



## Response of the Gene Actions Governing Grain Yield and Quality Traits in Wheat Parents and Their F<sub>1</sub> Progenies to Decreasing Soil-N Rate

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### Authors' contributions

This work was carried out in collaboration between all authors. Author AMMAN designed the study, wrote the protocol, produced the initial draft of manuscript and interpreted the data. Author ZER anchored the field study, gathered the initial data and performed preliminary data analysis. Authors RS and MMAEA managed the literature searches. All authors read and approved the final manuscript.

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### ABSTRACT

To start an accurate wheat breeding program for improving low-N tolerance, information on the type of gene action controlling the inheritance of grain yield and quality traits under contrasting N environments should be available, which is the objective of the present investigation. The diallel crosses (except reciprocals) among six divergent parents in low-N tolerance were made. Parents and F<sub>1</sub> crosses were evaluated in two seasons under two N environments; namely 0 kg N/fed (low-N) and 75 kg N/fed (high-N) in two separate experiments using a randomized complete block design with 3 replications. Results of analysis of combining ability across seasons showed that variances due to both general (GCA) and specific (SCA) combining ability were significant for all studied yield and quality traits, indicating the involvement of additive and non-additive types of genes in controlling these traits. Parents and F<sub>1</sub> crosses thus have different GCA and SCA effects,

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respectively. The best general combiners with positive effects for improvement of low-N tolerance were L26, L27 and L25 parents. Under low-N conditions, the best specific combinations for improvement of low-N tolerance were L25 x Gz168, Gem9 x Gz168 and Gem7 x Gem 9. Hayman analysis of variance indicated that spikes/plant (SPP), grains/spike (GPS), harvest index (HI) and grain yield/plant (GYPP) were controlled by additive and non-additive types of gene action, while 100 grain weight (100 GW) was controlled by an additive type of gene action. A high narrow sense heritability estimate was observed for GYPP (66.32%), SPP (42.52%), 100 GW (33.11%) and GPS (21.80%) under low-N.

**Keywords:** *Triticum aestivum*; low-N tolerance; diallel analysis; gene action; heritability;  $V_r$ - $W_r$  graph; combining ability.

## 1. INTRODUCTION

Wheat is one of the most important cereal crops of the world and provides over 20% of calories and protein for human nutrition for over 35% of the world's population in more than 40 countries including Egypt. Across the last five years, the average annual consumption of wheat grains is about 14 million tons, while the average annual local production is about 8 million tons with an average grain yield of 18.0 ardab / feddan (6.43 t/ha) [1]. Therefore, the gap between annual local production and consumption is about 6 million tons. This gap could be narrowed by increasing local production of wheat via two ways. The first way is through vertical expansion, i.e. increasing wheat production per unit area through the development of new cultivars of high yielding ability, early maturity, resistance to biotic and abiotic stresses, and the adoption of recommended cultural practices for growing these cultivars. The second way is through the horizontal expansion, i.e., by increasing the area cultivated with wheat. Potential expansion of wheat area is only possible in the Egyptian deserts. But the soil in these areas is sandy and very poor in nutrients required by wheat plants especially nitrogen. Using low-N tolerant wheat cultivars that consume less N fertilizer can tolerate nitrogen deficit in the soil could solve this problem.

To start an effective selection program for low-N tolerance in segregating generations of wheat hybrids, the additive genetic variance should play a major role in the inheritance of such adaptive traits. The type of gene action for agronomic and yield characteristics in bread wheat under low-N and high-N conditions was studied by several investigators, who indicated the role of both additive and dominance gene effects under both low-N stress and non-stress conditions [2-4] for yield and yield components. Additive was more important than dominance variance under both

conditions in controlling the inheritance of grain yield in wheat [5-7]. On the other hand, non-additive variance was more important than additive variance under low-N stress in the inheritance of wheat grain yield [8-10]. Moreover, the overdominance type of gene action which controlled grain yield per plant under high-N changed into partial dominance under low-N stress as reported by Al-Naggar et al. [11] and Subhani and Chowdhry [12].

Variation is partitioned into heritable and non heritable components, in order to estimate suitable genetic parameters such as genetic coefficients of variation, heritability estimates and gene action. The improvement of wheat yield is dependent upon a better understanding of the type of gene action underlying the inheritance of yield and its contributing characters. Genotype by environment interaction is often described as inconsistent differences from one environment to another [13].

The increase in grain yield by increasing N-levels may be due to the improved growth which may account for the superiority of yield components. In most of the wheat breeding programs, the materials in the segregating generations are grown under high fertility conditions till homozygosity is nearly attained and progenies are ready for bulking. Soil fertility as an environmental factor may differ from soil to another and might affect the assessment of characters in breeding programs, especially nitrogen levels.

The present work was carried out to study gene action, heritability and predicated genetic gain for yield and its components in bread wheat using  $F_1$  diallel crosses under low and high input level of nitrogen fertilizer. The ultimate goal of this study is to test the effect of two nitrogen levels, i.e. low (0 kg N/fed) and high (75 kg N/fed) level (recommended) on the different genetic

parameters controlling grain yield and its components and grain protein content and identifying the most promising genotypes to be involved in breeding programs for tolerance to low level of nitrogen fertilizer to sustain clean environment and hoping high grain yield with less nitrogen fertilizer to decrease costs in farmers fields.

## 2. MATERIALS AND METHODS

This study was carried out at Giza Research Station of the Agricultural Research Center(ARC), Giza Egypt (30° 02'N latitude and 31° 13'E longitude with an altitude of 22.50 meters above sea level), in 2005/2006 season and at Noubarya Research Station of the ARC, Noubarya, Egypt (30° 66'N latitude and 30° 06' E longitude with an altitude of 15.00 meters above sea level), in 2006/2007, 2007/2008 and 2008/2009 seasons.

### 2.1 Breeding Materials

Six bread wheat genotypes (*Triticum aestivum* L.) were chosen for their divergence in tolerance to low nitrogen, based on previous field screening carried out by Wheat Res. Dept., Field Crops Res. Inst., ARC, Egypt (Table 1).

### 2.2 Making the F<sub>1</sub> Diallel Crosses

In season 2005/2006, a half diallel of crosses involving the six parents (without reciprocals) was done at Giza Agric. Res. Stat., Agric. Res. Center, to obtain the F<sub>1</sub> seeds of 15 crosses. In summer 2006, a part of F<sub>1</sub> seeds was sown in greenhouse of Wheat Res. Dept. under controlled conditions to obtain the F<sub>2</sub> seeds. In season 2007/2008, the half diallel of crosses was again done to increase quantity of F<sub>1</sub> seeds.

### 2.3 Field Evaluation of 6 Parents and 15 F<sub>1</sub>'s

In the seasons 2007/2008, 2008/2009, parents (6), and F<sub>1</sub>'s (15) were sown on 17<sup>th</sup> of November each season in the field of Noubarya Res. Stat., under two levels of nitrogen fertilizer; the low level was 0 kg N/fed, i.e. without fertilization (LN) and the high level was 75 kg N/ feddan (HN); this is the recommended level of Ministry of Agriculture. This level of nitrogen fertilizer (in the form of Urea) was added in two equal doses, the first dose was added just before the sowing irrigation and the second dose just before the

second irrigation (21 days after irrigation). Two experiments were carried out, one for low-N and other for high-N, using a randomized complete block design with three replications. Each parent or F<sub>1</sub> was sown in two rows; each row was three meter long; spaces between rows were 30 cm and 10 cm between plants, and the plot size was 1.8 m<sup>2</sup>. All other agricultural practices were done according to the recommendation of Ministry of Agriculture for growing wheat in Noubarya region.

