Comparative performance of hybrid generations reveals potential application of F2 hybrids in upland cotton

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Research

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Abstract

Background: Heterosis has greatly improved productivity of cotton crop. However, major constraint for large-scale promotion of F_1 hybrid cotton is artificial emasculation and pollination. This study through comparative evaluation of hybrid generations proposed potential utilization of F_2 hybrids to improve upland cotton production.

Aims：The current study aimed to compare F_1 and F_2 hybrids and combine with the breeding practice of strong hybrid cotton to select the best combination of heterosis, provide reference for the feasibility of parental selection and utilization of F_2 heterosis in China.

Methods: We analyzed eight upland cotton varieties and made crosses according to NCⅡ incomplete diallel cross breeding design in two cotton belts of China.

Results: The results showed that Variance analysis revealed significant differences for agronomic, yield and fiber quality in both generations and environments. The broad-sense heritability of agronomic and yield traits were relatively higher than quality traits. Furthermore, narrow sense heritability of some traits was higher in F_2 than F_1 generation under both cotton belts. Overall, parental lines Zhong901, ZB, L28, and Z98 were observed with maximum combining ability while combinations with strong special combining ability were ZB ×DT, SJ48 ×Z98, L28 ×Z98, and ZB ×851. The yield traits heterosis was predominant in both generations. However, the level of heterosis was altered with trait, hybrid combination, generation, and environment. Interestingly, L28×Z98 performed outstandingly in Anyang. Its lint yield was 24.8% higher in F_1 and 11.6% in F_2 than that of the control Ruiza816. The performance of SJ48 × Z98 was excellent in Alar which showed 36.5% higher LY in F_1 and 10.9% in F_2 than control Zhongmiansuo 49. Further results revealed most hybrid combinations had shown low level of heterosis for agronomic and fiber quality traits in both generations. Comparatively, ZB ×DT and L28×Z98 showed hybrid vigor for multiple traits in both generations and cotton belts. Moreover, lint yield can be improved independently in both cotton belts in these combinations.

Conclusions: Through comparative analysis of variance, combining ability, and heterosis in F_1 and F_2 hybrids under different cotton belts, this study proposed potential utilization of F_2 hybrids to improve upland cotton productivity in China.

Background

Heterosis is a phenomenon by which hybrid progeny show superior performance compared to their parents in aspect of vegetative growth, reproductive growth and stress tolerance (Shahzad et al. 2019). Hybrids have widely been used to improve the crop yield of agronomic and horticultural crops including rice (Li et al. 2016), maize (Yu et al. 2020), tomato (Yu et al. 2021), and kohlrabi (Singh et al. 2019). The utilization of heterosis increased 10-20% yield of hybrid rice (*Oryza sativa*) than conventional cultivars (Luo et al. 2013). The soybean hybrids produced 15-25% more yield compared with conventional varieties (Wang et al. 2002). At present, about 80-90% of vegetable varieties are hybrids. Even countries such as the Netherlands, the United States and Israel have more developed hybrid vegetable seed industries. Utilizing heterogeneity is an extremely important genetic improvement technique to boost yield, quality, and resistance to diseases, insects, and pests. Global warming is a major threat for sustainable yield in recent years. Therefore, heterosis has important practical significance in meeting market demand, improved economic efficiency, and ensured food security.

Cotton is a major economic crop which has not only renewable natural textile fiber source in the world but also own ample amount of vegetable oil resource (Chen et al. 2007). Approximately 90% of the world cotton yield comes from upland cotton (*Gossypium hirsutum* L.) while Egyptian cotton (*Gossypium barbadense* L.) produces only 3% fiber (Fang et al. 2017). The upland cotton has shown significant heterosis for yield traits and altered across various traits, stages, and environments (Schnable et al. 2013). Moreover, hybrid cotton could be more adaptability and stability in varying environments (Shahzad et al. 2019). Cotton hybrids have been devolved through utilization of heterosis in China and planted in the main cotton provinces such as Hubei, Hunan, Jiangxi. The area of hybrid cotton planted was about 70% of the total cotton grown in these provinces (Xing et al. 2017). Heterosis has become a crucial way to increase cotton yield and improve fiber quality. Selecting and promoting hybrid cotton with strong heterosis have a meaningful impact on cotton production in China. However, artificial emasculation seed production is a main way to utilize cotton heterosis. Due to the high cost of seed production, the utilization of F_1 heterosis is largely restricted vast hybrid commercialization. To mitigate this challenge, the promotion and application of hybrid cotton increased rapidly with the expansion of cotton planting area in Xinjiang, and people gradually shift their attention to use F_2 generation of cotton hybrids.

Many cotton breeders have already been proposed utilization of F_2 cotton hybrids to reduce the cost of seed production and to meet the demands of cotton growers in diverse ecological environments. A large number of research findings showed that F_2 hybrids still have certain competitive advantages over inbred parents (Meng et al. 2019; Chen et al. 2021). An estimate of combining ability is an important index to determine the transmission ability of excellent characters, to correctly evaluate the advantages and disadvantages of combinations, and to select excellent parents and hybrid combinations to boost efficiency of any breeding program (Wang et al. 2012; Liu et al. 2019; Shi et al. 2021). In this study, we selected eight upland cotton varieties as experimental material and made crosses according to NCⅡ incomplete diallel cross (5×3) breeding design. The performance, combining ability, and heterosis were analyzed in F_1 and F_2 hybrids for multiple traits and locations. The main objective of our study is to compare F_1 and F_2 hybrids and combine with the breeding practice of strong hybrid cotton to select the best combination of heterosis, provide reference for the feasibility of parental selection and utilization of F_2 heterosis in China.

Materials And Methods

Experimental materials and field design

The field tests were conducted from 2020 to 2021. All 15 F_1 hybrid combinations used in this study were produced through adopting North Carolina mating design Ⅱ by crossing five upland cotton inbred lines as the female parents with three different inbred lines as the male parent with different nuclear backgrounds which have been reported in our previous studies (Li, et al. 2019; Shahzad, et al. 2019). Specifically, the inbred lines Zhong 901 (P1), ZB (P2), SJ48 (P3), L28 (P4) and K8 (P5) were used as female parents, while DT (P6), Z98 (P7) and 851 (P8) were used as male parents. In 2020, eight parental inbred lines and 15 F_1 hybrid combinations were planted in east experimental fields of the Cotton Research Institute of the Chinese Academy of Agricultural Science, Anyang, Henan Province, China (36°10'N, 114°35'E). All hybrids were self-pollinated and harvested to obtain corresponding 15 F_2 hybrids (Table 1). In 2021, eight parents, 15 F_1 and F_2 hybrid combinations were planted in two different cotton belts of China, i.e., in Anyang which located in Henan and in Alar which located in Xinjiang province (40°55'N, 81°28'E). Ruiza 816 and Zhongmiansuo 49 were used as the control varieties in Anyang and Alar, respectively. All experimental materials were planted in randomized complete block design. Seeds were sown in late April in sequential years and the crop management practices were followed in accordance to local recommendations.

