



RESEARCH ARTICLE

Assessment of GCA and SCA effects in wheat (*Triticum aestivum* L.) under sodic soil using line × tester mating design

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Abstract

The study utilised a line × tester mating design, crossing twelve diverse female lines with 3 male testers to develop 36 F₁ hybrids, evaluated along with three check varieties. The experiment was laid out in a randomized block design with three replications across two sowing environments: timely (E1) and late (E2) sown, for the study of 12 quantitative traits under sodicity conditions. Analysis of variance revealed highly significant genetic variability among genotypes for all traits in both environments. Combining ability analysis indicated the predominance of non-additive gene action for all studied traits, as specific combining ability (SCA) variance consistently exceeded general combining ability (GCA) variance, supported by high estimates of dominance variance and low narrow-sense heritability. Among parents, lines MP-1358 (for early maturity), UP-3043 (for plant height and grain yield) and DBW-302 (for spike length) were identified as superior general combiners. Tester LBRIL-102 also exhibited positive GCA effects for multiple yield components. Several crosses, notably PBW-821 × LBRIL-102 and GW-509 × LBRIL-102, demonstrated highly significant positive SCA effects for critical yield traits like grain yield per plant and harvest index. The study concludes that genetic expression, particularly of non-additive gene effects, was amplified under late-sown conditions (E2). The overwhelming predominance of non-additive gene action strongly suggests that heterosis breeding is the most promising strategy for genetic improvement of wheat for cultivation in sodic soils. The identified superior general combiners and specific cross combinations provide valuable genetic resources for developing high-yielding, stress-tolerant wheat hybrids.

Keywords: gene action; general combining ability; sodicity tolerance; specific combining ability; wheat

Introduction

Wheat (*Triticum aestivum* L.) is an important member of the Poaceae family and the world's second most important cereal crop after rice, providing nutrition to over 35 % of the global population (1). The crop is widely cultivated across diverse agro-ecological zones, with production often challenged by various abiotic stresses including soil salinity and alkalinity (2). Sodic soils, characterised by high pH and sodium saturation, present significant constraints to wheat cultivation, affecting approximately 6.73 million hectares in India alone (3). These challenging soil conditions necessitate the development of stress-tolerant wheat varieties with enhanced yield

potential and improved adaptability.

Wheat exhibits considerable genetic diversity for stress tolerance traits, making it amenable to improvement through systematic breeding approaches (4). The crop demonstrates both spring and winter growth habits, with facultative types showing intermediate responses to vernalisation requirements (5). Under sodic soil conditions, wheat plants experience multiple stress factors including high pH, sodium toxicity and reduced nutrient availability, which collectively impact plant growth, development and grain yield (6). The development of stress-tolerant cultivars requires comprehensive

understanding of genetic mechanisms governing tolerance traits and yield components under challenging environments.

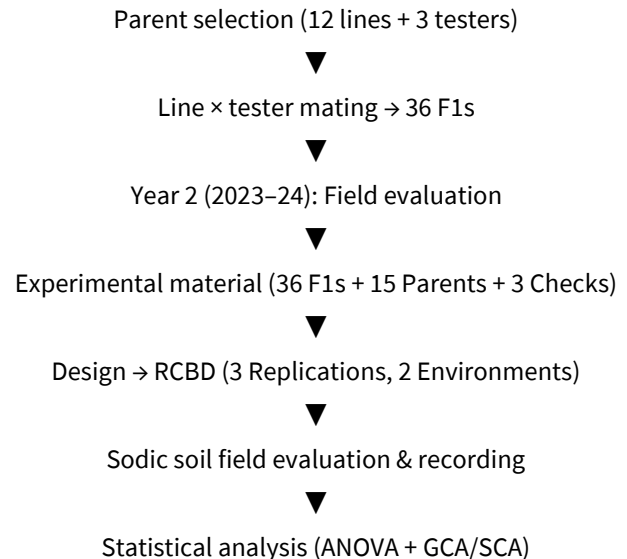
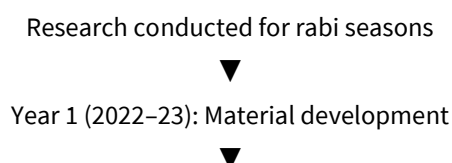
Recent wheat breeding programs have increasingly focused on developing varieties with enhanced stress tolerance, improved yield stability and superior grain quality characteristics (7). The identification of suitable parental combinations based on their combining ability represents a fundamental aspect of efficient breeding strategies (8). General combining ability (GCA) primarily reflects additive genetic effects, while specific combining ability (SCA) captures non-additive genetic variance including dominance and epistatic interactions (9). The line \times tester mating design has emerged as a powerful tool for evaluating combining ability, enabling breeders to assess the breeding potential of diverse genetic materials systematically.

The success of wheat improvement programs under stress conditions depends significantly on identifying parental lines with favourable gene combinations and superior combining ability for target traits (10). Certain genotypes demonstrate exceptional performance in hybrid combinations, producing progeny with enhanced stress tolerance and improved yield characteristics, while others may exhibit poor combining ability despite individual merit (11). Consequently, comprehensive evaluation of both GCA and SCA provides crucial insights into genetic mechanisms underlying trait inheritance and hybrid performance under stress environments.

