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ANALYZING COMBINING ABILITY AND HETEROSIS OF THERMO-PHOTO SENSITIVE GENIC MALE STERILE WHEAT LINES FOR HYBRID DEVELOPMENT

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ABSTRACT

This study was conducted to identify desirable wheat germplasm for superior hybrid cross combinations through 1) identifying the best parents with high combining ability (CA) and 2) estimating heterosis effects. Two thermo-photo-sensitive-genic-male-sterile lines (K456s and K78s) as female parents and 60 restorer lines as males were crossed according to line × tester hybridization method. The observed variation for most of the nine studied characters and <1 ratio for general (G)/specific (S) CA suggested governance of non-additive gene action. The GCA for K456s was higher than K78s in six out of nine characters, while restorers 2016Y_2-2776 and 2016Y_2-4117 had the highest in five characters. The crosses K78s/R31 and K456s/R2 had highest positive SCA values in five and six characters, respectively. The crosses K78s/R43 and K456s/R21 had the overall highest significant positive heterosis estimates for the best cross with respect to yield plant^{-1}and has the potential for utilization in hybrid wheat breeding program.

Keywords: Combining ability, heterosis, hybrid wheat, TPSGMS, traits improvement

INTRODUCTION

Wheat is the most widely grown and consumed cereal food crop in the world. A current annual production level is more than 651 million tons on a total production area of 217 million hectares. By the year 2050, the world population is estimated to be 9 billion and the demand for wheat will exceed 900 million tons (Tadesse et al., 2013). Hybrid wheat is being recognized as a preferred approach to improve wheat yield. The application of hybrid wheat will greatly increase the food production and make significant contribution to food security in the wake of population increase, climate change associated threats and diminishing natural resources. During 2009 to 2012，the new wheat hybrids were grown on about 66,700 hectares for demonstration with the average yield increase of 15.7 % in 11 provinces in China (Zhao, 2013).

Male sterility is an essential trait in hybrid seed production for self-pollinated crops like wheat. The use of cytoplasmic male sterile lines (CMS) or thermo photo sensitive genic male sterile (TPSGMS) line as female parent are preferred in wheat hybrid seed production. The TPSGMS lines are characterized by low-temperature and short-day induced sterility, while high-temperature and long-day induced fertility. The two line system using TPSGMS lines does not need maintainer lines and a wider restorer source. Moreover, it has a simple seed production procedure (Song et al., 2005).

Although the wheat hybrids with > 15% yield increase have been developed (Anonymous, 2015), accelerating yield improvements with stability and stress resistance with wider adaptability under varying agro-ecologies is still the key issue to be solved for the large-area application of hybrid wheat.

The knowledge of combining ability (CA) influencing yield and its components is useful to assess differences among the genotypes and also, elucidate the nature and magnitude of gene actions involved (Salgotra et al., 2009; Fasahat et al., 2016). Information of general and specific combining abilities influencing yield and its components has become increasingly important for plant breeders to select appropriate parents while developing hybrids (Rasheda et al., 2014). Line × tester analysis is one of the most powerful tools for predicting the general combining ability (GCA) of parents and selecting suitable parents and crosses with high specific combining ability (SCA) (Rashid et al., 2007; Saeed et al., 2001; Krystkowiak et al., 2008;

Jain and Sastry, 2012). Thus, the main goal of hybrid breeding is to systematically exploit heterosis. Heterosis of a hybrid is expected to increase with the genetic divergence between its parents (Melchinger, 1999). This study, thus, aimed to identify desirable wheat germplasm for superior hybrid cross combinations through 1) identifying the best parents with high combining ability (CA) and 2) estimating heterosis effects.

MATERIALS AND METHODS

Plant materials

Two TPSGMS lines (K78S and K456S), 60 restorer lines (R1 to R56 from Food Crops Research Institute and R57 to R60 from Mexico), two local checks (Yun mai 53 and Yun mai 56), and their 120 hybrid combinations were used in this study (Table 1).

