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Comparative performance of hybrid generations reveals the potential application of F_2 hybrids in upland cotton

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Abstract

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

Results: Eight upland cotton varieties were analyzed and crosses were made according to NCII incomplete diallel cross-breeding design in two cotton belts of China. Variance analysis revealed significant differences in agronomic, yield, and fiber quality in both generations and environments. The broad-sense heritability of agronomic and yield traits was relatively higher than quality traits. Furthermore, the narrow-sense heritability of some traits was higher in F_2 than in the F_1 generation in 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, 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 (LY) was 24.2% higher in F_1 and 11.6% in F_2 than that of the control Ruiza 816. The performance of SJ48 × Z98 was excellent in Aral which showed 36.5% higher LY in F_1 and 10.9% in F_2 than control CCRI 49. Further results revealed most hybrid combinations had shown a 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. It is feasible to screen strong heterosis hybrid combinations with fine fiber in early generations. In the two environments, the correlation of some traits showed the same trend, and the correlation degree of Anyang site was higher than that of Aral site, and the correlation of some traits showed the opposite trend. According to the performance of strong heterosis hybrid combinations in different environments, the plant type, yield and fiber traits associated with them can be improved according to the correlation.

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

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Keywords: Upland cotton, F_2 generation, Combining ability, Heterosis, Heritability

Background

Heterosis is a phenomenon by which hybrid progenies show superior performance compared to theirs in the aspect of vegetative growth, reproductive growth, and stress tolerance (Shahzad et al. 2019a). 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. 2021), tomato Yu et al., 2020), kohlrabi (Singh et al. 2019). The utilization of heterosis increased the 10%~20% yield of hybrid rice (*Oryza sativa*) more 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 to sustainable yield in recent years. Therefore, heterosis has the important practical significance in meeting market demand, improving economic efficiency, and ensuring food security.

Cotton is a major economic crop that has not only a renewable natural textile fiber source but also owns an ample amount of vegetable oil resources (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 adaptable and stable in varying environments (Shahzad et al. 2019b). Cotton hybrids have been devolved through the utilization of heterosis in China and planted in the main cotton provinces such as Hubei, Hunan, and 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 the main way to utilize cotton heterosis. Due to the high cost of seed production, the utilization of F_1 heterosis is largely restricted to 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 using the F_2 generation of cotton hybrids.

Many cotton breeders have already proposed the 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). 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 the efficiency of any breeding program (Wang et al. 2012; Liu et al. 2019; Shi et al. 2021). In this study, eight upland cotton varieties were selected as experimental materials and crosses were made according to the NC II 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 them with the breeding practice of strong hybrid cotton to select the best combination of heterosis and provide a 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 by 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. 2019b). Specifically, the inbred lines Zhong 901 (P1), ZB (P2), SJ48 (P3), L28 (P4), and K8 (P5) were used

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)

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 the east experimental fields of Institute of 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 is located in Henan, and in Aral which is located in Xinjiang (40°55′N, 81°28′E). Ruiza 816 and CCRI 49 were used as the control varieties in Anyang and Aral, respectively. All experimental materials were planted in a randomized complete block design, with 3 replicates. In Anyang, each material was planted in four rows without mulching, and in Aral adopts film mulching, and each material was planted under one film with six rows. Each block was 9.6 m^2, and guard rows were set up around. The density was set according to the different ecological environment types, as 45 000 plants per hectare in Anyang, and 150 000 plants per hectare in Aral. Seeds were sown in late April in sequential years and the crop management practices followed the local recommendations.