Table 1
Code numbers of all 15 hybrid combinations and their inbred parents

Female parents	Male parentsand hybrid combinations		
	P6	P7	P8
P1	1(P1×P6)	6(P1×P7)	11(P1×P8)
P2	2(P2×P6)	7(P2×P7)	12(P2×P8)
P3	3(P3×P6)	8(P3×P7)	13(P3×P8)
P4	4(P4×P6)	9(P4×P7)	14(P4×P8)
P5	5(P5×P6)	10(P5×P7)	15(P5×P8)

Investigation and methods of phenotypic traits

In mid-September, we investigated the plant height (PH), height of first fruit branch (HFFB), length of first fruit branch (LFFB), second fruit branch length (SFBL), fruit branch number (FBN) and boll number (BN) for each plant materials. 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). Weight of seed cotton per plot was used to calculate seed cotton yield (SCY) and lint yield (LY) per hectare. 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 assess fiber quality by using High Volume Instrument (HVI_900) machine. Following data were captured: fiber length (FL, mm; upper half mean length), fiber uniformity (FU, %), fiber strength (FS, $cN\cdot tex^{-1}$), micronaire (MIC) and fiber elongation (FE, %). Also, we denoted SCY, LY BN, BW, LP as yield traits; PH, HFFB, LFFB, SFBL, FBN as agronomic traits; FL, FU, FS, FE, MIC as fiber traits.

Date analysis

The test data were sorted and tabulated by Microsoft Excel, analysis of variance, combining ability (i.e., General Combining Ability,GCA; Special Combining Ability, SCA) and heritability analysis (i.e., broad-sense heritability, H^2; narrow sense heritability, h^2) with DPS software. Correlation analysis was performed with IBM SPSS statistics 25.0 software and Origin 2021 was used for figure drawing. The heterosis calculation based on the mean of parents (MP) and higher parent (HP) with the heterosis formula as follows: mid-parent heterosis (MPH)= (F_1/F_2-MP)/MP×100%, better-parent heterosis (BPH)= (F_1/F_2−HP)/HP×100%, competitive heterosis (CH)= (F_1/F_2−CK)/CK×100%, heterosis decline (HD)= (F_1−F_2)/F_1×100%.

Results

Variance analysis of F_1, F_2 hybrids, and their inbred parents at various cotton belt

The varianceFi analysis was performed for 15 F_1, F_2 hybrids, and their eight inbred parents. The variance was extremely significant ($P < 0.01$) for majority of traits in at various cotton belt (Table 2 and 3). All agronomic, yield and fiber quality traits except FU and FE showed significant differences in F_1 generation among the combinations in Anyang (Table 2). Similarly, the differences among the combinations of F_2 generation reached significant or extremely significant for all traits except FE and FS which indicated that the differences in these traits were mainly caused by genetic variation. The female inbred lines had non-significant variance for most of agronomic traits in both F_1 and F_2 generations. In contrast, female inbred lines demonstrated significant variance for majority of yield and fiber quality traits in both generations. The female variance was extremely significant and improved for in F_2 generation for SCY, LY, BN, BW, LP and FL. Furthermore, female inbred lines exhibited significant difference for PH, SFBL, FE, and FS only in F_2 as compared to F_1 generation. The male inbred lines had significant variance in eight traits in F_1 generation, while the difference was significant only in seven traits in F_2 generation. The female × male interaction variance was significant for majority of traits in both generations except HFFB, FE and MIC. Table 3 summarized the analysis of variance results for all traits in Alar. All combinations in F_1 displayed extremely significant differences in agronomic and yield traits whereas FL and FS related fiber quality traits had significant differences. Similarly, F_2 only showed significant difference in agronomic and yield traits. The variance was significant among female parents for most of traits in F_1 generation specifically in LFFB, SFBL, SCY, LY, BN, LP, FL, FS, and MIC. The variance for male inbred had significant difference in 80% agronomic and some yield traits. For example, LP had highly significant difference in F_1 generation. In contrast, PH, HFFB, SFBL, and FE had highly significant differences in F_2. Interestingly, the female × male interaction variance was extremely significant for PH, HFFB, LFFB, FBN, and BW.

Table 2
Analysis of variance and heritability analysis of each trait in Anyang

Trait	Generation	Block	Combination	F	M	M×F	Error	H^2(%)	h^2(%)
PH	F_1	2.55	9.54**	1.24	3.95*	5.09**	2.95	75.66	42.49
	F_2	0.81	5.80**	4.09*	5.67**	2.09	3.79	65.23	52.61
HFFB	F_1	7.93**	4.15**	1.65	11.56**	1.01	1.09	55.20	55.04
	F_2	8.90**	6.77**	7.10	16.73**	1.06	0.63	69.82	69.18
LFFB	F_1	1.77	17.65**	1.15	0.95	17.54**	1.05	85.04	2.57
	F_2	1.12	9.27**	1.49	1.89	6.99**	0.80	74.50	23.55
SFBL	F_1	1.30	17.73**	1.80	0.87	16.45**	1.90	85.77	12.46
	F_2	4.00*	12.74**	5.55*	1.26	7.39**	0.67	82.10	43.97
FBN	F_1	2.57	10.80**	3.25	4.87*	4.45**	0.08	78.86	54.53
	F_2	2.84	17.05**	0.81	4.30*	8.90**	0.06	85.49	47.30
SCY	F_1	2.89	10.84**	5.68*	4.14*	4.23**	0.04	79.46	57.38
	F_2	0.79	8.79**	10.79**	1.53	3.45**	0.04	76.56	57.45
LY	F_1	1.38	15.99**	18.99**	8.88**	2.75*	0.01	86.27	78.27
	F_2	1.86	14.98**	16.60**	1.88	4.31**	0.01	85.72	69.97
BN	F_1	0.81	4.84**	0.91	5.00*	2.27*	0.64	58.92	41.48
	F_2	1.40	3.37**	8.71**	2.23	1.37	0.42	50.43	44.27
BW	F_1	1.82	17.91**	9.73**	1.08	7.90**	0.03	87.44	58.57
	F_2	0.31	10.06**	20.39**	3.13	2.30**	0.07	79.78	71.04
LP	F_1	3.79*	27.26**	21.06**	1.94	6.59**	0.30	91.92	76.85
	F_2	2.42	16.44**	38.86**	4.41*	2.23*	0.40	87.30	82.10
FL	F_1	2.52	15.70**	19.00**	7.9**	2.83*	0.24	86.08	77.57
	F_2	1.12	6.43**	27.29**	13.44**	0.77	0.50	70.80	70.80
FU	F_1	1.54	1.46	7.13*	1.91	0.68	0.65	25.81	25.81
	F_2	3.10	2.70*	1.30	1.26	2.42*	0.69	37.17	7.44
FE	F_1	0.48	1.16	1.22	3.22	0.69	0.00	15.33	15.33
	F_2	0.74	4.84**	6.00*	5.62*	1.60	0.00	60.78	52.98
FS	F_1	3.67*	20.44**	0.98	0.51	23.87**	0.27	88.40	0.00
	F_2	0.29	6.64**	6.09*	2.75	2.98*	0.60	69.23	48.91
MIC	F_1	1.93	10.17**	33.57**	13.43**	1.10	0.04	79.83	79.13
	F_2	1.89	2.16*	4.68*	4.00*	0.91	0.07	34.43	34.43

*and ** denote significant differences at 0.05 and 0.01 levels, respectively. F (female), M (male).

