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Genetic analysis of thermotolerance and grain yield traits of bread wheat (*Triticum aestivum* L.) Using diallel analysis

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Heat stress alters the wheat crop productivity, causes a catastrophic loss of global wheat productivity. This study aims to find knowledge on genetic analysis of thermotolerance bread wheat genotypes altered by heat stress. Six bread wheat genotypes were crossed using a half-diallel producing 15 F1 crosses. All genotypes were sown in two different sowing dates (optimal sowing date ‘22nd November’, and late sowing date ‘5th January’) producing different heat stress conditions at two grown seasons 2015/2016, and 2016/2017 at Faculty of agriculture Farm, Zagazig University, Egypt. To investigate the thermotolerance and grain yield genetic analysis, we studied some physiological traits; days to heading and maturity, and two yield traits; 1000 grain weight and grain weight. Results indicate a significant difference between all the genotypes performance. Consequently, a reduction in all the studied traits is found under the heat stress conditions; days to heading (17.12%) and maturity (16.96%), 1000-grain weight (25.67%) and grain weight (56.62%). Studying the combining ability, results reveal that, both general ‘GCA’ and specific ‘SCA’ are presence high significant values. GCA/SCA ratio is above unity for days to heading, maturity, while it is less than unity for 1000 grain weight and grain yield/plant on the two sowing dates. It is noticed a low narrow sense heritability for all studied traits; while it is moderate for days to maturity. Covariance/Variance analysis discloses non-additive gene action with overdominance for all studied traits on the two sowing dates except days to maturity inherited by complete dominance. In conclusion, genotypes; Misr 1, Sids 14 and their F1 cross, are considered more thermotolerance corresponding to their yield under heat stress. Furthermore, they show negative and significant SCA. These results show new insights on the economic traits of the wheat crop productivity breeding program under the alterations on the climate changing. Furthermore, new genotypes candidates are identified as an ideal material for future thermotolerance breeding programs.

Keywords: ***Tritium aestivum* L, diallel analysis, gene action, GCA, SCA, sowing dates, heat stress**

INTRODUCTION

High temperature with resultant changes on the global climate alters bread wheat growth and production, ensuring an awful loss of the wheat global yielding. Wheat (*Tritium aestivum* L) considered one of the most strategic crops for edible foods necessary for about third of the world population. Changing in the climate environments through the growing season results in constraints disturbing yield potential (Asseng et al., 2013; Paymard et al., 2018). Environmental cues had a potential impact on plant growth and development

(Kamal et al., 2019a; Kamal et al., 2019b; Ormancey et al., 2019). Therefore, to reduce the climate change alterations, adaptation strategies and agriculture system obtaining high yield should be followed, and further the choice of appropriate sowing date (Cammarano et al., 2013; Luo et al., 2018; Lv et al., 2019). Reduction in the wheat productivity caused by shorter favorable growing period, high temperature with low humidity during the growing season (Akter and Rafiqul Islam, 2017; Jat et al., 2018). Heat stress is one of the major environmental cues alter the production and productivity of wheat crop (Joshi et al., 2007). Consequently, increasing the temperature during the reproductive phase cause a terrible loss due to the direct alterations on the number of grains and grain yield (Wollenweber et al., 2003). Consequently, various adaptation strategies are instantly required to reduce climate change alterations on agriculture (Dubey et al., 2019; Jat et al., 2018; Niles et al., 2015). Some of the adaptation for the wheat crop is, to use heat stress-tolerant genotypes and sowing dates (Jat et al., 2018) to avoid terminal heat stress.

Understanding the genetics analysis and gene interaction of heat stress tolerance are primary requirements for wheat crop improvement. The clarification of the genetic basis will enhance the efficiency of wheat improvement programs. Genetic analysis and inheritance determination by biometrical approaches are important for the breeding programs to identify new genotypes candidates (Poodineh and Rad, 2015), helps to figure out the nature of gene actions involved in a concerned trait. Developmental traits of the wheat crop are essential for improving adaption and yield potential. Improvement of wheat genotypes regarding each of earliness, yield and some yield attributes potential is largely depending on the knowledge of the relative number of genetic components, mode of gene action and the presence of non-allelic interaction of both traits in the plant material under investigation.

Here, in our present study, we aim to identify the best-combining parents using 6 genotypes of bread wheat and their generation crosses. Further, genetic analysis to analysis the genetic components and model of inheritance of heat tolerance, yield, and some contributing characters.

