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The effects of straw-returning and inorganic K fertilizer on the carbon–nitrogen balance and reproductive growth of cotton

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Abstract

Background: Many studies have indicated that straw-returning could meet part or even all of the potassium (K) demand for crop growth in the field, but few have compared the effects of crop straw as K source and inorganic K fertilizer on carbon–nitrogen (C–N) balance of cotton and the reproductive growth. To address this, field experiments were conducted using the cotton cultivar, Siza 3, under there treatments (CK as control group one, no crop straw and inorganic K fertilizer were applied; K150 as control group two, 150 kg·ha^{-1} of K_2O was applied; and W9000, 9 000 kg·ha^{-1} wheat straw, which could provide K_2O about 150 kg·ha^{-1}, was incorporated into soil).

Results: Although the final reproductive organ biomass did not differ between W9000 and K150, W9000 had a higher ratio of reproductive organ biomass to total biomass (RRT), suggesting that straw-returning was more conducive to the allocation of biomass to reproductive organs. The theoretical maximum biomass of reproductive organ was higher, but the average and maximum accumulation rates of reproductive organ biomass were 2.8%~8.3% and 2.5%~8.2% lower under W9000 than K150. Also, the duration of rapid-accumulation period for reproductive organ biomass (T) was 2.0~2.8 d longer under W9000 than K150, which was a reason for the higher RRT under W9000. Straw-returning altered the dynamics of leaf K with the growth period, so that W9000 had a more drastic effect on leaf C metabolism than K150. Consequently, lower soluble sugar/free amino acid and C/N ratios were measured under W9000 than K150 at boll-setting (BSS) and boll-opening (BOS) stages. Higher leaf net photosynthetic rate, sucrose phosphate synthase and sucrose synthase activities, and lower acid invertase activity were observed under W9000 than K150 at BSS and BOS and these were more conducive to sucrose accumulation. However, less sucrose was measured under W9000 than K150 at these stages. This should be because straw-returning promoted the assimilate transport capacity when compared with inorganic K fertilizer application, which also explained the higher RRT under W9000 than K150. The lower acid invertase activity under W9000 inhibited the conversion of sucrose to other sugars, hence lower contents of soluble sugar and starch were measured under W9000 than K150.

Conclusion: Under low K condition, crop straw as K source can increase the assimilate transport from source to sink, leading to lower C/N ratio in leaf and higher allocation of biomass to reproductive organs than inorganic K fertilizer.

Keywords: *Gossypium hirsutum* L., Crop straw, Inorganic potassium fertilizer, Reproductive growth, C-N balance

Introduction

Cotton (*Gossypium hirsutum* L.) is a complex structure crop with indeterminate growth habit, which makes it more sensitive to soil potassium (K) status than other field crops (Oosterhuis 2001). Soil K deficiency would decrease boll weight, boll number and lint percentage

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(Pettigrew 1999; Chen et al. 2021), finally leading to low cotton yield. Previous studies have noticed that biomass production is the basis of cotton yield formation (Bange and Milroy 2004) and the proportion of biomass allocated to reproductive organs determines the final yield (Yang et al. 2012). Nutrients are the important factors affecting crop growth and biomass production (Xia et al. 2016). Among many nutrient elements, K plays an irreplaceable role in biomass production of crops. Past investigations have found that soil K shortage will affect the accumulation of total biomass (Makhdum et al. 2007; Hu et al. 2015), and the negative effects of K shortage on the growth of reproductive organs was significantly greater than that on vegetative organs (Hu et al. 2015). Wang et al. (2012) and Hu et al. (2017) attributed this result to the restriction caused by K deficiency on the transport of carbon (C) and nitrogen (N) assimilation products from source organs to sink organs, resulting in large amounts of assimilates accumulating in the leaves, not in the reproductive organs.

Zhang et al. (2014) observed that leaf C/N ratio was closely related to reproductive growth. Potassium application altered the C metabolism in cotton leaves (Wang et al. 2012), increased the activities of enzymes related to sucrose synthesis, such as sucrose synthase (SuSy) and sucrose phosphate synthase (SPS), and decreased the activity of enzymes responsible for sucrose decomposition, such as acid invertase, in cotton leaves (Zahoor et al. 2017a). Potassium application also decreased the contents of unstructured sugars (hexose, sucrose, starch) in cotton leaves (Hu et al. 2016a). Also, the N metabolism in cotton leaves was promoted by K fertilizer application. Potassium fertilizer application could improve NO_3^- uptake by roots (Rufty et al. 1981), leading to high N concentration and nitrate content in cotton leaves (Hu et al. 2016b; Zahoor et al. 2017b). Hu et al. (2017) found that K fertilizer application decreased the C/N ratio and the ratio of soluble sugar to free amino acid in cotton leaves, since after adding K fertilizer, the transport of C assimilation products to the reproductive organs was improved more significantly than that of N assimilation products.

In recent years, K deficiency in soil has become one of the main limiting factors for cotton production around the world, and this phenomenon is found in many parts of China (Wang et al. 2012). Thus, the farmers have to apply large amounts of inorganic K to cope with the soil K deficiency. However, the long-term application of inorganic K will result in a series of environmental problems, such as soil crusts, soil acidification and underground water pollution (Paradelo et al. 2013; Udeigwe et al. 2015). Also, the increasing price of K fertilizer has become a heavy burden on cotton producers (Dong et al. 2010). Hence, it is imperative to minimize the dependence on inorganic K for cotton production. Previous studies have showed that crop straw usually contains high K content (Almaz et al. 2017; Sui et al. 2017) and the K cation in crop straw is more easily released than other nutrients (Li et al. 2014). Wu et al. (2011) reported that K cation in crop residue could be released more than 90% after 90 days post decomposition. Thus, crop straw has been considered as bio-K fertilizer instead of inorganic K fertilizer in many countries (Sui et al. 2015). Some experiments have indicated that straw-returning could meet part or even all of the K demand for crop growth in the field (Tan et al. 2007; Liu et al. 2010; Zhao et al. 2014). Since wheat (*Triticum aestivum* L.) and cotton double cropping is widely adopted in the Yangtze Valley region, lots of wheat straw can be harvested before planting cotton. Previous studies have showed that 0.9 $t\cdot ha^{-1}$ wheat straw returning to soil could replace about 150 $kg\cdot ha^{-1}$ K_2O which is the recommended quantity of K application for cotton production in the Yangtze Valley region (Sui et al. 2015; Yu et al. 2016) in the short term (≤ 3 years). However, the nutrients in the straw are released gradually (Wu et al. 2011), and the nutrient release pattern of straw is similar to that of slow-release fertilizer (Zhang et al. 2018). Hence, the effect of straw returning to the field on the dynamic growth of crops may be different from that of inorganic K fertilizer. However, little is known of the comparative effects of straw-returning and inorganic K fertilizer application on cotton growth.

