2004 BELTWIDE COTTON CONFERENCES, SAN ANTONIO, TX – JANUARY 5-9

GENETIC ANALYSIS OF BIOCHEMICAL TRAITS IN SHORT SEASON UPLAND COTTON OF CHINA

Shuxun Yu, Meizhen Song, Wankui Gong, Wu Wang, Shuli Fan, and Jiwen Yu
China Cotton Research Institute
Chinese Academy of Agricultural Sciences
Anyang, China

Abstract

Five short season cultivars (SSC) with no premature senescence were selected to cross with 5 SSC cultivars with premature senescence. The parents, F1, and F2 from the reciprocal crosses were field tested in replicated trials in 2001 and 2002. The results indicated that the activities of protecting enzymes of the antioxidant system such as CAT, SOD, and POD were higher in the early maturing SSC with no premature senescence than these in the SSC parental cultivars that showed premature senescence, while the MDA content in the former was lower than that in the latter. Various genetic variances and heritabilities for these biochemical traits and IAA, ABA, and chlorophyll contents were also estimated. There existed significant additive variance for CAT, POD, ABA and IAA, while CAT specific activity and SOD activity were largely controlled by dominant effects. Both maternal and dominant variances played equally predominant roles in POD and SOD specific activity, MDA and soluble protein contents. The relative contributions of the various genetic components to the phenotypic variation varied in boll-setting period.

Introduction

The competition for more planting acreages between cotton and food crops has become intense and will remain so in the near foreseeable future under the situation of a large population need for food and clothing in a limited farm land in China. Therefore, the coordinated development between them is the major concern of both policymaking and scientific research community, and double or multiple cropping farm practice provides a possible valuable way in doing so. It was estimated that the acreage of double or multiple cropping counted for 60% of total farming land in cotton producing areas in China, and the intercropping index, i.e., the harvest times per year per acreage, reached 165%. One of the critical measurements for the multiple cropping practices is the exploitation and planting of short season cotton cultivars (SSC). However, under the current double or multiple cropping farming systems, especially in the cotton producing area of the Yellow River Valley, the key obstacle for such practice is that the maturity of some SSC is still not early enough. Cotton plants in these cultivars usually show slower early growth and late maturity with high percentage of post-frost harvest, which greatly decreases lint yield and qualities. Therefore, increasing lint yield and improving fiber qualities are the most important purposes of cotton genetic improvement in SSC.

SSC is an ecotype of planting cotton that has relatively short growing period, adaptable to certain social-economical levels under specific ecological conditions. SSC has its own apparent morphological and developmental characteristics, and biochemical and cultivating properties. Yu (1989) categorized SSC in China into three sub-ecotypes: (1) the north typical early mature ecotype (NTEME); (2) the Yellow River Valley ecotype (YRVE); and (3) the Yangtze River Valley ecotype (YZRVE). NTEME is mainly distributed in cotton planting areas of north Xinjiang and Hexi Zoulang, where it is planted as mono cropping. YRVE, which is a newly developed sub-ecotype appeared in the 1980s, is mainly distributed in Huanghuaihai cotton planting area, where it is planted with wheat (or, rape, vegetables) in double or multiple cropping system. Its planting pattern is usually intercropping with wheat (or rape, vegetables), or transplanting or direct planting after wheat (or rape, vegetables). YZRVE was developed in the1970s and its planting pattern is transplanting or direct planting after wheat (or rape, vegetables). Our study will be focused on YRVE.

According to the growth/developmental status and yield potential, SSC can be further classified into three types: (1) Type A that shows earliness and premature senescence; (2) Type B that is early mature but with no premature senescence; and (3) type C that shows late maturity. The type A SSC (premature senescence) is that, instead of natural senescence during the mature period, the cotton plant prematurely terminates its growth with reduced photosynthesis within its effective growing period, rendering early-than-normally expected senescence in the physiological and biochemical processes. The early mature type with no premature senescence (Type B) can be defined as the ones that can sufficiently use the natural resources of heat units and sunlight in the climate, producing a satisfying economical product. The type C SSC is the one which does not mature on time in the according season and still maintains its vigorous vegetative growth. Type A and C SSC both result in reduced boll weight, decreased lint percentage, fibre strength and fineness, and yield loss. Especially for the premature senescence SSC (Type A), the earlier the premature senescence occurs, the greater the yield and fiber quality loss. In order to attain an early maturity of SSC that fits the requirements of double or multiple cropping practices in various cotton producing areas, one effective way to improve the premature senescence of early maturing SSC is through coordination of vegetative and reproductive growths. Our research group has developed a number of SSC cultivars that express early maturity without

premature senescence, which are grown in major cotton planting areas of China. The genetic basis of earliness was investigated (Cheng and Yu, 1994) and these SSC cultivars were also physiologically characterized (Yu et al., 1992, 1993, 1994, 1999). However, there is still lack of explanations on the mechanism of the biochemical inheritance of SSC. Our present study was to investigate the genetic basis of biochemical traits associated with antioxidant system and phytohormones such as activities of CAT, POD, and SOD, and contents of MDA, chlorophyll, soluble protein, IAA and ABA using SSC with and without apparent premature senescence.

