

DETERMINING THE GENE ACTION AND COMBINING ABILITY OF F₂ BREAD WHEAT BY DIALLEL ANALYSIS

MOHAMED. A. DARWISH¹, ZEINAB, E. GHAREEB², MUHAMMAD AAMIR IQBAL³, IBRAHIM AL-ASHKAR⁴, MOHAMMAD SOHIDUL ISLAM⁵ AND AYMAN EL SABAGH^{6,7*}

¹Wheat Research Department, Field Crops Research Institute, Agricultural Research Center, Giza, Egypt

²Central Laboratory for Design and Statistical Analysis Research, Agricultural Research Center, Giza, Egypt

³Department of Chemical Engineering, Louisiana Technical University, Ruston, LA 71272, USA

⁴Department of Plant Production, College of Food and Agriculture Sciences, King Saud University, Riyadh 11451, Saudi Arabia

⁵Department of Agronomy, Hajee Mohammad Danesh Science and Technology University, Dinajpur, Bangladesh

⁶Department of Field Crops, Faculty of Agriculture, Siirt University, Siirt, Turkey

⁷Department of Agronomy, Faculty of Agriculture, Kafrelsheikh University, Kafr El-Shaikh 33516, Egypt

*Corresponding author's email: aymanelsabagh@agr.kfs.edu.eg

Abstract

For ensuring the food security under changing climate and decreasing agricultural land area, genetic improvement of yield-related traits is the prerequisite for developing newer, better-performing varieties of bread wheat. Therefore, a study was conducted at the Sakha Agricultural Research Station Farm, Egypt, for investigating the ability and nature of gene action with the mode of inheritance for the grain yield and its component traits in F₂ bread wheat for identifying the superior genotypes for three consecutive seasons. An experiment was conducted to test ten parent genotypes of bread wheat along with their half-diallel hybrids (45 F₂ segregating populations) using the randomized complete block design (RCBD) with four replications. The results revealed that general combining ability (GCA) as well as specific combining ability (SCA) had significant differences for most of the traits under study. In addition, Baker's ratio confirmed the superior role of additive gene effect in controlling yield traits of wheat. Moreover, the GT-biplot data analysis and GCA effects (\hat{g}) illustrated that the Vorobey (P₃), Giza 171 (P₁₀), Line 1 (P₁), and Line 7 (P₉) had the highest values for the yield traits. Likewise, F₂ hybrids [Line 1 (P₁) x Line 5 (P₆), Line 2 (P₂) x Vorobey (P₃), and Line 1 (P₁) x Gemmeiza 11 (P₇)] remained superior for the yield contributing traits. Furthermore, the estimation of GCA incorporating the additive component (D) underscored the significance of additive gene effects more than the SCA incorporating dominance (H₁) for the traits under investigation. Lastly, the graphical analysis of W_r/V_r with $(H_1/D)^{0.05}$ pointed that the plant height, kernels number per spike and 100-kernel weight along with grain yield in F₂ tend to be determined by additive gene effect through partial dominance.

Key words: Biplot analysis, Diallel, Gene action, General combining ability, Griffing, Hayman, Staple crop.

Introduction

Globally, sufficient production of wheat (*Triticum aestivum* L.) is crucial to ensure the food security of increasing population especially in developing countries of Asia and Africa (Siddiqui *et al.*, 2019; Choudhary *et al.*, 2021; Chowdhury *et al.*, 2021; Iqbal *et al.*, 2021; Abbas *et al.*, 2023; Hossain *et al.*, 2023). It is regarded as king cereal because it provides foods to over 36% of the global population with 20% contribution towards required calories to human population (Alghawry *et al.*, 2021; Kizilgeci *et al.*, 2021). The changing climate, increasing human population, multi-dimensional biotic and abiotic stresses (El Sabagh *et al.*, 2019), decreasing profits of cereals production, increasing prices of farm inputs, declining land area for cultivation, etc. have necessitated increasing staple crops yield on per unit area basis (Iqbal *et al.*, 2018; Ahmad *et al.*, 2021; Raza *et al.*, 2023; El Sabagh *et al.*, 2021). Currently, Egypt has become the largest importer of wheat grain in the world, with local consumption of over 19 million tons (Gomaa *et al.*, 2014). For improving wheat yield sustainably, genetic improvement of yield-related traits and hybridization depend on additive, dominant, and non-allelic interaction effects (Hussain *et al.*, 2008). Hybridization has remained one of the most potent breeding techniques to break the yield barriers through development of varieties having

pronouncedly higher yield potential. However, the understanding and identification of superior parent genotypes are of immense pertinence to initiate the launching of effective and efficient breeding programs. Interestingly, selecting parent genotypes based on solely phenotypic performance could be flawed because phenotypically superior genotypes could yield poor recombination (Dehghani *et al.*, 2013). Thus, it becomes essential to select parent genotypes on the basis of genetic potential instead of phenotypic expression. The diallel analysis was developed by Hayman (1954) that could provide in-depth information regarding gene action involved in the expression of vital yield traits of crops.

To achieve these goals, the diallel mating design could provide a useful and convenient method for estimating different genetic parameters of wheat (Sabaghnia *et al.*, 2010). Recently, it has emerged as a standard tool in plant breeding to study the inheritance of traits (Freitas Júnior *et al.*, 2006; Souza *et al.*, 2008). Several biometrical analyses have been previously explored the genetic potential for the grain yield and yield attributes in the filial F₂ generation (Fellahi *et al.*, 2017; Ljubičić *et al.*, 2017; Qabil, 2017). The half-diallel methods have certain advantages, as it gives genetic information on the inheritance of quantitative traits to select the best parental combinations for hybrids (Hayman, 1954; Griffing, 1956). Likewise, the combining ability analysis is considered the most common biometrical tool to

