Response of Performance and Combining Ability of Wheat Parents and Their F$_2$ Progenies for N Efficiency Traits to Reducing N-Fertilizer Level

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Abstract: Because of high production cost of nitrogen (N) fertilizer and prevention of environmental pollution, it is important to improve N use efficiency (NUE) of wheat (*Triticum aestivum* L.). The objective of this study was to evaluate NUE traits of 6 x 6 diallel wheat F$_2$ progenies and parents at low (LN, no N fertilizer) and high (HN,75 kg N/fed) N levels. Two experiments were conducted during two seasons, the 1st under HN and the 2nd under LN using RCBD in three replications. Data analyzed across seasons indicated that L25, L26 and L27 showed high values of nitrogen use (NUE) and uptake (NUPE) efficiency and the best general combining ability (GCA) effects for these traits. The best F$_2$ crosses in *per se* performance and specific combining ability (SCA) effects were L26 x Gz168, L27 x Gem7, L26 x L27 and L25 x Gz168). Mean squares due to both GCA and SCA were significant under both low-N and high-N for all NUE components, 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 NUE, NUPE, nitrogen utilization efficiency (NUTE) and nitrogen harvest index (NHI) 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 NUE components.

Keywords: Combining ability, *Triticum aestivum*, N-use efficiency, low-N, N-harvest index, Diallel

I. INTRODUCTION

The consumption of nitrogen (N) fertilizer in the world as well as in Egypt increases year after year. Therefore, it is necessary to improve cultivars that have high N use efficiency. According to Moll *et al.* (1982), N use efficiency (NUE) in cultivar development can be divided into two component: (i) uptake efficiency (NUPE) (total plant N/N supplied), which is the ability of the crop to extract N from the soil; and (ii) utilization efficiency (NUTE) (Grain yield/total plant N), which measures the capacity of the plant to convert the already absorbed N in the plant into grain yield. Nitrogen utilization efficiency was further subdivided into nitrogen harvest index (NHI) and biomass production efficiency (grain dry weight / total above ground biomass N at maturity) (Ortiz-Monasterio et al., 1997).

In Egypt, progress in breeding wheat (*Triticum aestivum* L.) better adapted to less favorable fertilization regimes is still restricted for several reasons. Wheat breeders are frequently skeptical not only because of the complexity of the matter, but mainly due to limited data on both the variation among available wheat germplasm and the genetics of key characters involved. Hence, several important questions remain to be unsolved, especially in regard to the most effective breeding scheme, desirable plant ideotypes for low input ecosystems and appropriate selection criteria necessary for such breeding programs (e.g. Ceccarelli, 1996; Dawson *et al.* 2008 and Wolfe *et al.* 2008).

Among cereals, wheat is commonly identified as a species with higher requirements for nutrients, especially nitrogen. Thus, breeding wheat cultivars with improved adaptation to low N fertilization regime has gained importance. Furthermore, modern wheat cultivars are phenotypically different but, in essence, represent a limited gene pool. The majority of them were developed under favorable or even luxurious fertilization regimes used at most breeding stations without or with scarce selection pressure for components of nutrient use efficiency.

Genetic variability for N use efficiency in wheat has been reported (Ortiz-Monasterio *et al.*, 1997; Le Gouis and Pluchard, 1996; Le Gouis *et al.*, 2002). Dhugga and Waines (1989),working on bread and durum wheat, have reported that NUPE was the predominant component of NUE at all levels of N and the relative contribution of NUPE to NUE increased as the level of N increased in the soil. However, Ortiz-Monasterio et al. (1997) has shown

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that the level of N in the soil plays a very important role in the genetically expression of NUPE and NUTE of CIMMYT's bread wheat germplasm. Also they found better expression of NUPE under low N conditions and a better expression of NUTE under high N conditions. Van Ginkel *et al.* (2001) evaluated the improvement of NUE through plant breeding in six different wheat populations obtained from an incomplete 4×4 diallel. They selected the populations under five different selection regimes from F_2 to F_6. The alternate selection between high N in F_2, low N in the F_3-F_6 gave the highest grain yield, and grain yield of wheat was affected by N level in soil, NUTE, and NUPE. These N efficiency parameters were correlated with both environments and genotypes (Ma *et al.,* 2004). Thomason *et al.* (2002) reported that the most critical components of NUE were production system, cultivar, N fertilizer timing, and top dress N applications.

