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Genetic analysis of yield and fiber quality traits in upland cotton (*Gossypium hirsutum* L.) cultivated in different ecological regions of China

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Abstract

Background: Cotton is an important fiber crop worldwide. The yield potential of current genotypes of cotton can be exploited through hybridization. However, to develop superior hybrids with high yield and fiber quality traits, information of genetic control of traits is prerequisite. Therefore, genetic analysis plays pivotal role in plant breeding.

Results: In present study, North Carolina II mating design was used to cross 5 female parents with 6 male parents to produce 30 intraspecific F₁ cotton hybrids. All plant materials were tested in three different ecological regions of China during the year of 2016–2017. Additive-dominance-environment (ADE) genetic model was used to estimate the genetic effects and genotypic and phenotypic correlation of yield and fiber quality traits. Results showed that yield traits except lint percentage were mainly controlled by genetic and environment interaction effects, whereas lint percentage and fiber quality traits were determined by main genetic effects. Moreover, dominant and additive-environment interaction effects had more influence on yield traits, whereas additive and dominance-environment interaction effects were found to be predominant for fiber traits. Broad-sense and its interaction heritability were significant for all yield and most of fiber quality traits. Narrow-sense and its interaction heritability were non-significant for boll number and seed cotton yield. Correlation analysis indicated that seed cotton yield had significant positive correlation with other yield attributes and non-significant with fiber quality traits. All fiber quality traits had significant positive correlation with each other except micronaire.

Conclusions: Results of current study provide important information about genetic control of yield and fiber quality traits. Further, this study identified that parental lines, e.g., SJ48-1, ZB-1, 851-2, and DT-8 can be utilized to improve yield and fiber quality traits in cotton.

Keywords: Cotton, Hybrid, Genetic effects, Additive, Dominance, Correlation

Background

Cotton is the primary natural fiber crop used in textile industry, source of edible oil, and planted in more than 80 countries/regions of the world (Li et al. 2019). China is one of the major cotton producing and consuming countries in the world. The demand for fiber in the

textile industry keeps increasing. To fulfill this challenge, yield potential of recent cotton genotypes can be increased through hybridization. In this regard, hybrids are developed through utilization of heterosis and cultivated in considerable area of China (Xing et al. 2007a). Main task of cotton breeders is to develop varieties or hybrids not only with superior yield and fiber quality but also with resistance against major pests, diseases and abiotic stresses such as adverse climatic conditions. The preliminary step to achieve such breeding aims is to select good genetic materials with suitable breeding methods.

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Parents genetically superior, physiologically effective and having good combining abilities are generally useful to explore heterosis in commercial hybrids. Estimation of combining ability or genetic effects is an important strategy to sort out superior and inferior parents coupled with better crosses (Basal and Turgut 2005; Khan *et al.* 2015; Rauf *et al.* 2005). Combining ability can be broken down into two components, i.e., general combining ability (GCA) and specific combining ability (SCA). Genetic effects are comprised of additive and non-additive genetic effects. GCA is associated with the parental lines and underlies additive gene contributions, whereas SCA is related to the comparative performance of hybrids and determines non-additive gene action, viz., dominant and epistatic.

Along with development of molecular genetics and breakthroughs in bioinformatics, genetic engineering, and genome sequencing, major changes have taken place in crop breeding research. Modern breeding methods are based on genes with an emphasis on improvement of individual characters. So, breeders must have strong knowledge about genetic control of traits to empower applications of molecular genetics to improve yield and quality of cotton crop (Li *et al.* 2015; Wu *et al.* 2017a, 2017b; Yue *et al.* 2012; Zhang *et al.* 2018). To be in a concise perspective, genetic analysis has no substitute in crop breeding. Yield is a complex quantitative trait controlled by multiple genes frequently affected by environment. Estimation of genetic effects with quantitative genetic models is an important strategy to select future breeding materials. Four main genetic models are used in breeding to measure genetic effects, i.e., additive-dominance (AD) model (Ming *et al.* 2008), additive-dominance-environment (ADE) model (Tang and Xiao 2014; Ye *et al.* 2008), additive-dominance-epistatic (ADAA) model (Song *et al.* 2014, 2015b), and additive-dominance-maternal (ADM) model (Feng *et al.* 2011; Zhang *et al.* 2016). Genetic effects are influenced by materials, methods, and environments. Previous studies have shown that yield component traits are strongly influenced by dominant effects of genes, while additive-environment interaction effects also have certain contribution. In contrast, fiber quality traits are mainly controlled by additive effects of genes and are less affected by the environment (Cui *et al.* 2014; Jenkins *et al.* 2012; Song *et al.* 2015a; Zhang and Abdelraheem 2017; Zhang *et al.* 2017). Traits that are readily influenced by the environment can be effectively improved by adjusting cultivation measures, whereas traits whose phenotypic variation is mainly determined by genetic effects can be improved through genetics and breeding. High additive effects tend to facilitate early selection, and non-additive effects often suggest potential use of heterosis breeding.

Different mating designs are used in plant breeding to estimate the genetic variances of traits. However, choice of mating design is directly affected by objectives, time, space, and cost. Interestingly, North Carolina designs (NC) allow the breeders to measure additive, dominance and environment variances with less labor than diallel (Wen *et al.* 2015). In this study, NCII mating design was used to generate 30 F_1 intraspecific upland cotton hybrids by using 5 female inbred parents and 6 male inbred parents. Field experiments were performed at three different locations for two consecutive years to obtain reliable phenotypic data for genetic analysis. The objective of this research was to obtain information on the genetic control of yield and fiber quality traits and correlation among traits under study. Our results will be important to select the base population for future hybrid breeding in upland cotton.

