



Removal of early fruiting branches impacts leaf senescence and yield by altering the sink/source ratio of field-grown cotton



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ABSTRACT

Previous research shows that removal of early fruiting branches (FB) alters the sink/source ratio and delays leaf senescence in cotton. However, how the altered sink/source ratio regulates leaf senescence and yield formation is still poorly understood. In this study, 2 or 4 early FB were removed from two near isogenic cotton lines, late- and early-senescence lines, while plants with intact FB served as controls. The leaf chlorophyll content (Chl) and photosynthetic (Pn) rate in the late-senescence line were higher than those in the early-senescence line, but the malondialdehyde (MDA) accumulation and boll load per leaf area (BLLA) in the late-senescence line were lower than those in the early-senescence line. Removal of FB decreased the BLLA and MDA accumulation but increased the Pn rate, Chl concentration, and the expression of GhLHCB gene in both cotton lines, suggesting that FB removal reduced sink/source ratio and suppressed leaf senescence. However, it decreased ABA and JA contents by decreasing their biosynthesis related genes and increasing the expression of ABA catabolic related genes. Although FB removal increased the iP + iPA content, it had little effects on Z + ZR or DHZ + DHZR contents. The results suggest that the delayed leaf senescence following the decreased sink/source ratio associated with FB removal might be attributed to the increased iP + iPA and reduced ABA and JA contents, as well as the differentially expressed biosynthesis and catabolic related genes. Seedcotton yield increased by 6.3–10.2% following the removal of 2 FB but decreased by 5.7–11.7% following the removal of 4 FB in the early-senescence line; in the late-senescence line, the removal (whether of 2 or 4 FB) significantly decreased yield. Removal of 2 or 4 FB in the late-senescence line and 4 FB in early-senescence line significantly suppressed earliness. The overall results suggested that removal of early fruiting branches would practically regulate the sink/source relationship and suppress leaf senescence in cotton. Delaying leaf senescence would not necessarily increase cotton yield unless when earliness is not affected or when normal maturity is achieved.

1. Introduction

Senescence is the process leading to the natural termination of plant life or loss of organ function in crops, and plays a vital role in plant development by recycling many important nutrients (Chen and Dong, 2016). These nutrients are transferred from senescing leaves to actively growing tissues, thereby supporting plants in their overall growth and development (Himmelblau and Amasino, 2001; Hörtensteiner and Feller, 2002). During leaf senescence, photosynthesis declines and the metabolism of the leaf changes from anabolism to catabolism, including the degradation of chlorophylls, proteins, lipids and RNA (Matile et al., 1996; Hörtensteiner, 2006; Lim et al., 2007). Like many other plant species, cotton goes through a maturation process from seedling to maturity and from maturity to the aged and finally the termination of a

life cycle (Kong and Dong, 2011).

Maturity performance refers to the senescence appearance of cotton during the boll-opening stage, which is the manifestation and result of senescence (Kong and Dong, 2011; Chen and Dong, 2016). Generally there are three different maturity categories in cotton – normal maturity, premature senescence and late maturity (Chen and Dong, 2016). Appropriate senescence leads to normal maturity, which can help plants withstand adverse weather conditions, and efficiently utilize limited energy and material resources within the growing season to improve yield and quality. Senescence too late in the season would interfere with nutrient remobilization, thereby compromising photosynthetic activity in young leaves and decreasing cotton yield and fiber quality, which leads to late maturity. By contrast, too early senescence in cotton is referred to as premature senescence, which would reduce the plant's

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overall capacity to assimilate CO₂ and also decrease fiber yield and quality (Wright, 1999; Dong et al., 2006; Wingler et al., 2006). An understanding of the mechanisms of leaf senescence at morphological, physiological and molecular levels and the relationship between senescence and maturity may help to improve cotton yield and quality by avoiding premature senescence or late maturity through appropriate management.

Cotton variety is an internal factor determining senescence. Senescence may differ between genotypes because the genetic background, especially the senescence related genes are not exactly the same across cultivars. Generally, the chlorophylls (Chl), net photosynthetic (Pn) rate and soluble protein in the early senescence cotton are lower than in normal or late senescence cultivars, but the malondialdehyde (MDA) and superoxide dismutase (SOD) concentrations in the early senescence cotton are higher than normal or late senescence cultivars (Dong et al., 2005, 2008a; Chen and Dong, 2016). Dong et al. (2008a) studied two transgenic Bt cotton lines (K1 and K2) with different leaf senescence and found that K1 senescence earlier than K2 due to its lower cytokinin and higher ABA contents. We also found that the sink/source ratio differed between the two cultivars and suggested that the differences in leaf senescence and maturity may be due to differences in the sink/source ratios (Dong et al., 2008a).

Cultural practices and external environment can also affect cotton leaf senescence and maturity. Removal of the early squares or fruiting branches can reduce the sink/source ratio and delay cotton senescence (Chen and Dong, 2016). Therefore, removing the early fruiting branches has been used to prevent premature senescence in China (Dong et al., 2009). Previous studies have shown that the leaf Pn and Chl concentration were increased by removing early fruiting branches (Dumka et al., 2003; Dong et al., 2009). Our previous study also showed that girdling the basal main stem at squaring reduced root-canopy ratio and accelerated the leaf senescence of cotton (Dai and Dong, 2011). Also, grafting between early and late senescence lines changed the root-canopy relationship, thereby regulating the maturity of cotton (Dong et al., 2008a). These studies suggested that cultural practices such as removing early fruiting branches and girdling changed cotton senescence and maturity. And, without exception, the sink/source ratios were also changed by these cultural practices (Dong et al., 2008b, 2009; Niu et al., 2007; Dai and Dong, 2011). It seems that increasing sink/source ratios leads to premature senescence, but decreasing ratios usually leads to late maturity (Chen and Dong, 2016).