Materials and Methods

The present investigation was conducted over two consecutive rabi seasons. During the first season (2022–23), the experimental material was developed by selecting 12 genetically diverse female lines (PBW-822, PBW-821, PBW-752, UP-3043, WH-1270, VL-3020, VL-3021, DBW-302, VL-3022, DBW-328, MP-1358 and DBW-332) and 3 male testers (KRL-35, KRL-99 and LBRIL-102) as parents. The pedigree, origin and features of these parental lines are in supplementary Table 1. A line \times tester mating design was employed to generate unique F_1 crosses and data from the 5 plants per replication used for observation. In the following season (2023–24), the field evaluation was carried out at the Main Experiment Station Farm of Acharya Narendra Deva University of Agriculture and Technology, Ayodhya, Uttar Pradesh, India. The experimental material consisting of 36 F_1 crosses, their 15 parental lines and 3 check varieties (DBW-187, NW-1076 and HD-2967) was evaluated in a randomized complete block design (RCBD) with 3 replications across two sowing environments: E1 (timely sown on November 1, 2023) and E2 (late sown on December 1, 2023) under sodic soil conditions. Each plot measured 3 m in length with 25 cm row spacing and 10 cm plant spacing, following standard agronomic practices for sodic soil conditions. Sodic soil has initial pH of 8.6, electrical conductivity (EC) of <4 dS m^{-1} and exchangeable sodium percentage (ESP) of >15 . The soil texture was classified as sandy loam with low organic carbon content (0.38 %), available nitrogen (165.4 kg ha^{-1}), medium available phosphorus (12.8 kg ha^{-1}) and available potassium (218.6 kg ha^{-1}).

Flowchart of all the experimental steps performed during the research:



Phenotypic estimation of quantitative traits

The present investigation involved the study of 12 quantitative traits were recorded on 5 randomly selected plants per plot including plant height, flowering and maturity duration, flag leaf area, spike length, effective tillers per plant, peduncle length, grains per spike, 1000-grain weight, biological yield per plant, grain yield per plant and harvest index.

Statistical analysis

Analysis of variance was performed following combining ability analysis used line \times tester method to estimate GCA and SCA effects.

Results and Discussion

Analysis of variance

The analysis of variance revealed significant genetic diversity among experimental materials under both environmental conditions (Table 1). In E1, highly significant differences were observed among treatments for all 12 traits studied, with mean squares ranging from 2.38 (effective tillers/plant) to 196.14 (plant height). Under delayed sowing conditions (E2), treatment variance was more pronounced, with mean squares reaching 293.41 for plant height, confirming enhanced genetic expression under stress conditions.

The partitioning of treatment variance demonstrated highly significant differences between parents and crosses for most characters. Parent vs. crosses comparison revealed substantial heterotic effects, particularly for plant height (1547.66 in E1, 3228.97 in E2) and biological yield per plant (472.21 in E1, 2251.70 in E2), indicating significant heterosis in F_1 generation. These findings align with previous reports demonstrating the importance of non-additive genetic effects in wheat improvement programs (12, 13), supporting heterosis breeding as a viable strategy for genetic improvement under stress conditions.

Combining ability analysis

The analysis of variance for combining ability (Table 2) provided crucial insights into the genetic architecture underlying trait expression and the relative importance of general versus specific combining ability effects. Line effects were highly significant for all 12 characters in both environments, indicating substantial additive genetic effects among female parents. Tester effects showed variable significance patterns, with most yield components

Table 1. Analysis of variance for 12 characters in line × tester mating design of wheat in E1 and E2

Source	df	Days to 50 % flowering		Days to maturity		Plant height (cm)		Flag leaf area (cm ²)		Effective tillers/Plant		Spike length (cm)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
Replications	2	5.58	17.61	14.90	46.78	63.22	47.74	4.39	4.36	0.41	0.44	0.85	0.67
Treatments	50	13.94**	18.25**	37.67*	22.79**	196.14**	293.41**	19.44**	27.04**	2.38**	3.09**	9.55**	11.84**
Crosses	35	14.67**	13.47**	13.70**	19.55	152.78**	130.95**	19.64**	23.60**	1.50**	1.48**	12.26**	14.64**
Parent	14	6.56	29.87**	9.07	29.18	208.02**	489.90**	20.11**	34.85**	3.09**	5.96**	3.47**	4.98**
Lines (P)	11	5.20	35.35**	5.20	34.12**	251.97**	603.06**	21.93**	38.99**	3.35**	7.38**	2.05**	5.12**
Testers (P)	2	5.26	13.07	3.68	13.92	69.06**	96.41**	3.37**	16.52**	0.75**	1.15**	2.61**	4.47**
L (P) v T (P)	1	24.07	3.17	62.45*	5.43	2.49	32.02**	33.64**	26.00**	4.84**	0.03	20.81**	4.42**
Crosses vs Parents	1	91.74**	22.96**	1277.09**	46.78	1547.66**	3228.97**	2.86	38.16**	23.24**	18.83**	0.07	9.63**
Error	100	6.57	8.05	17.22	20.04	7.75	6.95	0.63	0.68	0.07	0.08	0.18	0.21
Total	152	9.63	11.53	25.67	21.30	70.45	101.72	6.86	9.40	0.83	1.07	3.27	4.04

