

Genetic analysis of the antioxidant enzymes, methane dicarboxylic aldehyde (MDA) and chlorophyll content in leaves of the short season cotton (*Gossypium hirsutum* L.)

Meizhen Song · Shuli Fan · Chaoyou Pang ·
Hengling Wei · Shuxun Yu

Received: 15 August 2013 / Accepted: 7 March 2014 / Published online: 25 March 2014
© Springer Science+Business Media Dordrecht 2014

Abstract Premature senescence is an important limited factor for the short season cotton (SSC), which decreases yield and declines fiber quality. The activity of antioxidant enzyme, methane dicarboxylic aldehyde (MDA) content and chlorophyll content is related with premature senescence. The present study is aimed to investigate the heredity and relationship of the antioxidant enzymes catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD), MDA content and chlorophyll content for breeding high yield and good quality of the SSC varieties. Six parents from two types of senescence varieties (type A, which matures early and displays premature senescence; type B, which matures early but does not display premature senescence) and their F_1 , F_2 progenies in a diallel crossing scheme were planted in the experiment field. Phenotypic data on the traits were analyzed according to the Additive–Dominance–Epistasis and Additive–Dominance–Maternal–Paternal effects genetic model. CAT activity of dominant genetic effects were significant and large from 9 to 85 days after planting, the variance components were 34.69, 8.41, 31.93, 19.57 and 27.96 % at 9, 36, 50, 66 and 85 days, respectively. Additive-by-additive epistatic effects on CAT activity

were significant and important from 9 to 85 days after planting. POD activity of additive genetic effects was significant and stable. There was not interaction by environment during 24 to 50 days after planting, the variance components were 9.82, 18.86 and 7.87 % at 24, 36 and 50 days, respectively. SOD activity of additive genetic effects was significant and stable. There was not interaction by environment during 66 to 100 days after planting, the variance components were 11.56, 11.80 and 13.84 % at 66, 85 and 100 days, respectively. MDA content of additive genetic effects was significant and stable. There was not interaction by environment during 50 to 100 days after planting, the variance components were 24.81, 13.81, 14.38 and 4.77 % at 50, 66, 85 and 100 days, respectively. Chlorophyll content was mainly controlled by significant dominance effects and main genetic effect from 9 to 66 days after planting, the dominant variance components were over 30 %. Maternal and paternal genetic effects on CAT and chlorophyll content were significant among 36–85 days after planting. Based on these results, it is suggested to selection of POD, SOD and MDA should be undertaken at early generation (F_2 , F_3) and selection of chlorophyll and CAT should be undertaken at late generation (F_4 , F_5) in SSC breeding programs.

M. Song · S. Fan · C. Pang · H. Wei · S. Yu (✉)
State Key Laboratory of Cotton Biology, Institute of
Cotton Research of Chinese Academy of Agriculture
Sciences, 38 Huanghedadiao Development District,
Anyang 455000, Henan, China
e-mail: yu@cricaas.com.cn

Keywords The short season cotton (*Gossypium hirsutum* L.) · Antioxidant enzymes · Additive effects · Dominance effects · Additive-by-additive epistatic effects

Introduction

Short season cotton (SSC) is an ecotype of upland cotton (*Gossypium hirsutum* L.) that has relatively short growing period. It is suitable for wheat, barley, rape and cotton double cropping farm practice in Yellow River and Yangzi River cotton areas and the short frost free regions in the northwest cotton areas in China (Yu et al. 2005) and in the high plains in America (Peabody and Johnson 2002). These patterns will be main cotton planting types in the large population areas in China. It was estimated that the acreage of double- or multiple-cropping farms accounted for 60 % of the total acreage of farming land in cotton-producing areas and the intercropping index (i.e. the harvest times per year per acreage) reached 165 % (Mao et al. 1999). So earliness is an important character for SSC, and the short season varieties often have premature senescence traits. Premature senescence can reduce yield and quality of SSC. Because senescence is a genetically regulated oxidative process (Gan and Amasino 1997; Nooden et al. 1997), which is mainly characterized as photosynthesis cessation, organelle structure disintegration, chlorophyll and proteins intensive losses, and dramatic increases in lipid peroxidation and membrane leakiness (Buchanan 1997). Premature senescence impacts dramatically on crop yields and quality and is related with altered regulation of thousands of genes and many metabolic and signaling pathways, resulting in major changes in the leaves (Breeze et al. 2011; Michelle and Huang 2007). The onset and progression of leaf senescence are regulated by both environmental and endogenous factors and their interactions. Environmental cues include stress factors that adversely affect plant development and productivity, such as drought, water-logging, high or low solar radiation, extreme temperatures, ozone and other air pollutants, excessive soil salinity, and inadequate mineral nutrition in the soil (Munne 'Bosch et al. 2004; Lim and Nam 2005; Schippers et al. 2007). Exposure of plants to stressful environmental conditions usually induces overproduction of reactive oxygen species (ROS), such as superoxide radicals (O_2^-), hydroxyl radicals ($\cdot OH$), singlet oxygen (1O_2) and hydrogen peroxide (H_2O_2), which contribute to lipid peroxidation and membrane damage, are generally enhanced during senescence (Pastori and del Rio 1997). Plants have developed an antioxidant defense