Table 1. Parent materials used for this study

Ser #	Parent	Ser #	Parent	Ser #	Parent
S1	K78s	R20	2016Y_2-3972	R41	2016Y_2-4123
S2	K456s	R21	2016Y_2-3988	R42	2016Y_2-4124
R1	2016Y_2-1987	R22	2016Y_2-3989	R43	2016Y_2-4132
R2	2016Y_2-2301	R23	2016Y_2-4001	R44	2016Y_2-4134
R3	2016Y_2-2652	R24	2016Y_2-4022	R45	2016Y_2-4181
R4	2016Y_2-2776	R25	2016Y_2-4032	R46	2016Y_2-4183
R5	2016Y_2-3613	R26	2016Y_2-4033	R47	2016Y_2-4184
R6	2016Y_2-3766	R27	2016Y_2-4052	R48	2016Y_2-4197
R7	2016Y_2-3768	R28	2016Y_2-4078	R49	2016Y_2-4201
R8	2016Y_2-3874	R29	2016Y_2-4090	R50	2016Y_2-4203
R9	2016Y_2-3876	R30	2016Y_2-4094	R51	2016Y_2-4205
R10	2016Y_2-3883	R31	2016Y_2-4097	R52	2016Y_2-4208
R11	2016Y_2-3884	R32	2016Y_2-4098	R53	2016Y_2-4217
R12	2016Y_2-3889	R33	2016Y_2-4102	R54	2016Y_2-4221
R13	2016Y_2-3901	R34	2016Y_2-4106	R55	2016Y_2-4223
R14	2016Y_2-3902	R35	2016Y_2-4108	R56	2016Y_2-4224
R15	2016Y_2-3907	R36	2016Y_2-4111	R57	2016CIM-1101
R16	2016Y_2-3913	R37	2016Y_2-4117	R58	2016CIM-2012
R17	2016Y_2-3917	R38	2016Y_2-4118	R59	2016CIM-6152
R18	2016Y_2-3919	R39	2016Y_2-4119	R60	2016CIM-6203
R19	2016Y_2-3962	R40	2016Y_2-4122	CK	Yun Mai 53 and Yun Mai 56

Field experiment

The present investigation was carried out at experimental field of Songming Agricultural Research Station, Yunnan Academy of Agricultural Sciences (25.4043° N, 103.625° E, 1872 m above sea level) during 2016 and 2017 growing seasons. In March 2016, two TPSGMS lines as female and 60 restorer lines as male were sown to produce 120 hybrid wheat crosses according to the 2 × 60 line × tester hybridization method. In October the parents (male, female and checks) and 120 F_1 crosses were sown in the field. The parents and F_1s were evaluated in a randomized complete block design in triplicate. Each genotype was grown in single row, 2 m long and 23.33 cm apart, with plant spacing of 15 cm. The experiment was surrounded by a protective row. The recommended package for Daejeon area was followed for cultural practices. At maturity stage, data were recorded on three randomly selected plants per row in each of the three replications.

Data recording

Data of nine biometrical traits including yield plant^{-1}(Y/P), number of spikes plant^{-1}(S/P), thousand grain weight (TGW), number of grains spike^{-1}(G/S), spike length (SL), spikelets numbers (SN), fertile spikelets number (FSN), sterile spikelets number (SSN) and plant height (PHt) was recorded. The Y/P of sterile lines is the yield of outcrossing.

Statistical analysis

All studied characters were statistically analyzed on plot mean basis according to Steel and Torrie (1980) to test the significance of 182 different genotypes. Mean squares for genotypes (parents and F_1s) were partitioned among parents, F_1 crosses and parents vs crosses (Kearsey and Pooni, 1996). Treatments were compared using the LSD values (Gomez and Gomez, 1984). Line × tester analysis was performed for all the studied characters. CA and gene effects were studied following Singh and Chaudhary (1985). The *t*-test was used to test whether CA effects were different from 0. These analyses were done using Excel and Agrobase 99 computer program (Anonymous, 1999)

The estimates of heterosis

Generally, the expression of increased vigor of the F_1 hybrid over its parents is called heterosis as proposed by Mather (1949) and Mather and Jinks (1982). However, following three approaches are usually used for estimation of heterosis:

1- Mid-parent heterosis or heterosis over the mean parents (MP). The amount of heterosis as proposed by Mather (1949) and Mather and Jinks (1982) was determined as the increase of the F_1 hybrid mean over the average of its two parents as follows:

$\%(MP) = [(F_1 - MP)/ MP] \times 100$.

2- Heterobeltiosis or heterosis over the better parent (BP). The heterosis of an individual cross was determined as the increase of the F_1 hybrid mean over its better parent, as follows:

$\%(BP) = [(F_1 - BP)/ BP] \times 100$.

3- Standard heterosis or heterosis over the best check cultivar (SH). The percent increase or decrease of F_1 hybrids over best check was calculated to estimate possible heterotic effects for the above mentioned parameters (Fonseca and Patterson, 1968) as follows:

$\% (SH) = [(F_1 - SH)/SH] \times 100$.

LSD values were calculated to test the significance of the heterosis effects over MP, BP and check cultivar, according to the formula that was suggested by Wynne et al. (1970).

RESULTS and DISCUSSION

Analyses of variance

The highly significant mean sum of squares (SS) due to genotypes (parents and hybrids) for all studied characters in this investigation (Table 2) and non-significant for replication indicated the existence of sufficient variation in the studied material (Fisher and Yates, 1967). These highly significant differences in all characters, indicating that the parents possessed alleles with different additive effects. Significant differences were noticed among the progenies, revealing that the parents were diverse for the studied characters and that this diversity could be transmitted to the offspring. A comparison of the parents versus F_1 crosses revealed significant differences for all characters except S/P, reflecting a sort of heterosis for these characters. This showed that there was significant variation among lines, testers and hybrids, hence it is possible to calculate the GCA and SCA in the populations. The <1 ratio of GCA to SCA variances for all studied characters indicated governance of predominantly non-additive gene action for these characters.