search out the parental genotypes from their potential to combine in hybrids (Griffing, 1956). It divides the genetic variation into general combining ability that measures the additive gene effects (AGE) and specific combining ability (SCA) that measures the dominance one. Hayman's (1954) models in F_2 generation provide clues on the nature of the gene action that are primarily involved in trait's inheritance. The AGE were the prime component in genetics whose efficient exploitation could be feasible by following phenotypic selection in F_1 generation (Abdallah *et al.*, 2015). Likewise, AGE and dominant gene effects (DGE) contributed pronouncedly to the genetics of grain yield (Badieh *et al.*, 2012; Aslam *et al.*, 2022). Therefore, genetic analysis allows for determining and obtaining promising genotypes in early segregating populations. A modified biplot called GGE (genotype, genotype x environment) biplot was proposed by Yan *et al.*, (2000) for genotypic analyses by environment data matrix that was constructed from experiments conducted in multi-environment. This method might also be utilized for analyzing two-way data including diallel data (Yan, 2001; Yan & Hunt, 2002). A biplot approach entailing diallel experimental data might effectively estimate the combining ability among different genotypes (Yan & Hunt, 2002). The prime advantages of biplot analysis compared to other biometric diallel analysis are its graphical presentation and better data interpretability, significantly enhancing the ability to understand the data patterns. The biplot approach of diallel data analysis reveals a much deeper understanding of parents (Yan & Kang, 2003). The biplot techniques for analysis of diallel data in cereals explores the combining ability and tends to distinguish the best genotypes in bread wheat (Farshadfar & Hasheminasab, 2012; Farshadfar *et al.*, 2012; Mostafavi & Zabet, 2013).

For developing genetically robust and high yielding cultivars, Cox & Murphy (1990) opined that development of a predominant genotype is more feasible if both of the parents tend to exhibit similar performance in comparison to genetic improvement which involved one superior parent in terms of one or more yield traits of wheat. However, it is emphasized that any of parent's performance could not be necessarily taken as its potential to be a good or poor combiner. Therefore, it becomes mandatory to determine the nature of gene effects along with their expression pertaining to the combining ability. Additionally, general combining ability (GCA) has been attributed to additive gene effects along with additive x additive epistasis and might be considered more flexible, at least theoretically. Contrastingly, SCA is attributable to non-additive gene action that could be owing to dominance and/or epistasis and has been declared non-fixable. Thus, there exist research and knowledge gaps pertaining to parent wheat genotypes that are genetically superior and diverse in terms of yield traits. Hence, the primary goals of this study were to employ graphical techniques for evaluating the combining ability of the examined parental bread wheat and its diallel genotypes within F_2 progenies. The specific objectives included deciphering the nature of gene action and determining the mode of inheritance for key grain yield traits in wheat. Ultimately, the overarching aim was to identify and select novel lines exhibiting superior yield potential and resistance to rusts, contributing valuable candidates to enhance wheat breeding programs.

Material and Methods

Plant genetic materials: The present experiment was carried out during three seasons from 2017/2018 to 2019/20, at Sakha Agricultural Research Station at the Agricultural Research Center, Kafr Elsheikh locality of Egypt. The geographical coordinates of the study locality were 31.10° North, 30.93° East. Ten parent genotypes of bread wheat were selected based on pronounced botanical differences among them (Table 1). Plant material was generated from hybrids among the ten-bread wheat parental genotypes to get F_2 plants.

Sowing and experimental design: All genotypes (including the selected parents and 45 F_2 populations obtained according to a half-diallel model) were sown by following the randomized complete block design (RCBD) having four replications. The sowing of the seeds was done in rows that were 4 m long and 30 cm apart, while the plants within rows were spaced by 20 cm. Two rows were reserved for each parent genotype, while 10 rows were maintained for each F_2 generation of every cross. After plants had attained physiological maturity, 30 plants of each parent genotype and 200 plants of F_2 were randomly selected for data recording pertaining to plant height, spikes number per plant, 100-kernel weight, and grain yield per plant.

Biometrical analyses: All data were subjected to analysis of variance. Data obtained from the 45 hybrids of F_2 and 10 parents were analyzed by Griffing (1956) method II, model 1. The analysis of combining ability was performed and simple correlation coefficients between all pairs of the studied traits were calculated based on the method proposed by Steel & Torrie (1987).

The analysis of the diallel data in F_2 generation was performed according to the model developed by Hayman (1954) and described by Sharma (2003). Estimates of genetic components due to the environment (E), additive effects (D), and dominance effects (H_1 , H_2 , and h^2) were determined. Additionally, different ratios in parents, as the average degree of dominance ratio (H_1/D)^{0.05}, dominant genes with positive or negative effects ratio ($H_2/4H_1$), and dominant and recessive genes ratio (K_D/K_R) were also estimated. Broad as well as narrow sense heritability (h^2_b and h^2_n) were also estimated by following the method of Mather & Jinks (1982).

Model for GGE biplot: The GGE biplots can efficiently analyze two-way data, where different experimental units are expressed in rows and columns (Yan & Hunt, 2002). Then, the GGE biplot might be modified to GGT (genotype main effect plus genotype-by-traits interaction). Yan & Rajcan (2002) used the genotype by trait (GGT) biplot for studying the genotype by recording the traits data. As different traits had atypical units, the biplot protocol was re-optimized by using the standardized mean values of all trait under investigation. The biplot analysis was performed by using the GenStat software package.

Table 1. Parents name, pedigree, and origin of 10 parental bread wheat genotypes.