system in response to the generation of ROS within plant, which is comprised of enzymatic and nonenzymatic components. Oxidants or antioxidant enzymes directly scavenge ROS, including superoxide dismutase (SOD; EC 1.15.1.1), catalase (CAT; EC 1.11.1.6), ascorbate peroxidase (APX; EC 1.11.1.11), peroxidase (POD; EC1.11), and a tocopherol; Oxidized antioxidants mainly include glutathione, glutathione reductase, ascorbate, and ascorbate reductase.

Two types of varieties (Type A and Type B) of the SSC were used in the present study. Type A matures early and displays premature senescence. Type B matures early but does not display premature senescence (Yu et al. 2005). In 2005 and 2006 year, the average cotton lint yield and fiber quality of type B varieties, Liao 4086, Zhong 061723 and Yuzao 1201 were significant higher than those of type A varieties, Zhongmiansuo 10, Zhong 652585, and Yuzao 28. The main objectives of this study were to estimate the genetic effects of the antioxidant enzymes, MDA and chlorophyll content among the biochemical characters. The selection strategies for CAT, POD, SOD, MDA and chlorophyll in SSC breeding program was discussed based on these results.

Materials and methods

Materials

Two types of the SSC (*G. hirsutum* L.) cultivars were used in the experiments: type A cultivars are those that senescence prematurely, including Zhongmiansuo 10 (designated as A_1), Zhong 652585 (A_2), and Yuzao 28 (A_3); type B cultivars are those that mature early without premature senescence, including Liao 4086 (designated as B_1), Zhong 061723 (B_2), and Yuzao 1201 (B_3). 6×6 diallel crossing design was used and 6 parents, and 30 reciprocal F_1 crosses, and 30 reciprocal F_2 crosses were planted in the experiment. F_1 and F_2 seeds, together with their parental lines, were planted in a randomized complete block design with three replications. The experiment was conducted in the fields at Institute of Cotton Research of CAAS, Henan, China. The plot size was three rows (8.5 m long/rows) for F_1 and five rows (8.5 m long/rows) for F_2 with row spacing of 0.7 m. The plant population was 42,500 plants/ha. Trials were repeated and the planting dates were around 21 May from 2005, 2006 and 2010.

Physiological and biochemical tests

The fourth leaves from the topmost leaf of plants were sampled during seedling, square, flowering, boll-setting and boll opening stages, which were 9, 24, 36, 50, 66, 85 and 100 days after planting. Ten leaves for parents (A_{1-3} , B_{1-3}), ten leaves for F_1 , 20 leaves for F_2 were bulked for analysis. Since F_2 is a segregating population and more plants should be sampling for a good representation. Samples were randomly collected from each line 8:00–9:00 a.m. Samples were kept in moist gauze and brought to Laboratory immediately. Samples were washed with ddH₂O and the main leaf veins were discarded. Approximately 350 mg fresh leaf tissue was frozen in liquid nitrogen, and stored at -80 °C until further analysis. Extraction of SOD, CAT, POD, MDA and chlorophyll was performed as previously described with modification (Wang et al. 1983; Beers and Sizer 1952; Yuan and Ding 1990; Hodges et al. 1999). Briefly, frozen leaves were homogenized with 4 mL of 150 mM ice-cold phosphate buffer (pH 7.0) with a mortar and pestle and centrifuged at $15,000\times g$ for 20 min at 4 °C. The supernatant was collected and used for determination of enzyme activity. MDA content was measured with a modified thiobarbituric acid–malondialdehyde (TBA–MDA) assay. Chlorophyll was extracted with the method of a 1:1 mixture of absolute ethanol and acetone. Absorbance values at 645 and 663 nm were measured to the determine chlorophyll content.

Data analysis

Data collected were analyzed with a genetic analysis model described previously (Zhu and Weir 1994a, b; Zhu 1995, 1997; Ye and Zhu 2000). The genetic analysis software of an Additive–Dominance–Epistasis (AD + AA) Model (Zhu 1995; Xu and Zhu 1999; Wu et al. 2006a, b) and an Additive–Dominance–Maternal–Paternal effects (ADMP) Model were used (Zhu 1995; Wu et al. 2006a, b). The ADAA model was used for the analysis of additive, dominant and additive epistasis effects, in which the total general genetic variance (V_G) is: $V_G = V_A + V_D + V_{AA}$, where V_A is the additive variance, V_D is the dominant variance, and V_{AA} is the epistatic variance. The ADMP model was used for the analysis of additive, dominant, maternal and paternal effects, in which the total general genetic variance (V_G) is:

$V_G = V_A + V_D + V_M + V_F$, where V_A is the additive variance, V_D is the dominant variance, and V_M is the maternal variance, V_F is the paternal variance. Phenotypic variance (V_P) was determined using the formula: $V_P = V_G + V_{GE} + V_e$, where V_{GE} is genotype and environment interaction variance, V_{AE} is components for additive by environment interaction variance, V_{DE} is dominance by environment interaction variance, V_{AAE} is additive \times additive epistasis by environment interaction variance, V_{ME} is maternal by environment interaction variance, V_{FE} is paternal by environment interaction variance, V_e is the residual variance. The minimum norm quadratic unbiased estimation method (MINQUE) was used to estimate all other variances and their percentages in the total variance. The linear unbiased prediction method was used to estimate the gene efficacy of all traits. The Jackknife method was used to compute the predictive value of all traits and their standard errors, and a t test was used to test the significance of differences.

Results

Additive genetic effects are equivalent to the general combining ability effects. Dominance effects are equivalent to specific combining ability (Wu et al. 2006a, b; Jenkins et al. 2007).

CAT activity

No significant for additive effects on CAT activity was detected, but additive genetic effect-by-environment interaction was significant at 24, 36, 66 and 100 days after planting, variance components were 3.06, 16.24, 16.29 and 8.76 %, respectively. Dominant genetic effects for CAT activity were significant and large from 9 to 85 days after planting, and variance components were 34.69, 8.41, 31.93, 19.57 and 27.96 % for 9, 36, 50, 66 and 85 days, respectively. Dominance genetic effect-by-environment interactions were significant and large at all growth stages, variance components were 9.75, 10.38, 44.46, 29.96, 30.52, 10.39 and 20.63 % for 9, 24, 36, 50, 66, 85, and 100 days, respectively. Additive-by-additive epistatic effects on CAT activity were significant and important from 9 to 85 days after planting, Variance components were 10.78, 25.15 and 12.70 % at 9, 24 and 36 days

Table 1 Estimated proportions of variance component for CAT activity at different stages

	9 days	24 days	36 days	50 days	66 days	85 days	100 days
ADAA model							
V_A/V_P	0	0	0	0	0	0	0
V_D/V_P	34.69**	0	8.41**	31.93**	19.57**	27.96**	0
V_{AA}/V_P	10.78**	25.15**	12.70**	3.47**	4.43**	4.74**	1.40
V_{AE}/V_P	0	3.06**	16.24**	0	16.29**	0.5	8.76**
V_{DE}/V_P	9.75**	10.38**	44.46**	29.96**	30.52**	10.39**	20.63**
V_{AAE}/V_P	7.34**	9.57**	0	0	0	5.37**	0
V_e/V_P	37.43**	51.84**	18.19**	34.65**	29.19**	51.01**	69.21**
ADMP model							
V_A/V_P	0	0	0	0	0	0	2.43**
V_D/V_P	30.78**	9.58**	0	14.84**	2.71**	2.49*	2.26
V_M/V_P	1.73	0	1.31	4.30**	5.19**	19.09**	0
V_F/V_P	0	0	12.04**	6.71**	17.53**	1.81*	0
V_{AE}/V_P	0	1.14	9.28**	0	9.68**	6.60**	0
V_{DE}/V_P	16.22**	26.77**	25.93**	15.97**	15.10**	4.84**	10.05**
V_{ME}/V_P	13.01**	27.73**	10.55**	0	10.52**	0	4.07**
V_{FE}/V_P	0	0	1.89**	9.30**	5.92**	6.21**	6.57**
V_e/V_P	38.26**	34.79**	39.01**	48.89**	33.35**	58.96**	74.62**

V_A , V_D , V_{AA} , V_{AE} , V_{DE} , V_e , V_P , V_{AAE} , V_M , V_F , V_{ME} , and V_{FE} represent additive variance, dominance variance, epistatic variance, additive by environment variance, dominance by environment variance, error variance, phenotypic variance, additive by additive by environment variance, maternal variance, is paternal variance, maternal by environment interaction variance and paternal by environment interaction variance, respectively

* and ** variance component are significant at 0.05 and 0.01 respectively

after planting respectively, then decreased. Additive-by-additive by environment interaction effects on CAT activity were only detected and small at 9 and 24 days after planting. Maternal and paternal genetic effects were significant among 36–85 days after planting. Maternal and paternal genetic effect-by-environment interaction was significant. The results showed that genetic effects on CAT activity were primarily dominance effects and additive-by-additive epistatic effects, the dominance effects and the epistatic effects also had interaction with environment (Table 1).