Material and methods

Plant materials, environment condition, and field design

In 2015, we used 11 inbred lines to produce 30 F_1 hybrids by using North Carolina mating design II (Li *et al.* 2019). The inbred lines Zhong 901–19 (P_1), L28–2 (P_2), SJ48–1 (P_3), ZB-1 (P_4), and K8–1 (P_5) were used as female parents, while GC-8 (P_6), 851–2 (P_7), A2–10 (P_8), DT-8 (P_9), Z98–15 (P_{10}), and RP24–10 (P_{11}) were used as male parents. Among them, P_4 , P_6 , and P_8 outperformed in the Yangtze River cotton belt, and P_5 and P_8 depicted better performance in the Northwest inland cotton belt, and all others were outstanding in the Yellow River cotton belt. Seeds of the resulting 30 hybrids and parental lines were planted in three different environmental regions of China. E_1 was in Anyang, Henan (114°35'E, 36°10'N; Yellow River cotton belt); E_2 was in Alar, Xinjiang (81°28'E, 40°55'N; Northwest inland cotton belt) and E_3 was in Wuwei, Anhui (117°75'E, 31°3'N; Yangtze River cotton belt). Planting and climate conditions at three locations are described in Additional file 1. All materials were planted in randomized complete block design with three replications in all above-mentioned environments during the period of 2016–2017. Seeds were sown in late April in consecutive years. Standard agronomic practices were followed throughout growing season.

Evaluation of yield and fiber quality traits

In mid-September, we counted total number of plants and total number of bolls for each line. Number of bolls (BN) per plant was calculated by dividing the total number of bolls by total number of plants. When more than 90% of bolls had opened, one fully opened boll was randomly selected from each of 50 individual plants, and weighed to estimate boll weight (BW). Seed cotton yield (SCY) was picked from each plot by hand and weighed

after drying. Weight of seed cotton per plot was used to calculate seed cotton yield (SCY) per hectare. Lint percentage (LP) was calculated as follows: lint weight/seed cotton weight $\times 100$. Lint yield (LY) was calculated by multiplying the seed cotton yield by the lint percentage estimated from the 50 bolls. Subsamples of lint collected from each plot were sent to Cotton Fiber Quality Testing Center affiliated with the Chinese Ministry of Agriculture and Rural Affairs (Anyang, Henan) to evaluate fiber quality using a model High Volume Instrument (HVI_900) machine. Following data was collected: fiber length (FL, mm; upper half mean length), fiber uniformity (FU, %), fiber strength (FS, cN \cdot tex $^{-1}$), micronaire (MIC) and fiber elongation (FE, %).

Data analysis

Genetic analysis was performed using QGASStation 2.0 software (<http://ibi.zju.edu.cn/software/qga/index.htm>) with ADE genetic model (Tang and Xiao 2014). The linear mixed model approach, i.e., minimum norm quadratic unbiased estimation (MIQNUE) was used to calculate variances and their contributions to the total variance. To estimate genetic effects, genotypic values based on population means were used with the adjusted unbiased prediction (AUP) method. The jackknife resampling method was used to calculate standard errors for each parameter by successive removal of individual blocks within each environment (Zhu 1992; Zhang *et al.* 2016). The *t*-test was used to assess significant differences.

Results

Genetic variance components of yield, yield components, and fiber quality traits

We estimated proportion of genetic variances for 30 hybrids and their parents based on three locations and 2 years data by using ADE genetic model for all traits under study. Results of all genetic variances can be seen in Fig. 1a. Result showed that additive variance (V_A) was significant for LP, FL, FU, FS, MIC, and FE with $P < 0.01$ (Additional file 2). Dominant variance (V_D) of genetic was significant for all traits except FL and FE. However, it was larger for BN, BW, LP, SCY, and LY. The V_D of BW, SCY and LY were greater than the V_A , while the opposite was true for LP and all fiber quality traits. Results of genetic-environment interaction showed that the variance of additive-environment (V_{AE}) interaction was larger than the variance of dominant-environment (V_{DE}) interaction. V_{AE} for BW, LP, and SCY were larger. However, it was smaller for BN. The V_{AE} and V_{DE} were equally important for LY. A significant V_{AE} was noticed for MIC and FU. V_{DE} was distinct for FL, FU, and FE. The ratio of genetic variance (V_G) to phenotype variance (V_P) for BW, LP, LY, and FL was > 0.80 . This ratio for

BN, SCY, FS, and FE was > 0.70 and for remaining traits was > 0.63 . These results indicated that these phenotypes were mainly inherited. Overall analysis results showed that BW, BN, SCY, and LY were mainly controlled by genetic and environment interaction effects (Fig. 1b). On the other hands, LP and fiber quality traits were mainly determined by the main genetic effects.

Additive effects for yield, yield components, and fiber quality traits

Additive effects (equivalent to GCA) are the average performance of a line in hybrid combinations due to additive gene action. It plays an important role to select superior inbred lines for specific trait or set of traits. Predicted additive effects of all parental lines based on all field tests for BN, LP, LY and fiber quality traits are listed in Table 1. The additive effects for BW and SCY were too small to analyze in this study. Result showed that female parent P_4 had the highest significant additive effect for BN. It was determined that female parents showed significant positive additive effects for BN. In contrast, most of male parents showed significant negative additive effects for BN. Further results showed that P_2 , P_3 , and P_4 had significant positive additive effects for LP. For LY trait, female parent P_3 had the highest additive effect and male parents P_7 had the lowest additive effect. The additive effects of P_2 , P_3 , and P_8 were significantly positive for LY. All parental lines had significant additive effects for FL except P_2 . Female parent P_3 showed the highest additive effect for FL. With regard to significant additive effects for FU, P_4 was the highest ranked genotypes among all parents. For FS, female parents P_5 had the highest additive effect. However, P_2 , P_6 , P_8 , and P_{11} had a significant but negative additive effect for FS. All parental lines had significant additive effects for MIC except for those of P_1 , P_2 , P_5 , and P_{10} . In context of additive effects for FE, female parent P_3 showed the highest and significant additive effects. Based on summarized results, it was concluded that parental lines P_3 and P_4 had the highest additive effects for yield and fiber quality traits. Whereby, P_7 and P_9 had the highest additive effects for majority of fiber quality traits.