Materials and Methods

Materials

Two types of SSC cultivars were used in the experiments: Type A cultivars are the ones that are prematurely senescence, including Zhongmiansuo 10 (designated as A_1), Zhong 450407 (A_2), Zhong 652585 (A_3), Zhong 619 (A_4), and Yuzao 28 (A_5); Type B cultivars are the ones that are early mature without premature senescence, including Liao 4086 (designated as B_1), Zhong 925383 (B_2), Zhong 061723 (B_3), Zhong 961662 (B_4), and Yu 1201 (B_5). Five reciprocal crosses between Type A and B were made in 2000, with their progenies referred to as A_nB_n, B_nA_n, respectively (n=1, 2, 3, 4, 5). The resulted F_1 seeds were planted in Hainan Winter Nursery to produce F_2 seeds during the winter. In 2001, all the F_1 and F_2 seeds together with their parent lines were planted in a random complete block design with 3 replications in the fields at China Cotton Research Institute, Chinese Academy of Agricultural Sciences, Anyang, Henan. The plot size was 3 rows x 8.5 m for F_1 and 5 rows x 8.5 m for F_2 with row spacing of 0.7 m. Plant population was 42500 plants per ha. In 2002, the 2001 trials were repeated. The planting dates for both years were May 21.

Physiological and Biochemical Measurements

The 4th leaves from the topmost leaf of cotton plants were sampled during flowering and boll setting stages. The samples were divided into two groups: (1) mixed group: 20 leaves were sampled from each of the crosses, with main leaf veins idscarded. Activities of antioxidant enzymes including catalase (CAT), peroxidase (POD), superoxide dismutases (SOD), and content of malondialdehyde (MDA), were measured; (2) The second group included only 3 crosses. In this group, leaves from 30 plants of each parental line and F_1, 100 plants of F_2 were sampled individually. Contents in MDA, soluble proteins, chlorophyll a, b, a+b, a/b, activities and specific activities (percentage between enzyme activity and content of soluble protein) of antioxidant enzymes including CAT, POD, and SOD were determined.

CAT activity was measured as described by Thompson (1997), and POD activity was determined using guaiacol method (Yuan, 1990). SOD activity was tested with reductive method under the light of nitroblue tetrazolium (NBT) (Wang, 1983). MDA content was measured using thiobarbituric acid method (Zhu, 1990). Chlorophyll was extracted with the method of 1:1 mixture of absolute ethanol and acetone. Absorbance values at 645 nm and 663 nm were measured, respectively for chlorophyll a and b content calculation. Soluble protein content was determined using the Coomassie Brilliant Blue G250 method (Lu, 1989). IAA and ABA contents were determined by ELISA method (He, 1990).

Data Analysis

Data collected were analysed using the genetic analysis model described by Zhu (Zhu and Weir, 1994; Zhu, 1995, 1997; Ye and Zhu, 2000). The software in diallel crossing and heterosis, and QTL were used. The following models were used: ADAA (ADE) model for the analysis of additive-dominant-epistatic effects, in which the total genetic variance is, $V_G = V_A + V_D + V_{AA} + V_{DD} + V_{AD}$; ADM model for the analysis of additive-dominant-maternal effects, in which the total genetic variance is $V_G = V_A + V_D + V_M + V_P$ (paternal effect); and AD model for the analysis of additive-dominant effects, in which the total genetic variance is $V_G = V_A + V_D$ in the absence of epistatic and maternal effects. Here, V_G is the total genetic variance; V_A is the additive variance; V_D is the dominant variance; V_{AA} is the epistatic variance due to additive x additive interaction; V_{DD} is the epistatic variance due to dominant x dominant interaction; V_{AD} is the epistatic variance due to interaction between additive x dominant effects. The phenotypic variance $Vp = V_G + Ve$, where, Vp is the phenotypic variance and Ve environmental variance. The minimum norm quadratic unbiased estimation method (MINQUE) was used to estimate all these variances and their percentages in the total variance. The linear unbiased prediction method was used to estimate the gene effects of all the traits. Jackknife method was used to compute the predictive value of all the traits and their standard errors, and t-test was used to test the significance of difference.