Table 2. Analysis of variance of 9 agronomic characters for genotypes, testers, lines and 120 hybrid wheat combinations and Line x Tester analysis.

SoV	df	Y/P	S/P	TGW	G/S	SL	SN	FSN	SSN	PHt
R	2	39.75	3.505	38.58	36.62	2.57*	5.85*	2.41	1.34*	28.69
G	181	34.63**	4.70**	150.74**	236.96**	3.95**	6.25**	6.71**	1.14**	136.8**
P	61	32.11**	4.27**	185.19**	256.91**	6.88**	8.19**	9.19**	1.03**	175.9**
C	119	35.96**	4.97**	126.26**	190.13**	2.44**	4.54**	5.38**	0.86*	115.5**
PvC	1	28.64*	1.75	961.15**	4591.9**	5.41**	91.65**	12.98**	40.80**	293.8**
L	1	100.59*	18.87**	42.38	3858.7**	3.85*	162.6**	209.4**	2.95**	13.23
T	59	45.53**	6.28**	176.60**	221.21**	3.64**	4.47**	5.08**	1.17**	195.2**
LxT	59	25.31*	3.42*	77.35**	96.88**	1.21**	1.92	2.221	0.51*	37.49**
R	362	16.61	2.666	37.38	56.714	0.678	1.508	1.898	0.293	13.217
V-GCA		0.04	0.01	0.18	0.35	0.01	0.01	0.01	0.00	0.29
V-SCA		2.90	0.25	13.32	13.39	0.18	0.14	0.11	0.07	8.09
GCA/SCA var. ratio		0.01	0.02	0.01	0.03	0.03	0.07	0.11	0.01	0.04

Note: “ * ” and “ ** ”represent significant differences at P＜5% and P＜1% levels, respectively. For characters Y/P represents Yield Plant^{-1}, S/P Spikes Plant^{-1}, TGW Thousand Grain Weight, G/S Grains Spike^{-1}, SL Spike Length, SN Spikelets Number, FSN Fertile Spikelets Number, SSN Sterile Spikelets Number, PHt Plant Height. SoV stands for Sources of Variation, R Replication, G Genotypes, P Parents, C Crosses, PvC Parents vs Crosses, L Lines, T Testers, LxT Line x Tester, R Residual

Analyses of combining ability

CA is an estimation of the value of genotypes on the basis of their offspring performance in some definite mating design (Allard, 1960). Average performance of parental line in series of cross combinations is generally referred to as GCA and is mainly attributed to additive and additive×additive gene effects. The GCA effect values of 9 agronomic traits of 120 hybrid wheat parents (Table 3) indicated that the third generation of wheat temperature and photosensitive sterile line K456s had GCA higher than K78s sterile line with respect to Y/P, TGW, G/S, SL, SN and FSN. K78s sterile line had the higher GCA of S/P, SSN and PHt. Three restorer lines recorded positive significant GCA effects for Y/P, among which 2016Y_2-2776 (R4) recorded the highest positive significant GCA effect (5.70) followed by 2016Y_2-4132 (R43) (5.06), and 2016Y_2-3919 (R18) (4.70) indicating that they were good general combiners for Y/P. 2016Y_2-4224 (R56), 2016Y_2-4117 (R37) and 2016CIM-1101 (R57) recorded the lowest negative GCA for Y/P. Four restorer lines recorded positive significant GCA effects for S/P, among which 2016Y_2-3884 (R11) recorded the highest positive significant GCA effect (2.47) followed by 2016Y_2-3919

(R18) (2.43), 2016Y_2-2776 (R4) (1.98) and (R10) (1.76) indicating that they were good general combiners for S/P. 2016Y_2-4217 (R53) and 2016Y_2-4224 (R56) recorded the lowest negative GCA for S/P.

Six restorer lines recorded positive significant GCA effects for TGW, indicating being good general combiners for this character. Among them, 2016Y_2-4118 (R38) recorded the highest GCA effect (12.3) followed by 2016Y_2-3889 (R12) (8.86), 2016Y_2-4217 (R53) (8.38), 2016Y_2-4201 (R49) (7.89), 2016Y_2-4221 (R54) (7.55) and 2016Y_2-3913 (R16) (7.15). 2016Y_2-4123 (R41), 2016Y_2-3766 (R6), 2016Y_2-3768 (R7) and 2016Y_2-3613 (R5) recorded the lowest negative GCA.