We hypothesized that crop straw as K source and inorganic K fertilizer would have different effects on C-N balance in cotton, which would influence the dynamic growth of reproductive parts. The objective of the current study was to explore and compare the effects of crop straw-returning and inorganic K fertilizer on the relationship between C and N metabolism, and the dynamics of cotton reproductive growth.

Materials and methods

Experimental materials and treatments

The cotton cultivar, Siza 3 was planted in the experimental field of Jiangsu Academy of Agricultural Sciences (clay soil with low available K content) in Nanjing (32° 20′ N and 118° 52′ E) from 2012 to 2013. The seeds were sown on 25 April in nutrient bowls. On 5 June, healthy and uniform seedlings were selected for transplanting in the field. There treatments [CK, no crop residue and K fertilizer as control group one; K150, 150 $kg\cdot ha^{-1}$ K_2O, which is the recommended quantity of K fertilizer in the Yangtze River cotton belt (Hu et al. 2015), was applied into the soil in the form of potassium sulfate before transplanting as control group two; and W9000, 9 000 $kg\cdot ha^{-1}$ wheat straw, which could supply about 150 $kg\cdot ha^{-1}$ of available K for cotton based on final cotton yield (Sui et al. 2015; Yu et al. 2016), was crushed and incorporated in

0～10 cm soil before transplanting] were designed for this experiment. A randomized complete blocks design with three replications was used for this experiment. The area of each plot was 7 × 4 m^2. The intra- and inter-row spacings were 0.3 m and 1.0 m, respectively. In addition, the placement of each plot was fixed in the 2 years. The nutrients in 0～20 cm soil before transplanting in each year are showed in the Additional file 1: Table S1. The nutrient (N, P and K) analysis of the crop straw performed using the Kjeldahl method (Nelson and Sommers 1972), the molybdenum blue colorimetric method (Rodriguez et al. 1994), and the flame atomic absorption spectrophotometer method (Hu et al. 2015), respectively, showed that the nutrients provided by 9 000 kg wheat straw were 96 kg N, 39 kg P_2O_5 and 161 kg K_2O in 2012 and 79 kg N, 37 kg P_2O_5 and 133 kg K_2O in 2013. In this study, sufficient N (300 $kg{\cdot}ha^{-1}$) and P (150 $kg{\cdot}ha^{-1}$ P_2O_5) were applied to all plots during the growth season (Yu et al. 2016).

Biomass accumulation

Three plants per plot were sampling at 80, 95, 110, 125, 140, 155 days after sowing (DAS) in 2012 and at 80, 95, 110, 125, 140 DAS in 2013 to measure the plant biomass. The plant samples were divided into vegetative organs (root, stem, fruiting branches, petiole and leaves) and reproductive organs including bolls, flowers, and buds. After the samples were oven-dried at 105 °C for 30 min and then at 80 °C to constant weight, the dry weight was recorded.

Sampling and processing

The functional leaf [the third (after tip pruning) or fourth (before tip pruning) from top to bottom of mainstem] was sampled at the peak flowering stage (PFS) on 15 July, 2012 and 18 July, 2013, at the boll-setting stage (BSS) on 15 August, 2012 and 15 August, 2013, and at the boll-opening stage (BOP) on 8 September 2012 and 10 September 2013. The sampled leaves were cleaned with deionized water. Then, the main veins of the leaves were abandoned. Half of the leaves to be used for the measurement of enzyme activities, were quick-frozen using liquid nitrogen before being stored at − 80 °C in an ultralow temperature freezer. The remaining leaves to be used for determining the concentrations of N, P and K and the contents of substance related to C and N metabolism, were dried in an 80 °C oven.

Net photosynthetic rate (P_n)

The P_n of functional leaf was measured between 9:00 and 11:00 using a Li-6400 gas exchange measuring system (Li-COR, Lincoln, NE, USA) in three replications. The leaf chamber condition was set at relative humidity of (65 ± 5)%, leaf temperature of (32 ± 2) °C, CO_2 concentration of (380 ± 5) $\mu mol{\cdot}mol^{-1}$, and quantum flux of 1 500 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$.

Leaf C, N, P and K contents

Leaf C content was assayed with the potassium dichromate wet digestion method according to Zhang et al. (2014). A H_2SO_4-H_2O_2 solution was used to digest the leaf tissues. Then, the contents of N, P and K in H_2SO_4-H_2O_2 solution were analyzed with the Kjeldahl method (Nelson and Sommers 1972), the molybdenum blue colorimetric method (Rodriguez et al. 1994), and the flame atomic absorption spectrophotometer method (Hu et al. 2015).

Carbohydrates and N compounds

Leaf tissues (0.1 g) and 80% (v/v) ethanol (5 mL) were placed into a 10 mL centrifuge tube. Then, the tube was heated for 30 min in an 80 °C water bath before centrifuging for 5 min at 4 000 $r{\cdot}min^{-1}$. The solid at the bottom of centrifuge tube was extracted twice more using 5 mL 80% (v/v) ethanol. After each centrifugation, the supernatant was collected. The final volume of the supernatant was fixed at 25 mL by adding 80% (v/v) ethanol. The anthrone colorimetric method was used for the assay of soluble sugar content and the resorcinol chromogenic method was used for the measurement of sucrose content in the final supernatant (Hendrix 1993). The final insoluble residue mentioned above was used for starch measurement. The starch in the residue was degraded to glucose using the perchloric acid decomposition method described previously (Hu et al. 2015). Then, the glucose content was assayed using the anthrone reagent (Morris 1948).

