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Effect of Low-N Stress on Performance and Combining Ability for Grain Yield and Quality Traits of Wheat Parents and their F_2 Progenies

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Abstract: Developing high-yielding wheat varieties under low-N requires adequate information on the nature of combining ability of available genotypes and the types of gene actions involved in the expression of grain yield and quality traits under such low-N stress. The objective of present study was to get information about performance and general (GCA) and specific (SCA) combining ability variances and effects for grain yield and quality traits of wheat to help its improvement under low-N environment. Two experiments were conducted during two seasons, the 1st under high-N (75 kg N/fed) and the 2nd under low-N (0 kg N/fed) using a randomized complete block design with three replications. The entries included six Egyptian wheat genotypes differing in low-N tolerance and their F_2 diallel crosses (without reciprocals). Data analyzed across seasons indicated that L25, L26 and L27 had high values of grain yield and quality traits and showed the best GCA effects for these traits. Under low-N, the best F_2 crosses in *per se* performance and in SCA effects were L25 x L27, L25 x L26 and L26 x G168. Mean squares due to both GCA and SCA were significant under both low-N and high-N for all studied traits, but the magnitude of GCA was greater than SCA, indicating that additive is more important than non-additive genetic variance in controlling the inheritance of all studied grain yield and quality traits. The results indicated that under low-N and high-N, the mean performance of a given parent is an indication of its general combining ability and the mean performance of a given F_2 cross is an indication of its specific combining ability effects for all studied grain yield and quality traits.

Keywords: Grain protein, Triticum aestivum, combining ability, Correlation, Low-N, Yield

I. INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the oldest and most important cereal crops in Egypt. Although wheat productivity in Egypt has increased during the past years, wheat production supplies only 45% of its annual domestic demand. Egypt still is one of the largest countries that import wheat. Wheat imports in 2011 were about 9.8 million tons, with a cost of about 3.2 billion US$ (FAOSTAT, 2011). Therefore, Egypt needs to make a great effort to increase wheat production. Extending wheat growing outside the Nile Valley is the first effort toward overcoming wheat problems. However, most of the area outside the Nile Valley suffers from some abiotic stresses, the most important are nutrient deficiency and low water holding capacity; therefore increasing tolerance of wheat genotypes to such stresses, is one of the cheapest methods to spread growing wheat in these areas.

Crop performance is a function of the genotype and the nature of the production environment (Cooper and Byth, 1996). Genotypic differences for grain yield observed in the absence of stress are largely unrelated to differences observed in the presence of severe stress (Banziger *et al.*, 1997; Ceccarelli, 1989; Ceccarelli and Grando, 1991; Ceccarelli *et al.*, 1992 and Mosisa, 2005). This may indicate that different physiological mechanisms are associated with high yield in favorable conditions and high yield in unfavorable conditions (Blum, 1997; Ccccarelli, 1996). Variation for quantitative characters is under the control of many genes and the contribution of the genes can differ among environments (Basford and Cooper, 1998; Delacy *et al.*, 1996 and Meseka *et al.*,2006). This conditional contribution of genes is the basis of genotype-by-environment (G x E) interactions.

Low-N stress is among the major abiotic stresses causing yield reductions in wheat (Lafitte and Edmeades, 1994; Beck *et al.*, 1996; Banziger *et al.*, 2000 and Banziger and Meyer, 2002). Understanding the genetic basis of hybrid performance under this stress is crucial to the design of appropriate breeding strategies (Hallauer and Miranda, 1988 and Betran *et al.*, 2003 a,b). Although improved N efficiency has been a desirable goal of wheat breeders, the

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information available regarding the relative contribution of general combining ability (GCA) effects and specific combining ability (SCA) effects for different traits related to grain yield under low-N is limited (Dass *et al.*, 1997 and Gorny *et al.*, 2011). Below *et al.* (1997) evaluated hybrids from a diallel mating design under high and low N availability (where low-N stress results in approximately 35% yield reduction) in a temperate environment and reported that the mean squares for general combining ability (GCA) and specific combining ability (SCA) were significant for all traits measured at both levels of N. They concluded that, based on the magnitude of the difference between GCA and SCA mean squares, the majority of the genetic effects were associated with GCA, indicative of additive genetic effects. Kling *et al.* (1997) conducted a diallel experiment in the tropical lowlands of West Africa for one season under high and low N conditions and reported that GCA for grain yield was significant under both N treatments while SCA was only significant under high-N. However, non-additive gene effects under low-N were common in other studies. Betran *et al.* (2003a) evaluated diallel crosses under high-N and low-N for one season and reported that under low-N, non additive genetic effects were more important for grain yield than the additive genetic effects. A significant crossover interaction was observed between the GCA of lines under low and high N conditions. Similar results were reported by Lafitte and Edmeades (1995). Banziger *et al.* (1997) found that N stress severity influenced genotype-by-N stress interactions. In addition to other environmental effects and type of families used, the contradictory results of different researchers may, therefore, be due to differences in the N stress level (testing environment) under which the genotypes were evaluated and/or genotypic difference among sets of genotypes included in the studies. A detailed study of the relative importance of GCA effects and SCA effects under contrasting N environments is crucial to generate precise information and design breeding strategies that serve the interests of resource-poor farmers (Banziger *et al.*, 2000).