For G/S, five restorer lines were good general combiners and recorded positive significant GCA effects, among them 2016Y_2-3972 (R20) recorded the highest positive significant GCA effect (13.9) followed by 2016Y_2-4181 (R45) (10.2), 2016Y_2-4117 (R37) (9.09), 2016Y_2-4090 (R29) (8.5) and 2016Y_2-2776 (R4) (8.19). 2016Y_2-3913 (R16), 2016Y_2-4078 (R28) and 2016CIM-6203 (R60) recorded the lowest negative GCA for G/S. 2016Y_2-4117 (R37), 2016Y_2-4201 (R49), 2016Y_2-3972 (R20), 2016Y_2-4022 (R24) and 2016Y_2-4217 (R53) recorded positive significant GCA for SL, while 2016Y_2-3919 (R18), 2016Y_2-4078 (R28) and 2016Y_2-3988 (R21) recorded the lowest negative GCA. The highest positive GCA for SN recorded by 2016Y_2-4117 (R37), 2016Y_2-3913 (R16) and 2016Y_2-4183 (R46), while 2016CIM-6152 (R59) and 2016CIM-2012 (R58) recorded the lowest negative GCA. The highest positive GCA for FSN recorded by 2016Y_2-4117 (R37), 2016Y_2-3972 (R20) and 2016Y_2-4197 (R48), while 2016CIM-2012 (R58) recorded the lowest negative GCA. 2016Y_2-3972 (R20), 2016Y_2-4197 (R48), 2016Y_2-4201 (R49), 2016Y_2-4117 (R37) and 2016Y_2-2776 (R4) recorded the lowest negative GCA for SSN. 13 restorer lines recorded positive and significant GCA effects for PHt. We can conclude that 2016Y_2-2776 (R4) had the highest general combining ability in five characters (Y/P, S/P, G/S, SSN and PHt). 2016Y_2-4117 (R37) had the highest general combining ability in five characters (G/S, SL, SN, FSN and SSN).

Deviation in the performance of a cross expected on the basis of average performance of parental lines is mainly attributed to dominant and epistatic effects and is termed as specific combining ability *i.e.,* non-additive part. Non-additive component is presence for the controlling traits necessitates exploitation of hybrid vigor in wheat breeding scheme.

The SCA effects of 120 hybrids for all studied characters were estimated and the highest 5% values for each character were presented in Tables 4. The best specific crosses for Y/P with first sterile line were K78s/R43, K78s/R31, K78s/R35, K78s/R4, K78s/R8 and K78s/R46. The best specific crosses for Y/P with second sterile line were K456s/R21, K456s/R17, K456s/R14, K456s/R2, K456s/R20 and K456s/R32. Non-significant positive and negative SCA values were recorded for S/P and SSN. The best specific crosses for TGW with first sterile line were K78s/R31, K78s/R37, K78s/R53, K78s/R42, K78s/R35 and K78s/R50, while with second sterile line were K456s/R51, K456s/R36, K456s/R27, K456s/R16, K456s/R32 and K456s/R57. The crosses K78s/R24 and K78s/R31 had positive and significant SCA values for SL. The crosses K78s/R57 and K456s/R16 had positive and significant SCA values for SN and FSN. Positive and significant SCA values for PHt were recorded by K78s/R35 and K456s/R14. The cross K78s/R31 had highest positive values in five characters, while K78s/R35, K78s/R24, K78s/R57and K78s/R53 crosses had highest positive values in three characters. K456s/R2 cross had highest positive values in six characters, while K456s/R17 and K456s/R14 had highest positive values in four characters. This information could be used for estimating and selecting superior cross combinations while exploiting heterosis and selecting homozygous lines in wheat, which is a self pollinated plant (Kose, 2017; Istipliler et al., 2015)

Estimates of heterosis effects

Many researchers have emphasized the utilization of heterosis percent as an important criterion for evaluation of hybrids. Therefore, the knowledge about the magnitude of heterosis would help in selection of best cross combination. Heterosis for Y/P, S/P, TGW and G/S was estimated and presented in Table 5. The highest combination for Y/P of heterosis over BP, MP and SH was K78s/R4, K456s/R20 and K456s/R21. K78s/R43 and K78s/R18 combinations recorded high positive heterosis over MP and SH for Y/P. The combinations K78s/R37, K78s/R27, K78s/R56, K456s/R31, K456s/R37, and K456s/R55 recorded lowest negative heterosis over MP and SH.

For S/P, heterosis were significant and positive in K78s/R11, K78s/R43, K78s/R34 crosses over BP and in K78s/R38, K78s/R48, K78s/R43, K456s/R59, K456s/R25, and K456s/R43 crosses over MP. The combinations K78s/R53, K78s/R37, K78s/R56, K456s/R55, K456s/R39 and K456s/R56 recorded lowest negative heterosis for S/P.