Dominant effects for yield, yield components, and fiber quality traits

Dominant effects (equivalent to SCA) refer average performance of a cross due to non-additive gene actions. It provides an opportunity for utilization of heterosis in hybrid breeding. Predicted dominant effects for yield and yield component traits are listed in Table 2. Results showed that 17 out of the 30 hybrids had significant positive dominant effects for BW. The optimal cross to enhance BW was $P_3 \times P_9$. Out of 30 crosses, 16 combinations

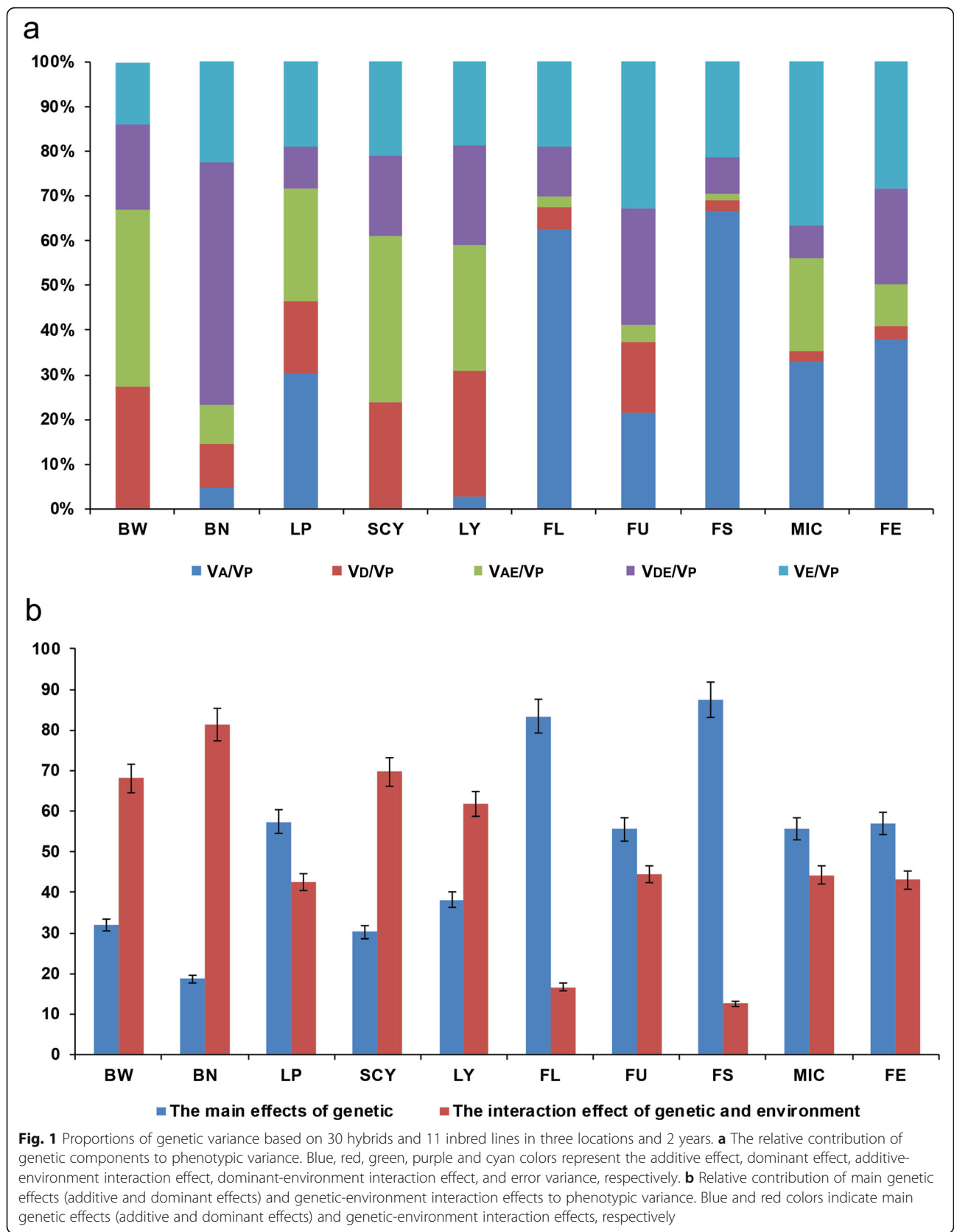


Table 1 Predicted additive effects for yield, yield components, and fiber quality traits

	BN	LP	LY	FL	FU	FS	MIC	FE
P ₁	0.087 ^b	-0.517 ^a	1.200	-0.416 ^c	0.059	-0.209	-0.003	-0.010 ^a
P ₂	0.491 ^a	1.034 ^c	24.340 ^b	-0.049	0.030	-0.785 ^c	-0.027	0.014 ^b
P ₃	0.087 ^c	0.908 ^c	24.445 ^b	1.045 ^c	0.082	0.890 ^c	-0.178 ^c	0.058 ^c
P ₄	0.331 ^c	0.609 ^c	0.499	0.486 ^c	0.482 ^c	0.903 ^c	0.070 ^c	0.047 ^c
P ₅	0.087	-0.437 ^c	-1.973	0.684 ^c	0.390 ^c	1.080 ^c	0.005	0.006
P ₆	-0.431 ^c	-0.330 ^b	3.696	-0.972 ^c	-0.140 ^b	-1.000 ^c	0.039 ^c	-0.022 ^a
P ₇	0.343	-1.673 ^c	-35.659 ^c	0.639 ^c	-0.124 ^b	0.814 ^c	-0.182 ^c	-0.018 ^b
P ₈	-0.143 ^a	0.331 ^b	16.153 ^a	-0.246 ^c	0.003	-0.826 ^c	0.187 ^c	-0.023 ^c
P ₉	-0.749 ^b	-0.044	-35.288 ^b	0.425 ^b	0.308 ^b	0.495 ^a	-0.114 ^c	0.012
P ₁₀	-0.403	0.185	9.577	-0.688 ^b	-0.428	-0.115	0.037	-0.021 ^b
P ₁₁	0.299	-0.064	-6.986	-0.907 ^c	-0.661 ^c	-1.247 ^c	0.167 ^c	-0.042 ^c

