{13}C-photosynthate to different organs during the period of early flowering to boll-opening stage, the peak flowering to boll-opening stage, and the peak boll-setting to boll-opening stage /%

	Growth period	Early flowering – boll-opening stage			Peak flowering – boll-opening stage			Peak boll-setting – boll-opening stage		
	Cultivar	J169	L21	99B	J169	L21	99B	J169	L21	99B
Vegetative organs	Root	5.22 a	5.15 a	4.20 b	10.20 b	13.78 a	7.83 c	15.27 b	22.82 a	14.20 c
	Stem	14.63 b	16.39 a	16.22 a	17.87 b	19.15 a	17.54 b	19.03 b	21.81 a	20.13 b
	Fruit branch	6.77 c	7.92 b	14.24 a	10.58 a	8.83 b	9.12 b	10.11 a	8.99 c	9.55 b
	Leaf	7.91 a	1.86 c	4.39 b	11.69 a	6.37 b	6.64 b	11.55 b	13.77 a	11.77 b
	Redundant shoot	3.66 c	5.69 b	6.83 a	4.74 c	5.02 b	7.19 a	6.90 c	7.43 b	8.53 a
	Total	38.19 b	37.02 b	45.88 a	48.81 a	44.68 b	43.55 b	53.09 b	59.18 a	54.87 b
Reproductive organs	Shell	10.10 b	9.77 b	11.79 a	8.17 b	10.00 a	10.07 a	8.00 a	8.07 a	7.53 a
	Fiber	11.31 a	10.84 a	7.97 b	8.61 b	8.93 b	9.65 a	9.31 a	7.74 b	9.17 a
	Seed	19.70 a	15.45 b	16.05 b	17.60 a	15.46 b	16.23 b	17.30 a	14.93 b	17.55 a
	Total	41.11 a	36.03 b	35.81 b	34.38 a	34.39 a	35.95 a	34.61 a	30.74 b	34.25 a
Shedding organs	Leaf	16.10 b	20.72 a	14.16 c	12.65 b	16.81 a	17.39 a	10.84 a	9.36 b	10.69 a
	Corolla	1.31 c	2.22 a	1.50 b	0.94 b	1.36 a	0.81 c	–	–	–
	Fruit	3.28 b	4.01 a	2.64 c	3.22 a	2.77 b	2.30 c	1.46 a	0.72 b	0.19 c
	Total	20.69 b	26.95 a	18.30 c	16.81 b	20.93 a	20.50 a	12.30 a	10.08 c	10.88 b

[a, b,] and [c] Values are mean±standard deviation. Values followed by a different small letter within same row are significantly different in a column at 0.05 probability level

Within-plant ^{13}C-photosynthate partitioning in bolls according to position and node Significant genotypic differences were demonstrated in the partitioning of photosynthate to bolls depending on spatial arrangement (Table 6). The distribution ratio of photosynthate to the lower bolls in L21 was 10.7% and 21.8% higher than that of J169, and 8.0% and 6.1% higher than that of 99B during two growth periods (early flowering to boll-opening stage, and peak flowering to boll-opening stage), respectively. However, from the peak boll-setting to the end of harvest, 99B partitioned 31.0% and 21.3% higher amount of photosynthate to the bottom bolls than J169 and L21, respectively. There was no significant difference in the distribution of assimilate to the middle bolls among the three cultivars during the period of early flowering to boll-opening stage. However, 99B transported the most photosynthate to the middle bolls, being 50.3% and 57.5% higher, respectively, than J169, and 51.2% and 12.1% higher, respectively, than L21 in the period of peak flowering to boll-opening stage and the period of peak boll-setting stage to the end of harvest. Significant differences were observed in the photosynthate

Table 6 Within-plant genotypic variance in ^{13}C-photosynthate partitioning in bolls according to position and node during the period of early flowering to boll-opening stage, the peak flowering to boll-opening stage, and the peak boll-setting to boll-opening stage /%