Nitrate content was extracted according to Ruiz and Romero (2002). Millipore-filtered water (10 mL) was used to extract nitrate in the dried leaves (0.2 g); 100 μL extract and 0.2 mL salicylic acid (10%) were added into a tube to wait for 20 min. Then, 4.75 mL NaOH (8%) was pipetted into the tube to wait for 30 min. The nitrate was calculated after measuring the absorbance of the mixture at 410 nm. The extraction of carbohydrates described above were used for assaying the free amino acid content using the ninhydrin method according to Yemm et al. (1955).

Enzyme activity

The crude enzyme solution was extracted according to Huber and Israel (1982). SPS (E.C. 2.4.1.14) activity was quantified according to the method of Hu et al. (2015); 200 μL crude enzyme solution and 350 μL reaction solution prepared with extraction buffer, fructose-6-P (50 mmol·L $^{-1}$), $MgCl_2$ (10 mmol·L $^{-1}$) and UDP-glucose (50 mmol·L $^{-1}$) were incubated for 30 min at 30 °C before adding 2 mol·L^{-1} NaOH (100 μL). After cooling, the mixture was heated again at 80 °C with 0.1% (w/v) resorcin (1 mL) which was prepared with 95% (v/v) ethanol and 30% (w/v) HCl (3.5 mL) for 10 min. The sucrose in the reaction mixture was measured at the wavelength of 480 nm. The assay method of SuSy (E.C. 2.4.1.13) activity was same as the method described above for SPS except that fructose 6-P was replaced with D-fructose.

For acid invertase (E.C. 3.2.1.26) activity assay, the crude enzyme solution of 100 μL was incubated at 30 °C with 2.2 mL acetic acid-NaOH (200 mmol·L $^{-1}$, pH 5.0) and 200 μL sucrose (1 mol·L $^{-1}$) for 30 min. After adding 1 mL 3,5-dinitro salicylic acid, the mixture was boiled for 5 min. The glucose in the reaction mixture was determined at the wavelength of 540 nm (Hu et al. 2019a). The assay method of alkaline invertase activity was similar to that of acid invertase except that sodium acetate-acetic acid (100 mmol·L $^{-1}$, pH 7.5) was used to replace acetic acid-NaOH.

Statistical analysis

The statistical analysis software SPSS (ver. 22.0, IBM, USA) was used for the analysis of variance (ANOVA) and means were compared using the LSD test at $P=0.05$. The mapping software Origin (Pro 8.0, OriginLab, USA) was chosen to make the figures. Yang et al. (2011) reported that the accumulation process of reproductive organ biomass can be fitted by a logistic formula as:

$$Bio = \frac{Bio_m}{1 + a * e^{b*DAS}} \tag{1}$$

where a and b are constants; Bio and Bio_m are the reproductive organ biomass at DAS, and the theoretical maximal biomass of reproductive organs, respectively. The initiation DAS (DAS_1) and termination DAS (DAS_2) of rapid accumulation of reproductive organ biomass, maximum accumulation rate of reproductive organ biomass (V_m) and occurrence time of V_m (DAS_m) were derived from Eq. (1) and estimated according to Eqs. (2)–(5):

$$DAS_1 = \frac{1}{b} ln\left(\frac{2 + 3^{1/2}}{a}\right) \tag{2}$$

$$DAS_2 = \frac{1}{b} ln\left(\frac{2 - 3^{1/2}}{a}\right) \tag{3}$$

$$DAS_m = -\frac{lna}{b} \tag{4}$$

$$V_m = -\frac{b*Bio_m}{4} \tag{5}$$

The duration of rapid-accumulation period of reproductive organ biomass (T) is equal to DAS_2 minus DAS_1 in Eq. (6). The average accumulation rate of reproductive organ biomass during T (V_T) was calculated according to Eq. (7):

$$T = DAS_2 - DAS_1 \tag{6}$$

$$V_T = \frac{Bio_2 - Bio_1}{DAS_2 - DAS_1} \tag{7}$$

Results

Reproductive organ biomass accumulation

The reproductive organ biomass was higher under K150 and W9000 than CK, with no obvious difference was found between K150 and W9000 (Table 1). The ratio of reproductive organ biomass to total biomass (RRT) increased by 4.8%~7.8% and 8.8%~13.6% under K150 and W9000, and being significantly higher under W9000 than K150. The reproductive organ biomass had a highly significant positive correlation with seed cotton yield ($P<0.01$) (Fig. 1).

Simulation of reproductive organ biomass accumulation

Equation (1) was used to fit the reproductive organ biomass accumulation, and the results in Tables 2 showed that the determination coefficient (R^2) for all treatments was higher than 0.95 and the P values were less than 0.01, suggesting that the formula could well describe the dynamic process of reproductive biomass accumulation.

Table 1 Reproductive organ biomass accumulation and ratio of reproductive organ biomass to total biomass (RRT) in 2012 and 2013

Treatment	2012		2013	
	Reproductive organ biomass/ (kg·ha^{-1})	RRT/%	Reproductive organ biomass/ (kg·ha^{-1})	RRT/%
CK	1 959.4 b	43.4 c	2 181.7 b	46.4 c
K150	3 679.4 a	45.2 b	4 403.4 a	50.0 b
W9000	3 691.6 a	47.2 a	4 480.0 a	52.7 a

CK, no crop straw and K fertilizer were applied as the blank control treatment; K150, 150 kg·ha^{-1} K_2O was applied before transplanting the cotton seedlings; and W9000, 9000 kg·ha^{-1} wheat straw was crushed and incorporated in 0~10 cm soil before transplanting. Values followed by different letters within the same column are significantly different at $P=0.05$. Each value represents the mean of three replications