^a, ^b and ^c denote significant differences at 0.1, 0.05 and 0.01 levels, respectively

had significant dominant effects in a desirable direction for BN. P₅ × P₁₁ was the best performing cross for this trait. Further, we found that 16 hybrids had significant dominant effects for LP and SCY. Top three crosses with higher dominant effects for LP were P₁ × P₁₁, P₁ × P₈, and P₁ × P₁₀. On the other hand, top three crosses with higher dominant effects for SCY were P₄ × P₇, P₄ × P₉, and P₅ × P₆. It was observed that 17 crosses had a significant dominant effect for LY. P₄ × P₉ was the optimal cross to maximize LY followed by P₄ × P₇ and P₃ × P₆. Results of estimated dominant effects for fiber quality traits are given in Table 3. In results of fiber quality traits, most crosses had non-significant dominant effects. Only, 7 crosses had significant dominant effects for FL and cross P₁ × P₉ had significant dominant effect for this trait. Results showed that only 11 and 8 hybrids had significant dominant effects for FU and FS, respectively. Cross with higher dominant effects for FU was P₄ × P₆ and for FS, it was P₁ × P₉. For MIC, only 13 crosses showed significant dominant effects. Cross P₁ × P₉ followed by P₂ × P₉ had higher dominant effects for this trait. According to results, only 7 out of total crosses had significant dominant effects for FE and cross P₄ × P₇ had highest significant dominant effect for this trait.

Additive-environment interaction effects for yield, yield components, and fiber quality traits

This study further analyzed the additive-environment interaction effects for yield and fiber quality traits for each environment. Analysis results can be seen in Table 4. Results showed that P₆ for BW, P₂ for BN, SCY, MIC, and FE, P₅ for LP, and P₃ for LY had more positive and significant additive-environment interaction effects in E₁. Analysis result in environment E₂ showed that P₉ for BW and MIC, P₁₀ for BN, P₈ for LP, P₇ for SCY and LY, and P₃ for FE had more positive and significant effects. In environment E₃, it was observed that P₇ for BW, SCY and LY, P₂ for BN, P₃ for FL, P₁₁ for MIC, and

P₄ for FE had more positive and significance additive into environment interaction effects. Collectively results represented that most of the additive-environment interaction effects for yield traits were significant but non-significant for fiber quality traits.

Dominance-environment interaction effects for yield, yield components, and fiber quality traits

Here, we calculated dominant-environment interaction effects for yield and yield-related traits (Additional file 3) and fiber quality traits (Additional file 4) in three locations based on 2 years of field experiments. A significant dominance-environment interaction effect was seen for yield parameters with most combinations, but these interaction effects varied among three locations. The effects of both crosses P₂ × P₁₁ and P₅ × P₉ for BW were significant in all locations. However, effect of P₂ × P₁₁ for BW was significant negative in E₁ and E₂, but significant positive in E₃. The effect of P₅ × P₉ was opposite to that of P₂ × P₁₁. The dominant-environment interaction effects of crosses P₁ × P₇, P₂ × P₁₁, P₃ × P₇, P₃ × P₁₀ and P₅ × P₇ for BN were significant but either positive or negative. For example, P₁ × P₇ had positive effect in E₁ and E₂ and negative in E₃, whereas P₂ × P₁₁, P₃ × P₇, and P₃ × P₁₀ had shown negative effects in E₁ and E₂ but positive in E₃. The effect of P₅ × P₇ was positive in E₁ but negative in E₂ and E₃. For LP, it was observed that the effect of P₁ × P₉ was significantly positive in E₂ and E₃ but negative in E₁, whereas P₅ × P₇ showed significant negative effect in E₁ and E₃ but positive in E₂.

According to results, crosses P₂ × P₁₀ and P₄ × P₇ had significant dominance-environment interaction effects for SCY across three locations. Particularly, the effect of P₂ × P₁₀ was positive in E₁ but negative in E₂ and E₃. P₄ × P₇ showed positive additive-environment interactive effect in E₁ and E₃ but negative in E₂. Only combination that had a significant additive-environment interactive effect for LY was P₂ × P₁₀. It had positive in E₁ but negative in E₂ and

Table 2 Predicted dominant effects for yield and yield component traits

	BW	BN	LP	SCY	LY
$P_1 \times P_6$	0.318 ^c	0.752	0.106	127.426 ^c	50.005 ^b
$P_1 \times P_7$	0.264 ^c	-0.320	-0.915 ^c	142.395	26.275
$P_1 \times P_8$	0.101 ^c	0.144	1.411 ^c	92.933 ^a	82.264 ^c
$P_1 \times P_9$	-0.034	0.241	0.589	151.437 ^b	69.819 ^b
$P_1 \times P_{10}$	0.079 ^b	0.068	1.167 ^c	94.123	71.308 ^b
$P_1 \times P_{11}$	-0.008	0.017	1.578 ^c	-1.003	46.430 ^b
$P_2 \times P_6$	0.090 ^b	-0.198 ^b	0.231	155.753 ^b	70.734 ^b
$P_2 \times P_7$	0.096 ^c	0.984 ^b	0.367 ^c	58.902 ^b	29.639 ^b
$P_2 \times P_8$	0.110 ^b	0.357	0.391	133.074 ^b	68.041 ^b
$P_2 \times P_9$	0.144	1.039 ^b	0.384	78.700	41.334
$P_2 \times P_{10}$	-0.040	-0.463	1.017 ^c	55.616	54.955
$P_2 \times P_{11}$	0.100 ^c	0.439	-0.070	107.889	38.172
$P_3 \times P_6$	0.074	0.592	0.881 ^c	200.342 ^b	108.113 ^c
$P_3 \times P_7$	-0.049	1.141 ^b	-0.217	23.613	-3.734
$P_3 \times P_8$	0.071	0.549 ^c	0.404 ^a	132.214 ^c	69.517 ^c
$P_3 \times P_9$	0.326 ^b	-0.964 ^b	0.715	48.601	49.444
$P_3 \times P_{10}$	0.093	1.172 ^b	0.511	210.484 ^c	107.284 ^c
$P_3 \times P_{11}$	0.175 ^b	-0.458	-0.023	28.722	10.129
$P_4 \times P_6$	0.039	-0.453	-0.175	25.584	8.341
$P_4 \times P_7$	0.128 ^c	1.069 ^c	0.817 ^b	251.70 ^c	118.717 ^c
$P_4 \times P_8$	0.052	0.514 ^a	-0.981 ^c	70.602	5.758
$P_4 \times P_9$	0.133 ^b	0.227	0.805 ^c	230.803 ^c	119.441 ^c
$P_4 \times P_{10}$	0.136	-0.514 ^b	-0.142	100.090 ^a	35.207
$P_4 \times P_{11}$	0.158 ^c	0.796 ^b	-0.492 ^b	138.248 ^b	38.249 ^a
$P_5 \times P_6$	0.076 ^a	0.991 ^b	0.519 ^c	225.022 ^c	106.719 ^c
$P_5 \times P_7$	-0.085	0.248	-0.445 ^a	-26.861	-27.692
$P_5 \times P_8$	0.182 ^a	0.809 ^a	0.121	198.922 ^a	83.575 ^a
$P_5 \times P_9$	0.113	-0.363 ^b	-0.179	-101.685	-38.597
$P_5 \times P_{10}$	0.103 ^b	-0.721 ^b	0.173 ^b	126.428 ^a	55.284 ^b
$P_5 \times P_{11}$	0.169 ^c	1.453 ^b	0.258 ^c	2.153	2.521