Investigation and methods of phenotypic traits

In mid-September, the plant height (PH), the height of first fruit branch (HFFB), length of first fruit branch (LFFB), the second fruit branch length (SFBL), fruit branch number (FBN), and boll number (BN) for each plant were investigated. 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). The weight of seed cotton per plot was used to calculate seed cotton yield (SCY) and lint yield (LY) per hectare, and the lint percentage (LP, the ratio of the fiber weight on the seed cotton to the weight of the seed cotton). Subsamples of lint collected from each plot were sent to the Cotton Fiber Quality Testing Center affiliated with the Chinese Ministry of Agriculture and Rural Affairs (Anyang, Henan) to assess fiber quality by using a 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, and LP as yield traits; PH, HFFB, LFFB, SFBL, and FBN as agronomic traits; FL, FU, FS, FE, and MIC as fiber traits.

Data 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 $(MPH) = (F_1/F_2 - MP)/MP \times 100\%$, better-parent heterosis $(BPH) = (F_1/F_2 - HP)/HP \times 100\%$, competitive heterosis $(CH) = (F_1/F_2 - CK)/CK \times 100\%$, heterosis decline $(HD) = (F_1 - F_2)/F_1 \times 100\%$.

Results

Variance analysis of F_1, F_2 hybrids, and their inbred parents in different cotton belts

The variance analysis was performed for 15 F_1, and F_2 hybrids, and their eight inbred parents. The variance was extremely significant ($P < 0.01$) for the majority of traits in different cotton belts (Tables 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 which indicated that the differences in these traits were mainly caused by genetic variation. The male inbred lines had a non-significant variance in LFFB and SFBL in both F_1 and F_2 generations. In contrast, male inbred lines demonstrated significant variance for the majority of yield and fiber quality traits in both generations. The male variance was extremely significant and improved in F_2 generation for SCY, LY, BN, BW, LP, and FL. Furthermore, male inbred lines exhibited significant differences for PH, SFBL, FE, and FS only in F_2 as compared with the F_1 generation. The female inbred lines had a significant variance in eight traits of the F_1 generation, while the difference was significant only in seven traits of the F_2 generation. The female × male interaction variance was significant for the majority of traits in both generations except HFFB, FE, and MIC. Table 3 summarized the analysis of variance results for all traits in Aral. 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 extremely significant differences in agronomic and yield traits other than BN. The variance was significant among male parents for most of the traits in the F_1 generation specifically in LFFB, SFBL, SCY, LY, BN, LP, FL, FS, and MIC. The variance for female inbred was inconsistent

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

Trait	Generation	Block	Combination	M	F	$F\times M$	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

F female, *M* male

*and ** denote significant differences at 0.05 and 0.01 levels, respectively

between the two generations for 80% of agronomic and some yield traits. For example, LP had a highly significant difference in the F_1 generation. In contrast, PH, HFFB, SFBL, and FE had significant differences in F_2. Interestingly, the female × male interaction variance was extremely significant for PH, HFFB, LFFB, FBN, and BW in F_1 and F_2.

Heritability analysis of F_1, F_2 hybrids, and their eight inbred parents in different cotton belts

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 with Anyang was detailed in Table 2. According to the results, the percentage of H^2 was strong for the majority of traits in both hybrid generations. In particular, LFFB, SFBL, FBN, SCY, LY, BW, LP, and FL stated that H^2 is greater than 70% in both hybrid generations. Conversely, FU had a lower percentage of H^2 relative to other 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 Aral detected that H^2 for PH, LFFB, SFBL, and BW was great than 65% in both F_1 and F_2. The heritability of fiber traits in Aral was relatively lower than in Anyang. Specifically, FU and FE had low h^2, which was less than 20% in F_1 and F_2. Interestingly, the h^2 of some traits in the F_2 generation was higher

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

Trait	Generation	Block	Combination	M	F	F × M	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

F female, *M* male

*and**denote significant differences at 0.05 and 0.01 levels, respectively

than that in the F_1 generation. For instance, SCY, BW, LP in Anyang and LY in Aral had higher h^2, in F_2 with more than 50%. These findings put forth a clue that it is significant to select these traits in the F_2 generation. The traits with lower heritability can easily be affected by the environment. Hence, these traits can be improved through longer screening cycles during breeding measures.