Results and Analysis

Population Distributions of Biochemical Traits in F2 between Type A and Type B

It is generally believed that the biochemical traits possibly associated with the early maturity of SSC are quantitative, which exhibit a continuously normal distribution in F_2 populations. The distribution properties in the F_2 populations are not only affected by the genotypic difference resulting from segregation of genes, but also by environmental factors. The statistic software, Statistic Analysis System (SAS) was used to analyse the distribution in the F_2 population from the reciprocal crosses between A_1 and $B_1$for the 5 different biochemical traits (Figure 1 to 5). Figure 1, 3, 4, and 5 showed that the distributions in CAT and POD activities and MDA and chlorophyll contents in the F_2 population fitted to a normal distribution, indicating

that these 4 biochemical traits all belong to typical quantitative traits. There existed two peaks in the distribution of SOD activity in the reciprocal crosses (Figure 2), which was significantly deviated from a normal distribution (data not shown), indicated that there might be major genes controlling it.

Relative Contributions of Various Genetic Effects

As indicated in Table 1, based on the Additive-Dominant-Maternal Effect Model (ADM Model) (Zhu, 1994, 1997), there existed significant maternal effects of cytoplasm in the activities of CAT, POD, SOD, and MDA, ABA and soluble protein contents. The activity of CAT, specific activity of SOD, and chlorophyll content were primarily affected by maternal effects and the dominant effects also played an important role; for specific activity of CAT and POD, SOD activity, and contents of soluble proteins, IAA, and MDA, dominant effects were the main contributing factor; and only the POD activity and ABA content were primarily affected by additive effects. Our study demonstrated that the inheritances of CAT activity, SOD specific activity, and chlorophyll content were primarily controlled by cytoplasm, while CAT and POD specific activities, SOD activity, and contents of soluble proteins, IAA, and MDA were primarily dominance-controlled traits. POD activity and ABA content were additively inherited, thereby, serving as biochemical indices for the selection of early mature materials in parental plants and progeny screening.

Heritabilities of the Biochemical Traits in SSC Populations

It can be seen in Figure 6 that POD activity and contents of ABA, IAA and chlorophyll had relatively higher narrow sense heritabilities, in that POD activity was the highest (52.96%), and ABA followed (51.67%). CAT specific activity, activities of POD and SOD, and contents of IAA and ABA had comparably higher broad sense heritabilities, in that POD activity was the highest (78.89%), IAA content came next (78.15%). Therefore, if early maturing lines without premature senescence are to be bred, an early generation selection based on POD activity and contents of ABA, IAA and chlorophyll could be effective.

Correlations among the Biochemical Traits

The activities of anti-oxidant system enzymes CAT, POD, and SOD had different expression levels and roles in different developmental stages of cotton plants. CAT and SOD play a major role in the early developmental stages of the cotton plant, while POD and SOD in the late developmental stages. Since these traits showed cytoplasmic inheritance, the Additive-Dominant-Maternal Effect Model (ADM Model) was chosen for correlation analysis (Table 2). It can be seen that CAT activity had a positive genetic and phenotypic correlations with SOD activity and IAA content, while it had a negative genetic and phenotypic correlations with POD activity, MDA, ABA and chlorophyll contents. The results indicated that CAT together with SOD and IAA could share some common roles in the early developmental stages of cotton. POD activity had positive genetic and phenotypic correlations with SOD activity, MDA and chlorophyll contents, but negative genetic and phenotypic correlations with IAA and ABA contents, indicating that POD and SOD could share some joint roles in the later developmental stages. ABA content had negative phenotypic correlation with IAA and MDA contents. The significant negative correlation between contents of IAA and ABA was in accordance with the growth and development of SSC. IAA mainly promotes the growth of cotton plants, while ABA mainly promotes the senescence of cotton and abscission of leaves, squares and bolls. It is important that appropriate selection be exercised for expression levels and ratio of these two hormones in different developmental stages in cotton breeding for earliness. Since SOD activity had positive genetic and phenotypic correlations with the CAT and POD activities, and IAA and MDA contents, negative genetic and phenotypic correlations with ABA content, it may render a major role in promoting early maturity without premature senescence of cotton plants. If cotton plants show late maturity, a selection pressure should be applied on the ABA content.