The soil analysis of the experimental soil at Noubarya Research Station, as an average of the two growing seasons, indicated that the soil is sandy loam (67.86% sand, 7.00% silt and 25.14% clay), the pH is 8.93, the EC is 0.55 dSm<sup>-1</sup>, the soluble cations in meq l<sup>-1</sup> are Ca<sup>2+</sup> (5.30), K<sup>+</sup> (0.70), Na<sup>+</sup> (0.31), Mg<sup>2+</sup> (2.60) and the soluble anions in meq l<sup>-1</sup> are CO<sub>3</sub><sup>2-</sup> (0.00), HCO<sub>3</sub><sup>-</sup> (2.10), Cl<sup>-</sup> (5.30) and SO<sub>3</sub><sup>2-</sup> (1.51).

### 2.4 Data Collection

The following characteristics were measured on a random sample of 10 plants of each genotype of parents and F<sub>1</sub>'s. 1. Number of spikes/plant (SPP): Number of fertile spikes per plant. 2. Number of grains\ spike (GPS): Number of grains per spike. 3. 100 grain weight (100GW) in g measured as weight of 100 grains taken from each guarded plant. 4. Grain yield/ plant (GYPP) in g measured as weight of the grains of each individual plant. 5. Harvest index (HI%) according formula: HI= 100 (GYPP/ BYPP), where BYPP= biological yield/plant. . 6. Grain protein content (GPC) measured as follows: GPC%= N<sub>g</sub> x 5.7 according to AACC [14], where N<sub>g</sub> is grain nitrogen content. Grain N<sub>g</sub> was determined using Kjeldahl procedure according to A.O.A.C. [15].

### 2.5 Statistical Analysis

Each environment (HN and LN) was analyzed separately across seasons as RCBD for the purpose of determining genetic parameters using GENSTAT 10<sup>th</sup> addition windows software. Least significant differences (LSD) values were calculated to test the significance of differences between means according to Steel et al. [16].

### 2.6 Genetic Analyses of F<sub>1</sub> Diallel Crosses

#### 2.6.1 Griffing approach

Diallel crosses in F<sub>1</sub> generation were analyzed to obtain general (GCA) and specific (SCA)

**Table 1. Designation, pedigree and tolerance to low N of the six wheat cultivars and lines used for making diallel crosses in this study**

Designation	Pedigree	Tolerance to low nitrogen
Line 25 (L25)	MYNA/VUL//TURACO/3/TURACO/4/Gem7.	Tolerant
Line 26 (L26)	MUNIA/CHTO//AMSEL.	Tolerant
Line27 (L27)	Compact-2/Sakha//Sakha61.	Tolerant
Gemeiza(Gem7)	CMH74A.630/SX//Seri82/3/Agent.	Sensitive
Gemeiza(Gem9)	Ald "s"/HUC "s; //CMH74A.630/SX.	Sensitive
Giza168(Gz168)	MRL/BUC//Seri.	Sensitive

Source: Wheat Res. Dept., Field Crops Res. Inst., ARC. Egypt.

combining ability variances and effects for studied traits according to Model I (fixed effect) Method 2. General (GCA) and specific (SCA) combining ability variances and effects were estimated according to Griffing [17] model I (*i.e.* the fixed model) method II. Estimates of both general ( $\delta^2_g$ ) and specific ( $\delta^2_s$ ) combining ability variances were calculated according to Griffing [17] as shown in Singh and Chaudhary [18].

### 2.6.2 Hayman's numerical approach

The genetic parameters and ratios were calculated according to methods developed by Jinks and Hayman [19], Jinks [20] and Hayman [21,22] and described by Sharma [23].

The variance and covariance statistics across replications were used to obtain estimates of the components of variation and their respective standard errors. The validity of the assumptions of diallel analysis was tested by the following formula (Sharma, 2003):  $t^2 = \{(n-2)/4[(MSS(Vr) - (MSS(Wr))^2 / \{MSS(Vr) \times [MSS(Wr) - MSP(Wr.Vr)]^2\})]$ . Where:  $W_r$  = covariance between parents and their off-spring and  $V_r$  = variance of each array in which a particular parent is involved. Significance of calculated "t" value was tested against the tabulated "F" value with 4 and (n-2) degrees of freedom. Significant value indicates failure of the assumptions (Hayman, 1954a and b). Another test was done by estimating the regression coefficient "bWr.Vr" of  $W_r$  on  $V_r$  as follows:  $b_{W_r.V_r} = [\text{cov}(W_r.V_r) / \text{var } V_r] = [MSP(W_r.V_r) / MSS(V_r)]$ . The standard error (SE) for the regression coefficient (b) value was estimated as follows:  $SE_b = [MSS(W_r) - bMSP(W_r.V_r)(n-2)]^{1/2}$  Where: n = number of parents. The significance of (b) different from zero ( $t_1$ ) and from unity (=1) ( $t_2$ ) can be tested by t-test as under:  $t_1 = (b-0)/SE_b$  and  $t_2 = (1-b)/SE_b$  the foregoing values were tested against the "t" tabulated value for (n-2) degrees of freedom according to Jinks and Hayman [19]. If all the assumptions were valid,

the regression coefficient would be significantly different from zero but not from unity. Hayman [21,22], derived the expectations for the statistics calculated from the F1 diallel table and the expected values of the component variations using least squares. The notations of Mather and Jinks [24] are used and described as follows:  $V_{0L0}$  ( $V_p$ ) (variance of the parents) =  $D + \hat{E}$ ,  $V_{1L1}(V_r)$ (mean of all the  $V_r$  values) =  $\frac{1}{4} D - \frac{1}{4} F + \frac{1}{4} H_1 + \frac{1}{4} H_2 + [\hat{E} + \hat{E} (n-2)/2n]$ ,  $V_r$  (variance of all the progenies in each parental array) =  $\frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} H_2 - \frac{1}{4} F + (n+1)/2n \hat{E}$ ,  $W_{0L01}(W_r)$  (mean of all the  $W_r$  values) =  $\frac{1}{2} D - \frac{1}{4} F + \hat{E}/n$ ,  $(M_{L1} - M_{L0})^2$  = dominance relationship =  $\frac{1}{4} h^2 + [(n-1) \hat{E}/n^2]$ . The components of  $\hat{E}$ , D,  $H_1$ ,  $H_2$ ,  $h^2$  and F were estimated in  $F_1$  as follows:  $\hat{E} = [(\text{Errors S.S.} + \text{Reps S.S.})/r] / [(r-1) + (c-1)(r-1)]$ .  $D = V_{0L0} - \hat{E}$ .  $F = 2 V_{0L0} - 4 W_{0L01} - [2 \hat{E} (n-2)/n]$ .  $H_1 = V_{0L0} + 4 V_{0L1} - 4 W_{0L01} - [\hat{E} (3n-2)/n]$ .  $H_2 = 4 V_{1L1} - 4 V_{0L1} - 2 \hat{E}$ .  $h^2 = 4(M_{L1} - M_{L0})^2 - [4 \hat{E} (n-1)/n^2]$ . Where n = number of parents.  $\hat{E}$  = expected environmental component of variance. D = variance due to additive effects of the genes. F = mean of the covariance of additive and dominance effects across all arrays.  $H_1$  = variance component due to dominance deviation.  $H_1 [1 - (u-v)^2]$ , where, u and v are the proportions of positive and negative genes, respectively in the parents.  $h^2$  = algebraic sum of dominance effects across all loci in heterozygous phase in all crosses. The following genetic parameters were also calculated: Average degree of dominance is estimated as  $(H_1/D)^{1/2}$ . 1. If the of this ratio is zero, there is no dominance. 2. If it is greater than zero, but less than one, there is partial dominance. 3. If it is equal to 1, there is complete dominance. 4. If it is greater than 1, it indicates over dominance. Ratio of dominant and recessive genes in the parents ( $K_D/K_R$ ) is estimated as follows:  $K_D/K_R = [(4DH_1)^{1/2} + F] / [(4DH_1)^{1/2} - F]$  If  $K_D/K_R \approx 1.0$ , it means nearly equal proportion of dominance and recessive alleles in parents, *i.e.* symmetrical distribution;  $p = q = 0.5$ . Any deviation from 1.0 indicates asymmetry of distribution ( $p \neq q$ ). Thus: Ratio > 1 refers to excess of dominant alleles