Source	df	Grains/Spike		Peduncle length (cm)		1000 grain weight (g)		Biological yield/Plant (g)		Harvest index (%)		Grain yield/Plant (g)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
Replications	2	17.20	26.42	3.97	1.13	9.86	1.55	12.66	0.39	9.31	0.52	1.68	0.02
Treatments	50	96.61**	204.27**	21.06**	55.58**	31.57**	54.26**	49.62**	161.37**	109.57**	240.95**	22.89**	54.47**
Crosses	35	72.98**	114.41**	20.88**	61.74**	41.68**	50.11**	49.82**	137.01**	104.50**	297.29**	17.30**	49.95**
Parent	14	145.00**	334.49**	19.78**	34.10**	3.75**	56.30**	18.93**	72.98**	97.76**	76.74**	22.12**	21.89**
Lines (P)	11	77.47**	311.24**	24.54**	41.61**	4.23**	64.37**	6.15**	26.18**	10.91**	46.96**	2.44**	4.14**
Testers (P)	2	52.07**	213.72**	3.50**	7.68**	0.91	2.05	5.85**	2.53	11.26**	41.90**	0.61**	2.49**
L (P) v T (P)	1	1073.70**	831.83**	0.00	4.32**	4.12**	76.10**	185.70**	728.75**	1226.07**	473.95**	281.73**	256.02**
Crosses vs Parents	1	245.96**	1526.35**	45.24**	140.75**	67.13**	170.92**	472.21**	2251.70**	452.64**	567.91**	229.37**	668.93**
Error	100	3.27	3.35	0.71	0.79	1.63	1.87	1.83	2.00	1.41	1.84	0.25	0.35
Total	152	34.16	69.74	7.45	18.82	11.58	19.10	17.69	54.41	37.09	80.48	7.71	18.15

*, ** significant at 5 % and 1 % level, respectively. (Note: E1 = timely sown, E2 = late sown, df= degree of freedom).

Table 2. Analysis of variance for combining ability for 12 characters in line × tester mating design of wheat in E1 and E2

Source	d.f.	Days to 50 % flowering		Days to maturity		Plant height (cm)		Flag leaf area (cm ²)		Effective tillers/Plant		Spike length (cm)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
Replications	2	3.78	8.09	78.03	39.91	32.02	41.57	2.92	3.16	0.34	0.39	0.83	0.88
Crosses	35	14.67**	13.47**	13.70**	19.55**	152.78**	130.95**	19.64**	23.60**	1.50**	1.48**	12.26**	14.64**
Lines (c)	11	34.90**	23.48**	33.46**	53.58**	135.97**	190.92**	57.65**	61.28**	3.45**	3.42**	34.79**	40.49**
Testers (c)	2	5.60	3.23	6.57	3.97	431.40**	264.71**	9.37**	20.18**	0.34**	0.34**	6.10**	7.82**
L × T (c)	22	5.39	9.40	4.47	3.95	135.85**	88.80**	1.57**	5.06**	0.63**	0.62**	1.55**	2.34**
Error	70	6.78	8.67	16.99	19.13	7.77	6.32	0.65	0.72	0.07	0.08	0.18	0.21
Total	107	9.81	10.23	17.05	19.65	55.65	47.74	6.90	8.25	0.55	0.55	4.14	4.94

Source	d.f.	Grains/Spike		Peduncle length (cm)		1000 grain weight (g)		Biological yield/Plant (g)		Harvest index (%)		Grain yield/Plant (g)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
Replications	2	15.64	38.48	3.46	2.24	6.75	1.22	10.08	0.74	7.58	0.47	1.28	0.00
Crosses	35	72.98**	114.41**	20.88**	61.74**	41.68**	50.11**	49.82**	137.01**	104.50**	297.29**	17.30**	49.95**
Lines (c)	11	193.25**	234.01**	59.60**	90.97**	95.27**	94.52**	84.01**	281.46**	242.38**	706.64**	42.05**	96.81**
Testers (c)	2	51.32**	131.75**	9.83**	63.63**	26.64**	36.05**	63.65**	64.53**	18.98**	4.53**	0.98**	4.96**
L × T (c)	22	14.82**	53.03**	2.53**	46.95**	16.26**	29.19**	31.47**	71.37**	43.33**	119.23**	6.40**	30.61**
Error	70	3.00	1.90	0.68	0.71	1.56	1.61	1.88	2.07	1.51	2.07	0.28	0.42
Total	107	26.13	39.39	7.34	20.70	14.78	17.47	17.72	46.18	35.31	98.61	5.87	16.61

*, ** significant at 5 % and 1 % level, respectively. (Note: E1 = timely sown, E2 = late sown, df= degree of freedom).

Table 4. Estimates of specific combining ability effects of crosses for 12 characters of wheat in E1 and E2