POD activity

Additive genetic effects on POD activity were significant and stable. They had no interaction by environment during 24 to 50 days after planting, variance components were 9.82, 18.86 and 7.87 % for 24, 36, 50 days, respectively. Dominance genetic effects on POD activity were significant at 9, 50, 66 and 100 days

after planting. Additive-by-additive epistatic effect-by-environment interaction was significant and large during 24 to 50 days after planting, variance components were 32.53, 53.78 and 28.18 % for 24, 36, 50 days respectively. No significant for maternal and paternal genetic effects were detected, but maternal and paternal genetic effect-by-environment interaction was significant during 24 to 50 days after planting. The results showed that genetic effects on POD activity were primarily additive genetic effects and additive-by-additive epistatic effects by environment interaction during 24 to 50 days after planting. So POD is also the key antioxidant enzyme at later growth stages in the SSC varieties (Table 2).

SOD activity

Additive genetic effects on SOD activity were significant and stable that was not interaction by environment during 66 to 100 days after planting, variance components were 11.56, 11.80 and 13.84 % for 66, 85,

Table 2 Estimated proportions of variance component for POD activity at different stages

	9 days	24 days	36 days	50 days	66 days	85 days	100 days
ADAA model							
V_A/V_P	0	9.82**	18.86**	7.87**	0	0	4.06**
V_D/V_P	12.52**	0	1.43	10.17**	18.92**	0	33.42**
V_{AA}/V_P	12.20**	0	0	0	0.31	12.29**	0
V_{AE}/V_P	10.67**	0.9	0	0	12.40**	15.18**	4.61**
V_{DE}/V_P	45.11**	0	0	0	0	41.50**	28.60**
V_{AAE}/V_P	0	32.53**	53.78**	28.18**	0	0	0
V_e/V_P	19.49**	56.75**	25.93**	53.78**	68.36**	31.03**	29.31**
ADMP model							
V_A/V_P	9.63**	5.31**	0.59	3.04**	0	3.63**	0
V_D/V_P	0	0	0	1.05	14.39**	0	5.21**
V_M/V_P	13.65**	0	1.15	0	0	1.42*	8.68**
V_F/V_P	0	0	0	0	3.94**	0	7.35**
V_{AE}/V_P	0	0	0	0	7.95**	14.33**	2.73**
V_{DE}/V_P	26.80**	13.81**	45.88**	4.94**	0	36.36**	9.04**
V_{ME}/V_P	0	30.35**	12.77**	11.92**	0	0	0
V_{FE}/V_P	20.84**	2.37**	15.10**	3.03**	0	11.90**	1.89*
V_e/V_P	29.08**	48.16**	24.51**	76.02**	73.72**	32.36**	65.11**

Table 3 Estimated proportions of variance component for SOD activity at different stages

	9 days	24 days	36 days	50 days	66 days	85 days	100 days
ADAA model							
V_A/V_P	17.13**	0.79	0	2.55*	11.56**	11.80**	13.84**
V_D/V_P	0	0	0	0	40.33**	5.17**	0
V_{AA}/V_P	0	7.60*	18.79**	0	0	0	0
V_{AE}/V_P	0	0	17.23**	8.32**	0	0	0
V_{DE}/V_P	0	0	42.01**	0	0	0	0
V_{AAE}/V_P	28.89**	41.52**	0	13.73**	24.93**	29.51**	41.28**
V_e/V_P	53.98**	50.09**	21.97**	75.41**	23.19**	53.51**	44.88**
ADMP model							
V_A/V_P	6.34**	3.75**	0	0	0	0	6.33**
V_D/V_P	9.44**	8.66**	0	2.13	7.19**	6.20**	0
V_M/V_P	0	0	2.97**	0	2.62**	10.49**	0
V_F/V_P	0	0	6.70**	0	1.19	0	0
V_{AE}/V_P	5.52**	0	7.32**	9.06**	9.13**	13.56**	0
V_{DE}/V_P	0	41.16**	53.01**	1.44	0	0	23.92**
V_{ME}/V_P	0	4.83**	4.60**	0	0	0	0
V_{FE}/V_P	0	5.06**	1.37	0	0	10.16**	0
V_e/V_P	78.69**	36.54**	24.02**	87.36**	79.8**	59.60**	69.75**

and 100 days, respectively. Dominance genetic effects on SOD activity were just significant at 66 days after planting. The variance components were 40.33 %.