^a, ^b and ^c denote significant differences at 0.1, 0.05 and 0.01 levels, respectively

E_3 . For fiber quality traits, it was noticed that $P_1 \times P_{11}$ had a significant dominance-environment interaction effect for FL in the three locations, but effect was positive in E_2 and negative in E_1 and E_3 . For FU trait, the effect of $P_5 \times P_8$ was significant in the three locations. The effect was significantly positive in E_1 and E_2 and negative in E_3 . The effect of $P_5 \times P_{11}$ for FS was significant negative in E_1 and E_2 but positive in E_3 . Analysis results for MIC trait showed that $P_2 \times P_9$ showed significant positive interactive effect in E_2 , while crosses $P_2 \times P_7$ and $P_5 \times P_9$ showed significant positive effects in E_3 . Five crosses, i.e., $P_1 \times P_7$, $P_1 \times P_9$, $P_1 \times P_{11}$, $P_3 \times P_9$, and $P_5 \times P_6$, showed significant effects for FE across all locations. From these, $P_1 \times P_7$, $P_3 \times P_9$, and $P_5 \times P_6$ had negative effects in E_1 and E_3 , but positive in

Table 3 Predicted dominant effects for fiber quality traits

	FL	FU	FS	MIC	FE
$P_1 \times P_6$	-0.119	0.495	-0.370	0.057 ^b	0.024
$P_1 \times P_7$	0.005	-0.018	0.102	-0.019	-0.008
$P_1 \times P_8$	-0.110	0.306 ^a	-0.092	0.103 ^a	0.007
$P_1 \times P_9$	0.488 ^c	0.445 ^b	0.573 ^b	-0.079 ^a	0.011
$P_1 \times P_{10}$	-0.082	0.471 ^a	-0.013	0.029	-0.009
$P_1 \times P_{11}$	-0.165 ^a	-0.320	-0.134 ^a	0.082	0.009 ^b
$P_2 \times P_6$	0.068	-0.072	-0.039	0.049 ^c	0.013
$P_2 \times P_7$	0.250 ^b	0.168	-0.326 ^a	0.005	0.014
$P_2 \times P_8$	0.034	0.372 ^b	-0.027	0.027	0.000
$P_2 \times P_9$	0.211	0.261	0.026	-0.054 ^b	0.008
$P_2 \times P_{10}$	-0.055	0.473 ^c	0.126 ^b	0.039 ^c	0.003
$P_2 \times P_{11}$	-0.040	-0.153	0.014	-0.017	-0.002
$P_3 \times P_6$	-0.017	0.064	0.206 ^b	-0.016	0.009 ^b
$P_3 \times P_7$	-0.010	0.068	0.020	0.023	-0.015 ^a
$P_3 \times P_8$	0.269	0.448	0.227 ^b	0.022	0.015
$P_3 \times P_9$	0.543	0.268	0.396	-0.058	0.017
$P_3 \times P_{10}$	0.246	0.096	0.021	-0.044 ^a	0.003
$P_3 \times P_{11}$	0.168	0.593 ^a	0.136	0.012	-0.001
$P_4 \times P_6$	0.020	0.633 ^b	0.003	0.051	-0.005
$P_4 \times P_7$	0.167	0.208	0.347	-0.013	0.010 ^b
$P_4 \times P_8$	0.244 ^a	0.208	0.300 ^a	-0.020	0.009 ^a
$P_4 \times P_9$	0.210	-0.406 ^c	-0.147	0.084 ^b	0.009
$P_4 \times P_{10}$	0.330 ^b	0.221	0.204	0.060 ^b	0.008
$P_4 \times P_{11}$	0.197 ^a	0.164	-0.104	-0.007	0.004
$P_5 \times P_6$	-0.020	-0.051	0.136	0.012 ^a	0.001
$P_5 \times P_7$	-0.080	-0.485 ^c	-0.072	0.032 ^b	0.007 ^a
$P_5 \times P_8$	-0.226	-0.184	0.074	-0.033 ^b	-0.018 ^a
$P_5 \times P_9$	0.228	0.329 ^b	0.292 ^a	0.045 ^c	-0.002
$P_5 \times P_{10}$	0.344 ^a	0.207	-0.074	-0.007	0.008
$P_5 \times P_{11}$	0.117	0.437 ^a	0.096	0.021	0.010

^a, ^b and ^c denote significant differences at 0.1, 0.05 and 0.01 levels, respectively

E_2 . In contrast, $P_1 \times P_9$ showed positive effect in E_1 and E_3 , but negative in E_2 . The effect of $P_1 \times P_{11}$ was positive in E_2 and E_3 but negative in E_1 .