and minority of recessive alleles ( $p > q$ ). Ratio  $< 1$  means minority of dominant alleles and excess of recessive alleles ( $p < q$ ). The ratio of dominant genes with positive or negative effects in parents ( $H_2/4H_1$ ) was determined. The maximum theoretical value of 0.25 for this ratio arises when,  $p = q = 0.5$  at all loci. A deviation from 0.25 would stem when  $p \neq q$ . Thus: if this ratio  $\approx 0.25$ , it means symmetrical distribution of positive and negative dominant genes in parents, while if this ratio  $\neq 0.25$ , it means asymmetry of distribution. Narrow-sense heritability ( $h^2_n$ ) was estimated using the following equation:  $h^2_n = [1/4D / (1/4D + 1/4H_1 - 1/4F + \hat{E})]$ . The expected genetic advance (GA) from direct selection as a percentage of the mean ( $\bar{x}$ ) was calculated according to Singh and Narayanan [25] based on 1% selection intensity as follows:  $GA = 100[(k \cdot h^2_n \cdot \delta_{ph})/\bar{x}]$  Where:  $k = 2.64$  (selection differential for 1% selection intensity), and  $\delta_{ph}$  = square root of the dominator of the narrow sense heritability.

### 2.6.3 Hayman's graphical approach

Based on parental variance ( $V_r$ ) and parent-offspring co-variance ( $W_r$ ) relationships diallel cross progenies, a two-way representation of parental arrays along a regression line of  $W_r$  on  $V_r$  was first suggested by Jinks and Hayman [19] and later refined by Hayman [21,22]. This two directional depiction is widely known as the  $W_r$ - $V_r$  graph. For drawing the regression line, the expected  $W_{rei}$  values were calculated as follows:  $W_{rei} = W_r - b\bar{V}_r + b\bar{V}_{ri}$ , where:  $W_r$  is array mean of variances,  $V_r$  is array mean of covariances and  $b$  = regression coefficient. The regression line was drawn by plotting  $W_{rei}$  against  $V_r$  values. The point of interception of the regression line with  $W_r$  ordinate, i.e., ( $a$ ) was obtained by the following equation:  $a = \bar{W}_r - b\bar{V}_r$ .

## 3. RESULTS AND DISCUSSION

### 3.1 Combining Ability Variances

Variances estimates for general (GCA) and specific (SCA) combining ability of the  $F_1$  diallel crosses of wheat for combined data across two years under high and low levels of nitrogen are presented in Table (2 and 3). Mean squares due to genotypes were highly significant for all studied grain yield and quality traits under the two levels of N. Mean squares due to GCA and SCA were also highly significant, for all studied traits, indicating that both additive and non-additive gene effects play an important role in the inheritance of all studied grain yield and quality traits under different N application rates.

In the present study, the magnitude of GCA mean squares was higher than that of SCA, since the ratio of GCA/ SCA mean squares was higher than unity for all studied traits under the two levels of nitrogen, except 100GW and GPC under low-N, where the ratio was below unity. Higher GCA/SCA ratio than unity, suggested the existence of a greater portion of additive and additive x additive than that of non-additive genetic variance in controlling the inheritance of grain yield traits under the two levels of nitrogen.

The greater importance of GCA relative to SCA variance as observed in this study was also reported by Al-Naggar et al. [26-32] for (GYPP) and its components. Le Gouis et al. [33] reported that in N-limited diallel  $F_1$  hybrids between modern French cultivars found markedly higher GCA/SCA ratios for grain yield, grain N yield and total above ground N than in those grown under high N nutrition.

**Table 2. Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied grain yield and quality traits in  $F_1$ 's under high N conditions across two years**

SV	df	MS					
		SPP	GPS	100 GW	GYPP	HI%	GPC
Genotypes (G)	20	12.75**	587.32**	3.79**	49.29**	106.62**	707.29**
GCA	5	31.91**	1609.27**	9.10**	116.77**	168.65**	1590.41**
SCA	15	6.36**	246.67**	2.02**	26.80**	85.94**	412.92**
GCA xY	5	3.12**	2.80	0.25	6.70**	85.94**	39.93*
SCA xY	15	1.19**	11.15**	0.24**	4.38*	15.63**	63.88**
GCA/SCA		5.02	6.52	4.51	4.36	1.96	3.85
GCA xY /SCAxY		2.62	0.25	1.05	1.53	5.50	0.62
error	80	0.30	1.73	0.14	1.78	6.75	16.14

\* and\*\* indicate significant at 0.05 and 0.01 probability levels, respectively

**Table 3. Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied grain yield and quality traits in F<sub>1</sub> diallel crosses under low N conditions across two years**

SOV	df	MS					
		SPP	GPS	100 GW	GYPP	HI	GPC
Genotypes (G)	20	13.85**	646.88**	2.42**	63.99**	175.40**	1325.14**
GCA	5	42.69**	1061.29**	7.55**	226.07**	305.16**	1844.74**
SCA	15	4.24**	144.50**	11.32**	9.97**	132.14**	1152.0**
GCA xY	5	1.33**	221.49**	0.094	4.96**	14.32**	21.0
SCA xY	15	6.05**	168.24**	0.08	4.97**	26.04**	7.50
GCA/SCA		10.06	7.34	0.66	22.68	2.30	0.72
GCA xY /SCAxY		0.21	1.31	1.18	0.99	0.54	2.80
error	80	0.35	2.03	0.06	1.74	5.38	29.0

\* and\*\* indicate significant at 0.05 and 0.01 probability levels, respectively

Results in Tables (2 and 3) indicate that mean squares due to SCA x year interaction were significant ( $P \leq 0.01$ ) for the all studied traits under the two levels of N, except 100GW and GPC under low N, indicating that non-additive variance was affected by years.

Mean squares due to the GCA x year interaction were also significant ( $P \leq 0.05$  or  $0.01$ ) for all studied traits under high and low N, except for GPS and 100 GW under high-N and 100GW and GPC under low-N, which were not significant, indicating that additive variance for most studied cases differs from one year to another.