Additive-by-additive epistatic effect-by-environment interaction was significant and large during all growth except 36 days. The variance components were 28.89,

Table 4 Estimated proportions of variance component for MDA content at different stages

	9 days	24 days	36 days	50 days	66 days	85 days	100 days
ADAA model							
V_A/V_P	0	3.45**	0	24.81**	13.81**	14.38**	4.77**
V_D/V_P	3.06**	1.26**	0	0	0	0	40.59**
V_{AA}/V_P	7.05**	0	2.96*	0	0	0	0
V_{AE}/V_P	0	0	0	0	0	0	0
V_{DE}/V_P	0	0	0	0	0	0	25.83**
V_{AAE}/V_P	86.24**	85.25**	28.64**	8.23**	19.16**	27.88**	0
V_e/V_P	3.64**	10.05**	68.40**	66.95**	67.03**	57.73**	28.82**
ADMP model							
V_A/V_P	0	0	1.94**	8.93**	8.53**	4.15**	0
V_D/V_P	0	0	5.34**	8.05**	4.68**	0.04	0
V_M/V_P	4.21**	1.74**	0	0	0	0	1.67*
V_F/V_P	6.08**	0	0	0.96	0	0	2.35**
V_{AE}/V_P	0	8.06**	0	0	0	1.89*	10.86**
V_{DE}/V_P	70.91**	64.44**	4.93**	0	0	0	23.23**
V_{ME}/V_P	6.37**	3.94**	39.41**	4.00**	8.84**	0	0
V_{FE}/V_P	4.60**	7.50**	0.3	0	0.87	0	0
V_e/V_P	7.83**	14.32**	48.08**	78.07**	77.08**	93.92**	61.89**

41.52, 13.73, 24.93, 29.51 and 41.28 % for 9, 24, 50, 66, 85, and 100 days respectively. No significant for maternal and paternal genetic effects were detected. The results showed that genetic effects on SOD activity were primarily additive genetic effects and additive-by-additive epistatic effects by environment interaction at all growth stages. So SOD was also the most key antioxidant enzyme at all growth stages in the SSC varieties (Table 3).

MDA content

Additive genetic effects on MDA content were significant and stable. They had no interaction with environment during 50 to 100 days after planting, variance components were 24.81, 13.81, 14.38 and 4.77 % for 50, 66, 85, and 100 days, respectively. No significant for dominance genetic effects were detected. Additive-by-additive epistatic effect-by-environment interaction was significant and large before 85 days after planting. The variance components were 86.24, 85.25, 28.64, 8.23, 19.16 and 27.88 % at 9, 24, 36, 50, 66, 85 and 100 days, respectively. Maternal genetic effect-by-environment interaction was also detected and significant before 66

days after planting. The results showed that genetic effects on MDA content were primarily additive genetic effects during 50 to 100 days after planting and additive-by-additive epistatic effects by environment interaction before 85 days after planting. Maternal and paternal genetic effects by environment interaction also existed before 66 days after planting (Table 4).

Chlorophyll content

Dominant effects for chlorophyll content were significant and main genetic effect from 9 to 66 days after planting. The dominant variance components were over 30 %. Dominance genetic effect-by-environment interactions were also significant and large for 24, 50 and 66 days after planting. The variance components were 26.85, 23.28 and 39.96 %, respectively. The Additive genetic effects for chlorophyll content were significant until 85 days after planting. The variance components were 7.28 and 11.61 % at 85 and 100 days, respectively. Additive genetic effect-by-environment interactions were detected at 9, 24, 50 and 66 days after planting. Additive-by-additive epistatic effects on chlorophyll content were significant at 24

Table 5 Estimated proportions of variance component for chlorophyll content at different stages

	9 days	24 days	36 days	50 days	66 days	85 days	100 days
ADAA model							
V_A/V_P	0	3.98**	0	0	0	7.28**	11.61**
V_D/V_P	49.91**	0	34.65**	36.20**	45.79**	0	0
V_{AA}/V_P	2.73	12.94**	0	0	3.81**	0	0
V_{AE}/V_P	4.02**	10.55**	0	5.88**	8.18**	0	0
V_{DE}/V_P	3.09*	26.85**	0	23.28**	39.96**	4.20**	0
V_{AAE}/V_P	0	0	29.48**	0	0	50.78**	29.93**
V_e/V_P	40.25**	45.67**	35.86**	34.64**	2.27**	37.74**	59.46**
ADMP model							
V_A/V_P	0	27.26**	0	0	0	0.26	1.75**
V_D/V_P	0	0	0	6.98**	0	0	0
V_M/V_P	16.49**	1.61	10.70**	0	28.41**	1.51*	0
V_F/V_P	12.36**	0	15.60**	10.99**	30.71**	0	0
V_{AE}/V_P	1.89**	2.23*	0	0	0	0	3.41**
V_{DE}/V_P	0	9.92**	16.67**	0	5.58**	54.96**	0
V_{ME}/V_P	3.25**	4.00**	3.33**	6.51**	8.96**	1.76	0
V_{FE}/V_P	2.12**	2.81**	0	10.08**	12.33**	2.03*	0
V_e/V_P	63.88**	52.17**	53.71**	65.44**	14.01**	39.48**	94.83**

and 66 days after planting. Additive-by-additive by environment interaction effects on chlorophyll content were significant at 36, 85 and 100 days after planting. The variance components were 29.48, 50.78 and 29.92 %, respectively. Maternal and paternal genetic effects were calculated by ADMP model were significant. The variance components were over 10 % at 9, 36, 50 and 66 days after planting. Maternal and paternal genetic effects by environment interaction were detected and significant. In general, the high dominance effects on chlorophyll content showed that the trait of chlorophyll content was not very stable until 85 days after planting (Table 5).