Gorny *et al.* (2011) reported that the soil N-treatments imposed had a substantial influence on gene actions responsible for the grain yield and N efficiency components and modes of inheritance. They found that under high N-fertilization, the grain yield components were inherited in a manner favorable for wheat selection (preponderance of additive effects), while the enhanced contribution of non-additive gene effects and increased dominance under N-limited conditions could impede wheat selection to improve the N efficiency and adaptation to less luxurious fertilization regimes. They concluded that selection methods that eliminate masking non-additive influences and take advantage of the additive variance should be employed to improve these traits.

This study aimed to determine *per se* performance of six Egyptian wheat parents and their 15 F_2 diallel crosses, estimate the relative importance of their GCA and SCA under contrasting N environments and investigate the relationship between *per se* performance and combining ability of parents and F_2 crosses.

II. 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. 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).

Table1. *Designation, pedigree and tolerance to low-N of the six promosing lines and Egyptian cultivars of wheat used for making diallel crosses of 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
Gemeiza9(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*

2.2. Making the F1 and F2 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_1 seeds of 15 crosses. In summer 2006, a part of F_1 seeds was sown in greenhouse of Wheat Res. Dept. under controlled conditions to obtain the F_2 seeds. In season 2007/2008, the half diallel of crosses was again done to increase quantity of F_1 seeds and in summer 2007 the F_1 seeds were again sown in the greenhouse under controlled conditions to obtain more seeds of 15 F_2 crosses

2.3. Field Evaluation of 6 Parents and 15 F2's

In the seasons 2007/2008, 2008/2009, parents (6) and F_2's (15) were sown on 17th of November each season in the field of Noubarya Res. Stat., in two experiments under two levels of nitrogen fertilizer; each experiment under one level of nitrogen. The low level (low-N) was without fertilization, i.e. 0 kg N/feddan (LN) and the high level (high-N) was 75 kg Nitrogen/ feddan (HN); this is the recommended level of Ministry of Agriculture (one feddan = 4200 m^2). This level of nitrogen fertilizer (equals 168 kg Urea/fed) 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). In this experiment, a randomized complete block design (RCBD) was used with three replications. Each parent was sown in two rows and each F_2 was sown in four 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^2 for parent and 3.6 m^2 for F_2. All other agricultural practices were done according to the recommendation of Ministry of Agriculture for growing wheat in Noubarya region.

Available soil nitrogen in 30 cm depth was analyzed immediately prior to sowing and N application at the laboratories of Water and Environment Unit, ARC, Egypt in the two seasons. Soil nitrogen was found to be 55 and 57 kg N/ fed in the seasons 2007/2008, 2008/2009, respectively. 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^{-1}, the soluble cations in meq l^{-1} are Ca^{2+} (5.30), K^+ (0.70), Na^+ (0.31), Mg^{2+} (2.60) and the soluble anions in meq l^{-1} are CO_3^{2-} (0.00), HCO_3^- (2.10), Cl^- (5.30) and SO_3^{2-} (1.51). All other agricultural practices were followed according to the recommendations of ARC, Egypt.

2.4. Data Collection

The following characteristics were measured on a random sample of 10 plants of each genotype of parents and 30 plants of F_2'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_g x 5.7 according to AACC (2000),where N_g is grain nitrogen content. Grain N_g was determined using Kjeldahl procedure according to A.O.A.C. (1990).

2.5. Statistical and Genetic Analyses

Each environment (HN and LN) was analyzed separately across seasons as RCBD for the purpose of determining genetic parameters using GENSTAT 10th addition windows software. Least significant differences (LSD) values were calculated to test the significance of differences between means according to Steel *et al.* (1997). Diallel crosses in F_2 generation were analyzed to obtain general (GCA) and specific (SCA) combining ability variances and effects for studied traits according to Griffing (1956) model I, i.e. fixed model, method II. Estimates of both general (δ^2_g) and specific (δ^2_s) combining ability variances were calculated as shown in Singh and Chaudhary (1985). Rank correlation coefficients calculated between *per se* performance of parents and their GCA effects in F_2's; between *per se* performance of F_2 crosses and their SCA_{F2} effects for studied traits under each environment across two seasons, using SPSS 17 computer software and the significance of the rank correlation coefficient was tested according to Steel *et al*. (1997). The correlation coefficient (r_s) was estimated for each pair of any two parameters as follows: $r_s = 1 - (6 \Sigma d_i^2)/(n^3-n)$. Where, d_i is the difference between the ranks of the i^{th} genotype for any two parameters, n is the number of pairs of data. The hypothesis Ho: $r_s = 0$ was tested by the r-test with (n-2) degrees of freedom.