General combining ability analysis of inbred parents in different cotton belts

General combining ability analysis is useful to screen superior inbred parents for specific or a set of traits. Based on the results of combining ability analysis, the GCA of the parental line was different and altered with generation, trait, and environment (Table 4). In Anyang, parental lines P1, P4, and P7 their GCA for SCY and LY were positive in both hybrid generations. Furthermore, these parental lines comparatively had better GCA manifestation for other traits in F_1 and F_2. In particular, P1 showed positive 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, FE and PH, and HFFB. P2 and P8 exhibited positive GCA in five or more agronomic characteristics and fiber quality traits. For P2 in PH, LFFB, SFBL, FBN, LP, FU, FE and MIC, and for P8 in LFFB, SFBL, FBN, FL and

Table 4 General combining ability of parents in Anyang and Aral

Environment	Parent	Generation	PH	HFFB	LFFB	SFBL	FBN	SCY	LY	BN	BW	LP	FL	FU	FE	FS	MIC
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	−1.35	3.71
		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	−3.65	1.86
	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	−1.60	3.71
		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	0.83	1.86
	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	1.69	−7.55
		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	2.60	−5.37
	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	2.47	−0.04
		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	−0.65	0.21
	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	−1.21	0.17
		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	0.87	1.45
	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	−0.21	−4.09
		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	1.24	−0.83
	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	−1.97	6.43
		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	−3.10	2.89
	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	2.17	−2.34
		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	1.86	−2.07
Aral	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	−4.06	5.33
		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	−0.83	0.76
	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	2.36	−1.39
		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	3.07	1.42
	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	−1.43	−2.51
		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	−1.43	−1.47
	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	−0.52	−0.49
		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	−1.35	1.87
	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	3.64	−0.94
		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	0.54	−2.58
	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	1.01	−0.09
		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	−1.66	0.89
	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	−3.11	2.47
		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	−0.68	1.42
	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	2.10	−2.38
		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	2.35	−2.31

FS. It was observed that GCA was quite undulating in Aral. The parental lines P2, P4, and P7 were detected with positive 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 was strong for SCY, LY, BN, LP, and MIC. In addition, P8 showed better GCA in six traits and had greater value in LFFB and SFBL. Overall, the GCA of P4 was improved for PH, LFFB, FBN, LY, BW, LP, FE and MIC in F_2 than F_1 in both cotton belts. However, seven traits of GCA of P6 in F_2 were improved 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 in Aral. These results revealed the importance of these inbred lines to improve specific traits or sets of traits in different cotton belts.

Special combining ability analysis of F_1 and F_2 hybrids in different cotton belts

The SCA revealed the performance of a cross and provide an opportunity for the utilization of heterosis in crop breeding. The SCA of all combinations was altered with traits and environments (Tables 5 and 6). In Anyang, it was observed that combinations 6, 8, 9, 10, 12, 13, and 14 have five or more than five traits with SCA values greater than zero in both generations. Among these, combinations 9, 10, and 12 all had positive SCA for SCY and LY in both F_1 and F_2 hybrids. Besides, combination 9 had also shown positive SCA for LFFB, BN, BW, FE, and MIC, and the SCA values of combination 10 were positive for BW, LP, FL, and FS. Meanwhile, combination 12 had better performances with positive SCA for LFFB, SFBL, BN, BW, FL, and FS (Table 5). The SCA analysis results in Aral were shown in Table 6. Among all combinations, only 2, 8, and 11 of SCY and LY were detected to be positive for 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, the SCA of this combination was improved in F_2 for FL, FU, FE, and FS. It was observed that Combination 8 showed better performance as well as positive SCA for SCY, LY, BW, LP, FU, and FE. Combination 11 exhibited positive SCA in eight traits including PH, HFFB, FBN, SCY, LY, BW, FE, and MIC. Besides these, combinations 3, 6, 9, 14, and 15, had positive SCA for most of the traits in F_2 as compared to F_1. These combinations most probably can be selected in the F_2 breeding generation to improve these traits in Aral. Overall, analysis results revealed that combinations 9 and 2 had improved performance in F_2 in both cotton belts which emphasizes the selection of these combinations in earlier generations would be effective for the future breeding program.