Relationship among activities of antioxidant enzymes and content of MDA and chlorophyll

CAT had significant positive genetic and phenotypic correlation at 36 and 85 days, and had significant negative genetic and phenotypic correlation at 66 days with POD, SOD MDA and chlorophyll after planting. POD had significant positive phenotypic correlation before 50 days, and had significant negative genetic correlation at 85 and 100 days with SOD, MDA and chlorophyll after planting. SOD had significant

positive genetic correlation at 100 days, and had significant positive phenotypic correlation at 24 and 36 days with MDA and chlorophyll after planting. MDA had significant positive genetic correlation at 66 and 100 days, and had significant positive phenotypic correlation before 50 days with chlorophyll after planting. The results showed that MDA content and chlorophyll content had a significantly positive genetic and phenotypic correlation with SOD at all growth. Therefore, SOD is the most key antioxidant enzyme at all growth in the SSC varieties. POD is also the critical antioxidant enzyme at the later growth in the SSC varieties (Table 6).

Discussion

Leaf senescence can either be naturally induced during development or stimulated by environmental factors including darkness, nutritional deficiency and various stresses (Lim and Nam 2005; Lim et al. 2007; Guo and Gan 2005). Premature senescence is an important factor leading to the decrease of crop yield and quality. The production of ROS such as the superoxide radical increased in leaf senescence, leading to disturbance in

Table 6 Estimated genetic and phenotypic correlation coefficients among biochemical traits

Traits	9 days	24 days	36 days	50 days	66 days	85 days	100 days
Genetic correlation coefficients							
CAT&POD	-0.288	0.176	0.565**	0.163	-0.210	0.662*	-0.852
CAT&SOD	-0.200*	0.212*	0.653	0.469	-0.442**	0.864**	0.310
CAT&MDA	-0.396	0.044	0.521**	0.417**	-0.414**	0.865**	0.184
CAT&chlorophyll	-0.039	0.044	0.476**	0.417*	-0.406**	0.860**	0.183
POD&SOD	0.300	0.457	0.369	0.366	0.605	-0.167	-0.867**
POD&MDA	0.516	0.344	0.433*	0.542	0.383	-0.221*	-0.863**
POD&chlorophyll	0.582	0.345	0.401*	0.542	0.373	-0.141**	-0.864**
SOD&MDA	0.288	0.404	0.373	0.323	0.832	0.498	0.357**
SOD&chlorophyll	0.341	0.404	0.380	0.323	0.815	0.517	0.357**
MDA&chlorophyll	0.523	0.486	0.483	0.502	0.495**	0.438	0.502*
Phenotypic correlation coefficients							
CAT&POD	0.034	0.050	0.177	0.061	-0.085*	0.123	-0.163
CAT&SOD	0.347	0.185**	0.255	0.258	-0.261**	0.437	0.131
CAT&MDA	-0.087	0.057	0.249*	0.170	-0.432**	0.266	0.076
CAT&chlorophyll	0.002	0.057*	0.229*	0.170	-0.420**	0.321	0.076
POD&SOD	0.445	0.485**	0.445*	0.341	0.341	-0.154	-0.045
POD&MDA	0.703**	0.389**	0.612*	0.607**	0.257	-0.227	-0.126
POD&chlorophyll	0.565*	0.389**	0.525	0.607**	0.249	0.155	-0.127
SOD&MDA	0.443	0.486**	0.464*	0.437	0.604	0.343	0.354
SOD&chlorophyll	0.347	0.486**	0.419*	0.437	0.589	0.572*	0.354
MDA&chlorophyll	0.541*	0.689**	0.610*	0.705*	0.609	0.398	0.705

Data were analysed by ADAA model

* and ** correlation coefficients are significant at 0.05 and 0.01 respectively

the redox homeostasis and also playing a key role in redox signaling in leaves (del Río et al. 1998; Foyer and Noctor 2003), POD and SOD activity increased in dehydrated and senescent Ramonda leaves (Sonja et al. 2006). MDA in detached leaves of Sponsor and Spokane (initially grown in the field or in a growth chamber) significantly increased 8 days after storage at 10 °C in the dark with RH \geq 95 % (Hodges et al. 2001). Antioxidant enzyme system such as CAT, POD and SOD activity and chlorophyll content of type B varieties is higher than that of type A with higher MDA content at the later growth of plant under natural stress (Yu et al. 2005). So cotton varieties without premature senescence have a high resistant to the natural stress, cotton varieties with premature senescence had a high MDA content and a low oxidative scavenging ability.