III. RESULTS AND DISCUSSION

3.1. Mean Performance

A comparative summary of means of all studied traits across all 21 genotypes (6 parents and 15 F_2's) subjected to two levels of nitrogen conditions and across two years is presented in Table (2). In general, low N caused a significant reduction in all studied traits, namely GYPP, SPP, 100GW, GPS, HI and GPC. Mean grain yield/plant

(GYPP) was significantly decreased due to low-N by an average of 18.96, and 15.40% for parents and F_2's, respectively. Reduction in grain yield of wheat due to low soil nitrogen was reported by several investigators. A positive relationship between N application levels and the grain yield has already been shown in many studies (Austin *et al.*, 1980; Desai and Bahatia, 1979). Significant reduction in grain yield as a result of low-N was associated with significant reductions in all yield components traits, *i.e.* SPP, 100GW and GPS. These reductions were relatively high in magnitude for number of spikes/ plant (SPP) for parents (23.65%) and F_2's (43.52%). This indicates that SPP is the most determining component of grain yield / plant of wheat under low-N stress. The importance of this trait (number of spikes or fertile tillers per plant) in wheat for grain productivity under abiotic stress conditions was previously reported by several investigators (Al-Naggar *et al.*, 2004,2007, 2011, and 2015 a,b,c). Geleto *et al.* (1995) reported that grain yield is closely related to the number of spikes per unit area. Fertilized plots produced more spikes than control. Such response can be attributed to the adequate nitrogen availability which might facilitate the tillering ability of plants, resulting in a greater spike population. Ayoub *et al*. (1994) also reported that spike population increased with increase in nitrogen level.

Table2. *Means of studied wheat traits under low–N (0 Kg N/fed) and high–N (75 Kg N/fed) and relative reduction compared to high–N combined across parents and F_2's across two seasons*

Traits	**Parameter**	**Parents**				**F_2 crosses**	
		High-N	**Low-N**			**High-N**	**Low-N**
GPS	Average	80.23	69.81			74.48	64.78
	Reduction%	---	13.47**			---	12.47**
100GW(g)	Average	4.66	4.05			3.37	2.61
	Reduction%	---	12.96**			---	21.72**
SPP	Average	11.88	9.11			12.95	7.31
	Reduction%	---	18.96**			---	43.52**
GYPP(g)	Average	27.53	22.41			25.65	21.54
	Reduction%	---	18.96**			---	15.40**
HI(%)	Average	43.67	40.73			43.50	41.37
	Reduction%	----	6.57**			---	3.96
GPC(%)	Average	16.18	12.12			14.04	13.83
	Reduction%	------	25.06**			------	23.31**

N= nitrogen, ** and** indicate significance at 0.05 and 0.01 probability levels, respectively. Reduction%= 100[(HN-LN)/HN]*

Moreover , low nitrogen caused a significant reduction in biological yield / plant (BYPP) by 12.49 and 11.24%, grain protein content (GPC) by 25.06 and 23.31% and harvest index (HI) by 6.57 and 3.69% for parents and F_2's, respectively.

Means of each parent, and F_2 cross for studied traits under two nitrogen levels (0 and 75 kg N /Fed) across two seasons are presented in Table (3). In general means of all studied grain yield traits and grain protein content and of the three parents L25, L26 and L27 were higher in magnitude than those of the three other parents Gem 7, Gem 9 and Giza 168 under both high-N and low-N levels. Reduction in GYPP, due to low-N stress was lower in the first three parents than that in the latter parents. The first three parents (L25, L25 and L27) were therefore considered as low-N tolerant (N-efficient) genotypes and the latter ones (Gem 7, Gem 9 and Giza 168) as low-N sensitive (N inefficient) parents. These parents are therefore proper genetic material for diallel analysis for studying inheritance of adaptive traits for low-N tolerance in wheat.

The rank of crosses in F_2 generation for most studied traits was changed from one environment (N-level) to another. The highest mean of GYPP under low-N was obtained from L25 x L27 followed by L25 x L26 and L26 x Gz168 in F_2 generation. These crosses also showed the lowest reduction due to low-N stress, and therefore were considered tolerant (efficient) to low-N stress.

Table3. *Mean performance of parents and F_2's under high-and low- levels of nitrogen across two years for studied traits*

	GPS			**100GW(g)**			**SPP**		
	High N	**Low N**	**Red%**	**High N**	**Low N**	**Red%**	**High N**	**Low N**	**Red%**
	Parents								
L25	91.29	81.02	11.24**	5.58	4.57	18.14**	13.43	10.83	19.35**