Growth period	Cultivar	Vertical distribution			Horizontal distribution	
		Lower	Middle	Upper	Inner	Distal
Early flowering – boll-opening stage	J169	55.26 b	33.56 a	11.18 a	87.03 a	12.97 c
	L21	61.19 a	32.38 a	6.43 c	73.77 b	26.23 b
	99B	56.65 b	34.06 a	9.29 b	62.71 c	37.29 a
Peak flowering – boll-opening stage	J169	29.34 c	29.73 b	40.93 a	82.89 a	17.11 c
	L21	35.74 a	29.56 b	34.70 b	81.85 a	18.15 b
	99B	33.67 b	44.69 a	21.65 c	70.87 b	29.13 a
Peak boll-setting – boll-opening stage	J169	28.16 c	29.65 c	42.19 a	86.43 a	13.57 c
	L21	30.40 b	41.66 b	27.94 b	72.31 b	27.69 b
	99B	36.89 a	46.71 a	16.40 c	64.28 c	35.72 a

[a, b,] and [c] Values are mean±standard deviation. Values followed by a different small letter within same row are significantly different in a column at 0.05 probability level

partitioning to the upper bolls between any of the labeled cultivars in which J169 the most, L21 the second, and 99B the lowest. Similarly, J169 allocated the highest amount of photosynthate to inner bolls during the three key periods of boll-forming, which was 20.0, 1.3, and 19.5 higher than of L21, and 38.8%, 17.0% and 34.5% higher than that of 99B, respectively. In contrast to findings for the inner bolls, photosynthate transported to distal bolls in 99B was the highest among the cultivars, followed by L21 and J169.

Discussion

The present study has further confirmed the common perception that genotypic variance in lint yield can be attributed to photosynthate partitioning. This study has also provided new insights into how photosynthate partitioning affects lint yield through mediating yield components and within-plant boll distribution.

Genotypic variation in yield and within-plant boll distribution

Cotton yield varied significantly depending on cultivar type and environment. The main reason for this yield difference was boll number and weight. The simultaneous growth of vegetative and reproductive organs through most of cotton's growth cycle often induces fruit forming at various times on different parts of a plant (Bednarz et al. 2005; Ritchie et al. 2009). This ultimately affects the overall yield and time of harvest. High yielding cotton cultivars produce more bolls in the inner nodes and upper branches (Mao et al. 2015; Dai et al. 2015; Nie et al. 2019). Results in this experiment showed that high yields are obtainable from newly cotton cultivars and this is attributable to their large boll weight in conjunction with a high number of bolls. Further analysis of plant boll distribution showed that high-yielding cotton cultivars: produced more bolls in the first and second nodes (the inner part of a fruiting branch), contained higher boll numbers in the upper branches, and distributed bolls in an optimal arrangement vertically up through the plant. A higher proportion of inner bolls is preferred during cotton harvests, as it helps improve fiber uniformity (Davidonis et al. 2004; Dong et al. 2014). Additionally, the increase of upper bolls can effectively weaken the apical dominance, thereby promote the no–topping and light and efficient cultivation of cotton (Dong et al. 2018).

Effects of photosynthate partitioning on boll distribution and yield formation

High yield crops not only have leaves with strong photosynthetic capacity, but also transport photosynthate to the reproductive organs in a timely and effective manner (Wullschleger and Oosterhuis 1990). Photosynthate partitioning to various organs has a significant effect on cotton yield and differs depending on the cultivar (Wells and Meredith 1984a, b). The results of this study showed that J169 and L21 cultivars partitioned more photosynthate to bolls than the 99B cultivar. In addition, the proportion of photosynthate transported to the fiber and seed of J169 was significant high than that of L21, so the yield of J169 was the highest, followed by L21 and 99B.

Photosynthate consumed by abscission organs not only waste plant nutrients, but also may disturb coordination growth of vegetative and reproductive organs, especially in the indeterminate growth habit of cotton. Premature and excessive transport of photosynthate to the reproductive organs usually induces early senescence in the middle-late stage. In our study, L21 partitioned much more photosynthate to the fruit in the early and peak flowering stages than the other cultivars, which induced the early senescence of photosynthetic organs and a reduction in the number of upper bolls formed. This finding was also reflected in the genotypic differences of photosynthate partitioning to the reproductive organs observed at each labeled stage, i.e., L21 had a high instantaneous photosynthesis rate and transfer efficiency of photosynthate to bolls while J169 had a low instantaneous transfer efficiency of photosynthate but a high redistribution of stored carbohydrate to bolls. These results suggest that the increase of photosynthetic rate may not be enough to increase the cotton yield, and it is of great significance to improve the redistribution of photosynthate for the breeding of high-yielding cultivars in the future.