Different cotton varieties have diverse senescence traits. Senescence is under genetic control and is related with different expression of specific genes in

natural stress. CAT activity was mainly controlled by dominance effects, additive-by-additive epistatic effects and dominance genetic effect-by-environment interactions. Chlorophyll content was mainly controlled by dominance effects and dominance genetic effect-by-environment interactions. POD activity, SOD activity and MDA content were mainly controlled by additive genetic effects and additive-by-additive epistatic effect-by-environment interactions. Epistasis is an important source of variation contributing to speciation (Wright 1931). Because breakdown of a certain combination of alleles already adapted to a local environment will decrease the fitness of the recombinants. Some studies showed that the epistatic variance can account for a large proportion of the genetic variance of quantitative traits among progenies of line crosses (Malmberg and Mauricio 2005; Malmberg et al. 2005). Maternal and paternal effects on these traits were also detected at different extent duration of all growth, which suggested that these

traits should be selected by performance of maternal and paternal plants. So POD, SOD, MDA and CAT activity has a strong additive genetic effects and additive-by-additive epistatic effects, using molecular assisted selection (MAS).

In this research type A varieties with premature senescence have a natural sensitivity and low potential productivity under natural stress. Type B varieties without premature senescence have a high resistance to the natural stress and have a high potential productivity and quality. Compared with type A varieties, type B varieties had higher antioxidant enzyme (such as CAT, POD and SOD) activity and chlorophyll content, and lower MDA content at later plant growth stages under natural stress conditions (Yu et al. 2005). CAT, POD and SOD activity for hybrid F₁ (type B × type A) was higher than hybrid F₁ (type A × type B) at the later growth stages. At the same time, antioxidant enzymes (CAT, POD and SOD) and chlorophyll and MDA had a positive or negative genetic and phenotypic correlation. Higher SOD, CAT, and POD enzyme activity with higher chlorophyll (Yu et al. 2005). So evaluation of the heredity of these biochemical traits (CAT, POD, SOD, MDA, chlorophyll, and so on) and their relationship are very important in the SSC breeding with high yield and good quality.

Present study has shown that two type cultivars of the SSC differing in their later senescence rates exhibit differences in their antioxidant dynamics. Results support earlier work with spinach (Hodges et al. 2000, 2001) and cotton (Yu 2005) which implied that H₂O₂ regulation may play a critical role in the onset and dynamics of senescence. Our results showed the additive genetic effects of POD, SOD and MDA were high, these traits is suitable to be selected in an early generation (such as F₂ and F₃) of SSC breeding program. The additive genetic effects were low and the dominant genetic effects of CAT and chlorophyll were high, these traits are suitable to be selected in a later generation (such as F₅ and F₆). Assistant selection of biochemical traits would significantly accelerate the pace and prospects of success for breeding to improve the yield and quality of the SSC without premature senescence. The continuous isolation of cotton adaptive genes would lead to a more comprehensive understanding of natural selection's effect on genes and genomes (Ehrenreich and Purugganan 2006).

Acknowledgments We thank Prof. Jun Zhu for providing genetic analysis model ADA and ADMP, Dr. Chee Kok Chin for Meizhen Song providing visiting research in Rutgers University in New Jersey in 2010–2011 year. We acknowledge support by the National Basic Research Program of China (973 Program, No. 2010CB126006).

References

- Beers RF, Sizer IW (1952) A spectrophotometric method for measuring the breakdown of hydrogen peroxide by catalase. *J Biol Chem* 195:133–140
- Breeze E, Harrison E, McHattie S (2011) High-resolution temporal profiling of transcripts during *Arabidopsis* leaf senescence reveals a distinct chronology of processes and regulation. *Plant Cell* 23:873–894
- Buchanan-Wollaston V (1997) The molecular biology of leaf senescence. *J Exp Bot* 48:181–199
- DaCosta M, Huang B (2007) Changes in antioxidant enzyme activities and lipid peroxidation for bentgrass species in response to drought stress. *J Am Soc Hortic Sci* 3:319–326
- Del Rí'o LA, Pastori GM, Palma JM, Sandalio LM, Sevilla F, Corpas FJ, Jimenez A, Lopez-Huertas E, Hernandez JA (1998) The activated oxygen role of peroxisomes in senescence. *Plant Physiol* 116:1195–1200
- Ehrenreich IM, Purugganan M (2006) The molecular genetic basis of plant adaptation. *Am J Bot* 93(7):953–962
- Foyer CH, Noctor G (2003) Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. *Physiol Plant* 119:355–364
- Gan S, Amasino RM (1997) Making sense of senescence. Molecular genetic regulation and manipulation of leaf senescence. *Plant Physiol* 113:313–319
- Guo Y, Gan S (2005) Leaf senescence: signals, execution, and regulation. *Curr Top Dev Biol* 71:83–112
- Hodges DM, Forney CF, Wismer WV (2001) Antioxidant responses in harvested leaves of two cultivars of spinach differing in senescence rates. *J Am Soc Hortic Sci* 126(5):611–617
- Hodges DM, Forney CF (2000) The effects of ethylene, depressed oxygen and elevated carbon dioxide on antioxidant profiles of senescing spinach leaves. *J Exp Bot* 51:645–655
- Hodges DM, DeLong JM, Forney CF, Prange RK (1999) Improving the thiobarbituric acid-reactive-substances assay for estimating lipid peroxidation in plant tissues containing anthocyanin and other interfering compounds. *Planta* 207:604–611
- Jenkins JN, McCarty JC, Wu J, Saha S, Gutierrez OA, Hayes R, Stelly DM (2007) Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with upland cotton cultivars: II fiber quality traits. *Crop Sci* 47:561–570
- Lim PO, Nam HG (2005) The molecular and genetic control of leaf senescence and longevity in *Arabidopsis*. *Curr Top Dev Biol* 67:49–83
- Lim PO, Kim HJ, Nam HG (2007) Leaf senescence. *Annu Rev Plant Biol* 58:115–136
- Malmberg RL, Held S, Waits A, Mauricio R (2005) Epistasis for fitness-related quantitative traits in *Arabidopsis thaliana*

