



## Cotton shoot plays a major role in mediating senescence induced by potassium deficiency

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### ABSTRACT

The objective of this study was to determine the roles of shoot and root in the regulation of premature leaf senescence induced by potassium (K) deficiency in cotton (*Gossypium hirsutum* L.). Two contrasting cultivars (CCRI41, more sensitive to K deficiency; and SCRC22, a less sensitive cultivar) were selected for self- and reciprocal-grafting, using standard grafting (one scion/one rootstock), Y grafting (two scions/one rootstock) and inverted Y grafting (one scion/two rootstocks) at the seedling stage. Standard grafting was studied in the field in 2007 and 2008. There were no obvious differences in senescence between CCRI41 and SCRC22 scions while supplied with sufficient K. However, SCRC22 scions showed significantly greater K content, SPAD values (chlorophyll content), soluble protein content and net photosynthetic rates than CCRI41 scions while grown in K deficient solution or soil, regardless of rootstock cultivars, grafting types, growth stage and growth conditions. Also, SCRC22 scions had greater yield and less variation in boll weight either between upper- and lower sympodials, or between proximal and distal fruit positions from the main stem in the field under K deficiency, probably owing to reduced leaf senescence. Although the effect of rootstocks on leaf senescence under K deficiency was significant in some cases, the scion cultivars explained the highest percentage of variations within grafting treatments. The shoot-to-root feedback signal(s), rather than high shoot demand for K nutrition, was involved in the shoot regulation of premature senescence in cotton plants, achieved possibly by altering root K uptake.

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### Introduction

Transgenic *Bacillus thuringiensis* Berliner (Bt) cotton (*Gossypium hirsutum* L.) has been adopted in most major cotton countries including China, where its adoption reached 70% in recent years (James, 2009). However, Bt cotton cultivars are more susceptible to potassium (K) deficiency (Zhang et al., 2007; Yang et al., 2011), although the mechanisms underlying this response are not well understood. In parallel with the inadequate input of K fertilizer, premature senescence, characterized by early chlorophyll degradation and reduced photosynthesis in mature leaves (Bednarz and Oosterhuis, 1995; Zhao et al., 2001) during flowers and boll

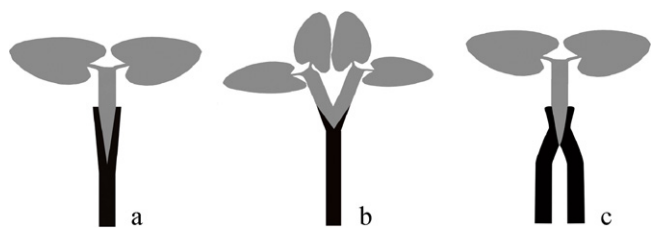
development (Wright, 1999), has been occurring on an increasing scale (Dong et al., 2006; Tian et al., 2008) and this has limited cotton productivity (Zhao et al., 2001).

Premature senescence of cotton induced by K deficiency was believed to result from faster fruit set, greater boll load and/or reduced root growth (Brouder and Cassman, 1990; Wright, 1999; Pettigrew, 2003), since the former would enhance remobilization of K from leaves and the latter would impair K supply to leaves. Dong et al. (2008) selected two Bt cotton lines with the same yield potential but contrasting senescence properties to study the factors controlling leaf senescence, and found that leaf senescence may result from root characteristics. Also, we observed that premature senescence/K-deficiency symptoms can occur in some cotton cultivars before first bloom when boll load is negligible in fields with low available K (unpublished data). Therefore, whether shoot demand or root supply or both dominate the premature senescence caused by K deficiency in cotton remains unclear and this has impeded the development of management solutions to the problem.

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**Fig. 1.** Sketch of the three types of grafting studied: (a) standard graft with one scion and one rootstock; (b) “Y” graft with two scions grafted onto one rootstock; (c) “inverted Y” graft with one scion grafted onto two rootstocks.

Grafting is commonly used for horticultural crops, and also has been used as a tool to explore root–shoot interactions governing a range of physiological responses, including abiotic stress tolerance (Ghanem et al., 2011b). Data for the relative importance of root (rootstock) and shoot (scion) in regulating growth and some physiological processes are variable. There is considerable evidence that elite rootstocks can mediate resistance to biotic (Anwar et al., 2002) and abiotic stress in plants, such as thermal stress (Rivero et al., 2003) and salt stress (Ruiz et al., 2006; Albacete et al., 2009, 2010; Ghanem et al., 2011a), thereby influencing scion growth and yield (Van Norman et al., 2004; Dodd et al., 2009; Jones et al., 2009) as well as delaying leaf senescence (Dong et al., 2008; Ghanem et al., 2011a). The importance of the shoot, in the regulation of growth (Chen et al., 2003; Tandonnet et al., 2010), leaf senescence (Faiss et al., 1997), branching (Beveridge et al., 1997; Foo et al., 2007), and drought tolerance (Holbrook et al., 2002) was also documented. Grafting studies indicate that both shoot and root are effective in the regulation of cambium development (Matsumoto-Kitano et al., 2008), growth (Werner et al., 2010), and the response of the plants to salt stress (Etehadnia et al., 2008). Other studies have shown that the relative role of root and shoot in grafted plants depended on the environment (Cornish and Zeevaert, 1988), species (Rivero et al., 2004), genotype (Beveridge, 2000; Holbrook et al., 2002; Dodd et al., 2009), growth stage (Ookawa et al., 2001), and growth processes (Holbrook et al., 2002).