Genetic Control of Biochemical Traits in SSC Cultivars with No Premature Senescence in Boll-setting Stage

CAT: The specific expression of CAT was estimated from the ADM model (Table 3). The results showed that from August 3rd to September 3rd (74-105 days after planting), the maternal effect on CAT activity persisted over the period. Also, the dominant variance on CAT activity increased gradually over time, reaching the highest on August 24th, while the additive variance was not detectable in the entire period. Figure 7 shows the heritability of CAT activity in the different developmental stages. The broad heritability of CAT activity reached highest on August 24th (63.41%), and then came August 10th (57.45%). After the peak expression, it decreased gradually with the senescence of cotton plants. The narrow heritability was low all the time and became detectable only on September 3rd (27.41%), indicating that CAT activity was mainly affected by the maternal effect and dominant effect during the time from August 3rd to September 3rd.

POD: The specific expression of POD was estimated from the ADM model (Table 4). During August 3rd and August 17th (74-88 days after planting), the POD activity was mainly controlled by dominant effect; after August 17th when cotton plants entered their late growing stage, maternal effect became predominant. Only after August 24th, the additive effect was detectable. Figure 8 showed that the broad heritability of POD activity remained a comparable higher level in the different developmental stages, but the narrow heritability reached a significant high level only till August 24th. This indicated that the additive gene effect controlling POD activity was turned off during the early boll setting stage, when the dominant gene effect and maternal effect predominated. Therefore, selection on POD activity for early maturity in the late developmental stages in breeding programme should be cautious.

SOD: The specific expression of SOD was estimated from the ADM model (Table 5). From August 3rd to September 3rd (74-105days after planting), the POD activity was mainly controlled by both maternal effect and dominant effect. The additive effect of SOD activity was only detectable on September 3rd (18.51%). Analysis of the heritability of SOD activity in the different developmental stages (Figure 9) revealed that the broad heritability of SOD activity maintained a high level on August 10th, 17th and September 3rd, while the narrow heritability became significant only on September 3rd. This indicated that, similar to SOD, during the time from August 3rd to late August, the additive gene effect controlling SOD activity was turned off.

MDA: The specific expression of MDA was estimated from the ADM model (Table 6). From August 3rd to September 3rd (74-105days after planting), maternal effect for MDA (19.31- 46.87%) was significant in all the sampling dates. Additive and dominant variances were also significant in two sampling dates (August 3rd and 17th), and the additive effect was predominant on August 17th (58.62%). Figure 10 showed the heritability of MDA content in different developmental stages, indicating that on August 3rd and August 17th, both broad sense heritability and narrow sense heritability maintained a high value, and then gradually declined. In the late developmental stages of cotton plants, various physiological and biochemical functions for growth tend to decline, which could trigger the expression of immune system of the plant, preventing itself from senescence.

Discussion

The Physiological and Biochemical Basis of Early Maturing Cultivars with No Premature Senescence

During the entire growing season, the cotton plant is undergoing the influences of biotic and abiotic stresses, such as drought, high temperature, irradiation, salt stress, and pathogen and insect invasion, which usually induces the plant cells to produce a number of reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2), hydroxy radical (·OH), singlet oxygen ($^1O_2$), and superoxide radical (O_2·-) (Geng et al., 2002; Lee and Bennett, 1982; Li et al., 2000, 2001; Shen and Yin, 1993; Wang et al., 1989). In the mean time, the metabolism in the cell itself also produces ROS. Usually the enzymatic and non-enzymatic anti-oxidant systems, which were developed during cotton evolution processes, are responsible for removing the ROS. The most documented enzymes in the antioxidant system include CAT, SOD, and POD, which are believed to have higher activities in the early maturing cultivars with no premature senescence than in the prematurely senesced cultivars. We used the early maturing cultivars with no premature senescence and with premature senescence and their hybrid progenies to test the activities of CAT, SOD and POD, and MDA content. The results revealed that CAT, SOD, and POD had higher activities in the early maturing cultivars with no premature senescence than in the early maturing cultivars with premature senescence. Meanwhile, we also analysed the changing patterns of the enzymatic activities of antioxidant system in their progenies. The result indicated that these biochemical traits usually showed hetereobeltiosis. As one of the final products resulting from the oxidization of the antioxidant enzymatic system, the MDA content was significantly lower in the early maturing cultivars with no premature senescence than in the parental cultivars with premature senescence.