Code No.	Parents name	Pedigrees	Origin
P ₁ (L1)	Line 1	KIRITATI//SERI/RAYON CGSS02Y00152S-099M-099Y-099M-11WGY-0B	Egypt
P ₂ (L2)	Line 2	SAKHA 8 / YECORA ROJO	Egypt
P ₃ (L3)	VOROBAY	VOROBAY CMSS96Y02555S-040Y-020M-050SY-020SY-6M-0Y	CIMMYT
P ₄ (L4)	Sakha 88	Sakha 88	Egypt
P ₅ (SD12)	Sids 12	BUC//7C/ALD/5/MAYA74/ON//1160.147/3/BB/GLL/4/CHAT"S"/6/MAYA/VUL//CMH74A.630/4*SXSD7096-4SD-1SD-1SD-0SD	Egypt
P ₆ (L5)	Line 5	GIZA 158 /5/ CFN /CNO "S" // RON /3/ BB / NOR 67 /4/ TL /3/ FN / TH // NAR 59*2 S10232-3S-2S-4S-0S	Egypt
P ₇ (Gem11)	Gemmeiza 11	BOW"S"/KVZ"S"/7C/SER182/3 /GIZA168/SAKHA 61 GM7892-2GM-1GM-2GM-1GM-0GM	Egypt
P ₈ (L6)	Line 6	GIZA 164 / SAKHA 61	Egypt
P ₉ (L7)	Line 7	WBLL1*2 / KIRITATI.CGSS01B00063T-099Y-099M-099M-099Y-099M-3WGY-0B.	Egypt
P ₁₀ (G171)	Giza 171	SAKHA 93 / GEMMEIZA 9 S.6-1GZ-4GZ-1GZ-2GZ-0S	Egypt

*Source: Wheat Research Department, FCRI, ARC, Egypt.

Table 2. Mean squares and Griffing analysis of variance for yield traits under investigation in F₂'s of bread wheat.

S.O.V	Df	Plant height	Number of spikes/ plant	Number of kernels/ spike	100-kernel weight	Grain yield/ plant
Replications	3	56.65**	113.72**	142.12**	1.07**	137.42**
Genotypes	54	114.19**	19.55**	132.20**	0.47**	88.14**
Parents	9	228.32**	28.96**	224.74**	0.81**	142.95**
Hybrids	44	92.58**	17.71**	106.50**	0.40**	78.89**
P <i>Vs</i> hybrid	1	37.81	15.53	430.12**	0.48*	1.92
Error	162	13.3	4.13	16.32	0.09	16.43
GCA	9	147.60**	20.30**	144.28**	0.56**	87.92**
SCA	45	4.74	1.80**	10.81**	0.03	8.86**
Error	162	3.33	1.033	4.08	0.02	4.11
Baker ratio		0.98	0.95	0.96	0.97	0.95

* and ** were significant at the p value of 0.05 and 0.01 probability levels, respectively

Results and Discussion

Analysis of genotypic variability and combining ability:

Analysis of variance depicted pronouncedly significant influences among genotypes, parents as well as hybrids for all yield traits under the investigation (Table 2). These findings explored the presence of pronouncedly higher genetic variability among the parent genotypes of wheat, and its 45 F₂ hybrids which allows for improving the studied wheat yield traits (plant height, number of spikes and kernels, and 100-kernel weight) and grain yield per plant. Similar results were obtained by Qabil (2017), Fellahi *et al.*, (2017), Abd-El-Hamid *et al.*, (2019) and Lance *et al.*, (2020), who reported a high degree of genetic variability among wheat genotypes. The parent *vs.* hybrid was highly significant and significant for the number of kernels per spike and 100-kernel weight, respectively, indicating adequate non-allelic interaction among hybrids in these traits.

As per recorded findings, the combining ability and gene action type were appropriate for estimating the traits under investigation. The significance of GCA as well as SCA for the diallel data traits have been illustrated in Table 2. The GCA variance was highly significant for all traits, indicating the importance of additive gene action in the studied traits. On the other side, SCA variance revealed highly significant non-additive for the number of spikes and kernels per spike along with grain yield per plant. Hence, the significant values of both GCA and SCA variances for most of the traits suggested that both additive and non-additive nature of gene actions had crucial roles

in the inheritance of these traits in all bread wheat genotypes. Then, combining ability employ the information about parental genetic value (as additive gene action) to produce superior hybrids (non-allelic interaction and dominance gene action).

These findings are supported by previous conclusions made by Farshadfar *et al.*, (2012) and Pagliosa *et al.*, (2017). Additionally, the research findings revealed that mean square values of GCA were recorded to be higher compared to SCA for all yield traits, whereas Baker's ratio approached near unity for all traits, indicating the importance of AGE more than non-additive ones (Baker, 1978). Therefore, GCA alone can predict the parents' performance and significance of additive gene action in controlling traits under investigation in durum wheat compared to non-additive ones (Sadeghzadeh-Ahari *et al.*, 2014). It was also reported that the plant height of wheat was qualitative that was affected by a single allele with few modifying factors, while the internodes length was found to be a quantitative characteristic which had their own unique and independent genetic patterns controlled by more than one genes. Few other related studies have demonstrated that the plant height remained positively correlated with internode length (Zhao & Wang, 2003). Thus, it was suggested that it could be useful in developing wheat breeding programs for understanding the inheritance of yield attributes.

Mean performance of the selected wheat genotypes:

The yield attributes and grain yield of parents along with their respective crosses have been described in Table 3.

Among 10 bread wheat parents, the mean values of spikes per plant varied between 10.50 and 16.90, spikes for Sids 12 (P5) and Vorobey (P3), respectively. For 100-kernel weight, the values ranged from 2.00 to 3.20g for Sakha 88 (P4) and Vorobey (P3), respectively. However, Line 2 (P2) and Vorobey (P3) recorded the minimum and maximum values for the plant height of 98.30 and 122.10 cm, the number of kernels per plant of 36.30 and 54.60, and the grain yield per plant of 19.34 and 35.32 g, respectively.