To investigate rootstock and scion effects on premature senescence in cotton, we have developed three types of grafting between two contrasting cultivars (Li et al., 2009). The first type is standard grafting involving one scion and one rootstock (Fig. 1a); this can evaluate the relative role of root and shoot in regulating senescence. The second type is “Y” grafting with two scions grafted onto one rootstock (Fig. 1b) to more precisely evaluate the role of shoot physiology at the same level of mineral and phytohormone supply. The third type is “inverted Y” grafting with one scion grafted onto two rootstocks (Fig. 1c) to evaluate interactions between two contrasting roots in regulation of leaf senescence. In the present study, the three types of grafts were studied at high (2.5 mM, as control) and low (0.03 or 0.01 mM, to induce premature senescence) levels of K in the growth chamber at the seedling stage. The standard grafts were also studied in the field at different levels of K fertilizer. A better understanding of rootstock and scion regulation of premature senescence in cotton would facilitate the development of approaches to manage this problem.

## Materials and methods

### Plant material

Two transgenic insect-resistant cotton (*Gossypium hirsutum* L.) cultivars, CCRI41 [containing *Bacillus thuringiensis* (Bt) and cowpea trypsin inhibitor (CpTI), developed by the Cotton Research Institute, Chinese Academy of Agricultural Sciences] and SCRC22 (containing Bt, developed by the Cotton Research Center, Shandong Academy

of Agricultural Sciences), were used in the present study. Although both genotypes contain the Bt gene, they exhibit different degrees of leaf senescence. CCRI41 is susceptible to senescence induced by K deficiency, whereas SCRC22 has relatively late senescence under K deficiency.

### Growth chamber experiment

#### Growth conditions

The experiment was performed in a growth chamber with 12 h light/12 h dark at  $30 \pm 2/22 \pm 2^\circ\text{C}$ , 70–80% humidity and  $600 \mu\text{mol m}^{-2} \text{s}^{-1}$  photosynthetically active radiation. Seeds were surface-sterilized with 9%  $\text{H}_2\text{O}_2$  for 30 min, and then germinated in a K-free sand medium. After emergence (4 d after germination), uniform seedlings were cultured hydroponically by transferring to  $16 \text{ cm} \times 13 \text{ cm} \times 16 \text{ cm}$  plastic pots filled with 2.2 L of 1/2-strength modified Hoagland’s solution. The constituents of the solution were (mM) 2.5  $\text{Ca}(\text{NO}_3)_2$ , 1  $\text{MgSO}_4$ , 0.5  $(\text{NH}_4)_2\text{HPO}_4$ ,  $2 \times 10^{-4}$   $\text{CuSO}_4$ ,  $1 \times 10^{-3}$   $\text{ZnSO}_4$ , 0.1  $\text{Fe Na EDTA}$ ,  $2 \times 10^{-2}$   $\text{H}_3\text{BO}_3$ ,  $5 \times 10^{-6}$   $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}$  and  $1 \times 10^{-3}$   $\text{MnSO}_4$ . The concentration of K in the form of potassium sulphate ( $\text{K}_2\text{SO}_4$ ) in solutions varied before and after grafting (see below).

Four uniform seedlings were raised per pot. All solutions were changed twice per week. De-ionized water was added daily to replace the water lost by evapo-transpiration. Solution pH was maintained at 6.5 by adding concentrated solution of NaOH and air was bubbled into the solution to provide  $\text{O}_2$  and achieve nutrient homogeneity.

### Grafting

Preliminary studies indicated that grafting did not affect the growth and development of cotton plants, irrespective of the type of grafting and growth environment (growth chamber or field). For example, there were no significant differences in SPAD values of the youngest fully expanded leaves (the 4th leaf from the top of plant) between ungrafted control and self-grafts in the growth chamber experiment, as well as lint yield in the field (Table 1). Therefore, only self-grafts were used as controls in the present study.

To properly evaluate the contribution of root and shoot to K deficiency-induced senescence, grafting at the root–shoot junction is necessary. However, the survival rate was too low for this kind of grafting to yield meaningful results. Consequently, the graft union in the present study was located at the cotyledonary node of the rootstock or just below it.

**Standard grafting:** When the rootstocks (4 d after germination, i.e. 4 DAG) were transferred to solutions containing 0.1 mM K, the scions started to germinate in sand. After full expansion of scion cotyledons (5 DAG), the 1st true leaf of the rootstock appeared, and grafting was carried out. Scions and rootstocks were joined at the cotyledonary node by the wedge-grafting technique (Fig. 1a), and grafted joints were wrapped with Parafilm (American National Can Inc., Chicago, USA) to prevent dehydration.

**“Y” grafting:** The sizes of scions and rootstock for Y grafting were the same as for the standard grafting. The scions from two separate seedlings were cut with a razor blade 2–3 cm below the apex. The rootstock was prepared by removing the shoot and cutting vertically downward approximately 2 cm at the cotyledonary node without damaging the cotyledons. Then two wedge-cut scions were placed into the gap of the rootstock, with the cut surfaces of scions and rootstock in complete contact (Fig. 1b). Parafilm was used to reinforce the union.

**“Inverted Y” grafting:** The scion plant and two rootstock plants were germinated at the same time. When their first true leaf appeared, two separate rootstocks were severed at the hypocotyls and a diagonal slice was made in each. An elastic band was placed over the two rootstocks, creating a V-shape slit at the junction of the

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