Genetic Basis of the Physiological and Biochemical Traits

The biggest obstacle for developing early maturing and high yield potential SSC cultivars is premature senescence of such cultivars. As early maturity and premature senescence are highly positive correlated, which makes it difficult to improve lint yield and quality, most SSC cultivars always show late maturity if they do not prematurely senesce. Therefore, it is difficult to develop SSC cultivars that are early maturing but with no premature senescence. New methods in cotton breeding for high yielding SSC should be taken into considerations. Biochemical breeding could be one of the solutions to such problems.

Our investigation indicated that, (1) The major enzymes in antioxidant system, such as CAT, POD, and SOD, and phytohormones such as ABA had significant maternal effect, showing a cytoplasmic inheritance; and then came the dominant effect inheritance. (2) The specific activities of CAT and POD, activity of SOD, contents of soluble proteins, IAA, and MDA were mainly dominant effect inheritance, but there also existed cytoplasmic inheritance. (3) POD activity and ABA content mainly showed additive effect inheritance, and there also existed cytoplasmic inheritance. Accordingly, the inheritance of these biochemical traits in cotton can be classified into two categories: that controlled mainly by cytoplasmic factors with a cytoplasmic-nuclear interaction and that controlled mainly by nuclear factors with a nuclear-cytoplasmic interaction. The traits, such as POD activity and ABA content, which had significant additive effect, can serve as biochemical criteria for selecting early maturing cotton genotypes with no premature senescence.

The relationship among the biochemical traits in cotton can be summarized as following, (1) CAT activity had positive genetic and phenotypic correlations with SOD activity, IAA content, and negative correlations with POD activity and contents of MDA, ABA and chlorophyll, indicating that in the early growth stage of cotton, CAT, SOD, and IAA acted cooperatively. (2) POD activity had positive genetic and phenotypic correlations with SOD activity, contents of MDA and chlorophyll, and negative correlations with contents of IAA and ABA, indicating that in the late growth stage of cotton POD and SOD had a coordinated effect. (3) ABA content had significant positive genetic and phenotypic correlations with contents of IAA and MDA. (4) SOD activity had significant positive genetic and phenotypic correlations with IAA content, positive genetic and phenotypic correlations with activities of CAT and POD, and MDA content, negative genetic and phenotypic correlations with ABA content, indicating that SOD played a major role in promoting early maturity.

Inheritance of Biochemical Traits during Boll-setting Period

During the boll setting stage from August 3rd to September 3rd, the activities of CAT, POD, and SOD were mainly the maternal effect, and in the next place was the nuclear controlled dominant effect. The nuclear controlled additive effect maintained a much low level or undetectable until after September. Therefore, through manipulating the genetic effect of the biochemical traits from August 3rd to September 3rd in early maturing SSC cultivars with no premature senescence, we can understand the developmental and genetic basis of the biochemical traits. This study has laid a foundation for further exploration on how and when the relevant genes or quantitative trait loci (QTLs) turn on and turn off and for the future QTLs localization on these biochemical traits.

References

Hongliang, C. and S. Yu. 1994. Studies on the earliness inheritance of upland cottons (*G. hirsutum* L.). Cott. Sci. 6(1):9-15.

Junyi, G., X. Zhang, R. Cui, Z. Wang, and F. Yan. 2002. Study on the SOD and POD activity and physiological biochemical mechanism in F_1 of cotton hybrid Jimian NO.18 Acta Agriculturae Boreali-Sinica 17(4):96-99.

Lee, E.H. and J.H. Bennett. 1982. Superoxide dismutase: A possible protective enzyme against ozone injury in snap beans (*Phaseolus vulgaris* L.). J. Plant Physiol. 6:1444.

Li, L., Y. Du, P. Wei, and L. Wen. 2001. Changes of IAA, ABA and MDA contents and activities of SOD and POD in the course of abscission of young cotton bolls. Acta Phytophysiologica Sinica. 27(3):215-220.

Li, Y., B. Han, and G. Jian. 2000. *Verticillium dahliae* toxin induces changes in the activities of peroxidase and SOD and in the experession of PR proteins in cotton callus. J. of China Agric. Univ. 5(3):73-79.

Shen, F. and C. Yin. 1993. The effect of salt stress on superoxide dismutase in cotton seeding cotyledon. Cott. Sci. 5(1):39-44.

Wang, J., H. Liu, and X. Tong.1989. The role of superoxide dismatase in stress physiology and senescence physiology of plant. Plant Physiol. Commum. 25(1):1-7.

Ye, Z. and Z. Jun. 2000. Genetic analysis on flowering and boll setting in upland cotton. Genetic behaviour at different developing stages. Acta Genetica Sinica. 27:800-809.