MATERIALS AND METHODS

Field Experiment design:

Field experiments were carried out at Ghazala Experimental Farm, Faculty of Agriculture, Zagazig University, Egypt during the two growing seasons of 2015/2016 and 2016/2017. Six genotypes of bread wheat (Table 1) were crossed in 6×6 diallel producing 15 F_1 crosses. Seeds of the six parent genotypes in addition to the 15 F_1 crosses were sown on two sowing dates, S1 (22nd November 'optimal sowing date in Egypt') and S2 (5th January 'late sowing date in Egypt') using a randomized complete block design for three replications. In each experiment, single rows of parent and F_1 were sown in 3m row length with a spacing of 5cm between plants and 20cm between rows. Temperature and humidity during the experiment are displayed in Figure 1

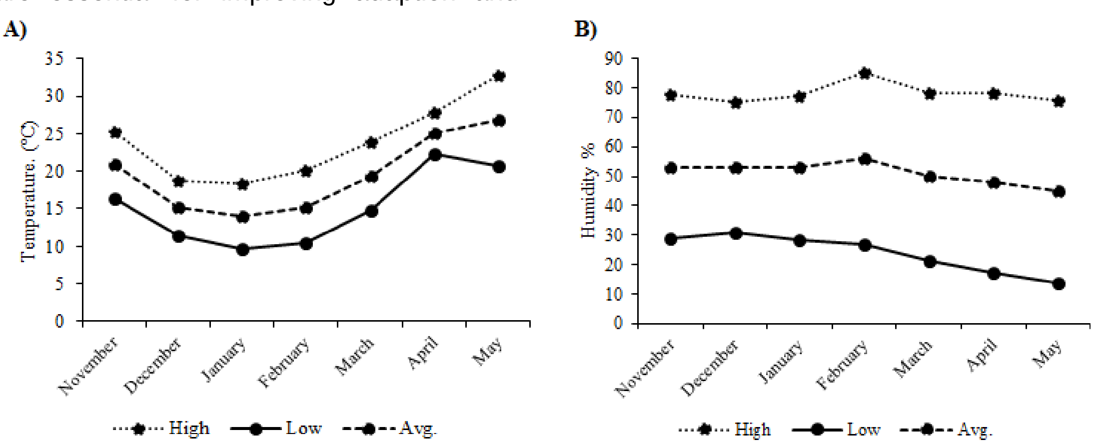

Figure 1. Meteorological data for monthly average during 2016/2017 growing season through November 2016 to May 2017.

A) represent high, low and average temperature (ºC). B) represent high, low, and average humidity %.

Table 1. Pedigree and origin of the 6 parental bread wheat genotypes

Genotype	Pedigree
Misr 1 (P1)	Oasis/SKAUZ//4*BCN/3/2*PASTOR.CMss00Y01881T -050M-030Y-030M-030WGY-33M-0Y-0S
Line 15 (P2)	WBLLI*2/BRAMBLING
Line 4 (P3)	BABAX/LR42//BABAX*2/3/BRAMBLING/
Sids 14 (P4)	SW8488*2/ KUKUNA- CGSS01Y00081T -099M-099Y-099M-099B-9Y-0B-0SD
Shandaweel 1 (P5)	SITE//MO/4/NAC/TH.AC//3*PVN/3MIRLO/BUC. CMSS93B00567S-72Y-010M-010Y-010M-0HTY-0SH.
Line 27 (P6)	ICB91-0539-7APP-0AP-3AP-0AP

. Five plants were used randomly for traits determination and observation in each experiment. We determined and analyzed some physiological and yield traits and its attributes; days to heading, days to maturity, 1000-grain weight and grain yield/plant.

Genetic analysis parameters:

Data were collected and analyzed using Microsoft office program 'Excel 2017'. Analysis of variance was estimated for the collected traits according to (Steel and Torrie, 1997). Estimation of both general (GCA) and specific (SCA) combining abilities were computed according to (Griffing, 1956) designated as method 2, model 1 for the studied characters. The traits showing significant genotypes differences were analyzed using diallel analysis technique as described by (Hayman, 1954a, b; Jinks and Jones, 1958). Furthermore, Heritability in narrow (T_n) sense was calculated according to (Mather and Jinks, 1982).

Graphic representation of the variance Vr (variance of the crosses involving particular parents or variance of each array) and Wr (covariance between parents and their offspring, which Wr is covariance of the array with non-recurring parents) were done. The values of Wr were plotted against the corresponding values of Vr to produce Wr/Vr graph.