- grown in the field and in the greenhouse. *Genetics* 171:2013–2027
- Malmberg RL, Mauricio R (2005) QTL-based evidence for the role of epistasis in evolution. *Genet Res* 86:89–95
- Mao SC, Song MZ, Zhuang JN, Zhang CJ (1999) Study on productivity of the wheat-cotton double maturing system in Huang-Huai-Hai Plain. *Agric Sin* 32:107–109 (in Chinese)
- Munne 'Bosch S, Alegre L (2004) Die and let live: leaf senescence contributes to plant survival under drought stress. *Funct Plant Biol* 31:203–216
- Nooden LD, Guiamet JJ, John I (1997) Senescence mechanisms. *Plant Physiol* 101:746–753
- Pastori GM, del Rio LA (1997) Natural senescence of pea leaves (an activated oxygen-mediated function for peroxisomes). *Plant Physiol* 113:411–418
- Peabody PJ, Johnson PN (2002) Profitability of short season cotton genotypes on the high plains of Texas. *Texas J Agric Nat Resour* 15:7–14
- Schippers JHM, Jing HC, Hille J, Dijkwel PP (2007) Developmental and hormonal control of leaf senescence. In: Gan S (ed) *Senescence processes in plants*, vol 26. Blackwell Publishing, Oxford, pp 145–170
- Sonja V-J, Biljana K, Branka S, Flavia N-I (2006) Senescence- and drought-related changes in peroxidase and superoxide dismutase isoforms in leaves of *Ramonda serbica*. *J Exp Bot* 57(8):1759–1768
- Wang AG, Luo GH, Shao CB, Wu SJ, Guo JY (1983) Studies on superoxide dismutase in soybean seed. *Acta Phytophysiol Sin* 9:77–83
- Wright S (1931) Evolution in Mendelian populations. *Genetics* 16:97–159
- Wu J, Jenkins JN, McCarty JC Jr, Wu D (2006a) Variance component estimation using the additive, dominance, and additive and additive model when genotypes vary across environments. *Crop Sci* 46:174–179
- Wu J, Jenkins JN, McCarty JC Jr, Saha S, Stelly DM (2006b) An additive-dominance model to determine chromosomal effects in chromosome substitution lines and other gem-plasms. *Theor Appl Genet* 112:391–399
- Xu ZC, Zhu J (1999) An approach for predicting heterosis based on an additive, dominance and additive model with environment interaction. *Heredity* 82(5):510–517
- Ye ZH, Zhu J (2007) Genetic analysis on flowering and boll setting in upland cotton. III. Genetic behavior at different developing stage. *Acta Genet Sin* 27:800–809
- Yu SX, Song MZ, Fan SL, Wang W, Yuan RH (2005) Biochemical genetics of short-season cotton cultivars that express early maturity without senescence. *J Integr Plant Biol* 47(3):334–342
- Yuan CX, Ding J (1990) Effects of water stress on the content of IAA and the activities of IAA oxidase and peroxidase in cotton leaves. *Acta Phytophysiol Sin* 16:179–180
- Zhu J (1995) Analysis of conditional effects and variance components in developmental genetics. *Genetics* 141(4):1633–1639
- Zhu J, Weir BS (1994a) Analysis of cytoplasmic and maternal effects: I. a genetic model for diploid plant seeds and animals. *Theor Appl Genet* 89:153–159
- Zhu J, Weir BS (1994b) Analysis of cytoplasmic and maternal effects: II. Genetic models for triploid endosperms. *Theor Appl Genet* 89:160–166
- Zhu J (1997) Genetic model analyze approaches. China Agricultural Publishing Company, Beijing