The highest values for the grain yield of 35.32, 30.76, 29.47, and 28.23 g per plant were exhibited by the Vorobey (P3), Giza 171 (P10), Line 7 (P9), and Line 1 (P1), respectively. Meanwhile, the Vorobey (P3), Line 6 (P8), Sakha 88 (P4), and Line 2 (P2) with showed the maximum values for spikes number per spike of 16.90, 15.60, 15.50, and 14.80, respectively. On the other side, the parent Vorobey (P3), Sids 12 (P5), Line 7 (P9), and Line 5 (P6) possessed the maximum values for the kernels number per spike with 54.60, 53.10, 46.90, and 45.70, respectively. Then, Vorobey (P3) recorded the highest performance for all related traits for grain yield per plant. Among hybrids as depicted in Table 3, 19 ones showed the highest mean values, more than the average mean values of 25.97 and 25.98 g for parents and hybrids, respectively. Hybrids H16, H23, H39, H110, H310, H18, and H35 involving the previous highly grain yield-related traits in parents recorded the highest values of grain yield (36.41, 32.91, 32.65, 32.37, 30.91, 30.40 and 29.49 g/plant, respectively). H16 hybrid concluded Line 1 (P1) with high grain yield x Line 5 (P6) and with a high number of kernels per plant in F₂'s. However, most of the hybrids (H23, H39, H310, and H35) involving one of these parents exhibited the highest value of grain yield coupled with another highest yield traits as Line 2 (P2) x Vorobey (P3), Vorobey (P3) x Line 7 (P9), Vorobey (P3) x Giza 171 (P10) and Vorobey (P3) x Sids 12 (P5) in F₂'s. These findings suggest that the parents Vorobey (P3), Giza 171 (P10), Line 7 (P9) and Line 1 (P1)) and F₂ hybrids [Line 1 (P1) x Line 5 (P6), Line 2 (P2) x Vorobey (P3), Vorobey (P3) x Line 7 (P9), Line 1 (P1) x Giza 171 (P10), Vorobey (P3) x Giza 171 (P10), Line 1 (P1) x Line 6 (P8) and Vorobey (P3) x Sids 12 (P5)] could be potent sources for improving the grain yield of bread wheat through a breeding program. Similar results were obtained by Farshadfar and Hasheminasab (2013) and Abdel Khalik *et al.*, (2018) pertaining to the grain yield.

Combining ability analysis of wheat genotypes

General combining ability: The GCA effects (\hat{g}_i) of each parent for all studied F₂ traits have been illustrated in Table 4 and Fig. 1B. These estimates are being used to compare each parent with other genotypes and facilitate selection of the desired parents with significant and high positive values for improving the grain yield. Comparison of the \hat{g}_i effects of each parent revealed that the six parental genotypes *viz.* Vorobey (P3), Line 5 (P6), Gemmeiza 11 (P7), Line 6 (P8), Line 7 (P9), and Giza 171 (P10) had the highest significant positive effects for the plant height. Meanwhile, the four parental genotypes *viz.* Line 1 (P1), Line 2 (P2), Vorobey (P3), and Sakha 88 (P4) gave highly significant desirable positive effects for the number of

spikes per plant. For kernels number per plant, three parent genotypes *viz.* Vorobey (P3), Sids 12 (P5), and Giza 171 (P10) showed the desirable highly significant and significant positive \hat{g}_i effects. The four parental genotypes, *viz.* Line 1 (P1), Vorobey (P3), Line 6 (P8), and Line 7 (P9) showed significant and highly significant positive \hat{g}_i effects for the 100- kernel weight. Regarding the grain yield per plant, four parental genotypes of Line 1 (P1), Vorobey (P3), Line 7 (P9), and Giza 171 (P10), expressed highly pronounced positive \hat{g}_i effects. Based on recorded findings, the desirable parent genotypes in each trait could be considered a good combiner for this trait. However, other negative significant, or insignificant parents had undesirable \hat{g}_i effects.

A biplot graph was used to compare parental genotypes based on the yield attributes and grain yield of wheat to identify and select the best \hat{g}_i effects in the studied F₂ wheat populations are shown in Fig. 1A. The GT biplot of yield traits explained by 98.37% of the total variation of the standardized data. The principal components (PC1 and PC2) explained by 66.81% and 31.56%, respectively. This relatively high proportion exhibited an intricate association between genotypes and yield traits under investigation. The results of first two PC results demonstrated a higher percentage (more than 60%) of the total variation which indicated the appropriateness of fit for the GT biplot model (Yan and Kang, 2003). Similar to these results, previous studies by Malla *et al.*, (2010), Boćanski *et al.*, (2011), Pagliosa *et al.*, (2017), and Kendal (2019) have also reported similar conclusions. The polygon sides reveal effective comparison between neighboring vertex genotypes. The parents Vorobey (P3) and Line 1 (P1) were on the positive end of both x and y axes, indicating that they had positive GCA effects for the grain yield (Gy) and the number of spikes per plant (Sp) (Yan & Hunt, 2002; Malla *et al.*, 2010; Pagliosa *et al.*, 2017). There is a similarity between the Griffing and GGE biplot analysis results reported by Darvishzadeh *et al.*, (2009), Malla *et al.*, (2010), Boćanski *et al.*, (2011), Pagliosa *et al.*, (2017), Kendal (2019). Finally, the GT biplot graph has been considered a successful and effective technique beside or instead of the diallel analysis method to predict combining ability and distinguish the most performing bread wheat genotype. Interestingly, \hat{g}_i effects associated with each parent explored parental genotype of Vorobey (P3) was an excellent combiner for the several traits (grain yield and yield contributing traits), followed by Line 1 (P1), Line 7 (P9) and Giza 171 (P10). Therefore, these parents are expected to have more additive genes for the desirable traits, and might be taken as a potential combiner for improving the grain yield. These findings are in agreement with those of reported by Pagliosa *et al.*, (2017) and Ahmad *et al.*, (2020) who suggested that superior parental genotypes must be utilized used in hybridization programs in order to develop superior recombinants for yield traits of wheat crop. Moreover, the outcomes of this trial explicitly reflect the existence of scope for combining the component traits of wheat parent genotypes, which led to improved yield attributes and grain yield in following generations.

Table 3. Yield attributes of ten bread wheat parents as well as their hybrids.