Table 3
Analysis of variance and heritability analysis of each trait in Alar

Trait	Generation	Block	Combination	F	M	M×F	Error	H^2(%)	h^2(%)
PH	F_1	3.93*	64.24**	0.12	6.76**	25.49**	4.25	96.08	64.03
	F_2	1.31	13.53**	3.87	4.55*	5.58**	9.35	82.75	56.43
HFFB	F_1	1.74	4.57**	0.31	1.68	4.17**	1.70	57.84	13.33
	F_2	0.09	32.00**	0.10	3.84*	19.01**	0.35	92.31	46.13
LFFB	F_1	0.28	12.06**	4.35*	7.06**	3.76**	1.07	80.09	63.70
	F_2	0.31	14.10**	4.05	2.04	8.14**	0.72	83.25	43.43
SFBL	F_1	0.34	30.88**	8.23**	8.31**	7.49**	0.69	92.23	75.40
	F_2	5.31**	6.15**	6.63*	4.89*	2.11	2.34	67.45	55.42
FBN	F_1	4.67*	5.09**	2.51	2.30	3.21**	0.32	60.33	31.16
	F_2	4.12*	5.73**	0.10	2.51	4.40**	0.30	65.17	25.69
SCY	F_1	0.05	5.76**	5.09*	2.82	2.74*	0.15	65.27	45.14
	F_2	0.23	4.78**	5.48*	2.16	2.43	0.09	60.18	41.27
LY	F_1	1.69	6.43**	7.74**	1.56	3.03**	0.03	68.99	48.02
	F_2	0.13	4.34**	10.44**	2.47	1.57	0.03	58.87	51.09
BN	F_1	0.43	4.09**	5.48*	5.88*	1.35	0.76	55.55	50.39
	F_2	0.20	1.26	2.24	0.41	1.25	0.74	15.67	8.68
BW	F_1	2.95	9.13**	1.73	2.02	6.54**	0.07	74.39	27.14
	F_2	3.34*	9.74**	0.93	2.15	7.39**	0.04	75.44	23.12
LP	F_1	1.49	6.99**	26.24**	8.50**	1.04	1.00	72.35	72.02
	F_2	0.49	3.59**	7.83**	2.45	1.50	1.41	52.27	44.25
FL	F_1	1.25	2.28*	5.67*	3.15	1.00	1.37	35.46	35.46
	F_2	3.40	1.27	6.88*	1.77	0.62	1.45	22.79	22.79
FU	F_1	2.19	0.75	0.22	0.09	1.19	0.85	6.06	0.00
	F_2	0.12	1.37	0.87	2.04	1.07	1.10	12.86	10.79
FE	F_1	2.03	1.02	1.00	2.29	0.75	0.00	9.66	9.66
	F_2	0.38	1.12	1.22	4.52*	0.55	0.00	18.28	18.28
FS	F_1	0.05	2.22*	7.63**	5.70*	0.68	2.04	39.46	39.46
	F_2	0.12	1.30	5.65*	2.77	0.60	1.74	23.22	23.22
MIC	F_1	0.93	1.06	6.63*	6.41**	0.32	0.10	23.60	23.60
	F_2	0.90	0.84	3.92	2.15	0.48	0.08	13.36	13.36

*****and******denote significant differences at 0.05 and 0.01 levels, respectively.F (female), M (male).

Heritability analysis of F_1, F_2 hybrids, and their eight inbred parents at various cotton belt

Heritability estimates the ratio of genetic variance to phenotypic variance. The broad-sense heritability (H^2) and narrow-sense heritability (h^2) were determined for all traits. Heritability analysis for Anyang is detailed in Table 2. According to the results, the percentage of H^2 was strong for majority of traits in both hybrid generations. In particular, LFFB, SFBL, FBN, SCY, LY, BW, LP, FL, and FS stated H^2 greater than 70% in both hybrid generations. Conversely, BN and FU had low percentage of H^2 relative to others traits in both hybrid generations. Further results determined that h^2 was strong and above 50% HFFB, SCY, LY, BW, LP, and FL in both F_1 and F_2 hybrids. LFFB and FU had very low h^2 in both generations than all other traits. Heritability analysis for Alar detected that H^2 for PH, LFFB, SFBL, and BW were great than 65% in both F_1 and F_2.The heritability of fiber traits in Alar were relatively more lower than Anyang. Specifically, FU and FE had low h^2. Interestingly, the h^2 of some traits in F_2 generation were higher than that in F_1 generation. For instance, SCY, BN, BW, LP in Anyang and LY in Alar had higher h^2. These findings put forth a clue that it is significant to select these traits in F_2 generation. The traits with lower heritability can easily affected by the environment. Hence, these traits can be improved through longer screening cycles during breeding measures.

General combining ability analysis of inbred parents at various cotton belt

General combining ability analysis is useful to screen superior inbred parents for specific or a set of traits. Based on results of combining ability analysis, GCA of the parental line was different and altered with generation, trait, and environment (Table 4). In Anyang, parental lines P1, P4, and P7 had higher GCA for SCY and LY in both hybrid generations. Furthermore, these parental lines comparatively had better GCA manifestation for others traits in F_1 and F_2. In particular, P1 showed higher GCA for HFFB, LFFB, SFBL, SCY, LY, BN, and MIC. P4 had greater GCA for SCY, LY, BW, LP and FU. P7 showed superior GCA for SCY, LY, BN, BW, LP, FU, and MIC. Apart from these inbred lines, P6 had better GCA for SCY, BW, FL, PH, HFFB. P2 and P8 exhibited positive GCA in more than five agronomic characteristic and fiber quality traits. It was observed that GCA was quite undulating in Alar. The parental lines P2, P4, and P7 were detected with higher GCA for SCY and LY in both F_1 and F_2. P2 GCA was specifically well in many traits such as PH, LFFB, SFBL, FBN, SCY, LY, BN, FL, FU, FE, and FS. P4 showed better GCA for SFBL, FBN, SCY, LY, BW, LP, and FL. GCA of P7 were strong for SCY, LY, BN, LP, and MIC. In addition, P8 showed better GCA in six traits and had greater value for LFFB and SFBL. Overall, the GCA of P4 was improved for LFFB, FBN, LY, BW, LP, and MIC in F_2 than F_1 in both cotton belt. However, GCA of P6 was improved for PH and HFFB in F_2 in both cotton belts. The P7 showed higher GCA in F_2 for SCY, LY, and BN in Anyang while P5 had improved GCA in F_2 for LFFB and SFBL at Alar cotton belt. These results revealed importance of these inbreed lines to improve specific trait or set of traits in different cotton belts.