The screening of hybrids with excellent heterosis in multiple traits

In this study, the level of MPH, BPH, CH, and HD for different traits, hybrid combinations, and in different cotton belts were analyzed. The analysis results revealed that the level of heterosis altered with the trait, hybrid combination, generation, and environment (Additional file 1). The majority of combinations in Anyang had shown the highest heterosis for yield traits as compared to agronomic and fiber quality traits. For instance, in the F_1 generation, combination 12 exhibited the highest MPH (45.9%) for LY, and the LY of combination 6 had the highest BPH at 36.3%. Moreover, the highest CH was 28.4% which had shown by combination 7 for BN. Most combinations of HD were positive for yield traits but negative for agronomic and fiber quality traits. It may be because of the negative MPH, BPH, and CH in agronomic and fiber quality traits. Among F_2 generation, the LY of combinations 5, 1, and 9 witnessed the highest MPH (24.0%), BPH (20.9%), and CH (11.6%) values, respectively. Intriguingly, combination 9 had outstanding MPH, BPH, and CH in multiple traits as compared to other combinations. The analyzed results in Aral showed F_1 had the highest CH for LY (36.5%). This was exhibited by combination 8. However, combination 2 had the highest MPH (21.9%) and BPH (19.7%) for SCY among others. Besides 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 the F_2 generation. Interestingly, combinations 2 and 9 had shown outstanding heterosis in multiple traits in Aral (Additional file 1). The overall analysis determined that combination 9 had the best hybrid vigor in both generations and cotton belts. Therefore, it can be considered an outstanding hybrid for both cotton zones.

Subsequently, this study further screened the 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 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 Aral. Besides this, some combinations exhibited strong vigor in both cotton belts but only in one generation. Such as combination

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 Aral

Combination	Generation	PH	HFFB	LFFB	SFBL	FBN	SCY	LY	BN	BW	LP	FL	FU	FE	FS	MIC
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	−1.03
	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	−0.89
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	0.99
	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	0.44
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	−1.26
	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	2.00
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	−1.93
	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	−0.67
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	3.23
	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	−0.89
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	−0.22
	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	−1.42
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	1.12
	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	−1.42
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	−0.45
	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	2.14
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	0.90
	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	−0.53
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	−1.34
	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	1.25
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	1.26
	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	2.31
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	−2.11
	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	0.98
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	1.70
	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	−4.14
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	1.03
	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	1.20
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	−1.88
	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	−0.36