The reduction percentage of means due to early or late sowing for all studied traits was calculated as [(mean value of optimum sowing trait - mean value of early or late sowing trait) / mean value of optimum sowing trait] x 100. Even though, heat susceptibility index (HSI) is estimated to detect the late sowing date tolerance 'thermotolerance' through the minimization of the grain yield reduction in grain yield (Fischer and Maurer, 1978) using the following formula.

$HSI = (1 - Y_{LS} / Y_{OS}) / (1- (X_{LS} / X_{OS})$

Where; Y_{LS} = mean of grain yield of a genotype in late sowing experiment.

Y_{OS} = mean of grain yield of a genotype in optimum sowing experiment.

X_{LS} = mean of all genotypes in late sowing.

X_{OS} = mean of all genotypes in optimum sowing.

RESULTS AND DISCUSSION

Genotypes materials mean performance:

Physiological traits; days to heading and days to maturity were evaluated for all the genotypes on the two sowing dates (Table 2, Table3). Results reveal that there are significant differences between the genotypes on the studied traits as well as between the two sowing dates (Table 3). Consequently, results of days to heading reveal that P2 and its F1 cross (P2 x P4) show level of earliness on the two sowing dates as '106 and 86 days', '105 and 86 days', respectively. Furthermore, P4 show earliness of days to maturity on the optimal date (153 days) and P2 on the late sowing date (127 days), while earliness maturity F1 crosses are P2 x P4 (153 and 126 days on the two sowing dates, respectively), as well as P2 x P5 (153, and 125 days).

Yield traits of the genotypes mean performance on the two sowing date were estimated by determining both 1000-grain weight and grain yield/plant (Table 2, Table3). It is noticed that the analysis of variance of the yield traits shows significant differences between the genotypes on the studied traits as well as between the two sowing dates (Table 3). Furthermore, the mean performance of the studied genotypes of 1000-grain weight traits indicates that the highest genotypes performance is P2, P3, F1 cross P2 x P5, and P3 x P4. While, P3, P6, and F1 cross P2 x P6 have the highest grain yield/plant on the normal sowing date (Table 2).

Heat stress by delaying the sowing date show significant alterations (reductions) on all the genotypes physiological and yield traits (Table 2, and Table 3). Reductions levels of days to heading, maturity, 1000-grain weight, and grain yield/plant are 17.12, 16.96, 25.67, 56.62 % (Table 2).

Table 2. Mean performance of parental genotypes and their F1 crosses for days to heading (days), days to Maturity (days), 1000-grain weight (g) and Grain yield/plant (g) on two sowing dates of bread wheat.

Genotypes	Days to heading (days)		Days to maturity (days)		1000-grain weight(g)		Grain yield/plant(g)		
	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2	HSI
Misr 1 (P1)	108.00	89.50	155.33	129.50	57.95	40.91	9.80	5.35	0.81
line15 (P2)	106.00	86.50	155.00	127.17	64.50	45.23	8.96	4.32	0.93
Line 4 (P3)	107.00	88.50	155.00	128.50	58.06	54.09	10.55	4.61	1.01
Sids 14 (P4)	106.50	90.00	153.50	128.33	58.82	30.08	8.39	4.79	0.77
Shandaweel (P5)	107.00	89.00	157.67	130.33	52.86	38.30	9.73	5.28	0.82
Line 27 (P6)	107.00	88.50	157.33	131.50	50.98	33.23	10.36	4.77	0.97
P1×P2	105.50	88.50	153.50	128.50	68.98	56.31	9.23	5.29	0.77
P1×P3	105.00	88.00	153.00	129.00	60.80	38.81	9.75	4.96	0.88
P1×P4	105.33	87.50	155.33	129.50	58.28	36.94	10.29	5.46	0.84
P1×P5	106.00	87.00	156.00	130.00	67.65	39.23	8.39	4.11	0.91
P1×P6	105.00	88.00	154.33	130.00	60.35	58.14	8.68	3.63	1.04
P2×P3	105.00	87.50	153.00	127.50	58.62	46.68	9.71	5.34	0.81
P2×P4	105.00	86.00	153.00	126.00	62.68	56.69	9.18	4.49	0.91
P2×P5	106.00	86.50	153.00	125.50	71.19	39.19	10.21	4.83	0.94
P2×P6	105.50	86.50	155.50	128.50	70.97	38.27	18.59	6.29	1.18
P3×P4	106.00	87.00	157.00	130.00	67.26	61.38	9.51	4.14	1.01
P3×P5	107.00	88.50	155.00	127.50	67.72	45.76	16.98	3.32	1.44
P3×P6	107.50	88.50	156.50	129.50	59.10	59.28	9.78	5.21	0.71
P4×P5	105.50	89.00	155.17	130.33	49.89	36.43	9.48	2.99	1.23
P4×P6	107.00	89.50	158.00	132.17	61.79	49.92	8.96	3.47	1.10
P5×P6	107.50	88.50	157.50	130.50	59.91	52.82	12.37	2.31	1.31
Mean	106.21	88.02	155.22	129.04	61.35	45.60	10.42	4.52	
Reduction %		17.12		16.96		25.67		56.62	
L.S.D 0.05	0.43	0.38	0.76	0.61	2.05	1.85	1.68	0.88	0.43
L.S.D 0.01	0.64	0.56	1.11	0.89	3.01	2.44	2.22	1.16	0.56