L26	87.50	76.85	12.18**	5.22	4.37	16.25**	12.43	10.93	12.06**
L27	96.02	89.08	7.23**	5.17	4.92	4.99**	12.22	10.85	11.19**
Gem7	67.80	61.94	8.64**	3.90	3.62	7.14**	11.75	5.90	49.79**
Gem9	69.52	51.68	25.66**	3.99	3.40	14.68**	10.52	7.32	30.43**
Giza168	69.25	58.28	15.84**	4.10	3.42	16.52**	10.93	8.85	19.05**
	F_2 crosses								
L25 X L26	87.17	66.98	23.17**	4.63	3.21	30.58**	14.72	10.63	27.75**
L25 X L27	92.23	77.73	15.73**	4.35	3.70	15.08**	14.27	10.15	28.86**
L25 X Gem 7	86.88	72.38	16.69**	3.58	2.93	18.06**	12.92	6.83	47.10**
L25 X Gem 9	65.77	69.50	-5.67*	3.53	3.45	2.27**	13.88	7.32	47.30**
L25 X Gz 168	67.96	66.31	2.44	2.35	2.49	-5.74**	13.78	7.57	45.10**
L26 X L27	72.21	72.38	-0.23	4.34	2.60	40.15**	13.15	11.53	12.29**
L26 X Gem 7	76.69	77.28	-0.77	2.99	2.00	33.18**	12.63	6.75	46.57**
L26 X Gem 9	65.84	51.14	22.34**	2.92	2.94	-0.46*	12.03	6.27	47.92**
L26 X Gz 168	70.87	55.66	21.47**	3.45	2.31	32.90**	13.32	6.52	51.06**
L27 X Gem 7	77.33	56.94	26.38**	3.36	2.58	23.15**	13.30	7.08	46.74*
L27 X Gem 9	83.33	72.06	13.52**	3.82	3.24	15.03**	11.42	5.27	53.87*8
L L27 X Gz168	77.69	60.77	21.78**	3.34	1.96	41.39**	13.62	5.03	63.04**
Gem 7 X Gem9	61.89	74.07	-19.7**	2.38	1.62	32.10**	13.32	4.95	62.83**
Gem 7 X Gz 168	62.25	46.16	25.85**	2.46	1.94	21.11**	11.63	6.13	47.28**
Gem 9 X Gz 168	69.02	52.42	24.05**	3.05	2.22	26.98**	10.27	7.68	25.16**
L.S.D.$_{0.05}$(G)	2.00	2.10		0.49	0.39		0.94	0.87	
(N)			4.00			0.80			1.30
(GN)			2.10			0.45			1.50

Genotypes	**GYPP(g)**			**HI(%)**			**GPC(%)**		
	High N	**Low N**	**Red%%**	**High N**	**Low N**	**Red%**	**High N**	**Low N**	**Red%**
	Parents								
L25	26.48	25.39	4.1**	39.74	41.06	-3.33	13.6**	11.7**	13.59**
L26	31.42	26.91	14.35**	45.95	44.16	3.89	15.7**	14.2**	9.86**
L27	29.86	26.28	11.99**	45.61	45.11	1.10	14.3**	11.6**	18.81**
Gem 7	25.96	18.37	29.22**	42.84	42.82	0.05	12.3**	8.6*	30.43**
Gem 9	25.76	17.89	30.53**	40.79	33.49	17.88**	11.3**	6.8*	39.52**
Giza 168	25.71	19.65	23.57**	47.12	37.77	19.85**	11.1**	8.9*	19.30**
	F_2 crosses								
L25 X L26	25.96	24.97	3.81**	42.52	42.62	-0.23	16.5**	12.0**	27.53**
L25 X L27	23.94	26.09	-9.02**	41.09	48.33	-17.64**	12.0**	12.7**	-5.45
L25 X Gem 7	23.33	23.88	-2.36	39.97	53.21	-33.1**	13.9**	12.2**	11.89**
L25 X Gem 9	22.97	15.97	30.49**	35.88	36.20	-0.89	15.6**	12.5**	20.10**
L25 X Gz 168	27.08	21.75	19.71**	42.14	35.30	16.23**	17.9**	12.5**	29.91**
L26 X L27	28.97	20.25	30.09**	44.48	34.09	23.37**	16.1**	11.7**	27.33**
L26 X Gem 7	23.95	23.51	1.84	36.58	40.19	-9.85**	14.7**	12.8**	12.75**
L26 X Gem 9	25.45	22.04	13.42**	44.14	40.99	7.15**	14.1**	15.4**	-9.48**
L26 X Gz 168	31.84	24.03	24.52**	54.07	43.71	19.17**	13.8**	15.9**	-15.31**
L27 X Gem 7	29.74	19.62	34.04**	56.26	37.25	33.78**	14.4**	12.4**	14.04**
L27 X Gem 9	24.07	20.07	16.61**	40.37	35.27	12.62**	11.5**	10.1**	12.00**
L27 X Gz168	26.21	23.39	10.77**	43.90	44.32	-0.96	10.0**	9.5**	5.50
Gem 7 X Gem9	25.41	19.18	24.50**	45.78	46.85	-2.34	8.3*	8.8*	-6.97*
Gem 7 X Gz 168	21.97	18.25	16.93**	41.39	34.01	17.84**	11.3**	9.0**	19.69**
Gem 9 X Gz 168	23.88	20.16	15.57**	43.98	48.25	-9.72**	12.7**	8.8*	30.60**
L.S.D.$_{0.05}$(G)	2.1	2.0		3.8	4.0		4.41	5.47	
(N)			2.5			3.0			10.03
(GN)			2.04			3.9			6.5

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

On the contrary, the three crosses Gem 7 x Gem 9, Gem 7 x Gz168 and L27 x Gem 9 in F_2 generation showed the lowest GYPP under low-N and high reduction due to low-N and therefore were considered sensitive (inefficient) to low-N stress.