Table 3. General combining ability value of 9 agronomic traits of sterile and restorer lines of hybrid wheat

Parents	Y/P	S/P	TGW	G/S	SL	SN	FSN	SSN	PHt
K78s	-0.5286	0.2289	-0.3431	-3.2739	-0.1035	-0.6722	-0.7627	0.0905	0.1917
K456s	0.5286	-0.2289	0.3431	3.27**	0.1035	0.67**	0.76**	-0.0905	-0.1917
R1	-3.3037	-0.9345	-4.9208	-2.4367	0.0552	0.3906	0.2668	0.1239	-5.725
R2	1.5213	0.3711	-2.7173	3.4191	0.1861	-0.7493	-0.69	-0.0593	-1.0583
R3	3.8322	0.899	4.6413	1.5725	0.0656	-0.4775	0.0834	-0.561	8.11**
R4	5.70**	1.98*	-4.0842	8.19*	0.0103	0.3942	0.9944	-0.60*	9.44**
R5	-0.3698	0.6766	-7.5098	0.9762	-0.1045	0.4203	0.5337	-0.1133	4.78*
R6	0.9752	1.2322	-11.8094	7.4619	0.392	0.6216	1.1528	-0.5312	4.78*
R7	-2.5006	-0.4623	-11.8425	6.5232	0.4026	0.2012	0.3816	-0.1804	5.44**
R8	2.3397	1.0933	1.3639	-0.7571	0.2315	0.131	-0.0292	0.1602	1.9417
R9	-0.4251	0.4822	-3.364	-2.0442	0.5251	1.152	1.2038	-0.0518	-0.0583
R10	1.9319	1.76*	1.7222	-7.3746	-0.2845	0.3523	-0.2692	0.6215	-3.225
R11	2.848	2.47**	-6.5294	0.3103	0.5909	1.1412	1.0439	0.0973	-3.225
R12	4.4369	0.9266	8.86**	-0.8854	-0.0815	-1.0295	-1.4726	0.4431	3.275
R13	-2.8837	-0.6845	-2.1615	-4.8277	0.8413	0.6403	-0.0504	0.6906	-9.225
R14	0.3669	-0.1845	3.0339	-1.6096	-0.9689	-0.2048	-0.2023	-0.0026	-5.5583
R15	-4.1184	-1.1428	-1.9217	-4.6839	0.4683	-0.6633	-0.0756	-0.5877	-7.3917
R16	-2.9776	-0.5178	7.15*	-14.0678	0.545	2.26**	1.4015	0.8626	-0.225
R17	-0.4887	-0.3095	2.5604	-5.31	-0.8967	-1.4378	-0.895	-0.5429	0.4417
R18	4.70**	2.43**	-0.965	-1.7035	-1.1604	-1.1575	-0.9894	-0.1681	-15.0583
R19	-2.1198	-0.8789	-6.907	2.8834	-0.6582	-0.2522	-0.6933	0.4411	-5.225
R20	2.5449	-0.365	-1.9065	13.95**	1.21**	1.1352	2.16**	-1.03**	-7.3917
R21	3.6363	0.4266	3.0019	4.215	-1.9388	-1.2421	-1.3034	0.0613	-5.5583
R22	0.7227	-0.6012	2.333	4.8208	-0.7646	-0.4777	-0.5691	0.0913	-1.5583
R23	-2.797	-1.1012	-1.6086	-1.0197	0.4958	0.0608	0.3672	-0.3064	-2.725
R24	0.4524	0.0377	-3.9886	4.4848	0.998*	0.367	0.299	0.0681	-6.3917
R25	1.813	1.3988	-3.3133	-1.8385	-0.3727	0.2145	-0.0336	0.2481	-5.225
R26	-2.3387	-0.1567	-3.9429	-5.2037	-0.5545	0.0407	-0.3643	0.405	-6.8917
R27	-3.3592	-0.3234	-4.9456	-7.3473	-0.8465	-0.0691	-0.1614	0.0923	-5.0583
R28	-2.3801	0.7044	-3.3226	-12.2625	-1.3955	-0.9984	-1.3723	0.3739	-2.225