significant on 0.05 and 0.01 levels of probability, respectively.
S_1= Normal sowing (22nd November), and S_2 = Late sowing (5th January).

Table 3. Mean squares of 6 parents and F_1 progenies of bread wheat for heading (days), days to Maturity (days), 1000-grain weight (g) and Grain yield/plant (g) on two sowing dates of bread wheat.

Source of variation	D.f	Days to heading (days)		Days to maturity (days)		1000-grain weight(g)		Grain yield/ plant(g)	
		S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2
Replicates	2	1.21	0.58	0.59	0.53	5.87	39.30	0.27	0.34
Genotypes	20	2.71**	3.79**	8.32**	8.42**	110.95**	267.74**	20.42**	2.43**
Parents	5	1.33**	4.40**	7.48**	7.22**	68.83**	223.95**	2.04	0.47*
Crosses	14	2.49**	3.09**	8.90**	9.38**	102.86**	252.01**	27.31**	3.19**
P. vs. C.	1	12.71**	10.41**	4.38	0.84	434.92**	707.00**	15.82**	1.58**
Error	40	0.31	0.23	0.92	0.59	6.77	4.98	1.07	0.23

*, **=significant on 0.05 and 0.01 levels of probability, respectively.
S_1= Normal sowing (22nd November), and S_2 = Late sowing (5th January).

It is noticed that there are significant differences between all the studied genotypes performance on all the determined traits. Results reveal that P2 (Line 15), P4 (Sids 14) and their F1 cross P2 x P5 show highest performance on the normal sowing data and more stable/tolerant for the heat stress by late sowing date. Earliness seems to have favored the plant to escape the losses due to terminal high temperature. P2 (Line15) and P4 (Sids14) could be utilized for transfer of genes responsible for earliness. This earliness is a desirable trait for high-temperature tolerance (Akter and Rafiqul Islam, 2017; Choudhary et al., 1996; Jat et al., 2018). Furthermore, reduction of 1000-grain weight and grain yield/plant due to late sowing could be attributed with heat stress al late growth stage, which resulted in increasing the grain filling in short time to escape from the stress conditions (Pandey et al., 2015; Stone, 2001).

Heat Susceptibility Index (HSI):

The heat susceptibility index (HSI) values refer to the thermotolerance of bread wheat genotypes based on reducing the grain yield losses under late sowing date compared to optimum sowing date (Pandey et al., 2015). HSI values less than 1.0 refer to the tolerant genotypes, while HIS more than 1.0 refer to the sensitive genotypes. It is found that heat susceptibility index for grain weight/plant was highly significant tolerance values (HSI < 1) for parents and F_1 crosses (Table 2, and Table 3).

Furthermore, genotype P4 (Sids 14), Misr 1 (P1) and F_1 cross P1×P4 have HSI values less than 1.0 (HSI < 1) (Table 2). Accordingly, these genotypes are considered more thermotolerant genotypes about to their grain yield/plant, Furthermore, the genotypes showing HSI values near 1.0 are moderate to late sowing, in this respect, P2 (Line 15) and F_1 crosses P2×P4, and P2×P5, have HSI values near one. A wide range of response to heat stress tolerance by delaying the sowing date of the bread wheat crop is reported (Abdallah et al., 2015; Ali and Abdul-Hamid, 2017; Khaled et al., 2013; Pandey et al., 2015).