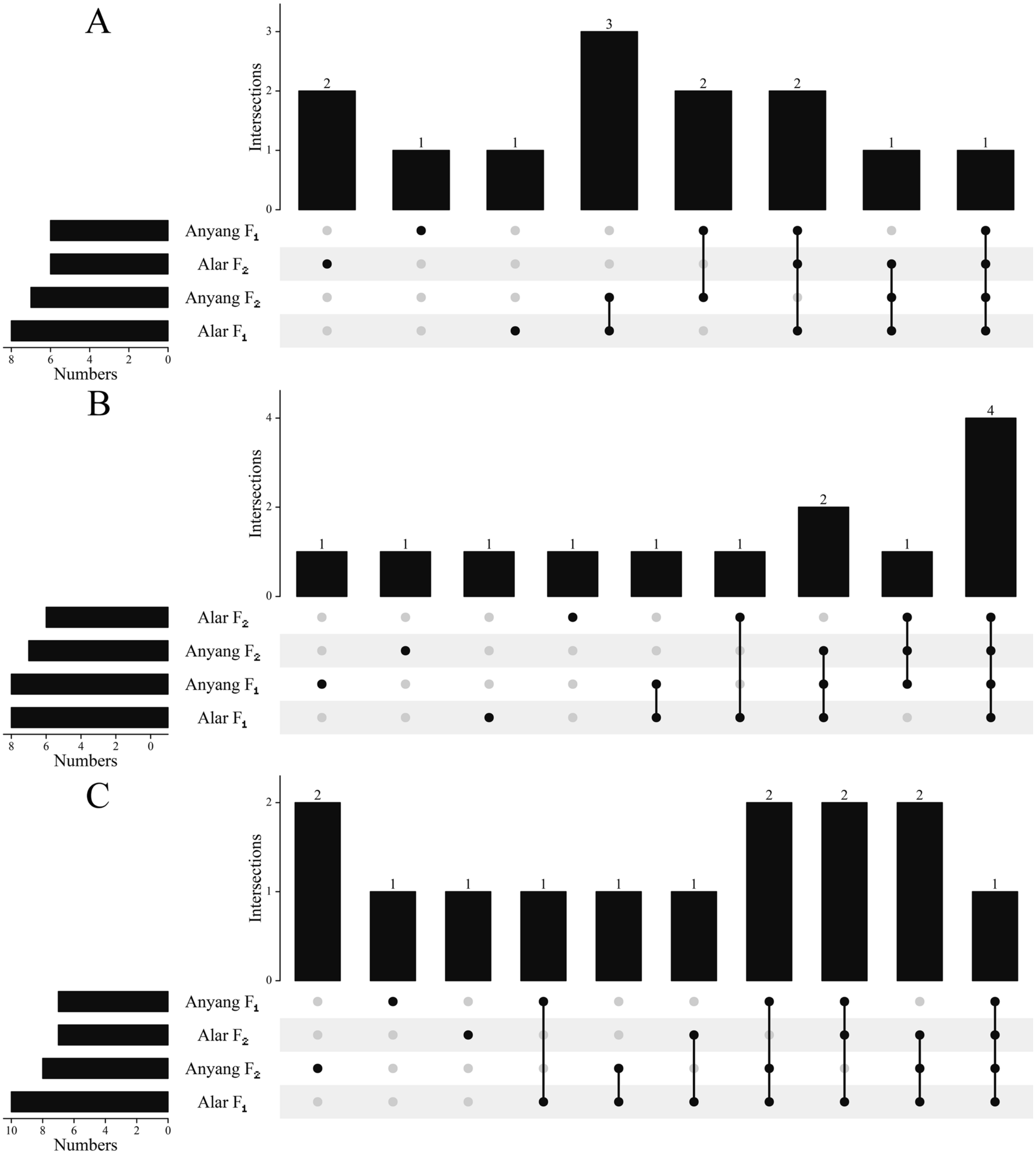

Fig. 1 Upset plot showing the details of the top eight hybrid combinations in BPH (**A**), CH (**B**), and MPH (**C**) for the F_1 and F_2 traits of the two environments. The connection of the black circle in the figure represents the intersection between the different groups, and the number of intersections is correspondingly represented in the upper bar chart

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. Comparatively, combinations 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.