The mean squares due to SCA x year was higher than those due to GCA x year for all studied traits under both high and low- N, except for SPP, GYPP, HI, GPC, under high-N and GPS, 100GW and GPC, suggesting that SCA (non-additive) variance (in 5 out of 12 cases) is more affected by year than GCA (additive) variance.

### 3.2 GCA Effects

Estimates of general combining ability (GCA) effects of parents for studied traits under the two levels of nitrogen across two years are presented in Table 4 (high-N) and Table 5 (low-N). Favorable significant GCA effects were expressed by positive estimates for all studied grain yield and quality traits.

In general, the best general combiners in F<sub>1</sub>'s for grain yield and quality attributes were L26 followed by L27 and L25 parents under both high-N and low-N, Gem 7 for GYPP and Giza 168 for HI under high-N and L26 and L27 for GPC under both high-and low-N conditions.

On the contrary, the worst general combiners in F<sub>1</sub>'s were Gem 9, Gem 7 and Giza 168 for most studied grain yield and quality attributes under both high-N and low-N environments.

It is worthy to note that the best general combiners in this study (L25, L26 and L27) showed also high *per se* performance for the most studied grain yield and quality traits under both high and low-N environments.

### 3.3 SCA Effects

Estimates of specific combining ability (SCA) effects of the F<sub>1</sub> crosses for the studied traits under the two levels of N are presented in Tables (6 and 7). The best crosses in SCA effects were considered those exhibited significant positive SCA effects for all studied traits.

The rank of F<sub>1</sub> crosses for SCA effects was changed from under high-N to under low-N conditions. Under high-N, the best cross for SCA effects of maximum number (4) of six studied traits (GPS, 100GW, HI and GPC) was the F<sub>1</sub> cross L25 x L26 followed by L27 x Gem7 in three traits (GYPP, HI and GPC), L26 x Gz168 for three traits (GYPP, GPS and GPC). These F<sub>1</sub>'s include at least one parent of high GCA effects under high N.

Under low-N conditions, the best SCA effects for maximum number (3 out of 6) of traits were shown the by F<sub>1</sub>'s Gem7 x Gem 9 for SPP, GPS and GPC, Gem9 x Gz168 for GYPP and GPS and L25 x Gz168 for GYPP.

It is observed from the previously mentioned results that for SCA effects, the best F<sub>1</sub>'s under high-N were not the same best F<sub>1</sub>'s under low-N.

**Table 4. Estimates of general combining ability effects ( $g_i$ ) of all studied traits in  $F_1$ 's under high N conditions across two seasons**

Parents	SPP	GPS	100 GW	GYPP	HI%	GPC
L25	1.01**	4.13**	0.47**	-1.38*	-2.96*	-0.10
L26	0.36*	2.89**	0.39*	2.38*	0.64	5.87**
L27	0.73*	7.97**	0.33*	1.45*	1.22	8.05**
Gem 7	-0.45*	-4.26**	-0.41**	1.45*	0.15	-3.72*
Gem 9	-1.04*	-6.61**	-0.43**	-1.38*	1.32	-4.18**
Giza 168	-0.61*	-4.11**	-0.36**	-0.35	2.26*	-5.91**
SE <sub>gi</sub>	0.29	0.70	0.20	0.71	1.39	3.43
SE <sub>gi-gj</sub>	0.45	1.09	0.31	1.11	2.14	2.14

\* and\*\* indicate significant at 0.05 and 0.01 probability levels, respectively

**Table 5. Estimates of general combining ability effects ( $g_i$ ) of studied traits in  $F_1$ 's diallel crosses under low N conditions across two years**

Parents	SPP	GPS	100 GW	GYPP	HI%	GPC
L25	0.49*	6.15**	0.26*	1.87**	3.46**	-4.12**
L26	0.89*	1.14**	0.10	1.88**	0.17	5.56**
L27	0.98**	8.87**	0.62**	1.97**	1.35	9.96**
Gem 7	-1.41**	-1.78**	-0.37*	-1.76*	0.77	-2.91*
Gem 9	-0.56*	-7.11**	-0.25*	-2.88**	-3.53**	-3.74**
Giza 168	-0.39*	-7.27**	-0.36*	-1.08*	-2.22*	-4.74**
SE <sub>gi</sub>	0.31	0.76	0.13	0.71	1.24	2.87
SE <sub>gi-gj</sub>	0.49	1.18	0.21	1.09	1.92	4.91

\* and\*\* indicate significant at 0.05 and 0.01 probability levels, respectively

**Table 6. Estimates of specific combining ability effects ( $s_{ij}$ ) of  $F_1$ 's under high N conditions across two seasons**

Crosses	SPP	GPS	100 GW	GYPP	HI	GPC
L25 X L26	0.18	3.40*	1.07**	1.20	3.94*	13.21**
L25 X L27	1.39*	4.00*	0.05	-2.96*	-3.04	0.64
L25 X Gem 7	0.63	5.34**	0.06	-0.93	-1.56	-2.26
L25 X gem 9	0.82	-11.96*	-0.75*	0.85	0.61	-9.21**
L25 X Gz 168	-0.39	-6.78*	-0.87*	0.71	-1.88	-9.11**
L26 X L3	0.87*	-13.42*	0.37	-0.34	-1.63	-9.47**
L26 X Gem 7	-0.17	2.76*	-0.69*	-0.82	-5.28**	0.17
L26 X Gem 9	-0.03	-3.90*	-0.14	1.12	1.25	3.37
L26 X Gz 168	1.21	7.77**	-0.65*	2.86*	1.79	7.12*
L27 X Gem 7	0.12	1.57	-0.71*	4.94*	9.45*	13.42**
L27 X Gem 9	-0.0003	6.34*	0.07	0.97	1.10	-0.17
L27 X Gz168	1.59*	1.41	0.06	0.82	-2.81	-5.13
Gem 7 X Gem9	0.18	-0.43	0.04	-1.69	-2.91	10.45**
Gem 7 X Gz 168	-0.57	-1.84	0.74*	0.98	4.62*	7.87*
Gem 9 X Gz 168	-0.68	4.54*	-0.04	-0.84	2.48	5.61
SE <sub>Sij</sub>	0.80	1.93	0.56	1.96	3.82	5.91
SE <sub>Sij-Sik</sub>	1.20	2.89	0.83	2.93	5.70	6.65
SE <sub>Sij-Ski</sub>	1.11	2.67	0.77	2.71	5.28	8.81

\* and\*\* indicate significant at 0.05 and 0.01 probability levels, respectively

### 3.4 Gene Action, Heritability and Selection Gain

Estimates of genetic components and ratios for studied grain yield and quality traits in  $F_1$ 's under

high- and low-N environments across two years are presented in Table (8). The dominance genetic component of variation ( $H_1$ ) was highly significant for all studied traits under both high and low-N environments, except for GPC under

low-N and high-N, indicating that the dominance gene effects in F<sub>1</sub>'s of this experiment are important for the inheritance of all studied grain yield traits under low-N and high-N (SSP, GPS, 100 GW, GYPP and HI).

The additive component of variation (D) was also significant (P ≤ 0.01 or 0.05) for all studied traits in F<sub>1</sub>'s under both high- and low- N, except for GPC under high-N and low-N, indicating that selection may be efficient for improving most studied traits.