R29	0.7244	0.6766	1.4559	8.51*	-0.5578	-0.0461	-0.2905	0.2444	3.94*
R30	-0.7192	0.0933	-4.6442	-1.6477	0.0945	-0.3237	0.0276	-0.3513	-4.5583
R31	-1.2748	-0.5178	-2.4588	0.9928	-0.7917	-0.6823	-0.1645	-0.5178	-0.0583
R32	-1.1376	-1.0317	6.6**	-3.8389	0.481	-0.6228	-0.8247	0.2019	10.61**
R33	-1.3628	-0.7956	7.79*	-6.6264	-0.8829	-1.0632	-1.0617	-0.0016	1.9417
R34	4.2088	1.7183	0.9979	3.9896	-0.945	-0.4497	-0.2106	-0.2391	-3.8917
R35	-1.0748	-0.1567	-6.3638	3.6579	0.3298	1.1654	1.0479	0.1174	1.4417
R36	0.9224	-0.1012	3.0403	0.4529	-0.5489	-0.3308	-1.0514	0.7206	-2.5583
R37	-5.0706	-1.7956	-11.4585	9.09**	2.50**	2.39**	3.05**	-0.68*	-5.8917
R38	4.0924	-0.3512	12.30**	5.6711	0.5943	1.2764	0.9751	0.3013	7.94**
R39	-1.6764	-1.3512	1.2537	4.2209	0.4731	0.3367	-0.1429	0.4796	4.94*
R40	1.2952	-0.1845	6.2258	0.6153	-0.9179	0.6194	0.4878	0.1316	15.11**
R41	3.0445	-0.4206	9.4589	5.2223	0.1549	-0.4551	-0.4646	0.0094	-0.5583
R42	-1.3312	0.1488	-0.1348	-4.6855	-0.0644	1.0073	0.8787	0.1286	0.775
R43	5.06**	1.3155	2.5406	4.791	-0.7031	0.7128	0.7234	-0.0106	8.11**
R44	-1.1839	0.1211	1.0192	-7.8534	-0.3456	-0.1739	-0.8475	0.6737	4.78*
R45	3.4991	0.8155	-1.7096	10.23**	0.2393	-0.1694	-0.3997	0.2303	1.275
R46	0.1411	-0.1567	-4.8847	6.9639	-0.4083	1.35*	0.7779	0.5678	-5.5583
R47	2.4741	0.7044	-0.0002	2.2039	-0.5278	-0.0543	-0.1027	0.0484	-1.8917
R48	1.3366	0.3988	2.849	1.9918	0.39	0.8353	1.83*	-0.997**	-1.0583
R49	2.3733	-0.9067	7.89*	8.56*	1.34**	0.1866	1.1693	-0.98**	0.9417
R50	1.2913	0.2044	-0.4267	3.5999	0.2965	-0.131	-0.5856	0.4546	-1.3917
R51	-1.8417	-0.8789	2.0158	-1.6746	-1.1216	-0.003	-0.4698	0.4668	-0.5583
R52	0.8088	-0.2123	6.2618	-1.754	-0.6289	-0.1843	-0.487	0.3027	5.61*
R53	-3.9653	-2.1289	8.38*	2.8036	0.930*	0.119	-0.1984	0.3174	1.4417
R54	0.4008	-0.9067	7.55*	2.8274	0.8369	-0.7765	-0.9585	0.182	-0.3917
R55	-2.8126	-1.8512	4.1623	1.6658	1.17**	-1.1599	-0.6354	-0.5245	-0.0583
R56	-5.1037	-1.7956	1.0457	-7.794	-0.1186	0.0178	0.2883	-0.2706	-2.0583
R57	-4.7395	-0.8512	-3.7601	-9.5145	0.0467	0.1136	0.0631	0.0505	-3.725
R58	-1.3837	-0.1845	4.2151	-6.8131	0.7044	-1.5765	-1.5083	-0.0682	7.78**
R59	-2.0598	0.6766	-6.6736	-6.9806	0.3271	-1.9141	-1.2277	-0.687*	6.44**
R60	-2.6906	0.4822	-1.5355	-14.2487	0.6641	-0.7754	-0.4063	-0.369	11.94**