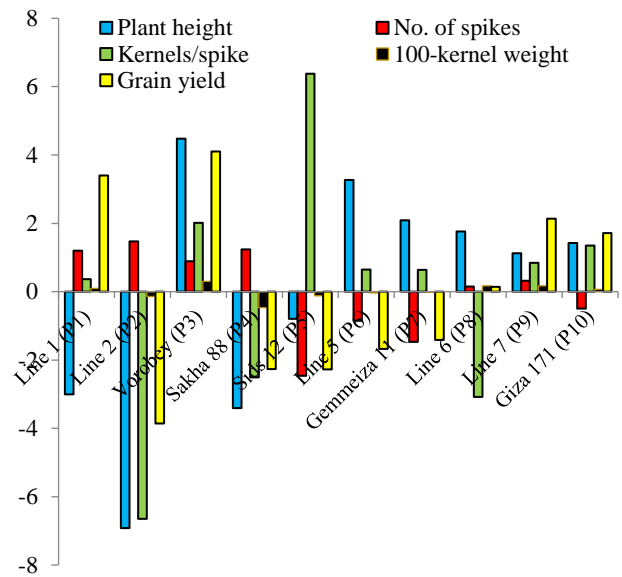
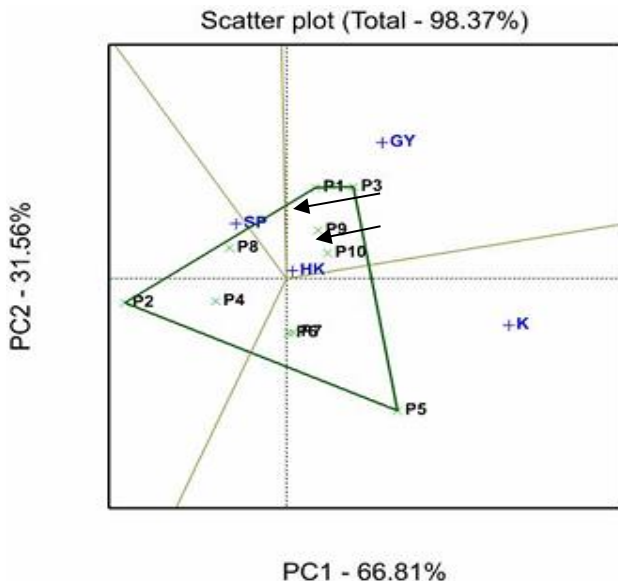
Genotypes	Plant height (cm)	Number of spikes/ plant	Number of kernels/ spike	100-kernel weight (g)	Grain yield / plant (g)
Line 1 (P1)	110.50	14.70	45.50	2.90	28.23
Line 2 (P2)	98.30	14.80	36.30	2.60	19.34
Vorobey (P3)	122.10	16.90	54.60	3.20	35.32
Sakha 88 (P4)	104.20	15.50	38.60	2.00	23.38
Sids 12 (P5)	111.00	10.50	53.10	2.60	22.49
Line 5 (P6)	120.80	12.90	45.70	2.60	22.55
Gemmeiza 11 (P7)	116.70	11.40	43.60	2.70	22.55
Line 6 (P8)	119.20	15.60	40.20	2.90	25.64
Line 7 (P9)	112.90	13.700	46.90	3.10	29.47
Giza 171 (P10)	116.80	14.40	45.00	3.00	30.76
Parents mean	113.30	14.00	45.00	2.80	25.97
H12	101.90	15.30	40.40	2.70	24.90
H13	112.60	15.40	40.10	2.80	24.11
H14	109.30	16.80	41.80	2.60	29.15
H15	107.90	14.00	48.70	2.90	29.41
H16	114.90	18.20	42.80	3.00	36.41
H17	115.50	14.20	41.70	3.00	29.36
H18	112.30	16.50	40.80	3.20	30.40
H19	110.90	14.60	44.10	3.10	26.82
H110	112.70	14.70	48.40	3.10	32.37
H23	112.10	16.50	41.30	3.30	32.91
H24	101.30	16.90	34.40	2.30	19.43
H25	107.00	11.80	39.20	2.60	20.68
H26	110.50	16.40	38.00	2.80	25.66
H27	109.30	15.10	35.90	2.70	21.93
H28	110.20	16.80	34.30	2.90	23.35
H29	110.60	16.90	35.90	2.80	23.29
H210	112.90	15.10	36.10	2.80	22.28
H34	117.90	13.80	45.00	2.90	26.25
H35	121.10	14.20	47.70	3.00	29.49
H36	120.30	13.20	42.20	3.00	25.22
H37	122.60	13.70	44.20	3.20	27.26
H38	119.60	14.30	40.40	3.20	28.89
H39	119.30	16.60	41.50	3.20	32.65
H310	119.60	14.40	42.70	3.50	30.91
H45	113.10	15.60	44.30	2.50	25.34
H46	113.10	15.20	40.00	2.30	21.78
H47	114.30	16.50	42.30	2.60	23.16
H48	111.80	15.30	38.50	2.50	21.67
H49	113.90	16.50	41.60	2.60	26.92
H410	111.40	15.20	41.90	2.50	25.78
H56	113.30	11.90	50.70	2.80	23.62
H57	115.30	11.60	48.60	2.50	22.90
H58	117.70	12.90	47.60	3.10	23.81
H59	114.80	13.20	46.10	2.70	25.48
H510	113.60	11.60	51.40	2.80	23.30
H67	119.20	12.50	43.40	2.70	23.70
H68	120.00	12.90	38.30	3.00	24.15
H69	124.20	12.90	42.10	3.00	23.44
H610	117.70	13.10	45.90	2.80	23.02
H78	115.20	11.60	42.40	2.90	21.73
H79	117.20	13.10	47.20	3.00	27.09
H710	118.50	12.90	43.60	2.80	24.04
H89	115.40	15.40	41.10	3.10	28.58
H810	115.90	14.10	40.50	2.70	29.05
H910	116.80	15.00	43.30	2.90	27.64
Hybrids mean	114.30	14.50	42.40	2.90	25.98
LSD _{0.05}	5.50	2.70	5.70	0.40	5.53

H_{ij}: Hybrid female * Male

Table 4. Estimates of GCA effects (\hat{g}_i) for studied traits in F₂'s bread wheat parents.