Table 4
General combining ability of parents in Anyang and Alar

Environment	Parent	Generation	PH	HFFB	LFFB	SFBL	FBN	SCY	LY	BN	BW	LP	FL	FU	FE
Anyang	P1	F_1	1.73	9.41	8.55	6.43	-1.21	2.68	2.49	1.68	1.01	-0.20	-3.58	-0.23	-0.46
		F_2	-0.68	4.67	1.45	4.8	-5.91	1.78	1.40	4.21	-2.37	-0.43	-3.89	-0.79	-0.75
	P2	F_1	0.37	-3.02	6.96	6.46	1.53	4.74	5.50	6.06	-1.16	0.87	-0.42	0.13	0.20
		F_2	0.90	-3.21	4.58	0.01	2.28	-3.48	-3.43	-0.01	-3.35	0.16	-0.64	0.53	0.07
	P3	F_1	1.95	-2.25	-5.96	-7.32	4.65	2.52	3.72	3.24	-0.67	1.30	3.45	-0.22	0.36
		F_2	2.63	0.09	-2.21	-3.36	3.27	-2.36	-0.74	-2.53	0.22	1.79	2.40	-0.32	0.07
	P4	F_1	-3.35	-2.89	-4.62	-0.23	-1.39	1.26	2.13	-2.36	3.78	0.86	-0.03	0.57	-0.13
		F_2	-2.53	-6.85	2.56	-1.01	2.11	6.80	8.13	1.15	5.31	1.12	0.41	0.53	0.23
	P5	F_1	-0.71	-1.25	-4.92	-5.33	-3.58	-11.20	-13.84	-8.63	-2.95	-2.84	0.58	-0.26	0.03
		F_2	-0.32	5.30	-6.38	-0.44	-1.75	-2.74	-5.35	-2.82	0.18	-2.64	1.71	0.06	0.39
	P6	F_1	0.65	1.15	-4.42	2.68	-1.33	2.61	-0.41	-1.83	4.51	-2.88	2.25	-0.10	0.16
		F_2	1.42	2.71	-2.03	-1.18	-1.33	2.47	-0.02	-2.57	5.25	-2.28	1.45	0.14	0.30
	P7	F_1	-1.07	0.61	1.92	-8.10	-0.97	4.02	9.09	1.93	2.18	4.93	-3.43	0.58	-0.13
		F_2	-0.45	-0.20	-1.39	-4.14	1.23	7.39	12.03	5.11	2.22	4.52	-3.14	0.36	-0.39
	P8	F_1	0.42	-1.76	2.50	5.41	2.31	-6.63	-8.68	-0.10	-6.69	-2.06	1.18	-0.48	-0.03
		F_2	-0.98	-2.50	3.42	5.32	0.10	-9.86	-12.01	-2.54	-7.47	-2.24	1.69	-0.50	0.10
Alar	P1	F_1	-12.90	3.41	16.69	1.95	-7.58	-4.84	-2.17	-10.15	3.41	2.39	-2.50	-0.03	-0.20
		F_2	-9.15	2.85	0.74	-1.47	-8.62	-1.00	0.36	2.19	0.33	1.33	-1.45	0.56	0.03
	P2	F_1	13.32	-1.98	15.19	23.89	4.53	8.33	6.38	10.67	-2.33	-3.30	1.63	0.07	0.29
		F_2	4.29	-0.16	6.44	10.91	3.28	5.48	5.13	2.14	2.82	-0.39	1.71	0.58	0.20
	P3	F_1	0.99	-0.41	-24.71	-25.07	-3.49	-0.70	0.39	2.88	-6.48	1.42	-2.17	-0.1	-0.36
		F_2	2.45	2.30	-19.32	-24.17	3.68	-4.12	-3.84	-1.38	-1.84	0.25	0.68	-0.87	0.03
	P4	F_1	-8.08	-6.24	-4.69	9.25	2.84	2.06	1.69	2.78	2.13	0.59	0.51	-0.11	-0.03
		F_2	-3.14	-11.38	5.94	13.99	6.16	1.68	3.15	-2.51	4.05	1.57	0.46	-0.27	0.36
	P5	F_1	6.66	5.22	-2.48	-10.02	3.70	-4.86	-6.29	-6.18	3.27	-1.10	2.53	0.17	0.29
		F_2	5.56	6.39	6.20	0.74	-4.50	-2.04	-4.8	-0.44	-5.35	-2.76	-1.41	0.01	-0.62
	P6	F_1	-0.13	-1.71	-6.07	-5.83	-4.62	-3.71	-4.68	-6.56	3.35	-1.21	1.45	0.07	0.13
		F_2	5.01	1.38	1.93	-0.44	-0.16	-0.59	0.08	0.14	0.67	0.73	-0.01	0.32	-0.13
	P7	F_1	-1.02	1.04	-5.82	-10.53	3.82	6.60	9.34	5.67	-0.62	3.47	-2.70	-0.16	-0.16
		F_2	-2.12	-1.67	-12.91	-13.31	-0.90	4.85	6.82	3.73	1.50	1.95	-2.11	-0.29	-0.03
	P8	F_1	1.16	0.68	11.89	16.36	0.80	-2.89	-4.66	0.89	-2.72	-2.26	1.25	0.09	0.03
		F_2	-2.89	0.29	10.98	13.75	1.06	-4.25	-6.90	-3.87	-2.16	-2.68	2.12	-0.03	0.16

Special combining ability analysis of F_1 and F_2 hybrids at various cotton belt

The SCA reveals performance of a cross and provide an opportunity for utilization of heterosis in breeding. Our analysis revealed all combinations SCA was altered with traits and environments (Table 5). In Anyang, some combinations including 9, 10, and 12 had higher SCA for SCY and LY in both F_1 and F_2 hybrids. Specially, combination 9 had shown higher SCA for LFFB, SCY, LY, BN, BW, FE, and MIC. Combination 10 had good SCA for SCY, LY, BW, LP, FL, and FS. Wherein, combination 12 had better performances with higher SCA for LFFB, SFBL, SCY, LY, BN, BW, FL, and FS. Furthermore, it was observed that combinations 1, 8, 13, and 15 had shown relatively higher SCA more than five traits in both generations. The SCA analysis results at Alar are shown in Table 6. Among all combinations, the 2, 8, and 11 were detected with better SCA in both F_1 and F_2. In particular, combination 2 had shown higher SCA for nine traits including SCY, LY, BW, LP, FL, FU, FE, FS, and MIC. Interestingly, this combination SCA was improved in F_2 for PH, HFFB, FL, FU, FE, and FS. It was observed that Combination 8 showed better performance as well as high SCA for SCY, LY, BW, LP, FU, and FE. The combination 11 exhibited higher SCA in eight traits including PH, LFFB, FBN, SCY, LY, BW, FE, and MIC. Beside these, combinations 3, 6, 9, 14, 15, had higher SCA for most of traits in F_2 as compared to F_1. These combinations most probably can be selected in F_2 breeding generation to improve these traits at Alar cotton zone. Overall, analysis results revealed that combinations 9 and 2 had improved performance in F_2 at both cotton belts which emphasize selection of these combination in earlier generations would be effective for future breeding program.