In general, F_2-means for most characters were within the range of parental genotypes. Some F_2- progenies under N-limited environment exhibited enhanced increased ability to accumulate protein in their grains, higher values of HI and SPP, suggesting transgressive effects in these characteristics. Gorny *et al.* (2011) reported a similar conclusion for grain dry weight produced per unit of N accumulated in grains (G_W/N_g).

It is worthy to note that the magnitude of N-induced alterations due to low-N stress in the majority of the studied traits was distinctly dependent upon the genotype, as evident by the significant genotype x environment interactions. These results are consistent with observations previously reported in wheat (El Bassam , 1998, Le Gouis *et al.* 2000 and 2002 , Al-Naggar *et al.* 2004, 2007 , 2011 , 2015 a,b,c), barley (Ceccarelli , 1994 and 1996 and Gorny and Sodkiewicz, 2001) and maize (Di Fonzo *et al.* 1982, Medici *et al.*, 2004, Preseterl *et al.*, 2008, Al-Naggar *et al.* 2011, 2014, 2015a,b), corroborating that an evaluation of breeding materials under diverse fertilization regimes is necessary for choice of the most efficient parental forms and / or cross combinations, as suggested by Brancourt-Hulmel *et al.*(2005), Laperche *et al.* (2006) , Dawson *et al.* (2008), Wolfe *et al.* (2008) and AL-Naggar *et al.* (2011 , 2014, 2015 a and b).

The rank of parents for GYPP was similar in the two N- environments, indicating less effect of interaction between parent and nitrogen level on GYPP. The three tolerant parents showed the highest GYPP under high-N and therefore were considered responsive parents. Moreover, L26 x Gz168 in F_2 generation had the highest GYPP under high-N and therefore considered responsive crosses.

3.2. Combining Ability Variances of F2's

Analysis of variance of general (GCA) and specific (SCA) combining ability of F_2 crosses of wheat for combined data across two years under high and low levels of nitrogen are presented in Table (4) for high–N and Table (5) for low-N. Mean squares due to genotypes were highly significant for all studied traits under the two levels of N. Results of F_2 crosses show highly significant estimates of GCA and SCA mean squares under both high-N and low-N for all studied traits.

Table4. *Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied traits in F_2's under high N conditions across two years.*

SV	**df**	**MS**						
		SPP	**GPS**	**100GW**	**GYPP**	**HI%**	**GPC**	
Genotypes (G)	20	12.77**	670.95**	5.03**	45.54**	140.44**	1917.10**	
GCA	5	27.48**	1806.64**	8.91**	79.92**	178.97**	5830.25**	
SCA	15	7.86**	292.40**	3.74**	34.08**	127.60**	612.73**	
GCA xY	5	5.06**	21.82**	0.41	7.53**	25.61**	468.05**	
SCA xY	15	2.56**	31.58**	0.19	10.80**	42.51**	162.17**	
GCA/SCA		3.49	6.18	2.30	2.35	1.40	9.52	
GCA xY /SCAxY		1.97	0.69	2.19	0.70	0.60	2.88	
error	80	0.36	1.62	0.11	1.78	5.16	19.81	

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

The ratio GCA/SCA mean squares was greater than unity for all studied traits of F_2 crosses under both high–N and low-N conditions, indicating that additive was larger in magnitude and more important than non-additive gene effects (dominance and epistasis) in controlling the inheritance of all studied traits under high-N and low N levels in the first segregating generation of the studied crosses.

These observations are in partial conflict with data reported by Le Gouis *et al.* (2002) who in N-limited diallel 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. More recently, a similar preponderance of GCA effects for grain yield was identified in F_2 and F_3 progenies of factorial hybrids between modern and exotic cultivars of barley grown under reduced N fertilization (Gorny and Ratajezak 2008). On the other hand, results of Gorny *et al.* (2011) on wheat appear to be in accord with similar N-shortage- induced increases in the importance of non-additive effects for grain yield previously reported in maize (Di Fonzo *et al*., 1982; Medici *et al*., 2004; Al-Naggar *et al*. 2011, 2015 a, b) and those for grain yield in barley (Gorny and Sodkiewicz 2001).