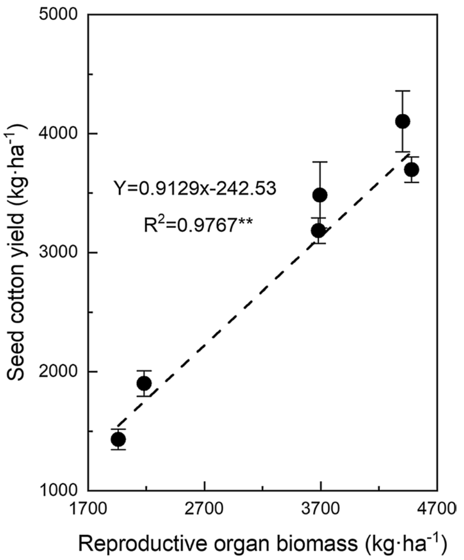

Fig. 1 Relationship between reproductive organ biomass and seed cotton yield. ** indicates a significant difference at $P = 0.01$ level

The Bio_m under K150 and W9000 was significantly increased relative to CK, and it was higher under W9000 than K150. The DAS_1 and DAS_2 were earliest under CK, followed by K150 and W9000; T and V_T increased under K150 and W9000 relative to CK, and T was longer under W9000 than K150, although V_T was lower under W9000. The variations in DAS_m and V_m among treatments followed the same trend as T and V_T, respectively.

Concentration of N, P and K in functional leaf

Leaf K level under K150 and W9000 was significantly higher than that under CK at all sampling dates in 2012 (except for PFS) and 2013 (Table 3). At PFS and BOS, leaf K concentration was similar under K150 and W9000, but it was lower under K150 than W9000 at BSS. Leaf N concentration under K150 and W9000 increased significantly at the BSS in 2013 and at the BOS in both years (Table 3). No significant difference was found in leaf P content across treatments and sampling dates (Table 3).

Table 2 The fitting of reproductive organ biomass accumulation and main eigenvalues of reproductive organ biomass accumulation for different treatments in 2012 and 2013

Year	Treatment	Regression equations	R^2	Fast accumulation period				Fastest accumulation point	
				DAS_1 /d	DAS_2/d	T/d	V_T/(kg·d^{-1})	V_m/(kg·d^{-1})	DAS_m/d
2012	CK	$Bio = 1\,979.8/(1 + 563\,429.6e^{-0.136\,5DAS})$	$0.991\,3^{**}$	87.4	106.7	19.3	59.6	67.5	97.0
	K150	$Bio = 3\,718.6/(1 + 722\,502.4e^{-0.113\,0DAS})$	$0.987\,8^{**}$	107.7	131.0	23.3	92.8	105.0	119.4
	W9000	$Bio = 3\,829.4/(1 + 238\,847.9e^{-0.100\,8DAS})$	$0.999\,2^{**}$	109.8	136.0	26.1	85.1	96.4	122.9
2013	CK	$Bio = 2\,220.2/(1 + 4\,127\,754.6e^{-0.138\,5DAS})$	$0.992\,6^{**}$	100.5	119.5	19.0	67.9	76.9	109.9
	K150	$Bio = 4\,617.7/(1 + 667\,640.8e^{-0.117\,0DAS})$	$0.991\,6^{**}$	103.3	125.8	22.5	119.3	135.1	114.6
	W9000	$Bio = 4\,926.3/(1 + 321\,420.9e^{-0.107\,0DAS})$	$0.996\,2^{**}$	106.2	130.7	24.5	116.3	131.8	118.5

CK, no crop straw and K fertilizer were applied as the blank control treatment; K150, 150 kg·ha^{-1} K_2O was applied before transplanting the cotton seedlings; and W9000, 9 000 kg·ha^{-1} wheat straw was crushed and incorporated in 0~10 cm soil before transplanting. DAS_1, DAS_2 and T mean the start time, termination time and duration of rapid accumulation of reproductive organ biomass; V_m and DAS_m present the maximum accumulation rate and occurrence time of maximum accumulation rate of reproductive organ biomass; V_T refers to the average speed of reproductive organ biomass accumulation during T. ** significant at $P < 0.01$

Table 3 Changes in leaf N, P and K concentrations for different treatments in 2012 and 2013

Year	Treatment	Peak flower stage (PFS)			Boll-setting stage (BSS)			Boll-opening stage (BOS)		
		K /(mg·kg^{-1})	N /(mg·kg^{-1})	P /(mg·kg^{-1})	K /(mg·kg^{-1})	N /(mg·kg^{-1})	P /(mg·kg^{-1})	K /(mg·kg^{-1})	N /(mg·kg^{-1})	P /(mg·kg^{-1})
2012	CK	29.45 a	32.01 a	3.17 a	13.59 c	25.02 a	2.95 a	8.84 b	16.38 b	2.25 a
	K150	31.24 a	31.65 a	2.98 a	18.55 b	27.04 a	3.23 a	16.09 a	20.29 a	2.54 a
	W9000	34.05 a	29.97 a	3.16 a	21.66 a	27.84 a	3.18 a	18.51 a	21.95 a	2.54 a
2013	CK	23.80 b	37.04 a	3.54 a	10.48 c	26.46 b	2.65 a	9.09 b	15.94 b	2.25 a
	K150	32.83 a	36.80 a	3.40 a	17.42 b	30.33 a	2.82 a	15.81 a	18.68 a	2.31 a
	W9000	30.45 a	35.57 a	3.32 a	21.89 a	29.06 a	2.68 a	16.49 a	20.11 a	2.38 a

CK, no crop straw and K fertilizer were applied as the blank control treatment; K150, 150 k·gha^{-1} K_2O was applied before transplanting the cotton seedlings; and W9000, 9 000 kg·ha^{-1} wheat straw was crushed and incorporated in 0~10 cm soil before transplanting. Values followed by different letters within the same column are significantly different at $P = 0.05$. Each value represents the mean of three replications