Yu, S., Z. Huang, R. Jiang, R. Yuan, X. Nei, Z. Su, and J. Xu .1992. Researches on the biochemical mechanism of high consistent yield of short season cotton Zhong Mian Suo 16. Scientia Agricultura Sinica. 25(5):24-30.

Yu, S., Z. Huang, R. Jiang, S. Liu, R. Yuan, Z. Chu, G. Zhang, and M. Mu.1993. Researches on the kinetics of fluorescence and SOD activity in cotyledon of short season cotton. Scientia Agricultura Sinica. 26(3):14-20.

Yu, S., Z. Huang, R. Jiang, R. Yuan, X. Nei, Z. Su, and J. Xu .1994. Researches on the biochemical mechanism of aging process of different short season cotton varietirs. Acta Agronomica Sinica. 20(5):629-636.

Yu, S., S. Fan, R. Yuan, X. Yu, and W. Gong. 1999. Genetic influence of eliminating active oxydase on the characteristic of early maturity but late senescence of cotton. Cott. Sci. 11(2):100-105.

Zhu, J. 1995. Analysis of conditional effects and variance components in developmental genetics. Genetics. 141(4):1633-1639.

Zhu, J. 1997. Genetic model analysis approaches. China Agricultural Publishing House.

Zhu, J. and B.S Weir. 1994. Analysis of cytoplasmic and maternal effects: I. A genetic model for diploid plant seeds and animals. Theor. Appl. Genet. 89:153-159.

Table 1. The ratios between various genetic variances to phenotypic variance for various biochemical traits.

Biochemical trait	Additive effect V_A/V_P	Dominant effect V_D/V_P	Maternal effect V_M/V_P	Residual error V_r/V_P	Phenotypic variance V_P
CAT(unit/g FW)	14.49	15.69	21.09*	48.73+	105959*
CAT specific activity	0	70.48*	14.53	14.99	27.54
POD(unit/g FW)	52.96*	25.93+	12.17*	8.94+	1857.01*
POD specific activity	0	42.23	22.67	35.10	0.10
SOD(unit/g FW)	0	60.76+	19.11*	20.12	86624.2+
SOD specific activity	0	44.95**	51.99**	3.06	261.62*
Soluble protein (mg/g FW)	0	47.05**	37.16**	15.80*	10579.7+
ABA(ng/mg FW)	51.67**	15.83**	11.61**	20.92	16760.7**
IAA(ng/mg FW)	26.22**	51.93	17.64	4.22**	158785**
MDA(μmol/mg FW)	0	21.24	13.75+	65.01*	0.000125**
CHLa+b (mg/g FW)	16.63	2.31	28.15	52.92	0.00759+

Note: Additive-dominant-maternal effects were computed based on the ADM model.

Table 2. Estimates of genetic and phenotypic correlation coefficients among biochemical traits in SSC.

Traits	CAT	POD	SOD	MDA	IAA	ABA	CHLa+b
CAT		-0.316	0.227	-0.100	0.453	-0.100	-0.299
POD	-0.310		0.024	0.207	-0.159	-0.139	0.392
SOD	0.189	0.082		0.150	0.106	-0.228	0.074
MDA	-0.570+	0.404	0.496		0.141	-0.536+	-0.341
IAA	0.514	-0.158	0.132**	0.266		-0.413**	-0.159
ABA	0.039	-0.212	-0.383	-1.000+	-0.445**		-0.485
CHLa+b	-0.653*	0.705+	0.227	-0.583	-0.208	-0.807	

Note: additive-dominant-maternal effect (ADM) model, in the below diagonal are the genetic correlation coefficients, and the above diagonal phenotypic correlation coefficients.

Table 3. Ratios of genetic variances to phenotypic variance of CAT activity in different developmental stages.

Sampling date	Additive effect V_A/V_P	Dominant effect V_D/V_P	Maternal effect V_M/V_P	Residual error V_r/V_P	Phenotypic variance V_P
August 3rd	0	26.77**	36.64**	36.59	2.30e+006
August 10th	2.68	54.78	35.42	7.13	1.60e+006
August 17th	0	39.90	42.63**	17.46	1.94e+006
August 24th	1.68	61.73**	24.69	11.90	1.23e+006
Sept. 3rd	27.41	12.91**	4.13**	55.54	879752

Table 4. Ratios of genetic variances to phenotypic variance of POD activity in different developmental stages.