Table 5
Hybrid combination F_1, F_2 Special Combining Ability in Anyang

Combination	Generation	PH	HFFB	LFFB	SFBL	FBN	SCY	LY	BN	BW	LP	FL	FU	FE	FS	MIC
1	F_1	1.79	0.18	-7.24	-3.62	-1.23	-7.71	-5.71	-5.32	-2.35	1.96	-1.39	-0.37	0.16	-0.43	1.79
	F_2	-1.83	-1.89	-0.89	-1.35	0.86	4.44	5.90	2.73	1.31	1.61	0.68	0.83	0.36	-0.82	3.10
2	F_1	-1.37	-1.91	2.93	7.92	0.81	0.85	1.17	-1.78	2.29	0.37	-0.35	-0.38	0.00	-3.26	1.79
	F_2	0.46	1.14	1.68	-2.72	-0.31	-1.18	-0.77	-0.87	-0.48	0.21	0.03	-0.17	0.03	-0.96	3.10
3	F_1	-0.42	1.74	4.31	-4.30	0.41	5.12	5.32	1.01	3.84	0.25	1.05	0.05	-0.16	-1.14	-1.96
	F_2	1.37	0.74	-0.78	4.07	-0.55	-3.40	-3.96	-0.55	-3.00	-0.74	0.14	-0.23	0.03	2.25	-1.45
4	F_1	-0.29	2.15	3.94	-0.89	-1.52	-3.03	-3.60	-1.77	-1.00	-0.51	1.08	0.27	0.33	-0.43	-0.08
	F_2	0.02	-0.09	-2.29	-3.21	-2.52	0.81	0.61	-0.73	2.14	0.10	-0.91	-0.25	-0.13	1.58	-2.07
5	F_1	-1.24	-0.78	2.22	3.03	2.04	4.77	2.83	7.85	-2.78	-2.07	-0.39	0.44	-0.33	5.26	-1.54
	F_2	-0.95	0.49	7.85	2.29	-0.78	-0.68	-1.79	-0.58	0.03	-1.18	0.07	-0.17	-0.30	-2.06	-2.69
6	F_1	1.53	-1.37	-6.16	-2.14	-0.52	0.64	2.79	3.47	-3.00	1.83	0.52	0.39	0.16	-0.47	0.04
	F_2	0.93	-0.40	-5.55	0.92	3.31	-3.54	-2.73	-0.19	-3.02	0.86	0.29	0.64	0.07	0.88	-0.62
7	F_1	0.81	0.29	7.12	8.35	0.00	-2.5	-4.23	1.61	-4.08	-1.81	-0.16	0.23	0.00	-4.15	-2.46
	F_2	-0.21	-1.82	-1.33	0.00	2.09	-3.92	-4.09	-1.21	-2.47	0.09	-0.90	0.42	-0.26	-1.07	-1.86
8	F_1	1.26	1.50	-7.56	-20.89	0.76	-1.82	-2.01	-2.28	0.13	-0.26	1.13	-0.20	-0.16	4.33	1.29
	F_2	-0.53	0.94	0.51	6.23	1.04	-1.89	-2.71	-3.24	1.53	-0.81	1.26	-0.69	-0.26	-2.09	1.03
9	F_1	-2.07	-1.79	0.44	12.54	-0.76	2.40	2.24	0.36	1.79	-0.31	-2.27	-0.57	0.33	-0.16	1.92
	F_2	0.74	0.88	0.82	-6.24	-3.12	8.87	9.22	4.96	3.18	-0.28	-0.76	0.26	0.07	-1.81	1.65
10	F_1	-2.26	-4.29	-8.99	-11.46	1.36	1.28	1.22	-3.16	5.16	0.54	0.77	0.15	-0.33	0.45	-0.79
	F_2	1.19	2.95	-1.78	0.85	-0.62	0.48	0.31	-0.31	0.78	0.14	0.11	-0.64	0.39	4.09	-0.21
11	F_1	0.13	3.44	-5.18	7.87	-4.47	7.07	2.93	1.84	5.36	-3.78	0.87	-0.03	-0.13	0.91	-1.84
	F_2	0.19	-0.01	-1.51	-4.12	3.64	-0.90	-3.17	-2.54	1.71	-2.47	-0.97	-1.47	-0.43	-0.06	-2.48
12	F_1	2.13	0.85	14.18	3.59	3.12	1.64	3.07	0.17	1.79	1.44	0.51	0.16	-0.30	7.41	0.67
	F_2	-1.38	-2.94	3.29	3.26	-3.02	5.10	4.86	2.07	2.95	-0.30	0.87	-0.25	0.23	2.03	-1.24
13	F_1	-0.06	1.68	5.17	7.62	1.39	-3.30	-3.30	1.27	-3.97	0.01	-2.18	0.16	0.03	-3.20	0.67
	F_2	0.82	0.84	6.30	3.71	0.20	5.29	6.67	3.79	1.47	1.55	-1.40	0.92	0.23	-0.16	0.41
14	F_1	1.23	-2.25	7.60	2.07	0.86	0.63	1.36	1.41	-0.79	0.81	1.19	0.30	0.03	0.59	-1.84
	F_2	0.84	-2.57	-8.52	-1.69	-3.59	-9.68	-9.83	-4.23	-5.32	0.18	1.67	-0.01	0.07	0.23	0.41
15	F_1	-1.17	0.57	-12.77	-9.70	-2.25	-6.04	-4.05	-4.69	-2.38	1.52	-0.39	-0.58	0.36	-5.71	2.34
	F_2	-1.66	1.73	2.23	-2.01	3.39	0.20	1.48	0.90	-0.81	1.03	-0.17	0.81	-0.10	-2.04	2.89