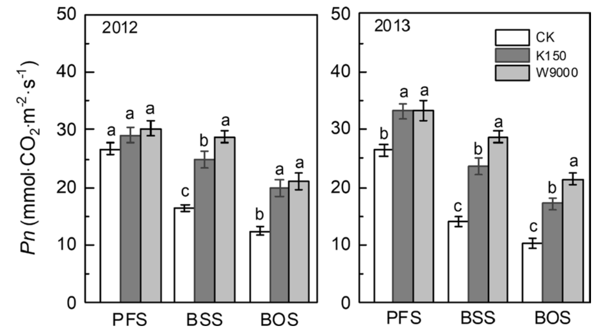

Fig. 2 Effects of straw-returning and inorganic K fertilizer on the net photosynthetic rate (*Pn*) of the functional leaf at the peak flowering (PFS), boll-setting (BSS) and boll-opening (BOS) stages of Siza 3 in 2012 and 2013. The data are means of three replications ± standard error. For each growth stage, bars bearing different letters are significantly different at $P = 0.05$

Net photosynthetic rate of functional leaf

The *Pn* of functional leaf under K150 and W9000 was noticeably higher than that under CK across sampling dates for both years (except for PFS in 2012, Fig. 2). Compared with K150, the *Pn* of functional leaf increased significantly under W9000 at the BSS (16.1%~21.6%) for both years and at the BOS (24.3%) in 2013.

Carbohydrates and N compounds in functional leaf

Soluble sugar content was markedly decreased under K150 and W9000 at BSS and BOS (Fig. 3), and the decrease was larger under W9000 (except for BOS in 2012). Sucrose content did not differ among treatments at PFS (except for 2013, Fig. 3), but was obviously decreased under K150 and W9000 at BSS and BOS in both years. Similar to soluble sugar content, a larger decrease in sucrose was observed under W9000 than K150 (except for BOS in 2013). At PFS, there were no differences in starch content among treatments (Fig. 3), but the starch content was significantly decreased under K150 and W9000 at BSS (18.6%~24.9% under K150; 21.4%~29.3% under W9000) and BOS (26.0%~35.2% under K150; 31.9%~44.5% under W9000).

At PFS, no significant differences in nitrate content were detected among treatments (Fig. 4). At BSS, the nitrate content increased significantly by 28.0%~32.1% under K150 and 25.0%~48.7% under W9000 in the 2 years. Similar increases in nitrate content were observed under K150 and W9000 at BOS in the 2 years (except for K150 in 2012). No significant change in nitrate content was observed between K150 and W9000 in the 2 years. The free amino acid concentration under K150 and W9000 significantly decreased at BSS (19.9%~21.8% under K150; 23.7%~25.0% under W9000) and BOS (17.3%~24.9% under K150; 20.4%~29.6% under W9000) in the 2 years (Fig. 4). There was no significant difference between K150 and W9000.

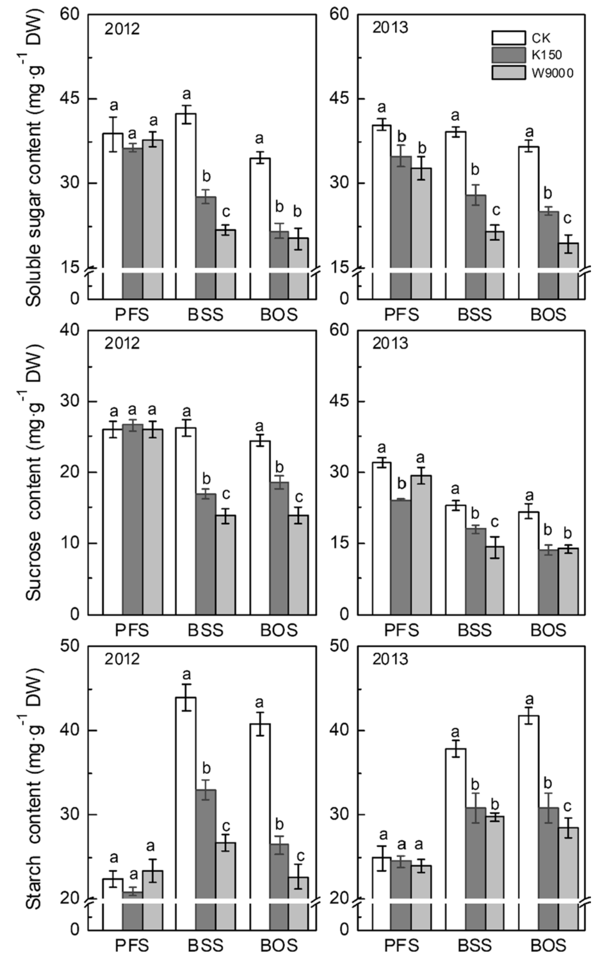

Fig. 3 Effects of straw-returning and inorganic K fertilizer on soluble sugar, sucrose and starch contents in the functional leaf at the peak flowering (PFS), boll-setting (BSS) and boll-opening (BOS) stages of Siza 3 in 2012 and 2013. The data are means of three replications ± standard error. For each growth stage, bars bearing different letters are significantly different at $P = 0.05$

The soluble sugar/free amino acid ratio did not differ among treatments at PFS in 2012 (Fig. 5), but was significantly decreased under K150 and W9000 at BSS and BOS in 2012 and at all sampling dates in 2013, and the decrease was larger in W9000 than K150 (apart from BOS in 2012). Similar to soluble sugar/free amino acid ratio, the C/N ratio significantly decreased under K150 and W9000 at all sampling dates (apart from PFS in 2012, Fig. 5), and compared with K150, W9000 had a lower C/N ratio (apart from BOS in 2012).