Analysis of heritability

Heritability is a genetic parameter that measures the relative ratio of genetic variation to phenotypic variation. Here, broad-sense heritability (h^2_B), narrow-sense heritability (h^2_N), broad-sense interaction heritability (h^2_{BE}), and narrow-sense interaction heritability (h^2_{NE}) were evaluated for all traits under study (Table 5). Results showed that heritability measures such as h^2_B and h^2_{BE} were highly significant and strong for all traits except for FS with non-significant h^2_{BE} . It was observed that h^2_N was significant for all traits except for BW and SCY. According to results, BW,

Table 4 Predicted additive-environment interaction effects for yield, yield components, and fiber quality traits in three locations based on 2 years field test

	BW	BN	LP	SCY	LY	FL	FU	FS	MIC	FE
E₁										
P ₁	0.001	1.083 ^b	-0.753 ^a	261.067 ^c	64.935 ^b	-0.067	0.188	0.054	0.162 ^a	0.019 ^c
P ₂	0.03	-0.111	0.64 ^a	6.02	31.275 ^b	0.126	0.116	0.014	0.047	0.031 ^b
P ₃	0.025	0.134	0.954	88.181 ^c	76.008 ^b	0.055	-0.007	-0.043	-0.028	-0.003
P ₄	-0.02	0.76 ^a	0.729	34.393	35.15 ^c	0.02	-0.109 ^b	0.016	0.017	-0.019 ^b
P ₅	-0.015	-0.279	0.406 ^b	-171.386 ^b	-55.857 ^a	0.034	0.098	0.151	-0.019	0.007
P ₆	0.151 ^b	0.061	-0.24	190.076 ^c	63.334 ^b	-0.166	-0.061	-0.025	0.017	-0.013
P ₇	-0.127 ^a	-0.592 ^b	-1.447	-496.371 ^b	-239.017 ^c	0.022	-0.12	-0.067	-0.051	-0.017 ^a
P ₈	0.153 ^a	-0.054	-0.362	138.314	46.767	0.104	0.058	0.045	-0.012	0.01 ^b
P ₉	-0.128 ^a	-0.684	1.78	-331.879 ^c	-76.805 ^a	0.114	-0.024	0.041	-0.049 ^b	0.015
P ₁₀	0.113 ^a	-0.157	-0.528 ^a	256.401 ^b	86.728 ^a	-0.051	-0.009	0.004	-0.053	-0.01
P ₁₁	-0.183 ^b	-0.162	-1.179	25.189	-32.515	-0.191	-0.129	-0.19 ^a	-0.031	-0.018
E₂										
P ₁	-0.057	0.321 ^b	0.426	-3.181	14.755	-0.06	-0.061	-0.107	0.073	-0.015 ^b
P ₂	-0.074 ^b	-0.368 ^b	-0.354 ^b	-42.001 ^a	-32.737 ^b	-0.099 ^a	-0.064	-0.095	-0.005	-0.003
P ₃	0.013	-0.509 ^b	-0.357	-28.529	-27.881	0.217	-0.115	0.235	-0.118	0.035 ^b
P ₄	0.24 ^c	-0.078	-0.09	113 ^b	37.14 ^c	0.156	0.011	0.126	-0.045 ^a	0.024
P ₅	-0.063 ^a	-0.105	-0.298 ^b	-9.847	-4.17	0.061	-0.068	0.164	0.004	0.003
P ₆	-0.014	-0.049	-0.132	-114.551 ^b	-45.52 ^b	-0.131	0.065	-0.108	0.03 ^b	-0.001
P ₇	-0.211 ^c	0.197	0.267	157.965 ^b	82.35 ^c	0.118	0.024	0.201	-0.136 ^b	0.001
P ₈	-0.089 ^b	-0.209	0.936 ^c	-47.223	-0.533	-0.194	-0.092	-0.301	0.104 ^c	-0.017 ^c
P ₉	0.507 ^c	0.421 ^b	-1.222	95.676	7.783	0.319	0.406	0.182	0.159 ^b	0.001
P ₁₀	-0.076 ^a	0.492 ^b	0.332	-24.098	-4.969	-0.132	0.019	-0.132	-0.042	-0.022 ^a
P ₁₁	-0.176 ^b	-0.113	0.492	-97.207 ^a	-26.216	-0.255	-0.125	-0.165	-0.024	-0.007 ^a
E₃										
P ₁	0.027	-1.314 ^b	-0.2	-204.661	-76.855	-0.055	-0.094	-0.021	-0.237	-0.01 ^a
P ₂	0.059 ^b	0.985 ^b	0.768 ^c	107.993 ^c	58.969 ^a	-0.049	-0.035	-0.199	-0.067 ^c	-0.019 ^b
P ₃	0.034	0.465 ^a	0.329 ^a	16.094	9.628	0.186 ^b	0.168	0.124	-0.017	0.008
P ₄	-0.312 ^c	-0.341 ^b	-0.018	-191.975 ^a	-71.112 ^b	0.036	0.367	0.179	0.092	0.028 ^b
P ₅	0.163 ^b	0.474	-0.554 ^c	204.393	55.365	0.204 ^a	0.188	0.07	0.02	-0.005
P ₆	0.021	-0.455	0.035	-29.585	-9.083	-0.129 ^a	-0.083 ^a	-0.223	-0.011 ^a	-0.002
P ₇	0.263 ^c	0.749	-0.526 ^b	242.421 ^b	72.417 ^c	0.14	0.027	0.156	0.02	0.003
P ₈	0.028	0.116	-0.237 ^a	-8.838	-8.072	-0.018	0.036	-0.038	0.08 ^c	-0.009 ^b
P ₉	-0.323 ^c	-0.509	-0.603	3.093	-14.351	-0.247	-0.21	-0.047	-0.214 ^b	-0.008
P ₁₀	-0.104	-0.751	0.385 ^a	-188.357 ^c	-59.131 ^a	-0.119	-0.249	0.087	0.128	0.017
P ₁₁	0.146	0.583 ^a	0.622 ^a	49.426	42.225	0.049	-0.115	-0.089	0.208 ^b	-0.004

^a, ^b and ^c denote significant differences at 0.1, 0.05 and 0.01 levels, respectively

SCY, and LY had significant and strong h^2_B , h^2_{NE} , and h^2_{BE} . These findings put forth a clue that these traits can be improved through genetics, breeding and proper selection of experimental populations. All heritability estimates of LP, FU, FE, and MIC were significant and equally important. Further results revealed that h^2_B and h^2_N of FL and FS were significant and strong as compared with h^2_{BE} and h^2_{NE} .