Table 6
Hybrid combination F_1, F_2 Special Combining Ability in Alar

Combination	Generation	PH	HFFB	LFFB	SFBL	FBN	SCY	LY	BN	BW	LP	FL	FU	FE	FS	MI
1	F_1	-1.51	4.72	19.99	15.79	-8.91	-3.06	-3.63	3.95	-2.67	-0.29	2.06	0.46	0.20	1.04	-1.0
	F_2	-2.45	-5.79	-12.34	2.04	-6.97	-5.03	-5.81	2.53	-1.58	-0.65	-0.10	-0.22	-0.03	-1.64	-0.8
2	F_1	-4.73	-4.42	-11.35	-3.32	3.04	2.96	2.93	-4.18	5.92	1.59	1.09	0.40	0.20	0.85	0.9
	F_2	1.35	-1.69	17.96	11.00	-6.17	7.78	8.33	5.31	0.80	0.47	2.36	0.54	0.30	2.81	0.4
3	F_1	12.55	2.84	2.17	-9.70	1.35	-4.76	-6.06	-3.23	-3.89	-1.79	-0.87	-0.49	-0.13	0.27	-1.2
	F_2	6.29	3.73	7.81	10.07	5.92	0.52	-1.05	4.54	1.46	-1.52	-0.35	-0.72	-0.03	0.40	2.0
4	F_1	-4.03	1.93	-3.71	-4.50	5.02	2.56	3.39	4.38	0.00	-0.07	-0.07	0.11	0.03	0.67	-1.9
	F_2	-1.58	-2.75	-16.18	-14.48	3.46	-3.33	-0.96	-6.90	-3.07	2.39	1.08	0.29	0.13	0.44	-0.6
5	F_1	-2.28	-5.07	-7.11	1.72	-0.50	2.31	3.38	-0.92	0.65	0.55	-2.21	-0.49	-0.29	-2.83	3.2
	F_2	-3.60	6.50	2.76	-8.63	3.76	0.06	-0.52	-5.48	2.38	-0.68	-3.00	0.10	-0.36	-2.01	-0.8
6	F_1	-3.08	-10.07	-5.85	-13.64	3.46	-0.24	0.67	0.51	-5.78	0.10	-1.17	-0.01	-0.49	-0.32	-0.2
	F_2	1.13	-0.40	3.78	0.75	0.55	1.87	4.29	3.38	-5.56	2.19	-0.32	-0.51	-0.13	1.94	-1.4
7	F_1	0.31	4.84	2.06	1.60	-0.09	-7.83	-7.72	-5.19	-1.59	0.40	-0.09	-0.54	0.00	-0.07	1.1
	F_2	3.96	5.54	-4.74	0.15	-0.85	-3.76	-4.34	-2.72	-1.17	-0.58	-0.50	0.49	-0.30	-1.40	-1.4
8	F_1	-6.05	2.99	-3.40	-2.59	-6.55	9.04	11.20	7.13	2.40	0.04	-1.61	1.00	0.16	-1.53	-0.4
	F_2	-7.23	-4.77	2.60	1.09	-5.64	0.44	2.15	-4.64	3.41	1.79	0.20	0.80	0.36	-0.47	2.1
9	F_1	2.21	-0.04	3.91	13.45	-1.60	-0.01	-1.49	-1.89	2.61	0.25	-0.70	-0.75	-0.16	-2.11	0.9
	F_2	-1.94	3.73	6.55	2.16	3.17	2.72	0.17	2.60	2.24	-2.56	-0.24	-0.70	0.03	0.46	-0.5
10	F_1	6.61	2.28	3.29	1.18	4.79	-0.96	-2.66	-0.56	2.36	-0.79	3.57	0.30	0.49	4.02	-1.3
	F_2	4.08	-4.10	-8.18	-4.15	2.77	-1.27	-2.27	1.39	1.07	-0.84	0.86	-0.08	0.03	-0.54	1.2
11	F_1	4.60	5.36	-14.13	-2.15	5.46	3.30	2.97	-4.46	8.46	0.18	-0.89	-0.46	0.29	-0.72	1.2
	F_2	1.32	6.19	8.56	-2.80	6.42	3.16	1.52	-5.91	7.13	-1.53	0.41	0.73	0.16	-0.30	2.3
12	F_1	4.41	-0.42	9.29	1.71	-2.95	4.87	4.79	9.37	-4.33	-2.00	-1.00	0.14	-0.20	-0.79	-2.1
	F_2	-5.31	-3.85	-13.22	-11.15	7.02	-4.02	-4.00	-2.58	0.37	0.11	-1.86	-1.03	0.00	-1.42	0.9
13	F_1	-6.50	-5.83	1.23	12.29	5.20	-4.28	-5.14	-3.90	1.49	1.76	2.47	-0.51	-0.03	1.26	1.7
	F_2	0.94	1.03	-10.4	-11.16	-0.29	-0.97	-1.10	0.10	-4.88	-0.27	0.15	-0.09	-0.33	0.07	-4.1
14	F_1	1.82	-1.89	-0.20	-8.95	-3.42	-2.55	-1.89	-2.49	-2.61	-0.18	0.77	0.64	0.13	1.44	1.0
	F_2	3.53	-0.98	9.63	12.32	-6.62	0.61	0.79	4.30	0.83	0.17	-0.84	0.41	-0.16	-0.90	1.2
15	F_1	-4.33	2.78	3.81	-2.90	-4.29	-1.35	-0.72	1.48	-3.01	0.24	-1.36	0.19	-0.20	-1.19	-1.8
	F_2	-0.48	-2.40	5.42	12.78	-6.53	1.21	2.79	4.10	-3.45	1.52	2.14	-0.02	0.33	2.55	-0.3

The screening of hybrids with excellent heterosis in multiple traits

In this study, we further analyzed the level of MPH, BPH, CH, and HD for different traits, hybrid combinations, and cotton belt. The analysis results revealed that level of heterosis altered with trait, hybrid combination, generation, and environment (Additional file 1). The majority of combination in Anyang had shown highest heterosis for yield traits as compared to agronomic and fiber quality traits. For instance in F_1 generation, the combination 12 exhibited highest MPH (45.9%) for LY. Combination 6 was top BPH producing among all combinations. It had 36.3% higher LY than better parent. Moreover, highest CH was 28.4% which had shown by combination 7 for BN. Most combinations HD was positive for yield traits but negative for agronomic and fiber quality traits. It may be because of negative MPH, BPH, and CH in agronomic and fiber quality traits. Among F_2 generation, LY had highest MPH (24.0%), BPH (20.9%), and CH (11.6%). This strong vigor was witnessed in combination 5, 1, and 9, respectively. Intriguingly, combination 9 had outstanding MPH, BPH, and CH in multiple traits as compared to other combinations. The analyzed results in Alar stated that F_1 had highest CH for LY (36.5%). This was exhibited by combination 8. However, combination 2 had highest MPH (21.9%) and BPH (19.7%) for SCY among others. Beside this, a positive HD was measured for most yield traits among all hybrid combinations. While agronomic and fiber quality traits had negative HD in most hybrid combinations. The results revealed hybrid combinations had shown positive MPH, BPH, and CH for yield traits in F_2 generation. Interestingly, combination 2 and 9 had shown outstanding heterosis in multiple traits at Alar cotton belt. Overall analysis determined that combination 9 had best hybrid vigor in both generation and cotton belt. Therefore, it can be considered an outstanding hybrid for both cotton zones.

Subsequently, this study further screened top eight hybrid combinations with superior performance in multiple traits. The results revealed CH, MPH and BPH in selected hybrids were altered with generation and cotton belts (Fig. 1, Additional file 2). It was determined that more than 6 combinations had better CH, MPH, and BPH in both generations and cotton belts. However, some of combinations had superior CH, MPH and BPH in both generations but one cotton belt. In this regard, combination 12 had similar performance in Anyang while combination 2 and combination 9 in Alar. Beside this, some combinations exhibited strong vigor in both cotton belts but only in one generation. Such as combination 2 and combination 7 had shown better CH, MPH and BPH in F_1. Combination 9 displayed better CH, MPH and BPH in F_2. Combination 2 was observed with strong CH and MPH in F_2. Comparatively, combination 2 and 9 showed excellent performance in multiple traits for both generations and cotton belts. These encouraging results evaluate the potential of F_2 hybrids to improve cotton productivity in China.

Correlations among various traits in two different cotton belts

Relationship between traits is dynamic factor in selection of plant breeding materials. The correlation analysis between agronomic, yield and fiber quality traits in Anyang is summarized in Fig. 2A. A significant positive correlation was observed among yield (SCY, LY) and yield components (BN, BW, LP). All fiber quality traits except FU showed negative correlation with yield traits. A significant positive correlation among FU and yield was detected. The correlation between yield and agronomic traits were either non-significant negative or positive. Similar results were observed among most of fiber quality and agronomic traits. Most of fiber quality traits including FL, FE, and FS had positive correlation with each other. However, MIC had strong negative correlated with FL and FS but positive correlation with FU. The correlations were undulating among agronomic traits. For instance, PH had significant negative correlation with LFFB and MIC, had significant positive with FBN and FS. A significant positive correlation was observed between SFBL and LFFB.