Sl. No.	Crosses	Days to 50 % flowering		Days to maturity		Plant height (cm)		Flag leaf area (cm ²)		Effective tillers/Plant		Spike length (cm)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
1	PBW-822 × KRL-35	0.67	-1.15	0.53	0.53	-9.87 **	-7.82 **	-0.18	0.51	-0.36 *	-0.36 *	-0.04	-0.09
2	PBW-822 × KRL-99	1.19	1.72	1.30	0.93	5.07 **	4.64 **	0.68	0.73	0.21	0.21	-0.34	-0.27
3	PBW-822 × LBRIL-102	-1.86	-0.57	-1.84	-1.46	4.80 **	3.18 *	-0.50	-1.23 *	0.15	0.15	0.38	0.35
4	PBW-821 × KRL-35	-0.15	0.21	-0.41	0.11	-0.48	0.67	0.27	0.75	-0.31	-0.30	0.10	0.05
5	PBW-821 × KRL-99	0.61	1.71	0.77	0.48	5.61 **	4.67 **	0.36	0.37	0.32 *	0.32	-0.71 **	-0.64 *
6	PBW-821 × LBRIL-102	-0.46	-1.92	-0.36	-0.59	-5.12 **	-5.34 **	-0.63	-1.12 *	-0.02	-0.02	0.61 *	0.59 *
7	PBW-752 × KRL-35	0.75	1.56	0.38	0.41	-1.22	-2.70	-1.03 *	-3.16 **	1.26 **	1.25 **	2.01 **	1.93 **
8	PBW-752 × KRL-99	1.17	-1.37	1.13	1.38	6.17 **	9.18 **	0.98 *	1.84 **	-0.41 *	-0.41 *	-0.43	-0.35
9	PBW-752 × LBRIL-102	-1.92	-0.19	-1.51	-1.79	-4.95 **	-6.48 **	0.04	1.32 **	-0.85 **	-0.84 **	-1.59 **	-1.58 **
10	UP-3043 × KRL-35	1.80	-0.17	1.40	-0.41	-3.77 *	-2.48	0.90	0.64	-0.41 *	-0.41 *	-0.37	-0.41
11	UP-3043 × KRL-99	-0.88	0.01	-0.53	0.84	2.13	-1.72	-0.09	0.16	0.33 *	0.32	0.22	0.28
12	UP-3043 × LBRIL-102	-0.92	0.15	-0.88	-0.43	1.64	4.19 **	-0.81	-0.80	0.09	0.09	0.15	0.13
13	WH-1270 × KRL-35	-0.56	0.92	-0.11	-0.78	3.43 *	3.62 *	0.55	1.18 *	-0.10	-0.10	-0.18	-0.22
14	WH-1270 × KRL-99	0.46	-1.18	-0.10	-1.32	0.51	-1.86	-0.49	-0.49	-0.40 *	-0.40 *	0.00	0.07
15	WH-1270 × LBRIL-102	0.10	0.26	0.20	2.10	-3.94 *	-1.76	-0.06	-0.69	0.50 **	0.50 **	0.17	0.15
16	VL-3020 × KRL-35	-1.85	-2.41	-1.50	-0.28	0.23	1.22	0.05	-0.63	0.04	0.04	-0.42	-0.32
17	VL-3020 × KRL-99	0.73	-0.53	0.79	0.51	4.63 **	-0.17	-0.98 *	-0.20	-0.15	-0.15	0.37	-0.63 *
18	VL-3020 × LBRIL-102	1.12	2.94	0.71	-0.23	-4.86 **	-1.05	0.93 *	0.82	0.12	0.11	0.05	0.95 **
19	VL-3021 × KRL-35	-1.04	-1.32	-1.34	-0.19	-1.40	3.58 *	-0.08	0.46	0.61 **	0.60 **	-0.28	0.09
20	VL-3021 × KRL-99	0.68	3.40 *	0.63	-0.07	-1.06	-7.65 **	-0.35	-1.14 *	-0.33 *	-0.33	0.14	0.01
21	VL-3021 × LBRIL-102	0.36	-2.09	0.71	0.26	2.46	4.08 **	0.44	0.68	-0.28	-0.27	0.13	-0.10
22	DBW-302 × KRL-35	-0.13	0.10	0.09	-1.06	-8.88 **	-1.71	-1.27 **	-0.45	0.12	0.12	0.02	0.18
23	DBW-302 × KRL-99	-1.38	0.04	-1.47	-0.69	5.21 **	4.46 **	0.14	0.82	-0.22	-0.23	0.64 *	0.60 *
24	DBW-302 × LBRIL-102	1.51	-0.14	1.38	1.75	3.67 *	-2.75	1.13 *	-0.37	0.11	0.10	-0.66 **	-0.78 **
25	GW-509 × KRL-35	-0.12	-0.52	-0.19	0.54	8.51 **	1.13	-0.06	-0.82	-0.21	-0.21	-0.44	-0.48
26	GW-509 × KRL-99	-0.43	-0.46	-0.30	-0.49	-4.90 **	1.96	0.20	-0.46	0.09	0.09	0.51 *	0.57 *
27	GW-509 × LBRIL-102	0.55	0.98	0.49	-0.05	-3.61 *	-3.09 *	-0.14	1.27 *	0.12	0.12	-0.07	-0.09
28	DBW-328 × KRL-35	1.22	2.06	1.43	1.23	4.46 **	3.58 *	0.15	-0.07	-0.27	-0.26	-0.47	-0.37
29	DBW-328 × KRL-99	-1.09	-1.35	-1.19	-0.50	-4.82 **	-3.58 *	0.00	1.10 *	0.15	0.15	0.56 *	1.25 **
30	DBW-328 × LBRIL-102	-0.13	-0.70	-0.24	-0.73	0.35	0.00	-0.15	-1.03 *	0.11	0.11	-0.10	-0.88 **
31	MP-1358 × KRL-35	-1.33	-0.15	-1.10	0.08	1.80	-0.76	0.72	0.87	-0.21	-0.22	-0.01	-0.50
32	MP-1358 × KRL-99	0.85	0.55	0.59	0.23	-12.19 **	-8.59 **	-0.23	-1.39 **	0.33 *	0.33 *	-0.39	0.49
33	MP-1358 × LBRIL-102	0.48	-0.40	0.51	-0.32	10.39 **	9.35 **	-0.49	0.52	-0.12	-0.12	0.39	0.01
34	DBW-332 × KRL-35	0.73	0.88	0.80	-0.19	7.20 **	1.65	-0.01	0.72	-0.16	-0.15	0.08	0.13
35	DBW-332 × KRL-99	-1.90	-2.54	-1.61	-1.29	-6.36 **	-1.35	-0.23	-1.34 **	0.09	0.08	-0.60 *	-1.39 **
36	DBW-332 × LBRIL-102	1.17	1.67	0.81	1.48	-0.83	-0.31	0.24	0.62	0.07	0.07	0.52 *	1.25 **
	SE (SCA effects)	1.503	1.700	2.380	2.525	1.609	1.451	0.465	0.488	0.158	0.168	0.245	0.266
	SE (best SCA effects)	2.126	2.404	3.365	3.571	2.276	2.052	0.658	0.691	0.223	0.237	0.347	0.376