General and Specific Combining Abilities:

General (GCA) and specific (SCA) combining ability were estimated using method 2 models 1 of (Griffing, 1956). Results present in Table 4 show the values of both general (GCA) and specific (SCA) combining ability of all the genotypes for all the studied traits. Analysis of variance of GCA and SCA show highly significant differences for all traits (Table 5), indicating that both additive and non-additive gene action controlled the genetic mechanism of these traits. The ratio of GCA/SCA variance for days to heading, days to maturity is more than unity on the two sowing dates, highlight the role of the additive gene in these traits. Whereas it is less than the unit for 1000-grain weight and grain yield/plant (Table 4), emphasizing the role of non-additive gene action. These findings of the major role of additive gene action for days to heading, maturity, and non-additive gene action for grain weight and yield/plant were reported by many studies (Ahmed et al., 2018; LjubiČIĆ et al., 2017).

General combining ability GSA effects (gi) for abilities (Table 4), results in a highlight that P2 has a negative and significant GCA effect for days to heading, days to maturity. While P2 has a positive and significant for 1000-grain weight grain yield/plant. These results indicate that this genotype could be the best candidate as one of the parental genotypes to improve any of these traits. On the other hand, results reveal negative and significant SCA effects of F1 cross P1 x P4 and P1 x P6 of days of heading traits. While, for days to maturity, negative and significant SCA effects are found in F1 crosses P2 x P4 and P2 x P5. Negative and significant SCA effects for earliness characters were also recorded by (Abd-Allah et al., 2013; Abdallah et al., 2015). Moreover, it is found a positive SCA with significant values in the F1 crosses P1×P2 and P3×P4 for 1000 grain weight on the two sowing dates. While grain yield/plant trait in F1 crosses (P1×P4 and P2×P6) has a positive and significant SCA. A similar finding was reported by (Abdallah et al., 2015; Khaled et al., 2013; Kumar et al., 2017; Yadav et al., 2017).

Gene Action (Physiological traits):

The values of additive (D) and dominance (H_1 and H_2) and its genetic analysis parameters were estimated for all the studied traits (Table 6).

Table 4. Estimates of general (GCA) and specific (SCA) combining ability effects of the bread wheat genotypes for heading (days), days to Maturity (days), 1000-grain weight (g) and Grain yield/plant (g) on two sowing dates of bread wheat.

Genotypes	Days to heading (days)		Days to maturity (days)		1000-grain weight(g)		Grain yield /plant(g)	
	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2
	GCA							
Misr 1 (P1)	-0.08	0.23	-0.47*	0.34	0.31	-1.00	-0.88**	0.24*
line15 (P2)	-0.56	-1.02	-1.07**	-1.62**	4.00**	1.05	0.23	0.33*
Line 4 (P3)	0.13	0.04**	-0.26	-0.35	0.02	5.11**	0.48	0.08
Sids 14 (p4)	-0.20	0.35**	-0.13	0.17	-1.49*	-2.21*	-1.10**	-0.26*
Shandaweel (P5)	0.32	0.17	0.68**	0.15	-0.92	-3.65**	0.49	-0.39**
Line 27 (P6)	0.38	0.23	1.24**	1.30**	-1.92**	0.71	0.77**	-0.01
$S.E._{(gi-gj)}$	0.160	0.14	0.277	0.22	0.751	0.64	0.298	0.14
	SCA							
P_1×P2	-0.07	1.27**	-0.19	0.74	3.32*	10.66**	-0.54	0.11
P1×P3	-1.26**	-0.29	-1.50**	-0.03	-0.88	-10.90**	-0.27	0.04
P1×P4	-0.60*	-1.11**	0.71	-0.05	-1.90	-5.45**	1.84**	0.88**
P1×P5	-0.45	-1.42**	0.56	0.47	6.91**	-1.73	-1.64**	-0.34
P1×P6	-1.51**	-0.48*	-1.67**	-0.68	0.61	12.83**	-1.64**	-1.20**
P2×P3	-0.78**	0.46	-0.90	0.43	-6.75**	-5.08**	-1.43*	0.33
P2×P4	-0.45	-1.36**	-1.02*	-1.60**	-1.18	12.25**	-0.38	-0.18
P2×P5	0.03	-0.67*	-1.83**	-2.07**	6.77**	-3.81**	-0.94	0.28
P2×P6	-0.53	-0.73**	0.10	-0.22	7.54**	-9.09**	7.17**	1.37**
P3×P4	-0.14	-1.42**	2.17**	1.13**	7.38**	12.88**	-0.30	-0.28
P3×P5	0.34	0.27	-0.65	-1.35**	7.27**	-1.30	5.58**	-0.98**
P3×P6	0.78**	0.21	0.29	-0.49	-0.35	7.86**	-1.89**	1.21**
P4×P5	-0.82**	0.46	-0.60	0.97*	-9.05**	-3.31**	-0.34	-0.97**
P4×P6	0.61*	0.89**	1.67**	1.65**	3.85**	5.82**	-1.13*	-0.86**
P5×P6	0.59*	0.08	0.35	0.01	1.40	10.16**	0.69	-0.89**
$SE_{(Sij-Sji)}$	0.320	0.28	0.554	0.45	1.502	1.29	0.597	0.28