Thus, a simultaneous exploitation of both additive and dominance variance to improve these parameters could be achieved by reciprocal recurrent selection. However, the magnitude of dominance (H<sub>1</sub>) was much greater than that of additive (D) component for all studied traits in F<sub>1</sub>'s under both high N and low N, except for SPP, GPS, 100 GW and GYPP traits under low-N, where the opposite was true, i.e. the additive was greater than dominance variance. This indicates that the dominance gene effects are more important than additive in F<sub>1</sub>'s and plays the major role in the inheritance of all studied traits under high N and HI and GPC under low-N.

The grain yield (SPP, GPS, 100 GW and GYPP) of F<sub>1</sub>'s under low-N showed more importance for additive than dominance variance. Selection for high values of these five traits in the segregating generations of the studied diallel crosses under

low-N would be efficient for obtaining improved high yielding and N- efficient wheat genotypes.

The overall dominance effects of heterozygous loci in Hayman's model (h<sup>2</sup>) controlling all studied traits of F<sub>1</sub>'s under both high- and low-N environments, except for SPP and GPS under high-N and 100GW under low-N were significant (P < 0.01 or 0.05); that could be due to the presence of a considerable amount of dominant genes for most studied traits in the parental genotypes.

The average degree of dominance (H<sub>1</sub>/D)<sup>1/2</sup> in F<sub>1</sub>'s was in the range of over-dominance (greater than unity) for all studied traits under the high level of nitrogen and HI and GPC under low-N, but SPP, GPS, 100 GW and GYPP traits under low-N showed partial dominance (smaller value than unity).

Lower ratio of (H<sub>2</sub>/4H<sub>1</sub>) than 0.25 (Table 8) indicated symmetrical distribution of positive dominant genes in parents for most studied traits of F<sub>1</sub>'s under both high- and low-N environments. The exceptions were SPP under low-N and GYPP under high-N, where H<sub>2</sub>/4H<sub>1</sub> was greater than 0.25, indicating asymmetry of distribution.

Under low-N, the ratio (K<sub>D</sub>/K<sub>R</sub>) in F<sub>1</sub>'s was more than unity for 3 out of 6 traits, indicating excess of dominant alleles and minority of recessive alleles (p > q) for SPP, GPS and HI traits. The

**Table 7 Estimates of specific combining ability effects (ŝ<sub>ij</sub>) of F<sub>1</sub>'s under low N conditions across two years**

Crosses	SPP	GPS	100 GW	GYPP	HI	GPC
L25 X L26	-0.62	-4.07*	0.10	0.48	-0.24	18.43**
L25 X L27	-0.50	-0.61	0.56*	-0.33	-0.36	-3.12
L25 X Gem 7	-0.91	2.06	-0.28	1.68	10.98**	-10.74**
L25 X gem 9	-0.03	5.88**	-0.18	-1.65	2.25	-21.52**
L25 X Gz 168	0.60	-2.33*	-0.49*	1.96*	0.23	-6.38
L26 X L3	1.56*	-1.13	0.14	0.95	2.13	-19.29**
L26 X Gem 7	0.83	8.03**	-0.26	-0.15	4.59*	-1.02
L26 X Gem 9	-0.43	-7.99**	-0.15	-0.71	1.37	5.94
L26 X Gz 168	-1.40*	-5.61**	-0.38*	-1.44	-2.40	13.84**
L27 X Gem 7	-0.04	4.77*	-0.59*	1.24	0.91	-3.68
L27 X Gem 9	0.33	1.01	0.15	-1.24	-4.76*	6.69
L27 X Gz168	-0.84	1.22	0.18	0.14	-1.58	3.72
Gem 7 X Gem9	0.91*	5.14*	0.09	-0.29	-2.64	26.47**
Gem 7 X Gz 168	0.03	-3.09*	0.11	-0.87	-6.07*	-1.81
Gem 9 X Gz 168	0.62	2.55*	0.11	1.99*	1.63	6.01
SE <sub>Sij</sub>	0.87	2.09	0.37	1.74	3.41	7.91
SE <sub>Sij~Sik</sub>	1.31	3.13	0.55	2.90	5.09	8.93
SE <sub>Sij~SkI</sub>	1.21	2.90	0.51	2.68	4.71	11.82

\* and \*\* indicate significant at 0.05 and 0.01 probability levels, respectively



**Table 8. Estimates of genetic parameters and ratios for studied traits under high and low-N in F<sub>1</sub> populations of 15 diallel crosses across two seasons**

Variance components	SPP	GPS	100GW	GYPP	HI	GPC
<b>High N</b>						
E	0.58*	0.05	0.10	0.59	2.25*	6.60**
D	0.54*	162.81**	0.458**	5.52**	6.81**	-3.31
H <sub>1</sub>	1.02**	171.19**	0.88**	15.18**	47.92**	-24.28
H <sub>2</sub>	0.89**	157.29**	0.93**	13.52**	47.18**	3.61**
F	-2.17**	48.74**	-0.37*	-3.99**	-7.61**	0.97**
h <sup>2</sup>	-0.20	0.19	0.23*	6.68**	4.21**	-4.24**
(H <sub>1</sub> /D) <sup>1/2</sup>	1.37	1.03	1.40	1.66	2.65	2.71
H <sub>2</sub> /4H <sub>1</sub>	0.22	0.23	0.26	0.22	0.25	0.20
K <sub>D</sub> /K <sub>R</sub>	-0.19	1.34	0.54	0.64	0.65	0.40
h <sup>2</sup> /H <sub>2</sub>	-0.23	0.00	0.25	0.49	0.09	0.22
h <sup>2</sup> <sub>b</sub> %	61.70	99.90	81.00	91.27	87.30	8.52
h <sup>2</sup> <sub>n</sub> %	9.20	56.89	21.40	20.41	9.60	0.00
GA%	2.50	15.87	9.24	5.11	23.90	0.00
<b>Low-N</b>						
E	0.68	0.02	0.12	0.58	1.79*	9.67**
D	3.90**	214.01**	0.31**	17.12**	17.53*	-2.63
H <sub>1</sub>	0.16*	113.32**	0.0	4.63**	90.63**	-30.23
H <sub>2</sub>	0.24**	92.05**	-0.002	3.98*8	-1.03*	-1.89*
F	0.86**	36.43**	-0.35*	-1.43**	71.53**	-22.59**
h <sup>2</sup>	-0.44*	10.57**	0.04	0.10*	4.99**	-9.72**
(H <sub>1</sub> /D) <sup>1/2</sup>	0.20	0.73	0.00	0.52	2.27	3.39
H <sub>2</sub> /4H <sub>1</sub>	0.36	0.20	0.06	0.21	0.20	0.19
K <sub>D</sub> /K <sub>R</sub>	3.32	1.26	0.00	0.85	1.13	0.30
h <sup>2</sup> /H <sub>2</sub>	-1.86	0.11	-27.80	0.02	-0.01	0.08
h <sup>2</sup> <sub>b</sub> %	54.42	100.00	57.50	91.00	93.50	20.00
h <sup>2</sup> <sub>n</sub> %	42.52	21.80	33.11	66.32	15.87	0.00
GA%	2.27	1.30	4.38	23.25	5.42	-5.70

\* and\*\* indicate significant at 0.05 and 0.01 probability levels, respectively

remaining traits of F<sub>1</sub>'s (100 GW, GYPP and GPC) under low-N, recorded less than unity K<sub>D</sub>/K<sub>R</sub> ratio, indicating minority of dominant alleles and the excess of recessive alleles (p<q).