Sl. No.	Crosses	Grains/Spike		Peduncle length (cm)		1000 grain weight (g)		Biological yield/Plant (g)		Harvest index (%)		Grain yield/Plant (g)	
		E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
1	PBW-822 × KRL-35	-4.63 **	-7.53 **	-0.26	0.70	0.17	-1.70 *	-0.54	-1.83 *	-0.17	4.26 **	-0.22	1.17 **
2	PBW-822 × KRL-99	3.00 **	1.63 *	-0.41	-3.11 **	-0.50	2.77 **	1.21	1.73 *	-1.50 *	-7.27 **	-0.28	-2.67 **
3	PBW-822 × LBRIL-102	1.63	5.90 **	0.67	2.41 **	0.33	-1.07	-0.67	0.11	1.67 *	3.01 **	0.50	1.49 **
4	PBW-821 × KRL-35	-0.16	-3.14 **	-0.29	-3.13 **	1.42	2.98 **	2.38 **	-0.51	-3.91 **	-3.35 **	-0.67 *	-1.43 **
5	PBW-821 × KRL-99	2.31 *	2.28 **	-0.47	4.42 **	1.61 *	1.13	2.80 **	5.87 **	-2.97 **	-4.01 **	-0.16	0.54
6	PBW-821 × LBRIL-102	-2.15 *	0.86	0.76	-1.29 **	-3.03 **	-4.11 **	-5.17 **	-5.36 **	6.88 **	7.37 **	0.83 **	0.89 *
7	PBW-752 × KRL-35	0.07	1.90 *	-0.33	2.05 **	3.83 **	5.92 **	1.04	-0.13	-2.45 **	-1.13	-0.59	-0.28
8	PBW-752 × KRL-99	-0.65	-1.14	-0.40	-1.71 **	-1.76 *	-3.24 **	-0.30	0.43	2.59 **	3.81 **	0.84 **	1.29 **
9	PBW-752 × LBRIL-102	0.58	-0.77	0.73	-0.34	-2.06 **	-2.68 **	-0.74	-0.29	-0.14	-2.68 **	-0.25	-1.01 **
10	UP-3043 × KRL-35	0.96	-1.78 *	-0.34	-0.97 *	0.25	-1.23	3.73 **	0.99	-2.97 **	-1.03	0.33	0.30
11	UP-3043 × KRL-99	0.10	-0.26	-0.53	-0.89	-0.01	0.37	-4.17 **	-0.33	2.28 **	-0.78	-1.01 **	-0.93 *
12	UP-3043 × LBRIL-102	-1.06	2.03 *	0.88	1.86 **	-0.23	0.86	0.44	-0.66	0.70	1.81 *	0.68 *	0.64
13	WH-1270 × KRL-35	1.42	-4.43 **	0.10	-0.24	0.44	1.34	-2.12 **	-0.73	0.98	1.01	-0.69 *	0.24
14	WH-1270 × KRL-99	-0.64	0.47	1.58 **	0.01	-0.04	0.70	0.58	1.27	0.40	2.32 **	0.32	1.08 **
15	WH-1270 × LBRIL-102	-0.78	3.96 **	-1.68 **	0.22	-0.40	-2.04 **	1.54	-0.54	-1.38	-3.33 **	0.37	-1.32 **
16	VL-3020 × KRL-35	-1.72	1.80 *	-0.33	-7.69 **	0.30	-1.13	-5.18 **	-4.96 **	7.74 **	4.81 **	1.02 **	-0.15
17	VL-3020 × KRL-99	-0.74	-0.08	-0.46	11.99 **	-4.36 **	-4.19 **	0.70	-0.10	-1.93 **	-6.52 **	-0.25	-2.56 **
18	VL-3020 × LBRIL-102	2.46 *	-1.72 *	0.79	-4.30 **	4.06 **	5.31 **	4.48 **	5.06 **	-5.82 **	1.71 *	-0.77 *	2.71 **
19	VL-3021 × KRL-35	0.76	6.15 **	0.40	0.14	-2.14 **	-1.61 *	-2.55 **	-3.91 **	2.03 **	-2.84 **	-0.12	-2.48 **
20	VL-3021 × KRL-99	0.00	-1.27	0.11	0.82	0.63	-1.91 *	0.48	1.62	-2.93 **	-4.94 **	-1.03 **	-1.63 **
21	VL-3021 × LBRIL-102	-0.76	-4.88 **	-0.51	-0.96	1.50 *	3.52 **	2.07 *	2.29 **	0.89	7.78 **	1.15 **	4.11 **
22	DBW-302 × KRL-35	2.03 *	0.81	0.94	3.42 **	1.69 *	2.30 **	0.15	-1.01	1.90 **	1.58	0.93 **	0.60
23	DBW-302 × KRL-99	-0.94	-5.05 **	0.84	-2.78 **	0.21	0.04	0.86	1.58	1.14	7.61 **	0.79 *	4.33 **
24	DBW-302 × LBRIL-102	-1.09	4.24 **	-1.78 **	-0.64	-1.90 **	-2.34 **	-1.01	-0.57	-3.03 **	-9.19 **	-1.72 **	-4.94 **
25	GW-509 × KRL-35	-0.80	-0.84	0.32	0.67	-3.46 **	-3.22 **	-1.62 *	7.70 **	-0.22	-9.36 **	-0.48	-2.63 **
26	GW-509 × KRL-99	-1.33	1.81 *	0.51	-0.34	1.82 *	1.65 *	-4.18 **	-14.44 **	-0.92	2.65 **	-1.46 **	-2.72 **
27	GW-509 × LBRIL-102	2.13 *	-0.97	-0.82	-0.32	1.64 *	1.57 *	5.80 **	6.73 **	1.14	6.70 **	1.94 **	5.35 **
28	DBW-328 × KRL-35	-0.37	5.02 **	-0.32	2.73 **	-2.86 **	-3.58 **	1.72 *	0.53	-0.83	3.47 **	0.28	2.11 **
29	DBW-328 × KRL-99	0.27	-2.19 **	-0.45	-3.51 **	2.48 **	2.82 **	0.80	1.53	0.02	0.65	0.27	0.72
30	DBW-328 × LBRIL-102	0.10	-2.82 **	0.77	0.78	0.38	0.76	-2.53 **	-2.05 *	0.81	-4.12 **	-0.55	-2.83 **
31	MP-1358 × KRL-35	3.06 **	2.15 **	-0.35	0.28	-0.33	0.08	-0.21	-1.36	-5.25 **	-3.20 **	-2.32 **	-2.02 **
32	MP-1358 × KRL-99	-3.90 **	-1.98 *	-0.47	-2.37 **	0.21	0.18	0.93	1.65 *	1.87 **	1.42	1.11 **	1.16 **
33	MP-1358 × LBRIL-102	0.84	-0.17	0.82	2.09 **	0.12	-0.26	-0.71	-0.29	3.38 **	1.78 *	1.21 **	0.86 *
34	DBW-332 × KRL-35	-0.61	-0.12	0.47	2.05 **	0.68	-0.15	3.22 **	5.22 **	3.16 **	5.77 **	2.54 **	4.57 **
35	DBW-332 × KRL-99	2.52 *	5.79 **	0.15	-2.53 **	-0.27	-0.32	0.27	-0.80	1.95 **	5.06 **	0.86 **	1.39 **
36	DBW-332 × LBRIL-102	-1.91	-5.67 **	-0.62	0.49	-0.41	0.47	-3.49 **	-4.42 **	-5.10 **	-10.83 **	-3.40 **	-5.96 **
	SE (SCA effects)	1.000	0.797	0.477	0.488	0.721	0.733	0.793	0.830	0.709	0.831	0.308	0.373
	SE (best SCA effects)	1.415	1.127	0.675	0.690	1.019	1.037	1.121	1.174	1.003	1.175	0.435	0.528