Parents	Plant height	Number of spikes/ plant	Number of kernels/ spike	100-kernel weight	Grain yield/ plant
Line 1 (P1)	-3.01**	1.20**	0.37	0.09*	3.40**
Line 2 (P2)	-6.92**	1.47**	-6.65**	-0.14**	-3.86**
Vorobey (P3)	4.48**	0.89**	2.01**	0.30**	4.10**
Sakha 88 (P4)	-3.41**	1.24**	-2.51**	-0.47**	-2.27**
Sids 12 (P5)	-0.80	-2.46**	6.38**	-0.12**	-2.28**
Line 5 (P6)	3.27**	-0.85**	0.65	-0.04	-1.68**
Gemmeiza 11 (P7)	2.09**	-1.47**	0.64	-0.02	-1.41*
Line 6 (P8)	1.76**	0.15	-3.08**	0.17**	0.14
Line 7 (P9)	1.12*	0.32	0.84	0.17**	2.14**
Giza 171 (P10)	1.42*	-0.50	1.35*	0.07	1.71**
S.E. (gi-gj)	0.74	0.41	0.82	0.06	0.83

* and ** Significant at the 0.05 and significant at the 0.01 probability levels, respectively



Sp: number of spikes/plant, K: number of kernels/plant, Hk: 100-kernel weight, and Gy: grain yield

Fig. 1. Graphs based on yield attributes and grain yield, showing the best combining ability (\hat{g}_i) effects in F₂'s bread wheat.

Concerning hybrid combinations, the values of SCA effects (\hat{S}_{ij}) have been presented in Table 5. Three hybrids (P₁×P₆, P₄×P₅, and P₄×P₇) exhibited highly significant values for the number of spikes per plant. Only one hybrid (P₅×P₁₀) had highly substantial positive \hat{S}_{ij} effects for the number of kernels per plant, and hybrid (P₃×P₁₀) for the 100-kernel weight. Meanwhile, six hybrids had highly significant values in P₁×P₆, P₂×P₃ and P₁×P₇, and significant in P₂×P₆, P₄×P₅, and P₈×P₁₀ for grain yield per plant. Therefore, for the GCA, the Vorobey (P3), Line 1 (P1), Line 7 (P9), and Giza 171 (P10) can be considered as the most efficient genotypes based on their performance, and the three hybrids [Line 1 (P₁) x Line 5 (P₆), Line 2 (P₂) x Vorobey (P₃) and Line 1 (P₁) x Gemmeiza 11 (P₇)] had the highest values for the grain yield. The trend of the \hat{S}_{ij} effect for the grain yield was more or less in agreement with the results reported by Pagliosa *et al.*, (2017) and Ahmad *et al.*, (2020). Therefore, such wheat hybrid combinations are promising for production improvement as they showed high \hat{S}_{ij} effects and involved one of the parents as an excellent general combiner.

Moreover, the gene action understanding of such polygenic characteristics could be essential for formulating

genetic strategies to improve wheat crop. Thus gene effects estimate and genetic variance investigated and interpreted in the present study could be helpful in understanding the genetic potential of the parent varieties of wheat and their subsequent use in genetic improvement of wheat.

Genetic parameter analysis in F₂ progenies: The variance's genetic components along with estimates of their derived parameters have been illustrated in Table 6. The nature of gene action controlling the inheritance of yield and its components revealed that the environmental variance (E) estimates were significant for all yield attributes 100-kernel weight, exploring that these were significantly affected by environment in the wheat F₂ populations of this experiment. Additive component (D) remained pronouncedly significant for all traits (plant height, spikes number per plant, kernels number per plant and 100-kernel weight along with grain yield), suggesting the importance of additive effects in the inheritance and selection of desired traits in wheat for segregating the generations could be effective. Dominance components of variation of H₁ and of H₂ remained pronouncedly significant for traits like plant

height, spikes and kernel number and significant for the grain yield per plant. Wherever, the H_1 estimate was greater than H_2 in F_2 , indicating that both positive as well negative alleles at loci for yield traits were not proportionally equal for parents. Meanwhile, the D estimates remained higher than H_1 , suggesting that additive genetic variance was comparatively more vital than dominance (non-additive) variance, and it might play prime role in the inheritance of most studied traits. Similar findings were reported by Al-Naggar *et al.*,

(2015, 2017), Qabil (2017), Ljubičić *et al.*, (2017), Fellahi *et al.*, (2017), and Ahmad *et al.*, (2020). Estimates for the average degree of dominance (H_1/D)^{0.5} remained less than 1 for all yield traits, indicating the existence of partial dominance gene action in controlling the inheritance of studied traits, and could be even more improved by individual phenotypic selection in F_1 generation. These results are in concurrence with those of Al-Naggar *et al.*, (2015, 2017) in F_2 generation, Ljubičić *et al.*, (2017) and Ahmad *et al.*, (2020).

Table 5. Estimation of specific combining ability effects (\hat{S}_{ij}) for yield traits under investigation in F_2 's d wheat.