The formation time and within-plant position of bolls affect the direction and distance of photosynthate partitioning (Sadras 1995). Previous studies have shown that the stability of lint yield within a certain density range was due to the strong self-regulation ability of the cotton plant and a high amount of assimilate being distributed to the dominant boll to achieve the optimal combination of boll number and weight (Dai et al. 2015; Mao et al. 2015). A high proportion of photosynthate partitioned to the shell usually results in a lower weight of seed cotton (Liang et al. 2005). In the present study, the high-yielding cultivar J69 not only partitioned high amount of photosynthate to the bolls and fibers, but also more than 80% of photosynthate was supplied to the inner bolls, which resulted the highest number of inner bolls and large bolls. Moreover, high proportion of assimilates transferred to leaves and fruiting branches of J169 could prolong the photosynthetic period and provide abundant carbohydrate for the bolls after the peak flowering stage, which was the main reason for the highest number of upper bolls. The increase of upper bolls not only optimized within-plant boll distribution, but also reduced the potential early senescence and boll rot caused by a

high proportion of lower bolls. L21 partitioned more photosynthate to fruit and fiber than 99B did, and the proportion of photosynthate partitioned to inner bolls was 12.5%–17.6% higher than that of 99B. The lowest photosynthate partitioned to the fruit was detected in 99B with more than 30% supplied to distal bolls, which resulted the highest number of distal bolls. The high proportion of photosynthate partitioned to the boll-shell in 99B was seriously affected the development of seed cotton and led to the lowest boll weight. The high proportion of photosynthate partitioned to the redundant buds in 99B induced a large amount of secondary growth, which not only restricted boll development, but also caused shadowing in the field and affected the opening of bolls. These results suggest that the high-yield cotton cultivars had the optimized pattern of photosynthate partitioning. The characteristics of photosynthate partitioning and the pattern of plant boll distribution of J169 are conducive to the concentrated distribution of high-quality bolls. Agronomic measures such as high plant density, chemical regulation with mepiquat chloride, and nitrogen fertilization at flowering can improve photosynthate partitioning to cotton bolls in the inner and middle of plants, and thus they are beneficial to the formation of fiber yield and quality.

Conclusions

This study has provided new insights into how photosynthate partitioning affects lint yield through mediating yield components and within-plant boll distribution. Specifically, the synergistic increase in the number of inner and large bolls resulted in a higher lint yield for the newly bred cultivars. This was related to a particular pattern of photosynthate partitioning, i.e., a high proportion of photosynthate partitioned to the leaves and fruiting branches in the middle-late growth stage; a high amount of photosynthate distributed to the fruit and fiber, especially the inner bolls; and an even distribution of assimilate caused by the high number of upper bolls. These results provide new guidance for high-yield cultivar breeding programs and cotton cultivation in terms of the optimization and improvement of boll-setting.

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Authors' contributions

Sun XZ and Song XL designed and performed the experiments. Nie JJ wrote the main manuscript text and prepared all figures. Nie JJ, Qin DL and Mao LL carried out the experimental work and data analysis. Sun XZ, Song XL, Dong HZ, and Liu YH revised and polished the manuscript. All authors contributed in the interpretation of results and approved the final manuscript.

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Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

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Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors have declared that no competing interests exist.

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References

Ainsworth EA, Bush DR. Carbohydrate export from the leaf: a highly regulated process and target to enhance photosynthesis and productivity. Plant Physiol. 2011;155:64–9. https://doi.org/10.1104/pp.110.167684.

Ashley DA. ^{14}C-labelled photosynthate translocation and utilization in cotton plants. Crop Sci. 1972;12:69–74. https://doi.org/10.2135/cropsci1972.0011183X001200010023x.

Bange MP, Milroy SP. Growth and dry matter partitioning of diverse cotton genotypes. Field Crop Res. 2004;87:73–87. https://doi.org/10.1016/j.fcr.2003.09.007.