*, ** significant at 5 % and 1 % level, respectively. (Note: E1 = timely sown, E2 = late sown).

most morphological and yield traits, including plant height (2.63 in E1, 2.33 in E2), flag leaf area (0.57 in E1, 0.79 in E2) and biological yield per plant (1.54 in E1, 1.08 in E2). The LBRIL-102 emerged as an outstanding male parent with favourable effects across multiple trait categories, indicating its broad utility in breeding programs. The identification of these superior general combiners provides valuable insights for parent selection strategies in future breeding initiatives.

Specific combining ability effects

The analysis revealed significant variation among 36 crosses for all traits (Table 4). Several crosses demonstrated exceptional SCA effects for yield-related traits. The PBW-821 × LBRIL-102 showed outstanding grain yield per plant SCA effects (0.83 in E1, 0.89 in E2) and harvest index performance (6.88 in E1, 7.37 in E2). The GW-509 ×

LBRIL-102 exhibited remarkable SCA effects for grain yield per plant (1.94 in E1, 5.35 in E2) and biological yield per plant (5.80 in E1, 6.73 in E2).

The larger values of specific combining ability effects emphasise the critical importance of evaluating specific cross combinations rather than relying solely on parental performance (18, 19). The superior SCA effects observed in crosses like PBW-821 × LBRIL-102 and GW-509 × LBRIL-102 suggest complementary gene action between divergent parental genotypes, resulting in transgressive segregation and hybrid vigour (20). These findings support the hypothesis that genetic diversity among parents enhances the probability of obtaining superior hybrid combinations. The identification of specific high-performing cross combinations provides immediate targets for hybrid development programs while

Table 5. Components of variance, degree of dominance, additive and dominance components and heritability in narrow sense for 12 characters of wheat under timely (E1) and late sown (E2) environments

Components	Days to 50 % flowering		Days to maturity		Plant height (cm)		Flag leaf area (cm ²)		Effective tillers/Plant		Spike length (cm)	
	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
COV (HS)	0.15	0.064	0.15	0.246	0.27	0.66	0.28	0.29	0.01	0.01	0.17	0.19
COV (FS)	2.40	0.932	1.15	0.280	74.75	56.39	6.55	8.50	0.43	0.42	4.15	4.98
σ^2A	0.293	0.128	0.291	0.491	0.533	1.33	0.569	0.292	0.027	0.014	0.337	0.194
σ^2D	0.46	0.245	4.17	5.060	42.69	27.49	0.31	1.45	0.19	0.18	0.46	0.71
σ^2g (GCA)	0.15	0.064	0.15	0.246	0.27	0.66	0.28	0.58	0.01	0.03	0.17	0.39
σ^2s (SCA)	0.46	0.245	4.17	5.060	42.69	27.49	0.31	1.45	0.19	0.18	0.46	0.71
DOD	1.26	1.38	3.79	3.21	8.95	4.55	0.73	2.23	2.60	3.64	1.17	1.91
Predictability ratio	0.387	0.34	0.065	0.09	0.012	0.05	0.650	0.168	0.129	0.070	0.424	0.215
NSH (%)	2.77	1.21	1.35	1.95	0.54	1.73	7.31	2.92	3.61	1.83	6.83	3.31