*, **=significant on 0.05 and 0.01 levels of probability, respectively.
S_1= Normal sowing (22nd November), and S_2 = Late sowing (5th January).

Table 5. Mean squares of general (GCA) and specific combining ability (SCA) for days to heading (days), days to Maturity (days), 1000-grain weight (g) and Grain yield/plant (g) on two sowing dates of bread wheat

Source of variation	df	Days to heading (days)		Days to maturity (days)		1000-grain weight(g)		Grain yield/plant(g)	
		S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2
GCA	5	2.98**	6.25**	16.57**	22.05**	109.60**	225.08**	14.85**	1.89**
SCA	15	2.62**	2.96**	5.57**	3.87**	111.40**	281.96**	22.28**	2.61**
Error	40	0.31	0.23	0.92	0.59	6.77	4.98	1.07	0.23
σ2GCA/ σ2SCA		1.14	2.11	2.98	5.70	0.98	0.80	0.67	0.73

*, **=significant on 0.05 and 0.01 levels of probability, respectively.
S_1= Normal sowing (22nd November), and S_2 = Late sowing (5th January).

Table 6. Additive (D), dominance (H) genetic variances and their derived parameters for days to heading (days), days to Maturity (days), 1000-grain weight (g) and Grain yield/plant (g) on two sowing dates of bread wheat

Genetic Component	Days to heading (days)		Days to maturity (days)		1000-grain weight(g)		Grain yield/plant(g)	
	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2
Genetic Parameters D	0.33	1.38**	2.19**	2.21**	20.70*	72.45**	0.52**	0.03
H_1	3.13**	3.52**	7.75**	5.29**	132.53**	372.56**	1.58**	0.19**
H_2	2.36**	3.22**	5.37**	4.05**	121.87**	316.69**	1.18**	0.13*
F	0.40	0.72	1.17	-0.93	12.37	89.58*	0.79*	0.06
h^2	2.68**	2.20**	0.78	0.07	92.72**	151.52**	0.36*	0.01
E	0.12	0.08	0.30	0.20	2.24	2.20	0.04	0.03**
Derived Parameters $[H1/D]^{0.5}$	3.10	1.60	1.88	1.55	2.53	2.27	1.74	2.74
$[H2/4H_1]$	0.19	0.23	0.17	0.19	0.23	0.21	0.19	0.18
$[h2/H_2]$	1.13	0.68	0.14	0.02	0.76	0.48	0.31	0.09
[KD / KR]	1.50	1.39	1.33	0.76	1.27	1.75	2.56	2.52
$T_{(n)}$	33	35	51	64	23	19	16	14

*, **=significant on 0.05 and 0.01 levels of probability, respectively.
S_1= Normal sowing (22nd November) and S_2= Late sowing (5th January)

Results reveal that both additive and dominance values are high significant for days to heading on the late sowing date and on two sowing dates for days to maturity, shown the role both additive and non-additive gene action controlling this trait (Hussain et al., 2013; Kumar et al., 2017; LjubiČIĆ et al., 2017; Sedek, 2009). The dominance component (H_1) is more than (H_2), on the two sowing dates for days to heading and maturity, indicating that dominance and recessive genes are inequitably disseminated in the parent's genotypes, in which the [H_2/ $4H_1$] value is less than (0.25).

F, for the relative rate of dominant and recessive genes in the parent's genotypes, is found to be positive and insignificant for days for heading and days to maturity on normal sowing dates. Negative (F) values are observed on late sowing date for days to maturity, showing the importance of recessive alleles in this character, which was supported by the low value of KD/KR than unity for this trait. The sum of dominant alleles, as indicated by (h^2), show positive values for earliness characters on two sowing dates, showing that dominant genes controlling the genetic mechanism of this character.