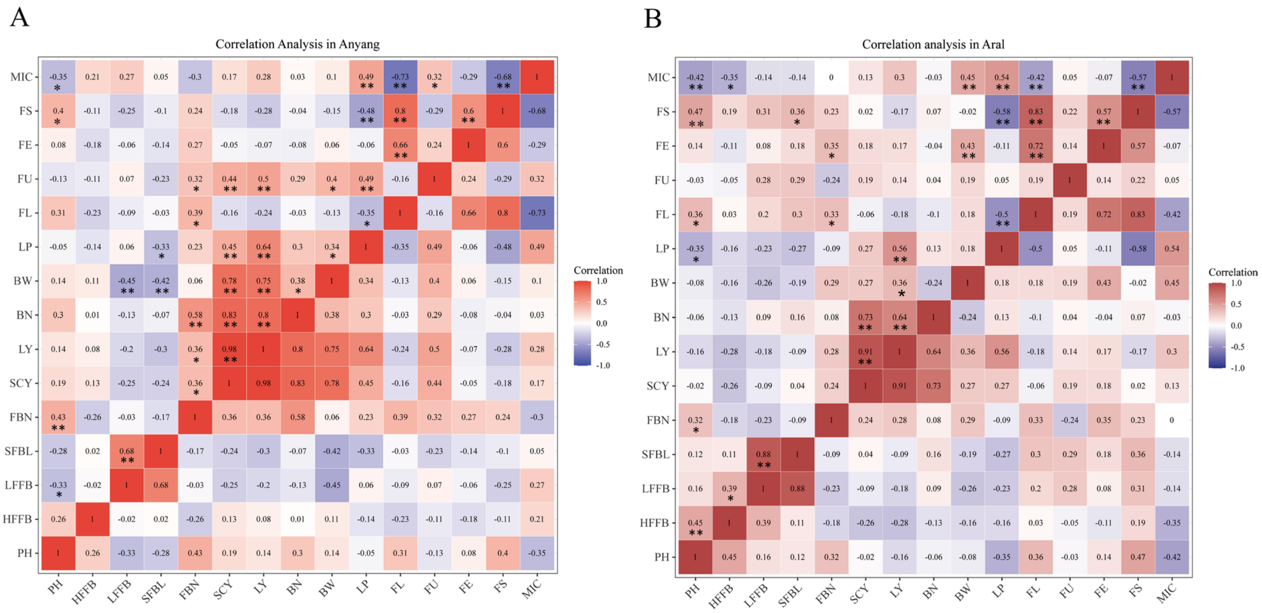

Fig. 2 Correlation analysis of yield, fiber, and agronomic traits in two ecological sites. Correlation analysis among 15 traits in Anyang (**A**) and Aral (**B**).* and** show significant differences at 0.05 and 0.01 levels, respectively

Correlations among various traits in two different cotton belts

The relationship between traits is a dynamic factor in the selection of plant breeding materials. The correlation analysis between agronomic, yield, and fiber quality traits in Anyang was 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 a negative correlation with yield traits. A significant positive correlation between FU and yield was detected. The correlation between yield and agronomic traits was either non-significant negative or positive. Similar results were observed among most of the fiber quality and agronomic traits. Most fiber quality traits including FL, FE, and FS had a positive correlation with each other. However, MIC had a strong negative correlation with FL and FS but a positive correlation with FU. The correlations were undulating among agronomic traits. For instance, PH had a significant negative correlation with LFFB and MIC but had a significant positive with FBN and FS. A significant positive correlation was observed between SFBL and LFFB.

The correlation analysis in Aral revealed SCY had a significant positive correlation with LY and BN whereas LY was positively correlated with BN and BW (Fig. 2B). The correlation of BW was significantly positive for FE and MIC. LP showed a significant negative correlation with FL and FS. In contrast, it had a significant positive correlation with MIC. Among fiber quality traits, FL had a significant positive correlation with FE and FS. MIC had a significant negative relationship with FL and FS. The agronomic traits had shown diverse correlations but few were significant. For instance, PH had an extremely positive correlation with HFFB, FBN, and FL. And PH negatively correlated with LP and MIC. Moreover, SFBL positively correlated with FS. FBN 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 exchange earnings. Genotypes with higher yield and fine fiber are desired in upland cotton. This synchronized improvement of multiple traits in upland cotton demands more crossing, assessment, screening, and useful resources. The utilization of heterosis is the most suitable method to achieve such vast breeding aims. 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 in two cotton belts. Further the potential utilization of F_2 hybrids was screened and discussed to improve cotton production in China.