Hybrids	Plant height	Number of spikes/ plant	Number of kernels/ spike	100-kernel weight	Grain yield/ plant
H12	-2.28	-0.67	0.76	-0.12	-0.70
H13	-2.97	-0.70	-5.40**	-0.35**	-8.22**
H14	1.62	0.80	0.45	0.14	2.42
H15	-2.38	0.61	0.28	0.10	1.83
H16	0.54	3.21**	-1.42	0.15	9.10**
H17	2.33	0.44	-0.61	0.24	4.92**
H18	-0.54	0.79	-0.83	0.12	0.77
H19	-1.32	-0.82	-0.03	-0.01	-3.13
H110	0.14	-0.03	2.31	-0.03	0.49
H23	0.39	1.10	1.61	0.21	6.31**
H24	-2.51	-1.20	-0.47	0.05	-3.34*
H25	0.63	-1.19	-6.43**	0.00	-1.39
H26	0.00	1.38	0.31	0.04	3.42*
H27	0.03	1.02	-2.54	0.02	-0.13
H28	1.27	0.96	-0.72	0.10	-0.63
H29	2.30	1.42	-3.00	-0.18	-0.88
H210	4.27**	-0.41	-1.40	0.04	-1.10
H34	2.72	-2.13*	1.61	0.17	-1.16
H35	3.28*	0.71	-2.50	0.02	1.83
H36	-1.58	-1.14	-2.31	0.02	-2.34
H37	1.87	0.54	-5.44**	-0.01	-1.34
H38	-0.73	-1.95*	-1.98	-0.11	-0.71
H39	-0.48	0.56	-5.45**	0.06	1.99
H310	-0.47	0.08	-2.96	0.46**	-0.71
H45	3.16*	2.72**	-2.18	0.11	3.34*
H46	-0.87	0.68	-1.56	-0.29*	-2.21
H47	1.48	2.35**	1.07	0.14	-0.23
H48	-0.65	-0.33	-0.21	-0.07	-3.02
H49	2.05	1.43	1.77	0.07	3.13
H410	-0.77	-0.35	-0.09	0.06	0.16
H56	-3.35*	0.02	2.88	0.15	0.98
H57	-0.09	-0.64	0.25	-0.27*	-0.58
H58	2.64	0.44	2.83	0.20	1.00
H59	0.31	-0.06	-1.67	-0.23	-1.67
H510	-1.19	-1.47	5.46**	0.03	-2.28
H67	-0.30	-0.36	-0.08	-0.03	-0.07
H68	0.81	-1.46	-3.63*	0.22	-1.11
H69	5.71**	-1.64	-1.55	0.11	-3.70*
H610	-1.13	0.34	1.39	-0.10	-1.65
H78	-2.82	-1.69*	3.09	0.00	-2.31
H79	-0.14	-0.11	2.24	0.12	1.61
H710	0.84	0.33	-1.39	-0.06	-2.11
H89	-1.64	1.13	0.42	0.06	2.05
H810	-1.45	-0.46	-1.68	-0.21	3.59*
H910	0.11	1.41	-0.87	-0.14	-0.25
S.E. (sij - sji)	2.10	1.17	2.33	0.17	2.34

* and ** Significant at the 0.05 and significant at the 0.01 probability levels, respectively

Table 6. Estimation of genetic variables for studied traits in the wheat F₂ populations.

	Plant height	Number of spikes/ plant	Number of kernels/ spike	100-kernel weight	Grain yield/ plant
E	3.52**	1.53**	4.65**	0.03	4.66**
D	53.56**	5.71**	51.53**	0.17**	31.08**
H1	12.15**	4.23**	37.97**	0.03	25.23*
H2	9.81**	3.28**	23.59**	0.04*	24.66*
h ²	2.48	0.99	40.91**	0.04	-1.49
(H1/D) ^{0.5}	0.48	0.86	0.86	0.42	0.90
H ₂ /4H ₁	0.20	0.19	0.16	0.13	0.24
KD/KR	1.38	0.99	1.49	0.75	1.15
h ² _B	0.88	0.73	0.87	0.77	0.81
h ² _n	0.80	0.59	0.70	0.69	0.56

* and ** Significant at the 0.05 and significant at the 0.01 probability levels, respectively

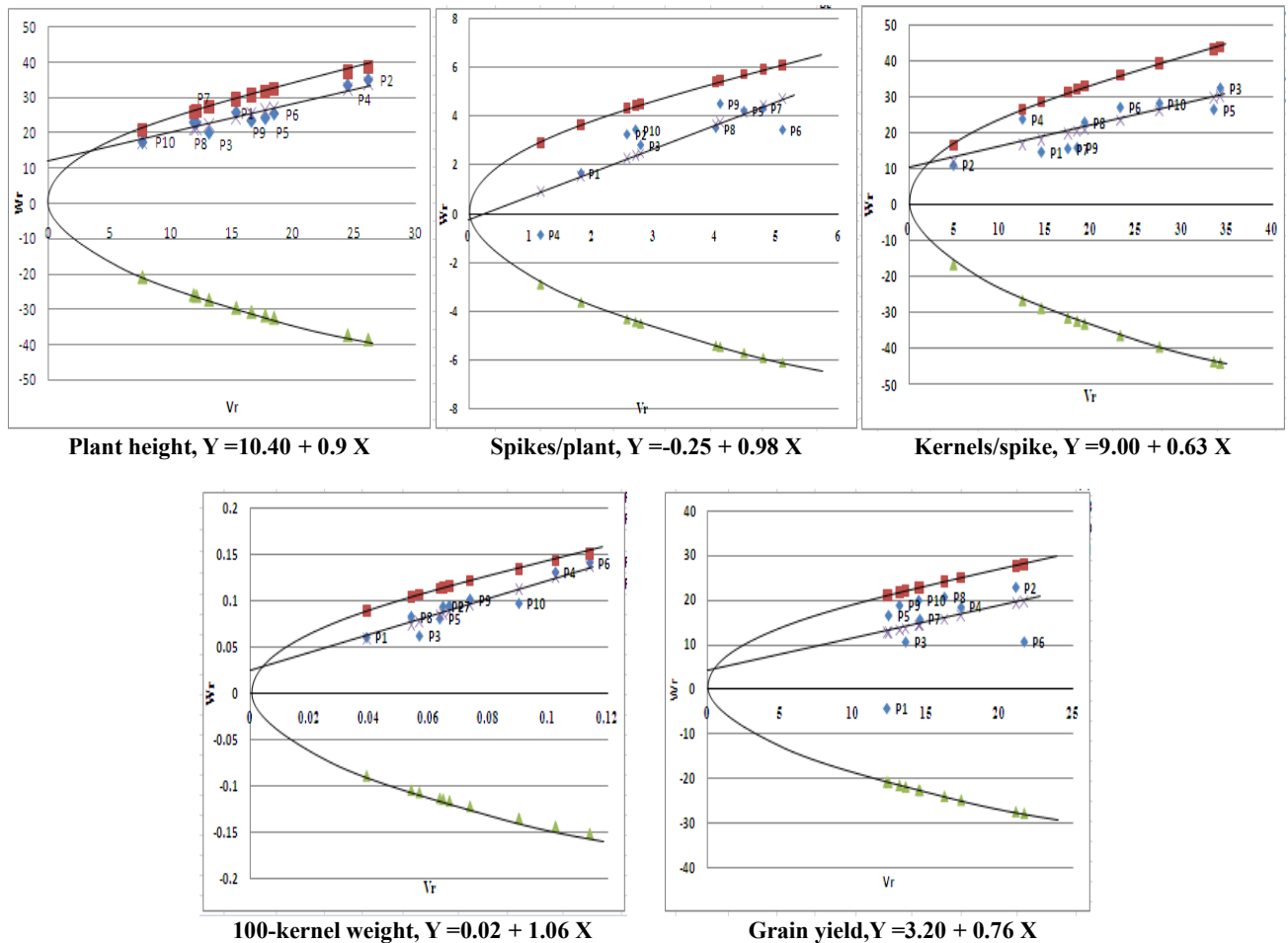


Fig. 2. Regression graph of (Wr/Vr) relationships for different traits of parental wheat genotypes.