Sampling date	Additive effect V_A/V_P	Dominant effect V_D/V_P	Maternal effect V_M/V_P	Residual error V_r/V_P	Phenotypic variance V_P
August 3rd	0	66.30	19.11	15.59	4106.2
August 10th	0	62.81**	32.78**	4.41	16490.5
August 17th	0	74.70**	16.81	8.49	36585.9
August 24th	43.03**	17.05	25.04	14.89**	45314.5
Sept. 3rd	27.30**	20.24	45.44**	7.01	326726

Table 5. Ratios of genetic variances to phenotypic variance of SOD activity in different developmental stages.

Sampling date	Additive effect V_A/V_P	Dominant effect V_D/V_P	Maternal effect V_M/V_P	Residual error V_r/V_P	Phenotypic variance V_P
August 3rd	0	0	16.82	83.18	10295.8**
August 10th	0	51.22**	28.90**	19.88	254754
August 17th	0	32.68	40.13	27.19	190413
August 24th	0	3.93	22.36**	73.71	106211
Sept. 3rd	18.51**	41.14	36.48**	3.87	143903

Table 6. Ratios of genetic variances to phenotypic variance of MDA content in different developmental stages.

Sampling date	Additive effect V_A/V_P	Dominant effect V_D/V_P	Maternal effect V_M/V_P	Residual error V_r/V_P	Phenotypic variance V_P
August 3rd	37.51**	25.69**	19.31**	17.49**	0.0002
August 10th	0	0.29	55.05**	44.66**	0.0002
August 17th	58.62**	7.70**	23.65**	10.02**	0.0002**
August 24th	3.91	45.80	23.04**	27.25**	0.0001**
Sept. 3rd	1.86	34.67	46.87**	16.60**	0.0005**

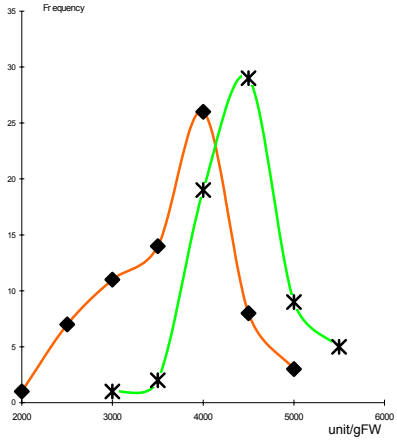

Fig. 1 CAT Activity Frequence of F2 of B1*A1.

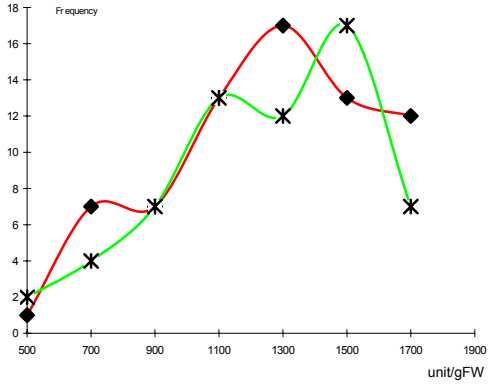

Fig. 2 SOD Activity Frequence of F2 of B1*A1.

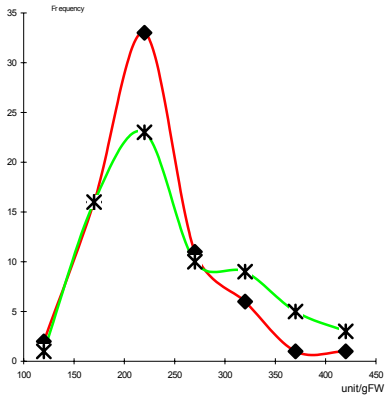

Fig. 3 POD Activity Frequence of F2 of B1*A1.

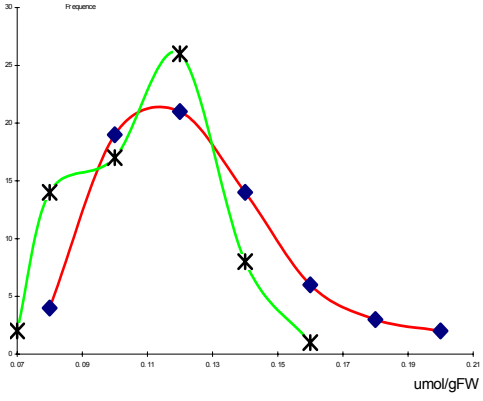

Fig. 4 MDA content Frequence of F2 of B1*A1.