Components	Grains/Spike		Peduncle length (cm)		1000 grain weight (g)		Biological yield/Plant (g)		Harvest index (%)		Grain yield/Plant (g)	
	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2	E1	E2
COV(HS)	0.92	0.97	0.29	0.23	0.40	0.33	0.29	1.03	0.96	2.80	0.17	0.30
COV(FS)	25.07	43.00	6.90	21.46	13.63	16.23	18.41	42.58	30.46	83.17	4.88	13.66
σ^2A	1.832	1.93	0.578	0.233	0.801	0.330	0.578	1.034	1.926	2.803	0.343	0.305
σ^2D	3.94	17.04	0.62	15.41	4.90	9.19	9.86	23.10	13.94	39.05	2.04	10.06
σ^2g (GCA)	0.92	0.97	0.29	0.47	0.40	0.66	0.29	2.07	0.96	5.61	0.17	0.61
σ^2s (SCA)	3.94	17.04	0.62	15.41	4.90	9.19	9.86	23.10	13.94	39.05	2.04	10.06
DOD	1.47	2.97	1.03	8.14	2.47	5.28	4.13	4.73	2.69	3.73	2.44	5.75
Predictability ratio	0.317	0.10	0.484	0.015	0.140	0.035	0.055	0.043	0.121	0.067	0.144	0.029
NSH (%)	5.74	3.31	6.77	0.64	3.91	1.22	2.05	1.47	3.76	2.00	4.16	1.13

NSH =narrow sense heritability, DOD=degree of dominance, E1 = timely sown, E2 = late sown.

establishing a foundation for future breeding initiatives.

Genetic variance components

Analysis of variance revealed that dominance genetic variance (σ^2D) was substantially larger than additive genetic variance (σ^2A) for all 12 traits in both environments (E1 and E2) (Table 5). The relative contribution of these variances was quantified by the dominance-to-additive variance ratio (σ^2D/σ^2A). This ratio was exceptionally high for morphological and yield-related traits. For instance, plant height exhibited a pronounced ratio of 80.1 in E1 and 20.7 in E2, indicating a very strong dominance effect governing its inheritance.

This majority of non-additive gene action was further corroborated by the comparison of variance components from the line \times tester analysis. The variance due to SCA consistently exceeded the variance due to GCA for every character. The SCA variance to GCA variance ratio ranged from 1.1 to 158.5 across the traits and environments. These results unanimously confirm that non-additive (dominance and epistasis) genetic effects play a predominant role in the inheritance of the quantitative traits evaluated in this study. The enhanced expression of dominance effects under stress conditions (E2) indicates that heterotic combinations become more valuable under challenging environments (21). This pattern suggests that hybrid breeding approaches are particularly suitable for developing wheat varieties adapted to sodic soil conditions, where environmental stress amplifies the relative importance of non-additive genetic effects (22). The environment-specific SCA variations observed emphasise the necessity of multi-location testing in breeding programs targeting stress tolerance.

The low narrow-sense heritability estimates across all characters indicate limited potential for genetic gains through conventional

selection methods (23). These findings strongly support investment in hybrid breeding technology as the most efficient approach for wheat improvement under sodic soil conditions (24).