Table5. *Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied traits in F_2 under low N conditions across two years*

SV	df	MS						
		SPP	GPS	100GW	GYPP	HI%	GPC	
Genotypes (G)	20	27.77**	789.82**	4.89**	60.04**	182.02**	1516.3**	
GCA	5	62.93**	1792.94**	6.37**	150.04**	61.93**	2450.8**	
SCA	15	16.05**	455.45**	56.62**	17.59**	222.05**	1204.8**	
GCA xY	5	5.06**	93.53**	4.94**	14.87**	67.16*	59.08	
SCA xY	15	4.83**	17.31**	2.33**	39.84**	149.93**	32.8	
GCA/SCA		3.92	3.94	0.11	8.53	0.28	2.03	
GCA xY /SCAxY		1.05	5.40	2.13	0.37	0.45	1.80	
error	80	0.34	2.06	0.08	1.71	8.12	43.14	

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

Results indicate that mean squares due to GCA x year and SCA x year interactions in F_2's were significant or highly significant in the two levels of N, except for 100GW under high–N and GPC under low-N, indicating that the additive and non–additive gene effects in most cases were affected by years.

The mean squares due to SCA x year were higher in magnitude than those due to GCA x year for all studied traits of F_2 crosses, except for SPP and 100GW under high–N and SPP, GPS, 100GW and GPC under low-N, suggesting that in F_2 crosses SCA (non-additive variance) is more affected by year than GCA for four traits (GYPP, GPS, HI nd GPC) under high-N and two traits (GYPP and HI) under low-N and GCA (additive variance) is more affected by year than SCA for other traits.

3.3. GCA Effects Of Parents In F2 Crosses

Estimates of general combining ability (GCA) effects calculated from the analysis of F_2 diallel crosses under the two levels of N are presented in Tables (6 and 7). The best general combiners based on F_2 diallel analysis were considered those having the highest positive GCA effects for the rest of studied F_2 traits.

Table6. *Estimates of general combining ability effects ($\hat{g}_i$) of all traits in F_2's under high N conditions across two years*

Parents	SPP	GPS	100GW	GYPP	HI	GPC	
L25	1.20**	6.22*	0.43**	-0.88*	-0.09*	-4.21**	
L26	0.41*	1.87*	0.34**	1.96**	-0.06*	9.01**	
L27	0.12	7.75**	0.40**	1.17**	-0.04**	13.04**	
Gem 7	-0.17	-4.03**	-0.45**	-0.87*	-0.01	6.13**	
Gem 9	-0.70**	-5.99**	-0.31**	-1.25*	0.084*	-9.41**	
Giza 168	-0.85**	-5.82*	-0.41**	-0.11	0.12**	-14.55**	
SE_{gi}	0.32	0.68	0.17	0.71	0.03	2.37	
SE_{gi-gj}	0.50	1.05	0.27	1.11	0.06	3.68	

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

Table7. *Estimates of general combining ability effects ($\hat{g}_i$) of all traits in F_2's under low N conditions across two years*

Parents	SPP	GPS	100GW	GYPP	HI	GPC	
L25	1.17**	6.43**	0.47**	1.36*	1.18	-4.91*	
L26	1.1**	1. 7**	0.08	2.01*	0.20*	7.25**	
L27	0.75*	6.81**	0.34*	1.18*	0.14	10.44**	
Gem 7	-1.41**	-1.6*	-0.36*	-1.42*	1.10	-1.27	
Gem 9	-1.1**	-5.1**	-0.11	-2.42	-1.72*	-6.61**	
Giza 168	-0.52*	-8.2**	-0.42**	-0.71*	-0.90	-4.89*	
SE_{gi}	0.31	0.77	0.15	0.70	1.53	3.50	
SE_{gi-gj}	0.48	1.19	0.23	1.08	2.36	5.44	

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

Data in Table (6) indicate that under high-N, the best general combiners based on F_2 diallel analysis were L27 for fou traits (GPS, 100GW, GYPP and GPC), L26 for five traits (SPP, GPS, 100GW, GYPP and GPC), L25 for three traits (SPP, GPS, and 100GW), and Gem7 for one trait (GPC).

Under low-N (Table 7), the best general combiners were L25 for seven traits (SPP, GPS, 100GW and GYPP) , L26 for five traits (SPP, GPS, GYPP, HI, and GPC), L27 for five traits (SPP, GPS, 100GW, GYPP, and GPC). The best combiners identified from both F_1 and F_2 diallel analyses under high-N and low-N are more or less similar in most cases under low-N conditions. L25, L26 and L27 are generally the best combiners for most grain yield and quality traits based on diallel analyses of F_2 crosses. These parents are expected to have more additive genes for the respective characters

3.4. SCA Effects Of F2's

Specific combining ability (SCA) effects of the F_2 crosses under two levels of N are presented in Tables (7 and 8). Under high-N, the best F_2 cross in SCA effects was L27 x Gem 7 for three traits (GYPP, HI and GPC), L26 x Gz168 for two traits (GYPP and HI), Gem7 x Gem9 for two traits (GPS and HI) and Gem 9 x Gz168, and L25 x Gem7 for one trait (GPS)