However, under high-N, the ratio (K<sub>D</sub>/K<sub>R</sub>) in F<sub>1</sub>'s was less than unity for all studied traits, except GPS, indicating minority of dominant alleles and the excess of recessive alleles (p<q) for most studied traits (Table 8). The exception under high-N was GPS, where the ratio (K<sub>D</sub>/K<sub>R</sub>) was more than unity, indicating excess of dominant alleles (p>q) for such trait.

Number of genes or groups of genes controlling the inheritance of a given trait (h<sup>2</sup>/H<sub>2</sub>) was one group of genes for most studied traits of F<sub>1</sub>'s under both high-N and low-N environments (Table 8). The exceptions were SPP and 100GW under low-N which were controlled by 2 and 28 genes or groups of genes, respectively.

Broad-sense heritability (h<sup>2</sup><sub>b</sub>) in F<sub>1</sub>'s for all studied traits (except GPC) in this experiment

was of medium to high magnitude and ranged from 61.7% (SPP) to 99.9% (GPS) under high-N and from 54.42% (SPP) to 100.0% (GPS) under low-N environments (Table 8), indicating that environment had a small effect on the phenotype of F<sub>1</sub>'s for most studied traits. Grain protein content (GPC) trait showed very small h<sup>2</sup><sub>b</sub> value under both high and low N environments (8.52 and 20.00%, respectively), indicating a large effect of environment on this trait.

Narrow-sense heritability (h<sup>2</sup><sub>n</sub>) in F<sub>1</sub>'s (Table 8) was generally of low to medium magnitude and ranged from 9.20% (SPP) to 56.89% (GPS) under high-N and from 15.87% (HI) to 66.32% (GYPP) under low-N. It is observed that GPC trait recorded 0.0% h<sup>2</sup><sub>n</sub> under both high- and low-N; the reason may be because its D value was negative; that is why we considered it zero.

The big difference between broad- and narrow-sense heritability estimated from F<sub>1</sub>'s in this experiment could be attributed to the high

estimates of dominance as compared to additive component.

It is observed that narrow-sense heritability ( $h^2_n$ ) in  $F_1$ 's of the present study was generally higher in magnitude under low-N than under high-N for all studied grain yield traits, except for GPS trait. This increase in  $h^2_n$  under low-N compared to high-N was more pronounced in SPP, GPS and GYPP traits; i.e. the most important components of grain yield in wheat.

Our results are in agreement with some researchers, e.g. Shabana et al. [34], Blum [35,36], Hefny [37], Al-Naggar et al. [27-32,38-40], who support the idea that heritability is higher under stressed than non-stressed environment. On the contrary, other investigators reported that heritability is higher under good (non-stressed) environment [41-45].

Expected genetic advance (GA) from selection (based on 1% selection intensity) across two years ranged from 2.50% for SPP under high-N to 23.9% for HI under high-N and from 1.30% for GPS to 23.26% for GYPP under low-N. The values of GA were higher under high-N than under low-N for GPS, 100 GW and HI traits. The trait GYPP showed much higher estimates of GA (23.25%) under low-N than those under high-N (5.11%). These results indicated that to improve grain yield trait in the present germplasm, it is better to practice selection for this trait under low-N conditions to obtain higher values of selection gain.

### 3.5 Graphical Approach of $F_1$ Diallel Analysis

The graphical analysis of diallel crosses purposed by Hayman (1954 a and b) will be illustrated on the following bases: (1) The parabola marks the limits within which the variance-covariance points ( $V_r, W_r$ ) should lie, (2) If the regression coefficient ( $b$ ) of ( $V_r, W_r$ ) is not different from unity, the genetic control system may be deduced to be additive without the complications of gene interactions, (3) Complementary gene effects (epistasis) generally reduces the covariance ( $W_r$ ) disproportionately more than the variance ( $V_r$ ), causing the slope of the regression line ( $b$ ) to be less than unity, (4) When dominance is complete, the regression line with  $b = 1$  would pass through the origin, (5) Over dominance causes the regression line to intercept the ( $W_r$ ) axis below the origin, while partial dominance causes the

regression line to intercept the ( $W_r$ ) axis above the origin point, (6) The closeness of the regression line or ( $V_r, W_r$ ) points to the limiting parabola indicates little dominance and (7) The order of the array points on the regression line is a good indicator of the dominance order of parents. The parents with more dominant genes are located nearer to the origin, while those with more recessive genes fall farther from the origin. The parents with equal frequencies of dominant and recessive genes occupy an intermediate position.

Based on the above information, in the  $F_1$  diallel Hayman's approach, it is clear, from Figs (1 to 3) for 6 studied traits, that the regression line intercepted the  $W_r$ -axis below the origin, i.e. cutting the  $W_r$ -axis in the negative region (intercept =  $a < 0$  (negative)) or  $D$  (additive variance)  $< H_1$  (dominance variance), indicating the presence of overdominance for 4 out of 12 cases, namely SPP (Fig. 1), GPS (Fig. 1), 100 GW (Fig. 2) and GPC (Fig. 3) under high-N.

The regression line passed through the origin ( $D = H_1$ ), indicating complete dominance for 1 out of 12 cases in  $F_1$ 's, namely GPC (Fig. 3) under low-N.

For 7 out of 12 cases in  $F_1$ 's, namely SPP, GPS, 100 GW, GYPP and HI under low-N and GYPP (Fig. 2), HI (Fig. 2) under high-N, the regression line intercepted the  $W_r$ -axis above the origin ( $D > H_1$ ), indicating partial dominance and the predominance of additive variance in these cases.

The dispersion of parents (1 = L25, 2 = L26, 3 = L27, 4 = Gem7, 5 = Gem9 and 6 = Gz168) around the regression line for SPP (Fig. 1) showed that under low-N, the parents 4, 5 and 6 (Gem7, Gem9 and Gz168) are close to the origin of the coordinate, and accordingly have more dominant genes; with Gem7 is the nearest parent to the origin (contains more than 75% dominant genes), while parents 1, 2 and 3 (L25, L26 and L27) have mostly recessive genes. Under high-N, dispersion of parents around the regression line, for SPP trait (Fig.1) showed that parents 4, 5 and 6 are very close to the origin, indicating that they contain more than 75% dominant genes, the parents 1 and 2 are very far from the origin, indicating that they mostly contain recessive genes, while dominant and recessive genes are located in the parent 3 (L27) for such trait.

For GPS trait (Fig. 1), under low-N, the dispersion of parents around the regression line reveals that parents 5 and 6 are close to the origin of the coordinate, end accordingly have > 75% of dominant genes while parent 4 has 50-75% of dominant genes, while parents 1, 2 and 3 are far from the origin and therefore have < 25% of dominant genes. Under high-N, the dispersion

of parents around the regression line showed that parents 2 and 4 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, parents 1 and 5 have 50-75% Of dominant genes, while parents 3 and 6 are far from the origin, therefore they have < 25% of dominant genes.