Bednarz CW, Shurley WD, Anthony WS, Nichols RL. Yield, quality, and profitability of cotton produced at varying plant densities. Agron J. 2005;97:235–40. https://doi.org/10.1051/agro:2004062.

Bhardwaj SN, Nath V, Mehra RB. Plant type in relation to fruiting coefficient in upland cotton (*Gossypium hirsutum* L.). Indian J Agr Sci. 1971;41:519–23. https://doi.org/10.1016/S2095-3119(15)61174-1.

Bie S, Tang SF, Zhang JH, et al. Transportation and distribution of ^{14}C-assimilation product within cotton leaf of vegetative shoot and fruit bearing shoot. Hubei Agri Sci. 1998;4(2):8–10. https://doi.org/10.3969/j.issn.0439-8114.1998.04.002 .

Brown CL. The influence of external pressure on the differentiation of cells and tissues cultured in vitro. In: Zimmermann MH, editor. The formation of wood in forest trees. New York: Academic Press; 1973. p. 389–404.

Constable GA, Bange MP. The yield potential of cotton (*Gossypium hirsutum* L.). Field Crop Res. 2015;182:98–106. https://doi.org/10.1016/j.fcr.2015.07.017.

Dai JL, Li WJ, Tang W, et al. Manipulation of dry matter accumulation and partitioning with plant density in relation to yield stability of cotton under intensive management. Field Crop Res. 2015;180:207–15. https://doi.org/10.1016/j.fcr.2015.06.008.

Davidonis GH, Johnson AS, Landivar JA, Fernandez CJ. Cotton fiber quality is related to boll location and planting date. Agron J. 2004;96:42–7. https://doi.org/10.2134/agronj2004.0042.

Ding J, Zhang DY, Sun HZ, Tang YW. Studies on the relation between translocation of photosynthetic product and the physiological shedding of buds and bolls of cotton plant. Acta Biol Experi Sin. 1960;7:147–60.

Dong HZ. International competitiveness of China cotton in seed industry and fiber quality. China Cotton. 2013;40(7):1–5 (in Chinese with English abstract).

Dong HZ, Mao SC, Zhang WF, Chen DH. On boll-setting optimization theory for cotton cultivation and its new development. Sci Agric Sin. 2014;47:441–51. https://doi.org/10.3864/j.issn.0578-1752.2014.03.004.

Dong HZ, Zhang YJ, Zhang DM, et al. New grouped harvesting-based population structures of cotton. Sci Agric Sin. 2018;51:4615–24. https://doi.org/10.3864/j.issn.0578-1752.2018.24.003.

Guinn G. Causes of square and boll shedding in cotton. US Department of Agriculture Tech Bull 1672. Washington, D.C.: USDA. 1982. https://naldc.nal.usda.gov/download/CAT87201601/PDF.

Hearn AB. The growth and performance of cotton in a desert environment: II. Dry matter production. J Agric Sci. 1969;73:75–86. https://doi.org/10.1017/s0021859600024.

Hu HB, Zhang WJ, Chen BL, et al. Changes in C/N ratio of subtending leaf of cotton boll and its relationship with cotton boll dry matter accumulation and distribution. Acta Agron Sin. 2008;34:254–60. https://doi.org/10.3724/SP.J.1006.2008.00254.

Iqbal M, Naeem M, Rizwan M, et al. Studies of genetic variation for yield related traits in upland cotton. Am-Eurasian J Agri Env Sci. 2013;13:611–8. https://doi.org/10.5829/idosi.aejaes.2013.13.05.835.

Kong FL, Jiang BG, Zhang QY, Yang FX. Genetic improvements of cotton varieties in Huang-Huai region in China since 1950s I. Improvements on yield and yield components. Acta Agron Sin. 2000;26:148–56. https://doi.org/10.3321/j.issn:0496-3490.2000.02.004 .

Lee JA. Cotton as a world crop. In: Kohl RJ, Lewis CF, editors. Cotton. Madison: American Society of Agronomy; 1984. p. 1–25.