Genetic and phenotypic correlations between yield, yield components, and fiber quality traits

Coefficients of genetic and phenotypic correlation between yield and fiber quality parameters can be seen in Table 6. Results revealed that SCY and LY had significant positive correlation with LP, BW, and BN. Further, SCY and LY had positive correlation with FL, FU, MIC,

Table 5 The heritability estimates of yield, yield components, and fiber quality traits based on three locations and 2 years field test

	Heritability(h^2_N)	Heritability(h^2_B)	Heritability(h^2_{NE})	Heritability(h^2_{BE})
BW	0.000	0.275 ^c	0.396 ^c	0.587 ^c
BN	0.048 ^a	0.145 ^c	0.089 ^a	0.631 ^c
LP	0.302 ^c	0.465 ^c	0.250 ^c	0.345 ^c
SCY	0.000	0.239 ^c	0.371 ^c	0.552 ^c
LY	0.028 ^a	0.310 ^c	0.281 ^c	0.502 ^c
FL	0.627 ^c	0.674 ^c	0.026 ^a	0.135 ^c
FU	0.214 ^c	0.373 ^c	0.039	0.299 ^a
FS	0.666 ^c	0.689 ^c	0.016	0.100
MIC	0.330 ^c	0.353 ^c	0.207 ^c	0.280 ^b
FE	0.380 ^c	0.408 ^c	0.094 ^b	0.308 ^c

Narrow-sense heritability (h^2_N), Broad-sense heritability (h^2_B), Narrow-sense interaction heritability (h^2_{NE}), Broad-sense interaction heritability (h^2_{BE})
^a, ^b and ^c denote significant differences at 0.1, 0.05 and 0.01 levels, respectively

Table 6 Estimated genetic and phenotypic correlations between yield, yield components, and fiber quality traits

Traits	LY	LP	BW	BN	FL	FU	FS	MIC	FE
SCY									
R_p	0.913 ^c	0.211 ^c	0.481 ^c	0.453 ^c	0.009	0.094 ^a	-0.055	0.187 ^b	0.080 ^a
R_G	0.918 ^c	0.246 ^c	0.531 ^c	0.606 ^c	0.030	0.110	-0.055	0.217	0.115 ^a
					LY				
R_p		0.524 ^c	0.489 ^c	0.425 ^c	0.045	0.128 ^a	-0.062	0.238 ^a	0.180 ^b
R_G		0.545 ^c	0.516 ^c	0.562 ^c	0.049	0.149	-0.078 ^a	0.248	0.224 ^b
					LP				
R_p			0.147	0.111 ^b	0.050	0.107	-0.095	0.242 ^a	0.311 ^b
R_G			0.119	0.153 ^b	0.025	0.124	-0.145 ^a	0.258	0.347 ^a
					FL				
R_p						0.540 ^c	0.765 ^c	-0.297 ^c	0.613 ^c
R_G						0.585 ^c	0.849 ^c	-0.424 ^c	0.694 ^c
					FU				
R_p							0.487 ^c	0.064	0.479 ^c
R_G							0.558 ^c	-0.071	0.626 ^c
					FS				
R_p								-0.357 ^c	0.538 ^c
R_G								-0.493 ^c	0.623 ^c
					MIC				
R_p									-0.082
R_G									-0.153 ^b

R_p phenotypic correlation coefficient, R_G genetic correlation coefficient
^a, ^b and ^c denote significant differences at 0.1, 0.05 and 0.01 levels, respectively

and FE. However, most of these correlations were non-significant, while correlation coefficients of SCY and LY with FS were negative and small. LP had significant positive correlation with BN and FE. Between fiber quality traits, results of both genetic and phenotypic correlation analysis showed that FL had significant positive correlation with FU, FS, and FE but, significant negative correlation with MIC. FU had significant positive correlation with FS and FE and negative correlation with MIC but, latter relationship was non-significant. According to results, FS had significant positive correlation with FE and negative correlation with MIC. MIC and FE showed significant negative correlation with each other but, only their genetic correlation was significant. Notably, all these results suggest that yield can be improved along with yield component traits independent of fiber quality traits.

Discussion

Cotton varieties with superior yield, fiber quality, and environmental adaptation are very important for sustainable cotton production. In plant breeding research, three mating designs (factorial, nested and diallel) are generally used to perform genetic analysis. In previous studies of cotton, most researchers used diallel and line-tester designs to perform genetic analysis (Song *et al.* 2015b; Ye *et al.* 2008). In this study, the NCII design was used to improve the efficiency of yield and fiber quality traits. We analyzed comprehensive data of 2 years and three locations of yield and fiber quality traits to reveal genetic variance and their effects, heritability, and correlations.