Parental selection has critical importance in hybrid cotton breeding. However, the identification of potential parents is a laborious job. 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 lines in the future breeding program. Previous studies have already shown 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, GCAs in the majority of parental lines were positive but the values altered with generation. Moreover, yield traits were detected with higher GCA and fiber traits with lower. Previous researches 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 the best GCA for multiple traits in F_1 and 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 the further breeding program to develop elite hybrids. Interestingly, our results showed that the GCA of P4 was improved for LFFB, FBN, LY, BW, LP, and MIC in F_2 as compared with F_1 in both environments. The abrupt increase may be the result of heterogeneous material with different effects in F_2 which probably lead to good adaptation in different 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 the majority of yield traits had strong H^2 and h^2 among different generations and environments (Tables 2 and 3). The traits with high heritability indexes 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 provide a foundation to screen highly dominant materials (Li et al. 2010a). However, combined performance across multiple generations and ecological zones could be an efficient method to identify elite breeding populations.

Estimates of SCA reflect the average performance of a hybrid combination and are mainly produced by the action of dominant or epistatic gene interaction. This non-additive gene action mediates the 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 a particular generation or environment (Soomro et al. 2012; Khan et al. 2015). Our study revealed that the magnitude of SCA varied with the traits, generations, and environments. Interestingly, combinations 9 and 2 had shown positive SCA effects in multiple traits in both F_1 and F_2 generation in two cotton belts, but for combination 3 and 15 in the two environments, the SCA of F_1 and F_2 showed opposite results in multiple traits related to yield, quality, and agronomic traits. This is consistent with previous studies on cotton F_1 hybrid combination with strong performance, and the dominance in F_2 was not necessarily well (Shang et al. 2012) (Tables 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. Besides this, those F_2 hybrid combinations with superior performance in a specific cotton belt would most likely be utilized to improve cotton productivity in such zone. Previous research stated that GCA and SCA were independent and higher GCA does not essentially interlink with higher SCA. Therefore, more emphasises should be on SCA effects rather than the GCA effects of inbred parents during the process of hybrid selection (Yang et al. 2009; Peng et al. 2015; Canavar et al. 2011). Correlation between traits plays a vital role in plant material selection (Liu et al. 2008). Our results showed 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. 2010b). These results enabled improvement in yield-related traits independent of fiber quality traits. Moreover, some agronomic traits showed a significant positive correlation with yield and quality traits in this study. Therefore, these agronomic traits should also be taken into consideration in the 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 the key ways to improve stagnant yield in upland cotton. However, the major challenge is the difficulty of producing F_1 seed through manual emasculation and pollination (Wu et al. 2004) which caused the 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, and the plant architecture, growth stages, and agronomic traits may not have a direct impact on the yield and fiber quality of F_2 generations (Wang et al. 2011; Kong et al. 2017). These unique cotton characteristics provide an opportunity for the 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 in both cotton belts (Fig. 1; Additional file 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 with 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, we systematically evaluated the potential breeding applications of F_2 hybrids by comprehensive comparative analysis of their field performance on yield, quality, and plant architecture-related traits. The combining ability variance and heritability of traits significantly differed across multiple traits in two generations and both environments, suggesting that it is meaningful to select and breed hybrid F_2 generations in upland cotton. The GCA of parents P4 (L28) and P7 (Z98), and the F_1 and F_2 generations of hybrid combination ZB × DT and combination L28 × Z98 in both environments were all outstanding in many traits such as yield, quality, and plant architecture. Therefore, it is feasible to breed cotton F_2 with potential for production and application by synthetically evaluating the yield, quality, plant architecture traits, and environmental adaptability of hybrid cotton F_2 through strict parent selection and in multi-plot experiments for several years.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42397-022-00125-8.

Additional file 1. Level of heterosis altered with the trait, hybrid combination, and generation in Anyang and Aral.

Additional file 2. Details of the top eight hybrid combinations in BPH, CH, and MPH for each trait in different generations and cotton belts.

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Author 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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