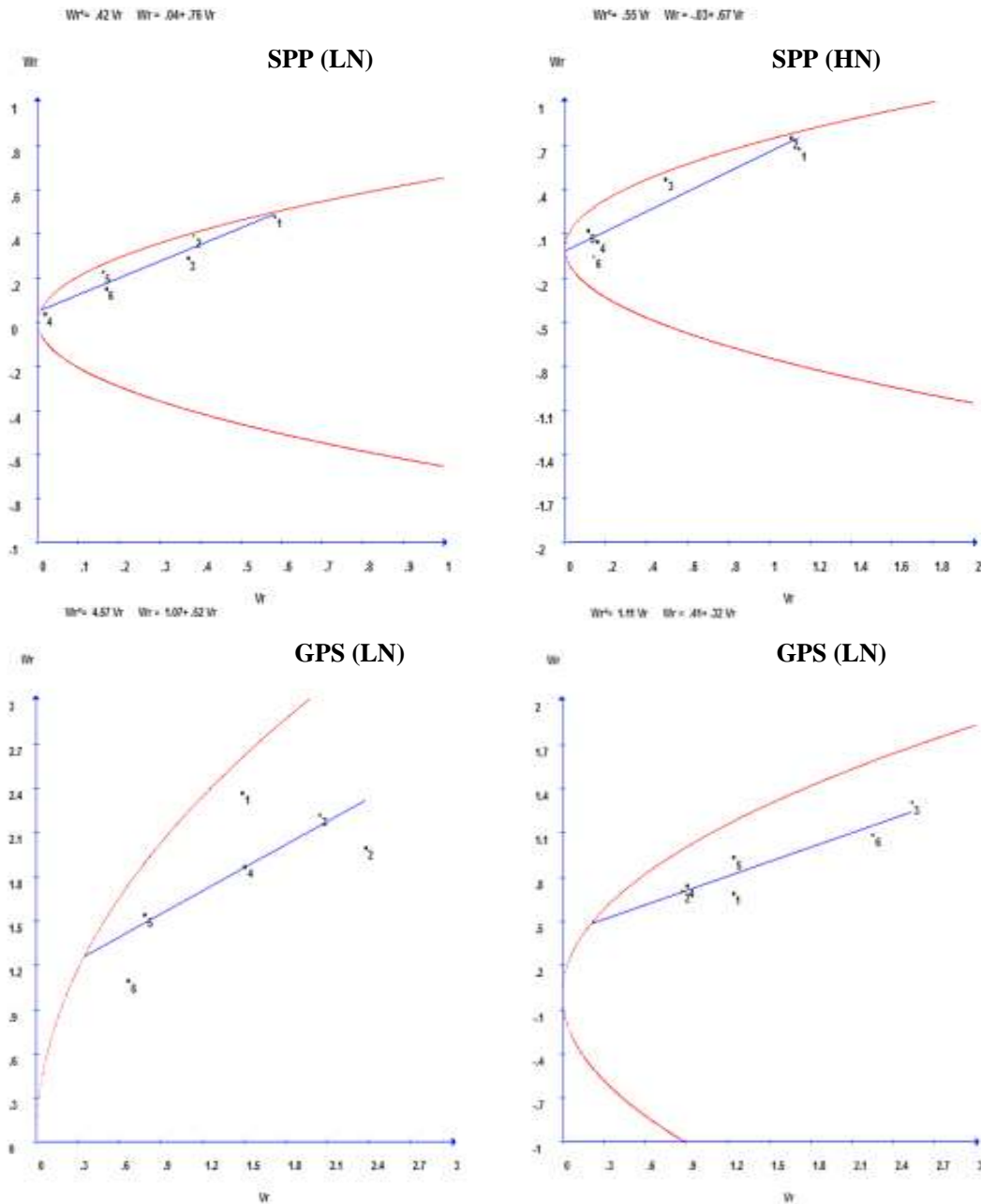
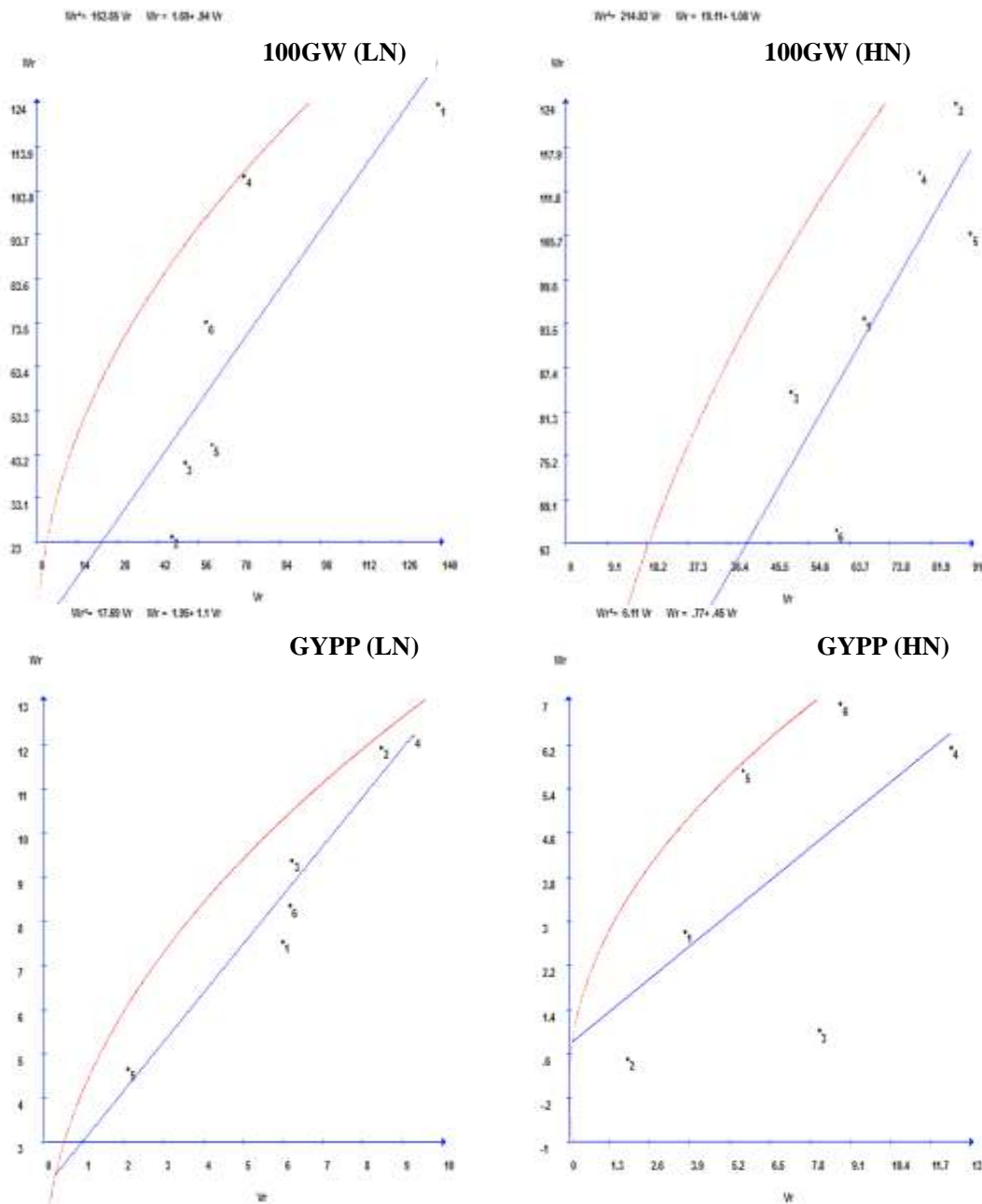