Genetic effects and their interaction with the environment

Previously, it was observed in agronomic crops that yield traits are quantitatively controlled by micro-functional polygenes, vulnerable to the environment (Nyombayire *et al.* 2018; Reddy *et al.* 2016). Therefore, comprehensive genetic analysis in different environments is an important strategy for a successful breeding program. Our results revealed that yield and fiber quality traits were determined by different effects of genetics. In this regard, yield traits were mainly controlled by genetic and environment interaction effects, whereas LP and fiber quality traits were mostly determined by main genetic effects. These findings are similar to the previous study by Song *et al.* (2015b). These authors reported that LP and fiber quality traits showed significant additive and dominant effects, thus controlled by main genetic effects. Further results showed that dominant effects had stronger influence on yield parameters and additive effects had stronger influence on fiber quality traits. These results predict that yield and its contributing traits have complex genetics with more influence of environmental

effects. Similar results have been reported by Ming *et al.* (2008), Li *et al.* (2016) and Song *et al.* (2015a, 2015b). However, some researchers also observed significant additive effects for yield traits related, but others reported contribution of additive and dominant effects for yield contributing traits (Liu and Zhu 2007; Xing *et al.* 2007b). To a particular interest, the inbred lines used in this study were developed by self-pollination over multiple generations belonging to three different cotton growing areas of China. Most of additive and dominant effects for yield and fiber traits were significant in this study. However, their interaction with environment was unstable across different locations. Results showed that parental lines P₂, P₃, and P₄ had more additive effects for yield and fiber traits. However, P₇, P₉, and P₁₀ were found to have high significant additive effects for most of fiber quality traits. According to results, significant positive dominant effects for yield traits were seen in more than 50% cross combinations, whereas most of crosses showed non-significant dominant effects for fiber quality traits. In context of dominance-environment interaction effects, P₁ × P₈, P₁ × P₁₀, and P₂ × P₁₀ in E₁, P₄ × P₆ in E₂, P₃ × P₇ and P₅ × P₁₁ in E₃ showed significant positive for yield traits. For fiber quality traits, significant positive dominance-environment interaction effects were produced by P₁ × P₉, P₄ × P₁₀, P₅ × P₉, and P₅ × P₁₁ in E₃. Because dominance underlies the potential utility of heterosis, these crosses can be improved through further hybridization.

Heritability of traits

Heritability is a statistic that determines the degree of phenotypic variance due to genetic variance. Results of current studies showed that broad-sense and its interaction heritability were extremely significant for all yield traits. In previous studies, it was described that seed cotton yield, lint yield, boll weight, lint percentage, boll number showed the highest broad sense by environment interaction heritability (Song *et al.* 2015a; Zeng and Pettigrew 2015). However, some researchers reported that many yield traits such as lint yield, boll number per plant, boll weight, and lint percentage showed little additive variance and low heritability (Tang *et al.* 1996). Further results showed that narrow-sense heritability was significant for all studied traits except for BW and SCY. These heritability estimates showed that broad and narrow-sense heritability were ubiquitous, thus indicating that potential of yield improvement in upland cotton through genetics and breeding is still large. Moreover, environmental factors have considerable influence on gene expressions. So, breeders should select plant materials which are adapted to different environments. Results for fiber traits showed that fiber length and strength had strong broad and narrow-sense heritability,

indicating that these traits can be improved through allopatric selection and shuttle breeding methods.

Correlations between traits

Relationships between traits play an important role in selection of plant material for future breeding. The results of this study showed that both phenotypic and genotypic correlations of SCY and LY were significantly positive with LP, BW, and BN. Thus, these yield-related traits with genetic effects should be considered as main criteria of genotype selection to improve yield. Previous studies have shown that yield and its contributing traits showed significant positive correlation among each other (Song *et al.* 2015a; Tang *et al.* 1996; Meredith 1990). In our results, SCY and LY also showed positive correlation with FL, FU, MIC, and FE and negative with FS, but most of these correlation coefficients were small and statistically non-significant. Other than this, FL, FU, FS, and FE showed significant positive correlation with each other but MIC showed negative correlation with other fiber quality traits. In the study of Song *et al.* (2015b), significant positive correlations were observed among fiber traits. However, FE showed significant negative correlation with other fiber quality traits in their study. Results of correlation analysis anticipate that SCY and LY can be improved coupled with BW, BN, and LP independent of fiber quality traits. Finally, this study identified that parental lines, e.g., SJ48-1 (P3), ZB-1 (P4), 851-2 (P10), and DT-8 (P9), can be used to improve yield and fiber quality traits in cotton through hybridization.

Conclusions

In this study, results of genetic analysis showed that yield traits were controlled by genetic and environment interaction effects. In contrast, fiber quality traits were mainly controlled by the main genetic effects. A significant positive phenotypic and genetic correlation was observed between yield and its component traits. Fiber quality traits also showed significant positive correlation with each other. However, yield and fiber quality traits had non-significant correlation among each other. Altogether, our results provide valuable information about genetic control of yield and fiber quality traits. It will help to develop high yield cotton hybrids with improved fiber quality traits in future.

Additional files

Additional file 1: Climate statistics and planting arrangement in three locations of this study. (DOCX 15 kb)

Additional file 2: Proportions of variance components for yield, yield components, and fiber quality traits based on 30 F₁ hybrids together

with their 11 parental lines of upland cotton tested at three locations in China during 2016–2017. (DOCX 17 kb)

Additional file 3: Predicted dominance-environment interaction effects for yield and yield component traits in three locations based on 2 years filed test. (DOCX 32 kb)

Additional file 4: Predicted dominance-environment interaction effects for fiber quality traits in three locations based on 2 years filed test. (DOCX 32 kb)

Abbreviations

ADE: Additive-dominance-environment; BN: Boll number; BW: Boll weight; FE: Fiber elongation; FL: Fiber length; FS: Fiber strength; FU: Fiber uniformity; LP: Lint percentage; LY: Lint yield; MIC: Micronaire; NCI: North Carolina II; SCY: Seed cotton yield

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Authors' contributions

Wu JY and Xing CZ conceived and designed the research. Qi TX, Gou LP, Tang HN, Zhang XX, and Wang HL constructed hybrid plant population. Zhang M, Zhang BB, and Qiao XQ helped field investigation. Li X performed data analysis. Shahzad K wrote the manuscript. Wu JY and Xing CZ contributed to the preparation of the final manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed in this study included in published article and additional files.

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The authors declare that they have no competing interests.

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