The environmental component of variation (E) reveals nonsignificant values for earliness characters on the two sowing dates, revealing the unimportant role of environmental factors in determining these traits. Moreover, the degree of dominance $(H_1/D)^{0.5}$ is higher than the unity for days to heading and maturity 'earliness traits' under two sowing dates, confirming the importance of over-dominance gene action in controlling the inheritance of these traits. In addition, genes with positive and negative effects in the parent's genotypes are detected by ($H_2/4H_1$). H2/4H1 values have deviated from the theoretical value (0.25) for these traits on the two sowing dates. These results advocate a proportioned dispersal of positive and negative gene alleles in the parent's genotypes. Furthermore, narrow sense heritability values are low for days two heading (33 and 35) and moderate for days to maturity (51and 64) among two sowing dates. These findings reveal that days to heading is an important attribute contributing to weight and direct selection can be adept in the early segregation generation (Abdallah et al., 2015).

Gene action (Grain yield traits):

Results of additive (D) and dominance (H_1 and H_2) values are significant for 1000 grains weight and grain yield/plant on two sowing dates (Table 6), showing the major role of both additive and non-additive gene action in the inheritance of these traits. However, the dominance genetic effects (H_1 and H_2) values display more than the additive gene effects (D) on the two sowing dates, showing that these characters are controlled by dominance gene action and could be improved through the hybrid breeding method. The dominance component (H_1) was more than (H_2) one, on the two sowing dates, indicating that dominance and recessive genes are inequitably disseminated in the parent's genotypes, in which the [H_2/ $4H_1$] value is less than (0.25).

Also, F values are found to be positive and insignificant for 1000 grains weight, indicating that parental genotypes have more dominant alleles than recessive alleles, supported by the ratio of KD/KR. The sum of dominant alleles, as indicated by (h^2), show positive values for grains yield traits on the two sowing dates, showing that dominant genes controlling the genetic mechanism of this character.

The environmental component of variation (E) is insignificant on two sowing dates for these characters, revealing the unimportant role of environmental factors in determining these traits. While, the degree of dominance $(H_1/D)^{0.5}$ was more than unity on the three sowing dates, confirming the importance of over-dominance gene action in controlling the inheritance of these traits. The proportions of genes with positive and negative effects in the parents as indicated by ($H_2/4H_1$) were near the theoretical value (0.25) for grain yield on the three sowing dates, suggesting asymmetrical distribution of positive and negative alleles among the parental genotypes.

Consequently, the proportion of dominant and recessive genes in the parents (KD/KR) were more than unity on two sowing dates, suggesting that dominance genes were more frequent than the recessive ones in the parental genetic make-up. Furthermore, results reveal low narrow sense values for 1000 grains and grain yield/plant, indicating a major role of the non-additive gene action. These findings were reported and suggesting by (Abdallah et al., 2015; Jain et al., 2017; LjubiČIĆ et al., 2017).

Hayman graphical analysis (Physiological traits):

Graphical analysis (Wr/Vr) was performed to elaborate on the genetic relationship among the parents and genotypes (Figure 2). The regression line position on the graph discloses the average degree of dominance (Singh and Chaudhary, 1995). Result of Wr/Vr of the days to heading reveals that the regression line cuts Wr-axis below the point of origin on the early and the late sowing dates concluding the major role of overdominance gene action in the genetics of days to heading (Figure 2A). The distribution of parental genotypes along the regression lines for days to heading on the two sowings show that genotype P2 has most dominant genes, P1 possess the most recessive genes, P3, P4, P5, and P6 possess 50:50 recessive to dominant genes on the normal sowing. On the late sowing date P1, P2 and P3 had the most dominant genes, while P4 possess the most recessive genes, P5 and P6 possess 50:50 recessive to dominant genes. (Figure 2A). While Wr/Vr analysis of days to maturity on the normal sowing are inherited by overdominance, in which the regression line meets the covariance axis below the point of origin, passing the negative region (Figure 2B). Even though, under late sowing date conditions are inherited by complete dominance, resulting as the regression line passes through the point of origin. Scattering of parent's genotypes around the regression line (Figure 2B) accomplishes that genotypes P1, P2 and P6 have the most dominant genes, while P4 and P5 exhibit most recessive genes and P3 possess 75:25 recessive to dominant genes on the normal sowing date. On the late sowing date P1, P2, and P3 show the most dominant genes, while P4 and P5 exhibit the most recessive ones and P6 has possessed 50:50 recessive to dominant genes.