Overall dominant effects of heterozygous loci (h²) remained pronouncedly significant for the number of kernels per plant, confirming the presence of many dominant genes in F₂ for this trait in the parental genotypes. The proportion of genes in the parents (H₂/4H₁) had values lower than 0.25 with positive effects for all the traits, suggesting the positive dominant genes symmetrical distribution in parents for the grain yield per plant (nearest value to 0.25) and asymmetrical distribution of positive and negative alleles in the parents in other traits of F₂ (lower ratios). For the K_D/K_R ratio (total number of dominant alleles to the recessive alleles) remained greater

than 1 for the plant height, number of kernels per spike and grain yield per plant, indicating the more dominant alleles presence in inheritance of these traits in F₂ generation (Ljubičić *et al.*, 2017; Ahmad *et al.*, 2020). However, the K_D/K_R ratio was less than one for the number of spikes per plant and 100-kernel weight, pointing to more recessive alleles in the parents than dominant ones in F₂. Broad-sense heritability (h_b²) and narrow-sense heritability (h_n²) for all the traits in F₂ were estimated and are tabulated in Table 6. The h_b² in F₂ estimate remained high for all the studied traits, and ranged from 0.73 for the number of spikes per plant to 0.88 for the plant height. However, the h_n² in F₂

was generally lower than h_b^2 , and ranged from 0.56 for the grain yield per plant to 0.80 for the plant height. In general, the traits such as the plant height, number of kernels per spike, and 100-kernel weight had higher heritable values. High estimates in F_2 heritability indicated that selection based on mean could potentially result in better wheat traits in early segregating generation F_2 s. Similar to our findings, previously a number of studies have reported such conclusions such as by Qabil (2017), Al-Naggar *et al.*, (2017) and Wasaya *et al.*, (2023).

Graphical diallel analysis: Graphical analyses (GDA) based on the regression of W_r of array variance (V_r), for depicting the inheritance for the studied traits in F_2 s, have been illustrated in Figure 2. The regression line of the trait that intersects the W_r axis above the origin point showed partial dominance. Meanwhile, axis below the origin's point indicated over-dominance with additive gene action for these traits. The parental arrays distribution along the line of regression suggested dominant and recessive alleles wide distribution among the parents. The scattering of parental arrays provided useful insights pertaining to the presence of varying alleles in different parents, which might be exploited further for the selection of parents in order to improve the desired traits in wheat.

Relationship of W_r/V_r parabola graph with yield traits have been illustrated in Fig. 2. The W_r/V_r graph constructed for plant height, kernels number per spike, 100-kernel weight and grain yield in F_2 revealed that the regression line intercepted the W_r -axis over the origin point of origin (intercept = positive values) that indicated partial dominance presence. Meanwhile, the regression line below the origin for the number of spikes per plant trait in F_2 's showed the over dominance or epistasis (inter-allelic interaction) effects in the inheritance of this trait. In the parabola graph, parental arrays distribution along the regression line showed that the closest parental genotypes to the origin point of the regression graph were P10, P7, P8, and P3 for the tallest plants. In contrast, the parents P4, P1, P2, and P3 for the spikes per plant, P2, P4, and P1 for the kernels per spike, P1, P8, and P3 for the 100-kernel weight and P1, P5, and P3 for the grain yield per plant, indicating dominant genes association for these traits. On the contrary, the farthest parental genotypes from the origin of the regression graph were P2 for the plant height, P3 for the number of kernels per spike, and P6 for the spikes per plant, 100-kernel weight, and grain yield per plant possessed the maximum recessive genes for these traits. These results corroborate with the findings of Rabbani *et al.*, (2009), Al-Naggar *et al.*, (2015), Fellahi *et al.*, (2017), Qabil (2017) and Ljubičić *et al.*, (2017).

Conclusion

The detailed analysis of combining ability was estimated based on the significant differences in results that indicate significant genetic variation among the studied genotypes (10 parental genotypes and 45 F_2 hybrids) for different yield traits. Both GCA as well as SCA variances remained significant for most of yield traits under investigation. Meanwhile, the GCA was recorded to be higher compared to SCA, suggesting the importance of

AGE more than non-additive effects in expressing the yield traits of wheat under investigation. Therefore, selection among the early F_2 segregating generations should be effective for improving these bread wheat genotypes. Graphically, the GT biplot data analysis and the GCA effects illustrated that Vorobey (P3), Giza 171 (P10), Line1 (P1), and Line 7 (P9) were the highest values for the yield traits. As well as, F_2 hybrids (Line 1 (P_1) x Line 5 (P_6), Line 2 (P_2) x Vorobey (P_3), and Line 1 (P_1) x Gemmeiza 11 (P_7)) had the highest ones for the yield traits. This study concluded that selection would be effective in F_2 improving the grain yield in early segregating generations. The graphical analysis with W_r/V_r pointed out that the plant height, kernels number per spike and 100-kernel weight along with grain yield in F_2 are controlled by the AGE, thence selection should be adequate for improving these traits. Thus, selection in segregation generation could be delayed for the spikes per plant trait. Moreover, these estimates could be of high assistance in formulating effective and efficient breeding procedure to impart pronounced improvement in wheat crop for ensuring food security of rapidly increasing populace.

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