Proportional contribution of lines and testers

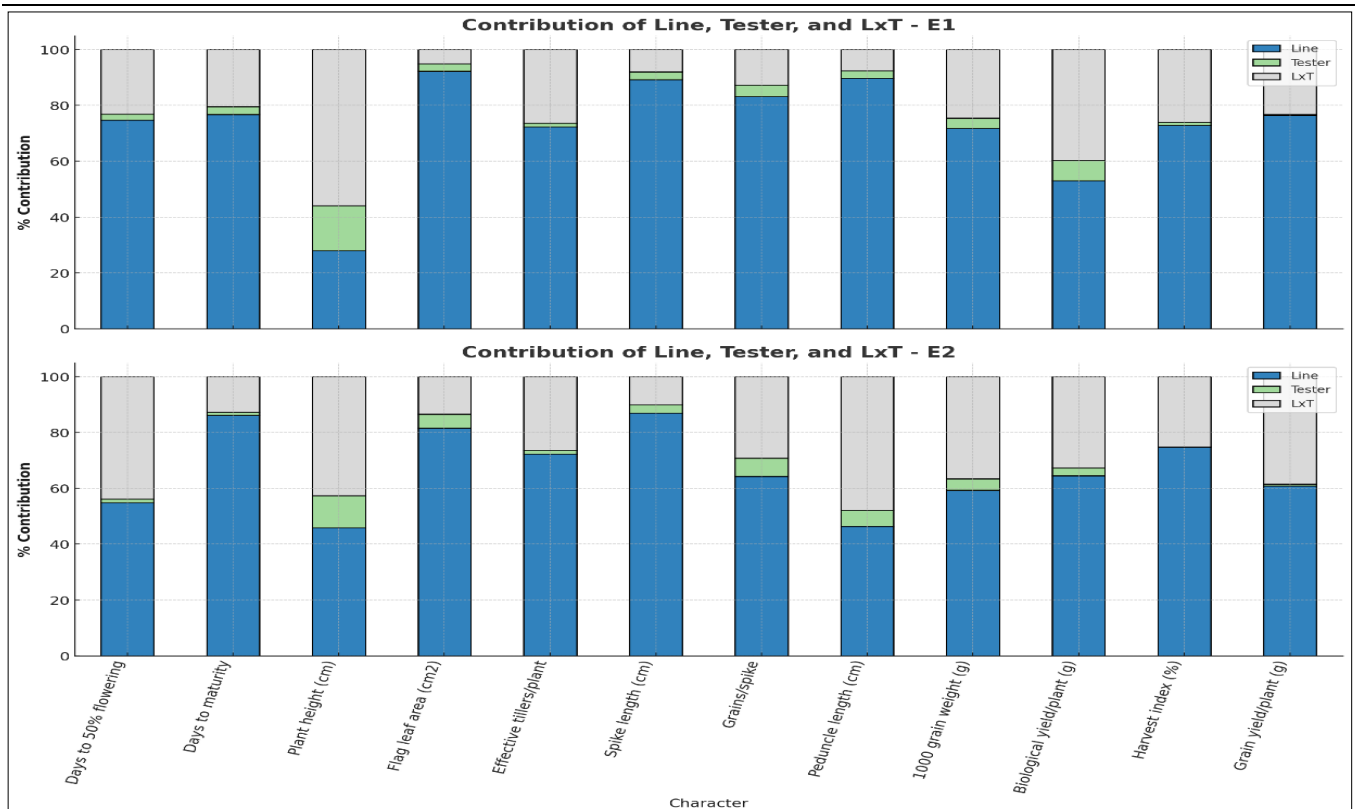
The proportional contribution of lines, testers and their interactions to total variance is presented in Table 6. Lines contributed the maximum share for most traits, particularly days to 50 % flowering, days to maturity, flag leaf area, spike length, effective tillers and harvest index, indicating predominance of additive gene action (Fig. 1). The proportional contribution analysis revealed that line effects contributed the largest proportion of total variance for most traits, indicating the primary importance of female parent selection (25). In contrast, line \times tester interactions contributed more to plant height, peduncle length, 1000-grain weight and grain yield, reflecting the role of non-additive gene action. However, the substantial line \times tester interactions for yield-related traits emphasise that hybrid performance cannot be predicted solely from parental GCA effects, necessitating comprehensive test cross evaluation programs (26).

Conclusion

The present study demonstrates that among parental genotypes, MP-1358, UP-3043 and DBW-302 represent superior general combiners for yield and related traits under sodic soil conditions. The crosses PBW-821 \times LBRIL-102, GW-509 \times LBRIL-102 and VL-3021 \times LBRIL-102 exhibited exceptional specific combining ability effects, indicating their potential for commercial hybrid development. The predominant non-additive gene action observed across all traits strongly supports heterosis breeding as the optimal

Table 6. Proportional contribution of lines, testers and their interactions to total variance in a set of line × tester crosses of wheat

Characters	Environments	Contribution		
		% Contribution	% Contribution	% Contribution
		(Line)	(Tester)	(L × T)
Days to 50 % flowering	E1	74.75	2.18	23.07
	E2	54.78	1.37	43.85
Days to maturity	E1	76.75	2.74	20.51
	E2	86.15	1.16	12.69
Plant height (cm)	E1	27.97	16.14	55.89
	E2	45.82	11.55	42.62
Flag leaf area (cm ²)	E1	92.25	2.73	5.02
	E2	81.63	4.89	13.49
Effective tillers/Plant	E1	72.25	1.3	26.45
	E2	72.3	1.31	26.39
Spike length (cm)	E1	89.19	2.84	7.97
	E2	86.92	3.05	10.03
Grain/Spike	E1	83.22	4.02	12.76
	E2	64.28	6.58	29.14
Peduncle length (cm)	E1	89.7	2.69	7.61
	E2	46.31	5.89	47.8
1000 grain weight (g)	E1	71.83	3.65	24.51
	E2	59.28	4.11	36.61
Biological yield per plant (g)	E1	52.99	7.3	39.71
	E2	64.57	2.69	32.74
Harvest index (%)	E1	72.9	1.04	26.07
	E2	74.7	0.09	25.21
Grain yield/Plant (g)	E1	76.41	0.32	23.26
	E2	60.91	0.57	38.52

**Fig. 1.** Proportional contribution of lines, testers and their interactions to total variance in a set of line × tester crosses of wheat.

strategy for wheat improvement under stress conditions. These findings provide valuable genetic resources for developing high-yielding, stress-tolerant wheat hybrids adapted to sodic soil cultivation. The comprehensive understanding of combining ability patterns established through this research offers a robust foundation for advancing wheat breeding programs targeting challenging environmental conditions. Validation of promising crosses through multilocation trials or molecular characterisation can be helpful in the identification of superior hybrids under stress condition.

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Authors' contributions

AKG carried out the trial and drafted the manuscript. RG contributed to data collection. MA helped in data interpretation. PG participated in the study design and assisted with statistical analysis. GM contributed to experimental setup and data acquisition. SKV helped with data tabulation. AS contributed to sequence validation and reviewed the manuscript. RKY and SKY participated in the design of the study and contributed to manuscript revision. PS conceived the study, participated in its design, coordination and supervised the overall project. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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