Table8. *Estimates of specific combining ability effects ($\hat{s}_{ij}$) of F_2's under high N conditions across two years*

Crosses	**SPP**	**GPS**	**100GW**	**GYPP**	**HI**	**GPC**	
L25 X L26	1.03*	2.96*	0.12	-1.31	0.84	9.49**	
L25 X L27	0.53	2.15*	-0.21	-2.53*	-1.05	4.92	
L25 X Gem 7	-1.58*	8.57**	-0.14	-1.1	-0.71	-12.7**	
L25 X gem 9	0.55	-10.57**	-0.33	-1.08	-3.05	-4.56	
L25 X Gz 168	0.32	-8.56**	-1.40**	1.90	-0.30	-1.05	
L26X L27	0.39	-13.52**	-0.13	-0.40	-1.73	-3.20	
L26X Gem 7	-0.65	2.72*	-0.63*	-3.32	-8.17**	4.94	
L26X Gem 9	-0.92*	-6.15**	-0.84*	-1.44	1.13	-12.32**	
L26X Gz 168	-0.15	-1.30	-0.21	3.80*	7.56**	6.22	
L27 X Gem 7	-0.64	-2.51*	-0.33	3.26*	11.05**	11.19**	
L27 X Gem 9	-1.29*	5.45**	-0.01	-2.04*	-3.10*	13.27**	
L27 X Gz168	-0.003	-0.36	-0.38	-1.03	-3.06*	8.38**	
Gem 7 X Gem9	2.44*	-4.21**	-0.60*	1.35	3.77*	3.69	
Gem7 X Gz 168	-0.81	4.02**	-0.41	-3.23*	-4.12*	12.9**	
Gem9 X Gz 168	-1.70*	4.71**	0.03	-0.94	0.21	-3.70	
SE_{Sij}	0.89	1.87	0.48	1.96	3.34	6.54	
$SE_{Sij-Sik}$	1.32	2.79	0.71	2.93	4.98	9.76	
$SE_{Sij-Skl}$	1.23	2.58	0.66	2.71	4.62	9.04	

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

Under low-N, the best F_2 cross for SCA effects was L25 x Gem 7 for two traits (GYPP and HI), Gem9 x Gz168 for SPP, L27 x Gem 9, for GPS and GPC and L27 x Gz168 for GPC. These F_2 crosses and especially those showing high SCA effects and including one parent of high GCA effects are expected to release more transgressive segregants if additive gene effects existed in the high general combiner parent and epistasis acts in the cross in the same direction for decreasing the undesirable characters and increasing the desirable traits. Results of Gorny *et al.* (2011) on wheat F_2 crosses appear to be in accord with similar N-Shortage – induced increases in the importance of non – additive effects for grain yield and components of NUE previously reported in maize (Di Fonzo *et al.*, 1982, Medici *et al.*, 2004, Al-Naggar *et al.* 2015a) and those for grain yield under low-N in grain sorghum (Al-Naggar *et al.*, 2008). Gorny *et al.* (2011) reported that under high N-fertilization, the grain yield components were incanted in a manner favorable for wheat selection (preponderance of additive effects) however the enhanced contribution of non-additive gene effects and increased dominance under N-limited conditions could impede wheat selection to improve the N efficiency and adaptation to less luxurious fertilization regimes. They concluded that selection methods that eliminate masking non-additive influences and take advantage of the additive variance should be employed to improve those traits.

Table9. *Estimates of specific combining ability effects ($\hat{s}_{ij}$) of F_2's under low N conditions across two years*

Crosses	SPP	GPS	100GW	GYPP	HI	GPC	
L25 X L26	0.54	-7.36*	-0.36	-0.19	0.06	16.62**	
L25 X L27	0.40	-1.73	-0.14	1.76	5.82*	-3.73	
L25 X Gem 7	-0.76	1.34	-0.20	2.15**	9.74*	-12.50**	
L25 X Gem 9	-0.60	1.99	0.07	-4.77*	-4.45*	-18.77**	
L25 X Gz 168	-0.91*	1.87	-0.58*	-0.70	-6.17*	-6.34	
L26X L27	1.86*	-2.35*	-0.85*	-4.73**	-7.45*	-8.61	
L26X Gem 7	-0.79	10.97**	-0.75*	1.13	-2.30	-0.11	
L26X Gem 9	-1.57*	-11.66**	-0.05	0.65	1.32	7.09	
L26X Gz 168	-1.89*	-4.05*	-0.37*	0.94	3.22	5.73	
L27 X Gem 7	-0.08	-14.49**	-0.43**	-1.93*	-5.18*	0.82	
L27 X Gem 9	-2.22*	4.15*	-0.01	-0.48	-4.34*	23.47**	
L27 X Gz168	-3.02*	-10.25**	-0.99**	1.13	3.89	25.36**	
Gem 7 X Gem9	-0.39	14.57**	-0.94**	1.23	6.28*	-0.59	
Gem 7 X Gz 168	0.23	-10.25**	-0.30*	-1.41	-7.39*	-6.50	
Gem 9 X Gz 168	1.5*	-0.47	-0.26*	1.50	9.69*	-3.96	
SE_{Sij}	0.85	2.11	0.41*	1.92	4.19	9.66	
$SE_{Sij-Sik}$	1.27	3.15	0.61*	2.87	6.26	14.40	
$SE_{Sij-Skl}$	1.18	2.92	0.57*	2.66	5.79	13.34	