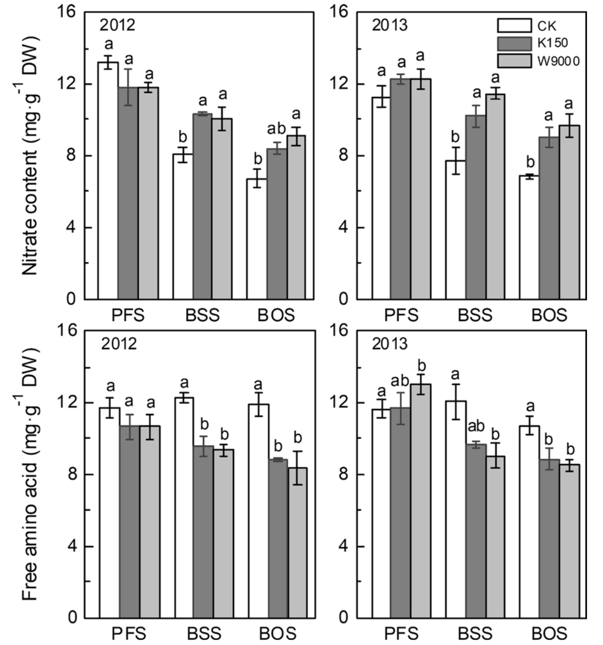

Fig. 4 Effects of straw-returning and inorganic K fertilizer on nitrate and free amino acid contents in the functional leaf at the peak flowering (PFS), boll-setting (BSS) and boll-opening (BOS) stages of Siza 3 in 2012 and 2013. The data are means of three replications ± standard error. For each growth stage, bars bearing different letters are significantly different at $P = 0.05$

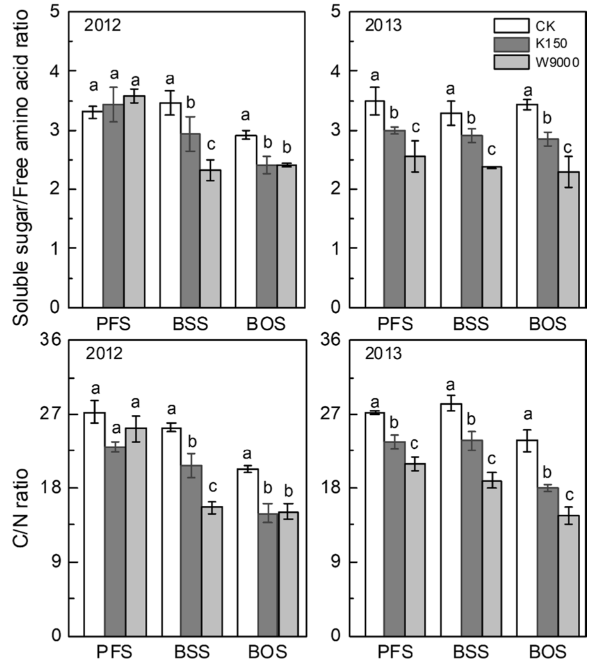

Fig. 5 Effects of straw-returning and inorganic K fertilizer on soluble sugar/free amino acid ratio and C/N ratio in the functional leaf at the peak flowering (PFS), boll-setting (BSS) and boll-opening (BOS) stages of Siza 3 in 2012 and 2013. The data are means of three replications ± standard error. For each growth stage, bars bearing different letters are significantly different at $P = 0.05$

Enzyme activities related to C metabolism

Sucrose phosphate synthase activity was little affected by K150 and W9000 at PFS, but was significantly increased under K150 and W9000 at BSS and BOS (Fig. 6), and the increase was more significant under W9000 (45.2%~116.8%) than K150 (27.7%~62.3%). The activity of SuSy was markedly influenced by K150 at PFS (Fig. 6). An increase of 27.7%~123.8% was observed in SuSy activity under K150 at BSS and BOS; an increase of 54.1%~170.2% was found under W9000 at BSS and BOS. Besides, the increase under W9000 was greater than that under K150 (apart from BSS in 2013).

Acid invertase was markedly reduced under K150 and W9000 at BSS and BOS in 2012 and at all sampling dates in 2013 (Fig. 7). Also, the decrease under W9000 was more obvious than that under K150 (except at the PFS in 2013). There were no significant differences in alkaline invertase among treatments in 2012 (Fig. 7). In 2013, the alkaline invertase was much lower under K150 at BOS and under W9000 at BSS and BOS.

Discussion

Previous studies showed that additional inorganic K fertilizer increased cotton productive organ biomass and yield under K deficiency (Makhdum et al. 2007; Hu et al. 2015). It also influenced the physiological metabolism in cotton, which was beneficial to C (Hu et al. 2015) and N (Drosdoff et al. 1947; Wang et al. 2012) metabolism. Hu et al. (2017) further showed that inorganic K fertilizer had a more significant effect on C metabolism than N metabolism. Hence, a lot of results on the effect of inorganic K fertilizer on cotton have been obtained. In this study, we focused on comparing the effects of wheat straw as K source and inorganic K fertilizer on cotton under low K condition.

Comparative effects of straw and inorganic K fertilizer on cotton reproductive biomass under low K condition

Previous studies have found that under low K, the seedcotton yield and lint yield were much higher under the straw-returning and K fertilizer treatments compared with blank control (Sui et al. 2015; Yu et al. 2016), since both straw-returning and K fertilizer application could increase available K in soil and promote root growth, which in turn facilitated nutrient absorption. Moreover, straw-returning could also alter soil C and N characteristics and microbial activities, which improved the growth environment of root, and was beneficial to the growth of

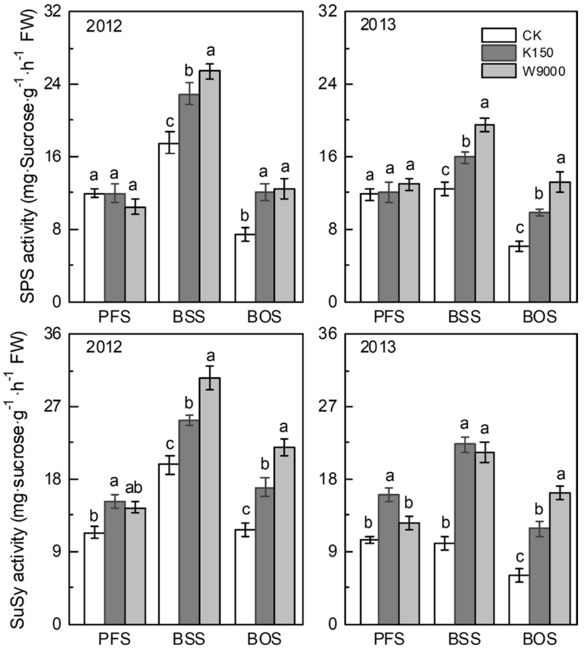

Fig. 6 Effects of straw-returning and inorganic K fertilizer on sucrose phosphate synthase (SPS) and sucrose synthase (SuSy) activities in the functional leaf at the peak flowering (PFS), boll-setting (BSS) and boll-opening (BOS) stages of Siza 3 in 2012 and 2013. The data are means of three replications ± standard error. For each growth stage, bars bearing different letters are significantly different at $P = 0.05$