The correlation analysis in Alar revealed SCY had significant positive correlation with LY and BN whereas LY was positively correlated with BN and BW (Fig. 2B). The correlation of BW was significant positive only for FE and MIC. LP showed significant negative correlation with FL and FS. In contrast, it had significant positive correlation with MIC. Among fiber quality traits, FL had a significant positive correlation with FE and FS. MIC had significant negative relationship with FL and FS. The agronomic traits had shown diverse correlations but few were significant. For instance, PH had extremely positive correlation with HFFB, FBN and FL. It had negatively correlated with LP and MIC. Moreover, SFBL was positively correlated with FS. FBN was positively correlated with FL and FE. Overall, analysis results propose that agronomic, yield, and fiber quality traits can be improved independently in both cotton belts.

Discussion

Cotton plays a critical role in textile industry development, employment opportunity, and foreign earning. Genotypes with higher yield and fiber quality are desired in upland cotton. This synchronized improvement of multiple traits in upland cotton demands more crossing, assessment, screening, and resources. Utilization of heterosis is most suitable method to achieve such vast breeding aim. Worldwide, difficulties in producing F_1 hybrid seeds have restricted the commercial use of heterosis in cotton. However, this study compared the performance, combining ability, and heritability in both F_1 and F_2 generations under two cotton belts. Further screened and discussed potential utilization of F_2 hybrids to improve cotton production in China.

Parental selection has critical importance hybrid cotton breeding. However, identification of potential parents is most laborious job in upland hybrid cotton breeding. In the utilization of heterosis, selected parental materials should have superior performance, physiology, combining ability, and heritability. GCA refers to the average performance of a parental line in hybrid offspring and mainly anticipates the role of heritable additive genes contribution (Liu et al. 2019; Shang et al. 2012). Therefore, statistics of GCA determined the selection of parental line in future breeding programme. Previous studies have already been showed that parents with high GCA can be well exploited through heterosis to produce superior hybrids(Hassan et al. 2000;Lukonge et al. 2008). In our study, majority of parental lines GCA were positive but altered with generation. Moreover, yield traits were detected with higher GCA and fiber traits with lower. Previous research in F_1 and F_2 hybrids stated similar statistics for combining ability in upland cotton (Tang et al. 1993; Khan et al. 2009). Among all inbred parental lines used in this study, P4 and P7 had best GCA for multiple traits in F_1, F_2 generations, and in both cotton belts (Table 4). These inbred lines superior performance in multiple traits, generations, and environments proposed their utilization in further breeding programme to develop elite hybrids. Interestingly, our results showed that GCA of P4 was improved for LFFB, FBN, LY, BW, LP, and MIC in F_2 as compared to F_1 in both environments. The abrupt increase may be results of heterogeneous material with different effects in F_2 which probably lead to well adaptation in different rage of environments. The estimate of heritability defines the range of genotypic and phenotypic variances. Therefore, it reveals the potential of parents to be selected and exploited to develop high yielding genotypes. High heritability and GCA increased the probability of selecting hybrid offspring with good performance in early generations (Sun et al. 1994; Jia et al. 2017). Our results displayed that majority of yield traits had strong H^2 and h^2 among different generations and environments (Table 2 and 3). The traits with high heritability index showed are less vulnerable to diverse environments. Thus, simple selection in early generations would be an effective strategy to improve these traits (Soomro et al. 2010). In cotton breeding, GCA and heritability analysis provides a foundation to screen highly dominant materials (Li et al. 2010). However, combined performance across multiple generation and ecological zones could be efficient method to identify elite breeding population.

Estimates of SCA reflect the average performance of a hybrid combination and mainly produced by action of dominant or epistatic genes interaction. This non-additive genes action mediates mechanism of heterosis in upland cotton (Ahuja and Dhayal. 2007; Shahzad et al. 2020). Thus, estimates of SCA provide an opportunity to screen potential hybrid combinations in particular generation or environment (Soomro et al. 2012; Khan et al. 2015). Our study revealed although the magnitude of SCA were altered with trait, generation, and environments. Interestingly, combination 9 and 2 had shown positive SCA effects in multiple traits in both F_1 and F_2 generation across two cotton belts (Table 5 and 6). In particular, yield and yield components were identified with higher SCA effects in these hybrids. Such promising results proposed that superior combinations may be utilized as F_2 hybrids to increase yield or as an elite population in advance breeding experiments. Beside this, those F_2 hybrid combinations with superior performance at specific cotton belt most likely would be utilized to improve cotton productivity in areas of that cotton zone. Previous research stated that GCA and SCA were independent and higher GCA does not essentially interlinked with higher SCA. Therefore, more emphasis should be on SCA effects rather than GCA effects of inbred parents during process of hybrid selection (Yang et al. 2009; Peng et al. 2015; Canavar et al. 2011). Correlation between traits play vital role in plant material selection (Liu et al. 2008). Our results observed that a negative correlation between yield and quality characters in both cotton belts (Fig. 2). These results were consistent with those previously reported by different researchers (He et al. 2009; Li et al. 2010). These results enabled improvement in yield related traits independent of fiber quality traits. Moreover, some agronomic traits showed significant positive correlation with yield and quality traits in this study. Therefore, these agronomic traits should also be taken into consideration in breeding of hybrids across mechanical harvest cotton zones. Apart from this, how to improve fiber quality is still an important research topic in hybrid cotton breeding.

The utilization of heterosis improved the productivity of crops. Utilization of heterosis is one of key way to improve stagnant yield in upland cotton. However, major challenge is difficulty of producing of F_1 seed through manual emasculation and pollination (Wu et al. 2004) which caused high cost of production and seed impurity. To mitigate this challenge, the commercial use of F_2 hybrids is proposed by many researchers (Li et al. 2000; Iqbal et al. 2015). The upland cotton belongs to allotetraploid, its F_2 segregation is not severe as in diploid rice and maize (Chen et al. 2020). Additionally, cotton has a long harvest period, the plant architecture, growth stages, and agronomic traits may not have a direct impact on yield and fiber quality of F_2 generations (Wang et al. 2011; Kong et al. 2017). These unique cotton characteristics provide an opportunity for utilization of F_2 hybrids to improve productivity. In this study, some combinations of F_2 hybrid generation performed well in multiple traits. For instance, combination 9 had shown excellent performance in multiple traits at both cotton belts(Fig. 1, Additional fiel 1). It illustrated that combinations with strong vigor performed well in F_2 (Liu et al. 2007; Zhang et al. 2018). Moreover, heterogeneity in F_2 most like enabled wider environment adaptation as compared to F_1 and inbred parents. Commercialization of elite F_2 hybrids not only reduced production costs but also increased yields and promotes hybrid cotton.

Conclusions

In this study, results of combining ability analysis showed that P4 and P7 had good GCA in both generations and cotton belts. There were many hybrid combinations with higher SCA and better heterosis performance in yield traits than other traits. Hybrid combination 9 performed outstandingly in Anyang wherein hybrid combination 8 was prominent than control Zhongmiansuo49 in Alar. Moreover, there was a significant positive correlation between yield components. In concise, our results revealed potential utilization of F_2 hybrids in upland cotton breeding. Furthermore, these results provide a strong basis for F_2 selection and ecological shuttle breeding to enhance cotton yield in china.