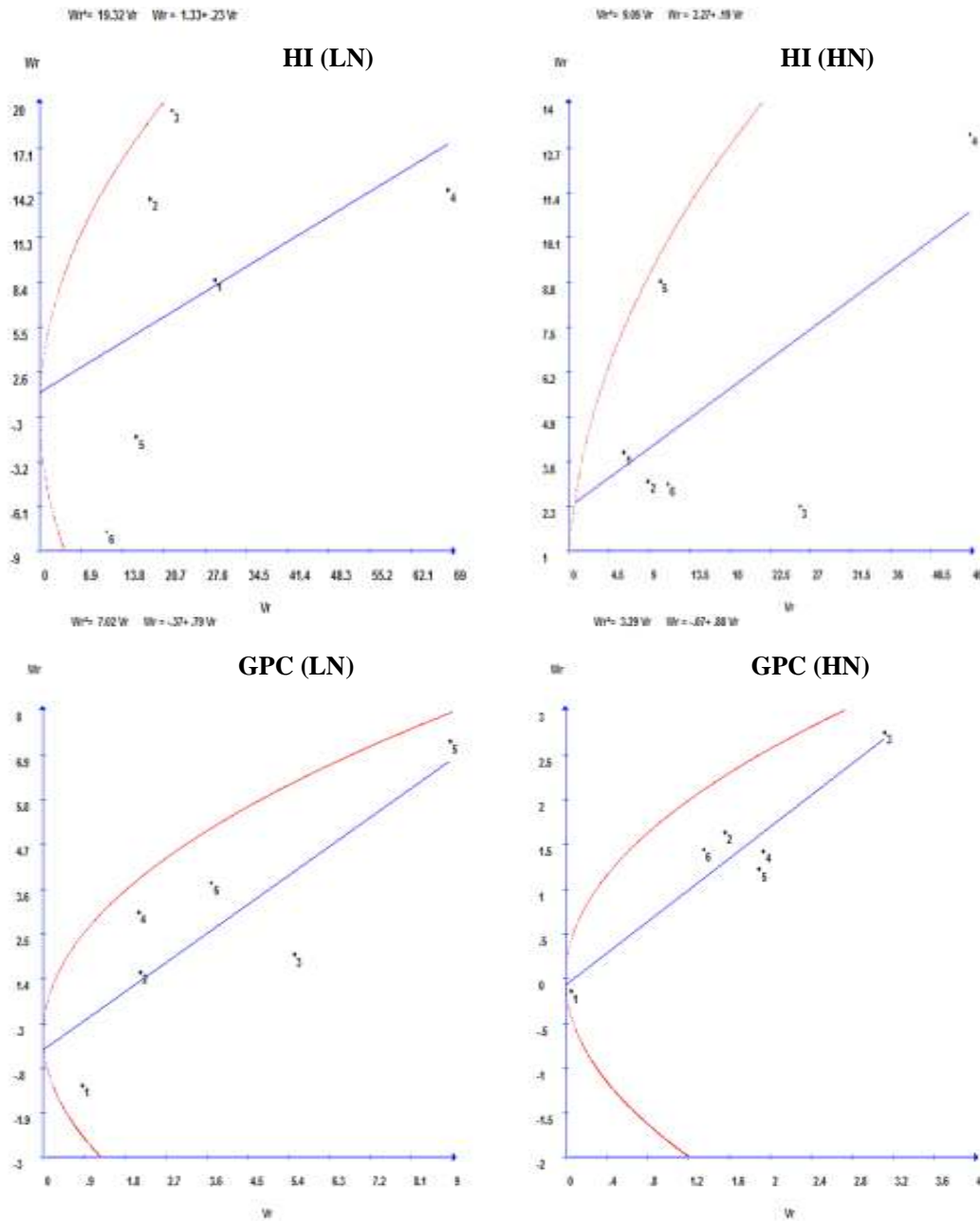
Fig. 1.  $W_r$ - $V_r$  graph of spikes/plant (SPP) and grains/spike (GPS) of  $F_1$ 's for combined data across two seasons under low – (LN) and high - (HN) nitrogen



**Fig. 2.  $W_r$ - $V_r$  graph of 100 grain weight (100 GW) and grain yield/plant (GYPP) of  $F_1$ 's for combined data across two seasons under low – (LN) and high - (HN) nitrogen**

Regarding 100 GW trait (Fig. 2), under low-N, the dispersion of parents around the regression line reveals that parents 2, 3 and 5 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes while parents 4 and 6 have 50-75% of dominant genes, while parent 1 is far from the origin and therefore has < 25% of dominant genes. Under high-N, for 100 GW, the

dispersion of parents around the regression line showed that parent 6 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 1 and 3 have 50-75% of dominant genes, while parents 2, 4 and 5 are far from the origin, therefore they have < 25% of dominant genes.



**Fig. 3.  $W_r$ - $V_r$  graph of harvest index (HI) and grain protein content (GPC) of  $F_1$ 's for combined data across two seasons under low – (LN) and high - (HN) nitrogen**

With respect of GYPP trait (Fig. 2), under low-N, the dispersion of parents around the regression line reveals that parent 5 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes while parents 1, 3 and 6 have 50-75% of dominant genes, while parents 2 and 4 are far from the origin and therefore have < 25% of dominant genes. Under high-N, for GYPP, the dispersion of parents around the

regression line showed that parent 2 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 1 and 3 have 50-75% of dominant genes, while parents 4, 5 and 6 are far from the origin, therefore they have < 25% of dominant genes.

For HI trait (Fig. 3), under low-N, the dispersion of parents around the regression line reveals that

parents 5 and 6 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes while parents 1, 2 and 3 have 50-75% of dominant genes, while parent 4 is far from the origin and therefore has < 25% of dominant genes. Under high-N, for HI, the dispersion of parents around the regression line showed that parent 1, 2 and 6 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, parents 3 and 5 have 50-75% of dominant genes, while parent 4 is far from the origin, therefore it has < 25% of dominant genes.

Regarding GPC trait (Fig. 3), under low-N, the dispersion of parents around the regression line reveals that parent 1 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes while parents 2, 3, 4 and 6 have 50-75% of dominant genes, while parent 5 is far from the origin and therefore has < 25% of dominant genes. Under high-N, for GPC, the dispersion of parents around the regression line showed that parent 1 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 2, 4, 5 and 6 have 50-75% of dominant genes, while parent 3 is far from the origin, therefore it has < 25% of dominant genes.

#### 4. CONCLUSIONS

In general, analysis of combining ability indicated that the best general combiners with positive effects for improvement of grain yield and quality attributes were L26, L27 and L25 parents under both high-N and low-N. Under low-N conditions, the best SCA effects were shown by the  $F_1$ 's L25 x Gz168 for GYPP, Gem9 x Gz168 for GYPP and GPS and Gem7 x Gem 9 for SPP, GPS and GPC. Genetic analysis indicated the involvement of additive and dominant types of gene action in the inheritance of SPP, GPS, 100 GW, HI and GYPP. Thus, a simultaneous exploitation of both additive and dominance variance to improve these parameters could be achieved by reciprocal recurrent selection. Highest narrow-sense heritability was observed for GYPP, SPP, GPS and 100 GW under low-N, hence the role of additive variance was higher than dominance variance that is likely to involve a few major genes in the genetic control of these traits. The results indicated that to improve grain yield trait in the present germplasm, it is better to practice selection for this trait under low-N conditions to obtain higher values of selection gain.

#### COMPETING INTERESTS

Authors have declared that no competing interests exist.

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