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

3.5. Correlations Between Xp And GCAF1 And Between XF2 And SCAF2 Effects

Rank correlation coefficients calculated between mean performance of parents (Xp) and their GCA effects of F_2's for studied grain yield and quality characters are presented in Table (9). Significant ($P \leq 0.05$ or 0.01) correlations between Xp and GCA_{F1} effects and between Xp and GCA_{F2} effects existed for all studied traits under both high-N and low-N, except for HI between Xp and GCA_{F2} under high-N conditions. In general, the magnitude of correlation coefficient between Xp and GCA_{F2} effects was very high (> 0.93 in 8 out of 12 cases) and was higher at low-N than high-N in 4 out of 6 traits. The highest correlation coefficient under low-N between Xp and GCA was observed for GYPP (0.98) and 0.97 for SPP, 0.93 for GPS and 0.89 for 100GW. On the contrary, the lowest correlation coefficient between Xp and GCA effects was shown under high-N for HI (0.25). These results indicate that the best performing parents for grain yield components are also the best general combiners and *vice versa*, and therefore, the mean performance of a given parent under low-N and high-N is an indication of its general combining ability. This conclusion was previously reported by Le Gouis *et al.*, (2000) and Yildirim *et al.* (2007) in wheat and Meseka *et al* (2016) and Al-Naggar *et al.*, (2015a) in maize. Le Gouis *et al.* (2000) reported that when GCA effects are largely superior to SCA effects, the correlation between *per se* value and GCA would give an indication about the possibility to use the means of the two parents to predict the value of hybrid. Yildirim *et al.* (2007) reported that *per se* values of parent for grain yield traits were positively correlated with GCA effects of themselves at N0 level; this can be used to obtain high N use efficient lines.

Table10. *Rank correlation coefficients among means performance of parents (Xp) and their GCA effects for F_2's (GCA_{F2}) and between mean performance of F_2's (X_{F2}) and SCA_{F2} effects under high and low–N environments across two seasons.*

Traits	X_P *vs* GCA_{F2}				X_{F2} *vs* SCA_{F2}	
	HN	**LN**			**HN**	**LN**
SPP	0.98**	0.71**			0.71**	0.38**
GPS	0.98**	0.70**			0.70**	0.13
100GW	0.98**	0.88**			0.88**	0.37**
GYPP	0.94**	0.83**			0.83**	0.13
HI%	0.25	0.91**			0.91**	-0.06
GPC	0.77**	0.32**			0.32**	0.34**

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

For F_2 crosses, under both low-N and high-N, the correlation coefficient between mean performance of F_2's (X_{F2}) and their SCA_{F2} effects were highly significant and positive; in all studied traits under high-N and SPP, 100GW and GPC under low-N (Table 9). This indicates that the mean performance of a given F_2 cross could be used as an indication of its specific combining ability effects for all studied characters under high-N and SPP, 100GW and GPC under low-N. This conclusion was also reported by Le Gouis *et al*., (2000) and Yildirim *et al.* (2007) under low-N conditions.

Summarizing the above mentioned results, it cloud be concluded that low-N stress affects on the associations between mean performance of parents and $F_{2's}$ on GCA and SCA effects of $F_{2,}$ respectively and so conclusions generated from results under high-N differ from those generated from results under low-N. Only indication under high-N and low-N are similar for the association between mean performance of parents and their GCA effects for F_2 (GCA_{F2}). Thus, under either low-N or high-N the mean performance of a given parent could be considered an indication of its general combining ability estimated from F_2's. But under high-N only, the mean performance of a given F_2 cross could be considered an indication of its SCA effects in F_2 generation.

IV. CONCLUSIONS

This study identified wheat genotypes (the promising lines L25, L26 and L27 and their F_2 crosses L25 x L27, L25 x L26 and L26 x G168 of high mean performance and combining ability effects for grain yield and quality traits under low-N conditions. These genotypes could be offered to wheat breeding programs for developing low-N tolerant varieties. Breeding programs that utilizes both additive and non-additive genetic variances could be used to improve grain yield and quality traits, with more emphasis on selection methods in segregating generations of wheat hybrids that utilize additive and additive x additive genetic components under low-N conditions. The results indicated that under low-N and high-N, the mean performance of a given parent is an indication of its general combining ability and that the mean performance of a given F_2 cross could be used as an indication of its specific combining ability effects for all studied grain yield component traits and grain protein content.

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