Declarations

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Authors’ contributions

Chen LL conducted the most of experiments and data analysis, and drafted the manuscript. Tang HN, Zhang XX, Qi TX, Guo LP, Wang HL, Qiao XQ and Zang R participated in data collection and performed part of the statistical analysis. Zhang M and Shahzad K helped polish the language and revise the manuscript. Xing CZ, Wu JY and Zhang M conceived, designed and funded the study. All authors have read and approved the final manuscript.

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Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no conflict of interest.

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Figures

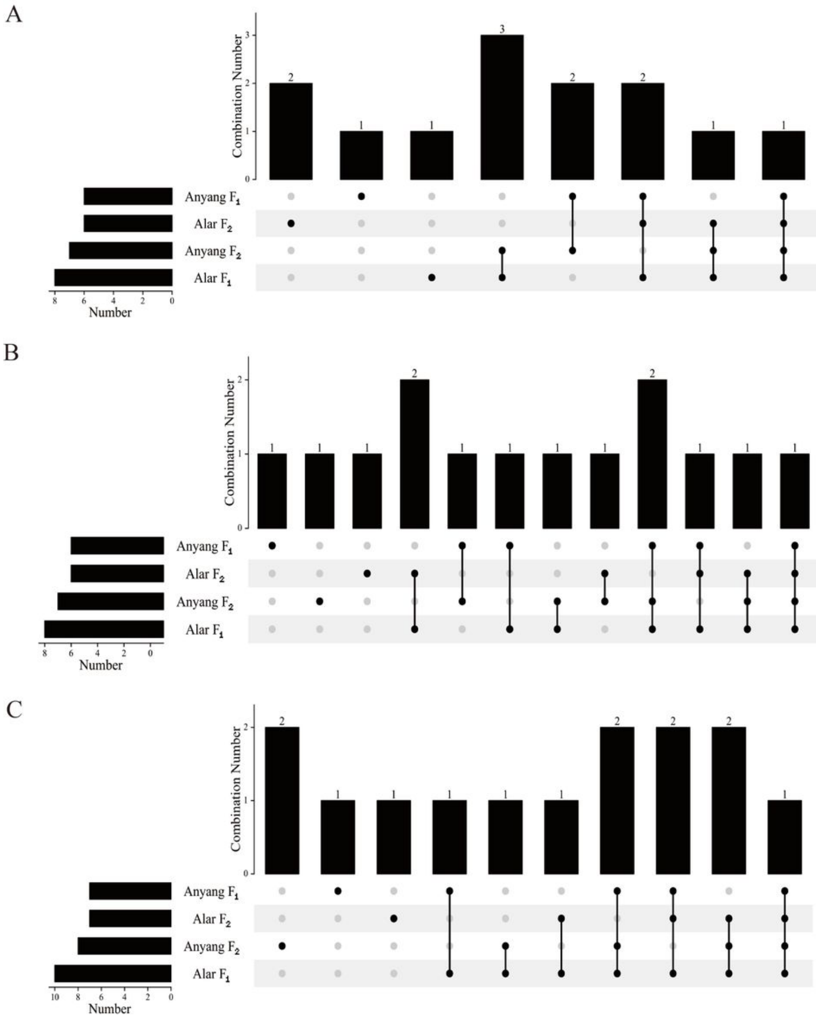

Figure 1

Top 8 hybrid combinations with strong BPH (**A**), CH (**B**) and MPH (**C**) in different generationsandcotton belts.

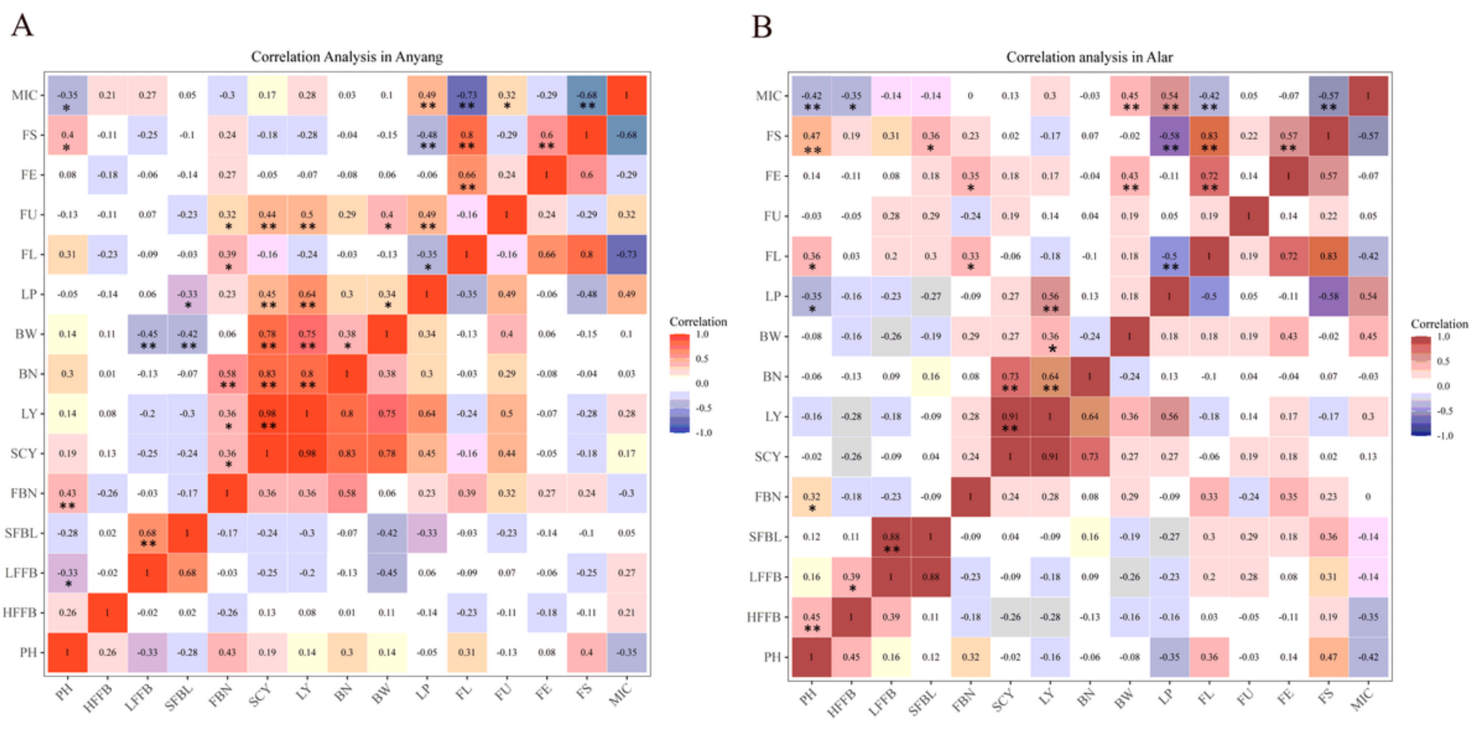

Figure 2

Correlation analysis among 15 cotton traits in Anyang (**A**) and Alar (**B**) ecological sites.***** and****** showsignificant differences at 0.05 and 0.01 levels, respectively.

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