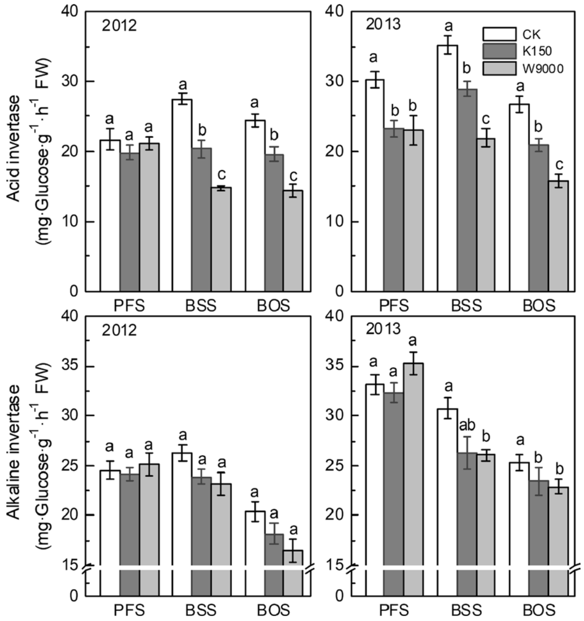

Fig. 7 Effects of straw-returning and inorganic K fertilizer on acid and alkaline invertases activities in the functional leaf at the peak flowering (PFS), boll-setting (BSS) and boll-opening (BOS) stages of Siza 3 in 2012 and 2013. The data are means of three replications ± standard error. For each growth stage, bars bearing different letters are significantly different at $P = 0.05$

cotton plants (Hu et al. 2019b). The yield formation of cotton is closely related to the biomass of reproductive organs (Li et al. 2020). The results of correlation analysis in the current study showed that the reproductive organ biomass had a positive correlation with seed cotton yield ($P < 0.01$) (Fig. 1), which confirmed the previous conclusion of Li et al. (2020). Although no significant difference in the reproductive organ biomass was measured between K150 and W9000, the W9000 had a significantly higher RRT than K150 (Table 1), indicating that straw-returning was more conducive to the allocation of biomass to reproductive organs than inorganic K fertilizer.

Liu et al. (2018) reported that the K release rate of wheat straw was much slower in dry land than in paddy field, and about 90 days were needed for K ion to release completely in dry land. Thus, the wheat straw returning to the dry land was similar to a kind of slow-release fertilizer which could change the dynamic accumulation and allocation of crop biomass by changing nutrient supply intensity and rate (Fan and Li 2009). As shown in Table 2, the eigenvalues of reproductive organ growth (Bio_m, V_T, V_m, T and DAS_m) were increased in both K150 and W9000, meaning that both inorganic K fertilizer and straw-returning changed the reproductive organ accumulation pattern. Meanwhile, Bio_m was higher in W9000 than K150, which indicated that crop straw had greater potential to accumulate the biomass of reproductive organs than inorganic K fertilizer. The V_T, V_m, T and DAS_m are the important parameters determining biomass accumulation (Yang et al. 2012; Du et al. 2016). The V_T and V_m were lower under W9000 than K150, suggesting that inorganic K fertilizer could better promote the rate of accumulation of reproductive organs than crop straw. However, T was 2.0~2.8 d longer under W9000 than K150, meaning that the duration of rapid reproductive growth period was extended by straw-returning relative to inorganic K fertilizer application, and the extension of rapid reproductive growth period was beneficial for yield formation (Yang et al. 2011). Consequently, T should be dominant compared with V_T, leading to the higher RRT under W9000 than K150. Moreover, DAS_1, DAS_2 and DAS_m were late by 2.1~2.9 d, 4.9~5.0 d and 3.5~3.9 d, respectively, under W9000 compared with K150, indicating that crop straw-returning could delay the start and end times of rapid reproductive growth in relation to inorganic K fertilizer, which might be because crop straw return to soil can effectively retard the senescence of crops and prolong the growth period (Mu et al. 2012).

Comparative effects of straw-returning and inorganic K fertilizer on cotton C–N balance under low K condition

Song et al. (2015) reported that straw-returning could replace inorganic K fertilizer under low K condition to increase the cottonseed K concentration. Similar results were observed in the current study. Leaf K level was much higher under K150 and W9000 than CK (Table 3). Compared with K150, W9000 did not change leaf K concentration at PFS and BOS, but increased leaf K concentration at BSS, suggesting that crop straw incorporation altered the dynamics of leaf K during growth period. A change in leaf K concentration would affect the C–N balance in cotton (Hu et al. 2017). Thus, the leaf C/N and soluble sugar/free amino acid ratios were significantly decreased under K150 and W9000 at BSS and BOS (Fig. 5). And compared with K150, W9000 caused greater reductions in both years (apart from BOS in 2012). A change in the C–N balance in leaves could influence the reproductive growth of crops (Zhang et al. 2014). Hence, the difference in C/N ratios between K150 and W9000 might be one of the reasons for the inconsistency in dynamic accumulation of reproductive organ biomass which was manifested through different accumulation eigenvalues (V_T, V_m, T, DAS_1, DAS_2 and DAS_m). Greater decreases in C/N ratio and soluble sugar/free amino acid ratio also led us to speculate that crop straw as K source might have a more drastic effect on C or N metabolism than inorganic K fertilizer. Zahoor et al. (2017b) and Hu et al. (2016b) found that extra K fertilizer could obviously increase leaf N and nitrate–N contents. Similarly, leaf N concentration and the content of nitrate as the substrate for N assimilation were higher in K150 and W9000 than CK at BSS in 2012 and at BOS in both years, but did not differ between K150 and W9000 (Table 3, Fig. 4). Also, the content of free amino acid, one of the main products of N assimilation, did not differ between K150 and W9000 (Fig. 4). These indicated that the impacts of straw-returning and K fertilizer application on N metabolism in cotton leaf were consistent, and did not support the above speculation that crop straw-returning had a more drastic effect on N metabolism than inorganic K fertilizer application. Previous studies showed that leaf K status could influence soluble sugar, sucrose and starch accumulation in leaves (Hu et al. 2015; Zahoor et al. 2017a). In support of these reports, we measured lower soluble sugar, as well as sucrose and starch contents under K150 and W9000 relative to CK at BSS and BOS in both years (Fig. 3), and the decrease was larger in W9000 than K150, suggesting that straw-returning had different effects on C metabolism than inorganic K fertilizer at some stages, which supported our above speculation that crop straw-returning had a more drastic effect on C metabolism.