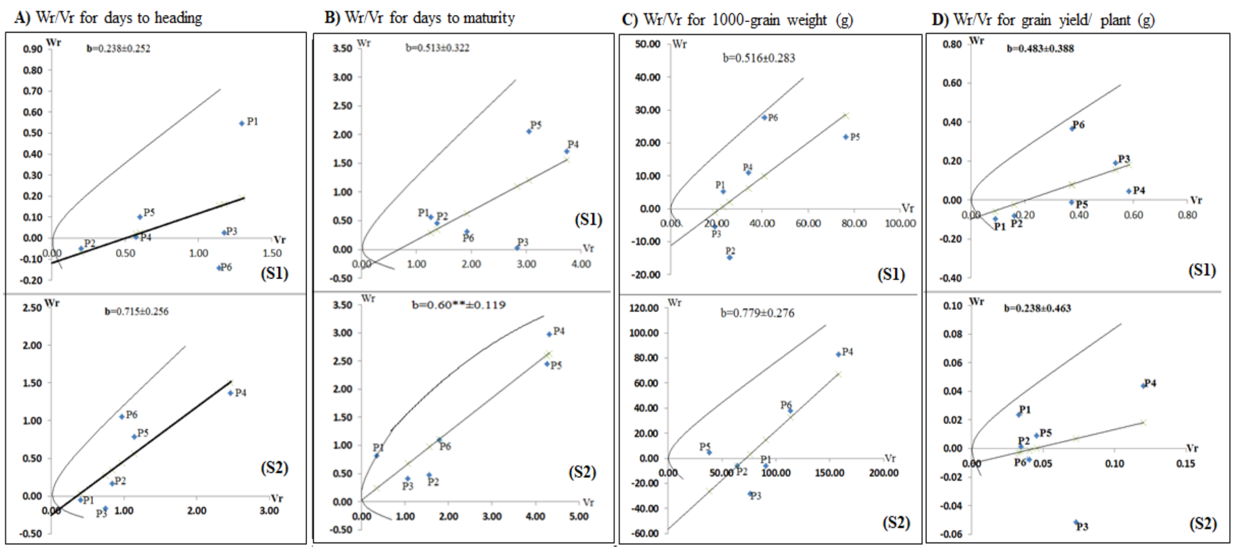

Figure 2. Covariance/Variance (Wr/Vr) graph for physiological and grain yield traits under two sowing dates; optimal sowing date (S1), and late sowing date (S2). A) Wr/Vr for days to heading. B) Wr/Vr for days to maturity. C) Wr/Vr for 1000-grain weight. D) Wr/Vr for grain yield/plant.

Hayman graphical analysis (Grain yield traits):

1000-grain weight and grain yield/plant on the two sowing dates are inherited by overdominance, proposing that selection for desirable transgressive segregates would not be possible through selection in the early generations (Figure 2C, and 2D). The pattern of distribution of parental genotypes along the regression line indicates that P5 and P6 possess the most recessive genes, while genotypes P3 and P2 contain most of the dominant genes 'near to the origin', P1 possess 25:75 recessive to dominant genes on the normal sowing. Moreover, on the late sowing Genotypes, P4 has the most recessive genes, while P5 has the most dominant genes and P2, P1 and P3 possess 25:75 recessive to dominant genes (Figure 2C). While, on grain yield/plant, dispersion of parents around the regression line for grain yield/plant indicate that genotypes P1 and P2 have the most dominant genes, while P6, P3, and P4 exhibit most recessive genes and P5 possessed 75:25 recessive to dominant genes on the normal sowing date. Moreover, on the late sowing date, wheat genotypes P1, P2, P5, and P6 has the most dominant genes, while P4 exhibited most recessive genes.

CONCLUSION

In conclusion, genetic analysis of thermotolerance wheat genotypes is very important to provide new knowledge for the heat tolerance breeding program. Physiological and yield traits show sciginfcat alterations under the study. Among our investigated genotypes, we found that Misr 1 (P1), Sids 14 (P4), and their F1 crosses presence more thermotolerance with a negative and significant SCA.

CONFLICT OF INTEREST

The authors declared that the present study was performed in the absence of any conflict of interest.

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AUTHOR CONTRIBUTIONS

All authors are conceived and designed the experiments. E. A. and M.A.A.A performed the experiment. E.A. analyzed the data. E.A. and K.Y.K. wrote the manuscript. All authors reviewed the manuscript.

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