Plant hormones play key roles in response to senescence. Cytokinins (CTKs) and ABA are the two endogenous hormones most studied for plant aging and premature senescence. CTKs have been considered the most effective hormones in delaying leaf senescence (Sakakibara, 2006; Dong et al., 2008a). However, ABA is considered an aging enhancement factor rather than the main factor triggering leaf senescence (Zhang and Zhou, 2013). The content of CTKs and the expression of isopentenyltransferase (*IPT*) gene involved in cytokinin biosynthesis decreased but the ABA content and expression of 9-*cis*-epoxycarotenoid dioxygenase (*NCED*) gene involved in ABA biosynthesis increased during cotton senescence (Dong et al., 2008a; Kong et al., 2013, 2016). Dong et al. (2008b) reported that the content of CTKs increased significantly in the main-stem functional leaves and leaf senescence was significantly delayed after sink reduction treatment by removing early squares or early fruiting branches. These results suggested that cotton senescence was related to CTKs and ABA and their biosynthesis genes. CTKs delay while ABA promotes leaf senescence.

The sink/source ratio plays important roles in senescence of cotton but the underlining mechanism of regulating senescence is still unclear. Therefore, the main purpose of this study was to determine how the sink/source ratio impacts cotton senescence by regulating hormones and their expression as well as senescence related genes and the relationship among senescence, maturity and cotton yield. Specifically, this study focused on the: a) difference in sink/source ratio between early- and late-senescence cotton lines and the relationship between

sink/source ratio and senescence; b) effect of removing early fruiting branches on sink/source ratio and leaf senescence; c) effect of changed sink/source ratio on hormones, and the expression of hormone and senescence related genes; and d) relationship among sink/source ratio, senescence, maturity and cotton yield.

2. Materials and methods

2.1. Experimental design

An early-senescence (ES) and a late senescence (LS) cotton (*Gossypium hirsutum* L.) line were used in the experiment. Both lines share the same genetic background but differ in leaf senescence. Field experiment was conducted from 2014 to 2016 at the Shandong Cotton Experimental Station, Linqing (115°42'E, 36°61'N), Shandong, China.

A randomized complete block design with three replications was used to determine leaf senescence variation between the two cotton lines in the first experiment in 2014, and a factorial design in randomized complete blocks was used to study the effect of removal of early fruiting branches on leaf senescence in the second experiment in 2015 and 2016. In the second experiment, one factor was cotton line (an early- and a late-senescence line) while the other was the number of early fruiting branches removed (0, 2 and 4 FB). Each plot contained six rows with row length of 9.58 m and in-row spacing of 76 cm.

Seeds were sown on 28 April 2014, 20 April 2015 and 22 April 2016. The first two early-fruiting branches on the main stem were manually removed on 17 June 2015 and 21 June 2016 (5 days after squaring) (Supplemental Fig. 1), and the other two FB were removed 5 days after the first removal for the treatments with 4FB removal.

2.2. Data collection

Data were collected for net photosynthetic (Pn) rate, chlorophyll (Chl) content and malondialdehyde (MDA) concentration from 2014 to 2016.

Data for plant biomass, leaf senescence related physiological parameters and gene expression, as well as yield, yield components, final biomass, earliness and harvest index were collected from 2015 to 2016.

2.2.1. Biomass accumulation and partitioning and harvest index

Leaf area and dry weights of plant organs and physiological parameters were determined from three randomly sampled plants per plot at 5, 20, 35, 50 and 65 days after removal of early fruiting branches (DAR). Specifically, plants were manually removed from soil and partitioned into roots, stems, branches, leaves and fruiting forms including bolls, squares and flowers. Leaf area of each plant was determined by passing the leaves through a LI-3100 leaf area meter (LI-COR, Lincoln, NE, USA). The dry weight of vegetative (stems, leaves and branches, VO) and reproductive organs (squares, flowers, young bolls and open bolls, RO) as well as total biomass were determined after oven-drying at 80 °C to a constant weight. Sink/source ratio as indicated by boll load per leaf area (BLLA, g/m²) was determined by the ratio of dry weight of reproductive organs to leaf area.

2.2.2. Yield, yield components, harvest index and earliness

Seedcotton in each plot was harvested on 14 September, 14 October and 27 October 2015 and 8 September, 23 September and 11 October 2016. During each harvest, 50 bolls were randomly sampled per plot to determine boll weight. After sun-drying for ten days, seed cotton was weighed. Seed cotton yield (kg/ha) as well as the average boll weight was determined for each plot. Earliness as indicated by the percentage of the first harvest yield to total yield of seedcotton was also determined. After complete harvest, 20 randomly selected plants were removed from each plot and weighed after sun-drying for 30 d. Plant biomass and harvest index (seed cotton yield/biological yield) were then determined.

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