Note: " * " and " ** "represent significant differences at P＜5% and P＜1% levels, respectively. For characters Y/P represents Yield Plant^{-1}, S/P Spikes Plant^{-1}, TGW Thousand Grain Weight, G/S Grains Spike^{-1}, SL Spike Length, SN Spikelets Number, FSN Fertile Spikelets Number, SSN Sterile Spikelets Number, PHt Plant Height.

Table 4. The specific combining ability values of the studied traits for top 5% of 120 hybrid wheat crosses.

	Y/P	S/P	TGW	G/S	SL	SN	FSN	SSN	PH
k78s line combination	K78s/R43	K78s/R43	K78s/R31	K78s/R31	K78s/R24	K78s/R57	K78s/R57	K78s/R14	K78s/R35
	5.236**	1.938	9.652**	13.405**	1.437*	2.588**	2.035*	0.742	7.142**
	K78s/R31	K78s/R8	K78s/R37	K78s/R29	K78s/R31	K78s/R24	K78s/R24	K78s/R37	K78s/R33
	4.313**	1.493	8.550**	9.320**	1.345*	0.966	1.071	0.627	4.308
	K78s/R35	K78s/R34	K78s/R53	K78s/R53	K78s/R19	K78s/R21	K78s/R55	K78s/R57	K78s/R53
	3.501**	1.146	7.067**	8.191**	0.912	0.926	1.027	0.553	4.142
	K78s/R4	K78s/R58	K78s/R42	K78s/R55	K78s/R21	K78s/R28	K78s/R31	K78s/R34	K78s/R25
	2.858**	1.104	6.960**	7.185**	0.772	0.746	0.902	0.506	3.808
	K78s/R8	K78s/R48	K78s/R35	K78s/R6	K78s/R16	K78s/R18	K78s/R18	K78s/R19	K78s/R42
	2.786**	1.077	6.112**	4.990**	0.719	0.698	0.820	0.476	3.808
	K78s/R46	K78s/R12	K78s/R50	K78s/R39	K78s/R53	K78s/R55	K78s/R33	K78s/R27	K78s/R9
	2.378*	0.938	3.611**	4.265**	0.388	0.612	0.775	0.389	2.975
K456s line combination	K456s/R21	K456s/R2	K456s/R51	K456s/R48	K456s/R7	K456s/R16	K456s/R16	K456s/R31	K456s/R14
	5.353**	1.451	5.848**	8.464**	1.094	2.100*	2.225*	0.706	5.192**
	K456s/R17	K456s/R53	K456s/R36	K456s/R37	K456s/R37	K456s/R35	K456s/R2	K456s/R33	K456s/R22
	3.967**	1.396	5.345**	7.227**	0.981	0.748	0.980	0.505	4.858
	K456s/R14	K456s/R24	K456s/R27	K456s/R21	K456s/R2	K456s/R2	K456s/R14	K456s/R13	K456s/R34
	3.584**	1.284	5.197**	7.196**	0.665	0.741	0.958	0.465	4.192
	K456s/R2	K456s/R17	K456s/R16	K456s/R14	K456s/R47	K456s/R32	K456s/R37	K456s/R55	K456s/R2
	3.550**	1.215	5.152**	6.545**	0.530	0.678	0.903	0.414	3.692
	K456s/R20	K456s/R42	K456s/R32	K456s / R34	K456s / R60	K456s/R41	K456s/R17	K456s/R54	K456s/R31
	3.013**	1.173	5.047**	5.600**	0.508	0.585	0.669	0.389	3.692
	K456s/R32	K456s/R30	K456s/R57	K456s / R16	K456s/R59	K456s/R17	K456s/R12	K456s/R53	K456s/R16
	2.859**	1.062	4.933**	5.062**	0.476	0.576	0.584	0.356	3.192

Note: " * " and " ** "represent significant differences at P＜5% and P＜1% levels, respectively. For characters Y/P represents Yield Plant^{-1}, S/P Spikes Plant^{-1}, TGW Thousand Grain Weight, G/S Grains Spike^{-1}, SL Spike Length, SN Spikelets Number, FSN Fertile Spikelets Number, SSN Sterile Spikelets Number, PHt Plant Height.

For TGW, highly significant positive mean heterosis estimates were observed in SH. This showed the tendency of superiority by K456s/R38, K78s/R53, K456s/R16, K78s/R52, K456s/R32 and K78s/R54 in this trait. However, the BP heterosis was significant to highly significant positive in K456s/R12, K456s/R12, K78s/R47, K456s/R36, K78s/R38 and K78s/R23. The combination K78s/R53 recorded the highest positive heterosis over MP. The lowest negative heterosis recorded by K456s/R37 over SH, BP and MP.

For G/S, highly significant positive mean heterosis estimates were observed in only two cross (K456s/R20 and K456s/R37) in SH. However, highest significant positive heterosis recorded by K456s/R20, K456s/R34, K456s/R21 and K78s/R37 over BP. K78s/R29, K78s/R31 and K78s/R45 crosses had the highest significant positive heterosis estimates over MP. We summarized that cross K78s/R43 was the best in Y/P and S/P, however K456s/R21 was the best in Y/P and G/S. This exploitation of heterosis in wheat hybrid development could be of significant economic importance considering the role of wheat in food security around the globe (Hochholdinger and Baldauf, 2018).

Contribution of lines, testers and their interactions towards yield testing

The proportional contribution of lines, testers and their interactions to total variances for different traits revealed that maximum contribution for all traits was due to tester effect. These lines showed more contribution than line x tester interaction for SN and FSN (Table 6).