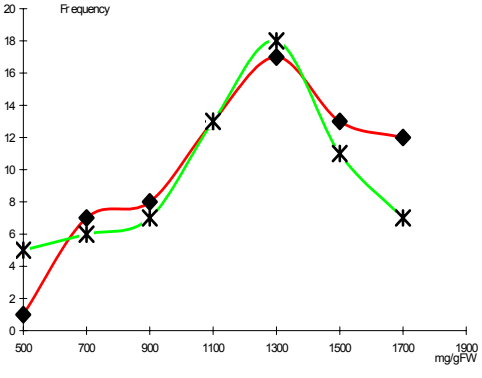

Fig. 5 Chlorophyll content Frequence of F2 of B1*A1.

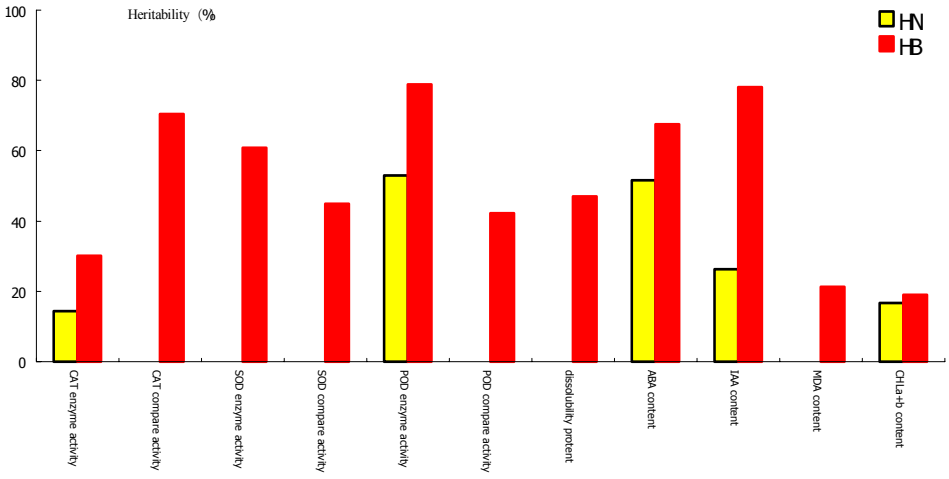

Figure 6. Heritabilities of biochemical properties (HN: narrow sense heritability; HB: broad sense heritability).

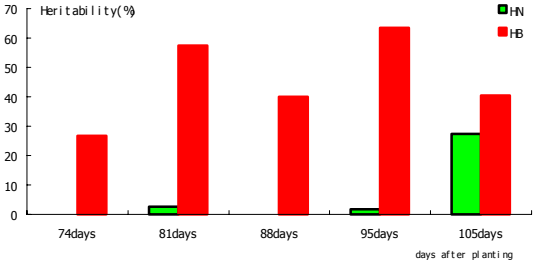

Figure 7. Heritability of CAT activity in various developmental stages.

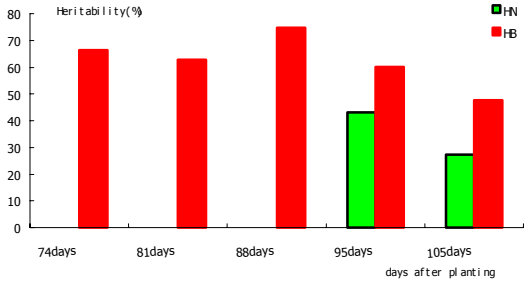

Figure 8. Heritability of POD activity in various developmental stages.

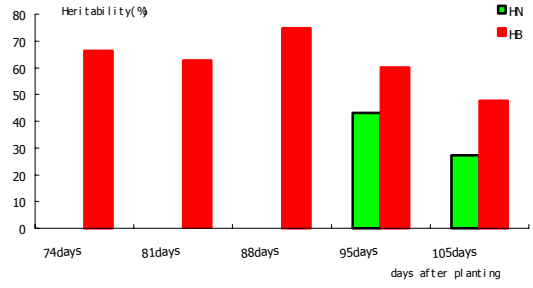

Figure 9. Heritability of SOD activity in various developmental stages.

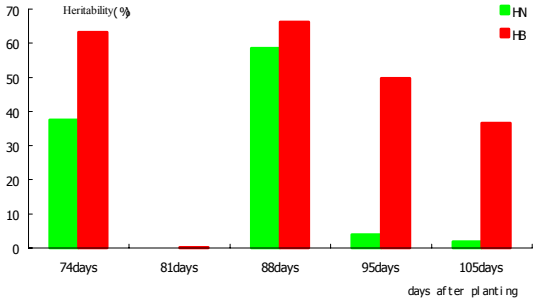

Figure 10. Heritability of MDA content in various developmental stages.