Previous results of inorganic K fertilizer affecting C metabolism showed that K application increased *Pn*, SPS, and SuSy activities, decreased acid invertase (SAI) activity and had no effect on alkaline invertase activity in cotton leaves (Hu et al. 2015; Zahoor et al. 2017a). Same results were confirmed in this study (Figs. 2, 6, 7). And, compared with K150, the *Pn* significantly increased under W9000 at BSS (16.1%~21.6%) for both years and at BOS in 2013 (24.3%), indicating that straw-returning can increase C assimilation capacity at the middle and later stages of cotton development. SPS and SuSy as the two key enzymes controlling sucrose biosynthesis (Hendrix and Huber 1986) were much higher under W9000 than K150 at BSS and BOS (except for SPS at BOS in 2012 and SuSy at BSS in 2013), indicating that straw-returning was more conducive to sucrose production at the middle and later stages of cotton development. Acid and alkaline invertases are the main enzymes that catalyze the decomposition of sucrose in leaves (Loka et al. 2020). In the current study, alkaline invertase did not differ between K150 and W9000, but acid invertase was lower under W9000 at BSS and BOS, which could lead to a decrease in sucrose hydrolysis. Overall, the above results suggested that straw-returning would favor a higher sucrose accumulation than inorganic K application at the middle and later stages of cotton development. However, sucrose content was markedly lower under W9000 than K150. Wang et al. (2012) and Hu et al. (2017) have reported that high leaf K concentration was beneficial to increasing the sucrose transfer rate in phloem. Thus, the higher leaf K content under W9000 than K150 at BSS suggested that the lower leaf sucrose under the straw-returning treatment than inorganic K fertilizer treatment was associated with the different assimilate transport capacity. Also, an inhibited sucrose hydrolysis due to lower invertase activity would reduce the conversion of sucrose to other sugars, such as hexose and starch (Loka and Oosterhuis 2016). Thus, lower contents of soluble sugars and starch were measured under W9000 relative to K150.

Conclusion

Although the reproductive organ biomass did not differ between straw-returning and inorganic K fertilizer treatments, straw-returning better increased the RRT. Inconsistent eigenvalues of reproductive growth (V_T, V_m, T, DAS_1, DAS_2 and DAS_m) were observed between straw-returning and inorganic K fertilizer treatments, and the larger T was the main reason for the larger allocation of biomass to reproductive organs in straw-returning treatment than inorganic K fertilizer treatment. Straw-returning altered the dynamics of leaf K concentration with the growth period, resulting in a more drastic effect on C metabolism in relation to inorganic K application.

Consequently, lower soluble sugar/free amino acid and C/N ratios at BSS and BOS were measured in straw-returning treatment than inorganic K fertilizer treatment. Further analysis of C metabolism (*Pn*, SPS, SuSy and acid invertase activities) indicated that straw-returning was more conducive to sucrose accumulation than inorganic K fertilizer at the middle and later stages. However, sucrose content was markedly lower in straw-returning treatment than inorganic K application treatment at BSS and BOS. This might be because straw-returning led to higher assimilate transport capacity than inorganic K fertilizer, which also could explain the larger RRT in straw-returning treatment than inorganic K fertilizer treatment. Also, compared with inorganic K fertilizer, straw-returning inhibited the conversion of sucrose to other sugars, resulting in lower contents of soluble sugars and starch.

Abbreviations

RRT: Ratio of reproductive organ biomass to total biomass; Bio_m: Theoretical maximum biomass of reproductive organs; DAS: Days after sowing; DAS_1: Initiation DAS of rapid-accumulation period of reproductive organ biomass; DAS_2: Termination DAS of rapid-accumulation period of reproductive organ biomass; T: Duration of rapid-accumulation period of reproductive organ biomass; V_T: Average accumulation rate of reproductive organ biomass; V_m: Maximum accumulation rate of reproductive organ biomass; DAS_m: Occurrence time of V_m; PFS: Peak flowering stage; BSS: Boll-setting stage; BOS: Boll-opening stage; SPS: Sucrose phosphate synthase; *Pn*: Net photosynthetic rate; C/N ratio: Carbon/nitrogen ratio; SuSy: Sucrose synthase.

Supplementary Information

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Additional file 1: Table S1. The chemical and physical properties of the soils before transplanting cotton seedlings into the field in 2012 and 2013 (Yu et al. 2016).

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Authors' contributions

Conceived, designed and performed the experiments: Hu W, Yu CR, Zhao WQ and Zhou ZG. Analyzed the data: Hu W and Yu CR. Contributed reagents/materials/analysis tools: Yang CQ, Liu RX and Zhou ZG. Wrote the paper: Hu W and Yu CR. All authors read and approved the final manuscript.

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Availability of data and materials

All relevant data are within this article.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All co-authors have consent for submission of manuscript.

Competing interests

The authors have declared that no competing interests exist.

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