Table 5. Heterosis estimation using various approaches for yield and yield components

Entry			SH			BP			MP		
Yield plant^{-1}	Highest combination	K78s	R43	R4	R18	R6	R4	R38	R43	R4	R18
			34.4**	23.8	7.58	126.7**	82.2**	67.5**	238.8**	212.0**	170.9**
		K456s	R21	R20	R49	R21	R20	R2	R21	R20	R33
			32.9 *	11.9	9.8	131.4**	94.8**	89.6**	165.6**	116.8**	113.4*
	Lowest combination	K78s	R37	R27	R56	R57	R60	R56	R56	R27	R37
			-60.6**	-63.7**	-63.9**	-60.5**	-60.1**	-57.9**	-8.9	-8.4	-0.7
		K456s	R31	R37	R55	R31	R37	R44	R31	R37	R55
			-56.4**	-52.4**	-51.7**	-52.1**	-47.1**	-44.5**	-24.1	-17.1	-15.8
Spikes plant^{-1}	Highest combination	K78s	R11	R43	R34	R11	R43	R34	R38	R48	R43
			-4.1	-5.3	-9.5	38.5**	36.8 *	30.8*	112.0**	93.9**	72.0**
		K456s	R18	R2	R47	R2	R47	R11	R59	R25	R43
			-21.9 *	-25.4 *	-27.8**	18.9	15.1	12.5	157.9**	50.7	46.4
	Lowest combination	K78s	R53	R37	R56	R53	R37	R56	R37	R17	R24
			-77.5**	-66.9**	-62.1**	-67.5**	-52.1**	-45.3**	-41.7	-36.8*	-32.5
		K456s	R55	R39	R56	R16	R40	R3	R56	R15	R16
			-63.3**	-63.3**	-61.0**	-50.0**	-49.0**	-44.4**	-35.3	-33.5	-32.1
Thousand grain weight	Highest combination	K78s	R53	R52	R54	R47	R38	R23	R53	R52	R54
			69.9**	54.5**	53.9**	31.4**	30.0**	29.4**	65.7**	50.7**	50.2**
		K456s	R38	R16	R32	R32	R12	R36	R12	R33	R3
			71.5**	63.3**	61.7**	37.7**	35.7**	30.0**	53.2**	50.9**	48.2**
	Lowest combination	K78s	R7	R19	R27	R27	R45	R44	R19	R27	R57
			-4.4	-2.6	0.8	-21.5**	-21.4**	-20.4**	-5.0	-1.6	2.3
		K456s	R37	R6	R35	R37	R59	R46	R37	R6	R35
			-23.9 *	-9.5	-3.6	-48.5**	-35.4**	-25.9**	-35.2**	-22.9*	-17.9
Grains spike^{-1}	Highest combination	K78s	R29	R31	R45	R37	R6	R29	R29	R31	R45
			12.7	6.6	6.3	40.0**	19.0 *	7.0	152.8**	139.0**	138.4**
		K456s	R20	R37	R21	R20	R34	R21	R22	R34	R20
			25.7**	21.7**	13.0	88.8**	64.8**	63.1**	127.6**	104.7**	90.7**
	Lowest combination	K78s	R16	R28	R60	R16	R56	R1	R16	R28	R60
			-53.9**	-46.4**	-39.7**	-53.4**	-44.6**	-44.5**	3.4	20.2	35.2
		K456s	R60	R31	R57	R60	R59	R55	R60	R31	R57
			-38.6**	-30.0**	-26.8**	-32.2**	-21.4**	-16.9 *	-7.8	5.2	10.0

Note: “ * ” and “ ** ”represent significant differences at $P < 5\%$ and $P < 1\%$ levels, respectively.

Table 6. Contribution of lines, testers and their interactions to total variances for 9 agronomic traits.

Contribution	Y/P	S/P	TGW	G/S	SL	SN	FSN	SSN	PH
Lines	2.35	3.19	0.28	17.05	1.33	30.15	32.73	2.89	0.1
Testers	62.76	62.68	69.35	57.68	74.13	48.89	46.8	67.84	83.8
Line X tester	34.88	34.13	30.37	25.26	24.54	20.97	20.47	29.27	16.1

Note: For characters Y/P represents Yield Plant^{-1}, S/P Spikes Plant^{-1}, TGW Thousand Grain Weight, G/S Grains Spike^{-1}, SL Spike Length, SN Spikelets Number, FSN Fertile Spikelets Number, SSN Sterile Spikelets Number, PHt Plant Height.

CONCLUSION

The non-additive gene action was predominantly governing all characters studied. The TPSGMS line K456s recorded highest GCA in Y/P, TGW, G/S, SL, SN and FSN. The restorer 2016Y$_2$-2776 (R4) and 2016Y$_2$-4117 (R37) showed the highest GCA in five characters. The cross K78s/R31 possessed highest positive SCA values in five characters, while K456s/R2 exhibited highest positive values in six characters. The crosses K78s/R43 and K456s/R21 showed the highest significant positive heterosis estimates over standard check (34.41 and 32.91, respectively), and MP (238.77 and 165.57, respectively) estimates with respect to Y/P. Also, the crosses K78s/R4 had significant positive heterosis estimates over BP (82.19), MP (211.96) and standard check (23.77) estimates with respect to Y/P. These promising materials could be utilized for parental lines traits improvement and heterosis level enhancement for hybrid wheat breeding program.

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