Liang ZJ, Zhao HZ, Qi HL. Studies on genetic improvement and effects on production and distribution of photosynthate among different genotypes of cotton. Cotton Sci. 2005;17(1):18–22. https://doi.org/10.3969/j.issn.1002-7807.2005.01.004 .

Liu HJ, Shi CY, Chai SS. Difference and related reason for assimilate distribution of sweetpotato varieties with different root tuber yields. Acta Agron Sin. 2015;41(3):440–7. https://doi.org/10.3724/SP.J.1006.2015.00440.

Mao LL, Zhang LZ, Eversc JB, et al. Yield components and quality of intercropped cotton in response to mepiquat chloride and plant density. Field Crop Res. 2015;179:63–71. https://doi.org/10.1016/j.fcr.2015.04.011.

Mao SC. Global cotton 60 years review and outlook. China Cotton. 2010;37(8):2–6. https://doi.org/10.3969/j.issn.1000-632X.2010.08.001.

Mason TG, Maskell EJ. Studies on the transport of carbohydrates in the cotton plant. I. A study of diurnal variation in the carbohydrates of leaf, bark, and wood, and of the effects of ringing. Ann Bot. 1928a;42:189–253. https://doi.org/10.1093/oxfordjournals.aob.a090110 .

Mason TG, Maskell EJ. Studies on the transport of carbohydrates in the cotton plant. II. The factors determining the rate and the direction of movement of sugars. Ann Bot. 1928b;42:571–636. https://doi.org/10.1093/oxfordjournals.aob.a090131.

Mason TG, Maskell EJ, Phillis E. Further studies on transport in the cotton plant. III. Concerning the independence of solute movement in the phloem. Ann Bot. 1936;50:23–58. https://doi.org/10.1093/oxfordjournals.aob.a090582.

Nie JJ, Yuan YC, Qin DL, et al. Spatial distribution of bolls affects yield formation in different genotypes of Bt cotton varieties. J Integr Agr. 2019;18:2492–504. https://doi.org/10.1016/S2095-3119(19)62617-1.

Ritchie GL, Whitaker JR, Bednarz CW, Hook JE. Subsurface drip and overhead irrigation: a comparison of plant boll distribution in upland cotton. Agron J. 2009;101:1336–44. https://doi.org/10.2134/agronj2009.0075.

Sadras VO. Compensatory growth in cotton after loss of reproductive organs. Field Crop Res. 1995;40:1–18. https://doi.org/10.1016/0378-4290(94)00088-T.

Tang B, Jenkins JN, Mccarty JC, Watson CE. F_2 hybrids of host plant germplasm and cotton cultivars. I. Heterosis and combining ability for lint yield and yield components. Crop Sci. 1993;33:700–5. https://doi.org/10.2135/cropsci1993.0011183X003300040012x .

Verhalen LM, Mamaghani R, Morrison WC, McNew RW. Effect of blooming date on boll retention and fiber properties in cotton. Crop Sci. 1975;15:47–52. https://doi.org/10.2135/cropsci1975.0011183X001500010014x.

Wells R, Meredith WR. Comparative growth of obsolete and modern cotton cultivars. II. Reproductive dry matter partitioning. Crop Sci. 1984a;24:863–8. https://doi.org/10.2135/cropsci1984.0011183X002400050008x.

Wells R, Meredith WR. Comparative growth of obsolete and modern cotton cultivars. III. Relationship of yield to observed growth characteristics. Crop Sci. 1984b;24:868–72. https://doi.org/10.2135/cropsci1984.0011183X002400050010x.

Wullschleger SD, Oosterhuis DM. Photosynthetic and respiratory activity of fruiting forms within the cotton canopy. Plant Physiol. 1990;94:463–9. https://doi.org/10.1104/pp.94.2.463.

Yang GZ. Evolution and international comparison of export competitiveness of textile and garment industry of China. Wool Textile J. 2014;42:52–8.

Zheng ZZ, Chen JX. Studies on the relation between reproductive growth and shedding of buds and bolls in cotton plant. Sci Agric Sin. 1980;13:51–8.

Zhi XY, Han YC, Li YB, et al. Effects of plant density on cotton yield components and quality. J Integr Agr. 2016;15:1469–79. https://doi.org/10.1016/S2095-3119(15)61174-1.