The manner in which target traits are inherited has, of course, major consequences for the whole breeding strategy. However, our understanding of the inheritance of the N efficiency components in wheat, as in other cereals, is still extremely limited. There is some information regarding various characteristics decisive for the uptake efficiency in juvenile wheat plants (Gamzikova 1992; An *et al.* 2006; Gorny *et al.* 2006b and Laperche *et al.* 2006b), but the limited data may lead to uncertain conclusions on N efficiency over the whole growing season. However, the genetic control of whole-season N efficiency has rarely been examined in wheat. Recent extensive molecular studies (Charmet et al., 2005; Habash *et al.* 2007; Laperche *et al.* 2008 and Fontaine *et al.* 2009) identified numerous genome regions (QTLs) responsible for grain yield structure and nitrogen yield under N limitations, grain protein content and N metabolism in the uppermost foliage as well as for the activity of glutamine synthetase and glutamate dehydrogenase, the key enzymes involved in N assimilation.

Further advancement in the yield of this important species requires adequate information regarding the nature of combining ability of the parents available in a wide array of genetic material to be used in the hybridization program and also the nature of gene actions involved in the expression of quantitative and qualitative traits of economic importance. The general and specific combining ability effects are very effective genetic parameters in deciding the next phase of the breeding program. According to Baker (1978), the combining ability is a better biometrical tool to circumvent the plant breeding program.

In earlier investigations (Le Gouis *et al.* 2002), both additive and non-additive genetic effects were crucial for agronomic NUE components in F1 hybrids between modern cultivars. In contrast, additive gene action was only important for NUE components among F2 progenies of wheat cultivars (Yildirim *et al.* 2007).

To the best of our knowledge, however, information are scarce in wheat for the major physiological measures of N efficiency, *i.e.* the uptake and utilization efficiencies (NUPE and NUTE) when whole-season indices and conventional genetic/ breeding approaches are considered, and this may have an impact on current breeding methods, aspirations and goals. Gorny *et al.* (2011) reported that the soil N-treatments imposed had a substantial influence on gene actions responsible for the efficiency components and modes of inheritance. They found that under high N-fertilization, the efficiency 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. Thus, the objectives of present study were: (i) to evaluate NUE traits of 6 x 6 diallel wheat F_2 progenies and parents at low (LN, no N fertilizer) and high (HN,75 kg N/fed) N levels, (ii) to identify the best combining wheat parents and their crosses on the basis of their general and specific combining ability effects for nitrogen use efficiency traits, and (iii) to investigate the relationships between *per se* performance of parents and crosses and their general and specific combining ability effects, respectively.

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
Gemmeiza(Gem7)	CMH74A.630/SX//Seri82/3/Agent.	Sensitive
Gemmeiza9(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 with three replications. The low level was without fertilization, *i.e.* 0 kg N/fed (LN) (fed=feddan=4200m^2) and the high level was 75 kg Nitrogen/ fed (HN); this is the recommended level of Ministry of Agriculture. 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 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. Available soil nitrogen after adding nitrogen fertilizer was therefore 55 and 130 kg N/fed in the first season and 57 and 132 kg N/fed in the second season for the two treatments, i.e. LN and HN, respectively. The available nitrogen to each plant (including soil and added N) was calculated for each environment to be 0.79, 1.85 g/plant in 2007/2008 season and 0.81 and 1.89 kg/fed in 2008/2009 season, with an average across the two seasons of 0.80 and 1.87 g/plant for the two environments LN and HN, 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).

2.4. Data Collection

Grain yield/ plant (GYPP) was measured as weight of the grains of each individual plant using an average of 10 plants each entry. At physiological maturity stage, five random guarded plants were removed from each plot by cutting at the soil surface. The plants were bulked as one sample per plot. They were separated into straws (including leaves, stems and spike residues) and grains. Samples were oven dried at 70°C to a constant weight and each part was weighed separately. Samples were ground in powder and nitrogen of straws (N straw) and grains (N_g) was determined using Kjeldahl procedure according to A.O.A.C. (1990). Total plant nitrogen (N_t) was calculated as follows: $N_t = N_g + N_{straw}$. The following traits were recorded: **1. Nitrogen use efficiency (NUE) g/g**= (GYPP / N_s). **2. Nitrogen uptake efficiency (NUPE) %** =100 (N_t / N_s). **3. Nitrogen utilization efficiency (NUTE)** (g/g)

= (GYPP/N_t). **4. Nitrogen harvest index (NHI %)** = $100(N_g/ N_t)$. Where GYPP is grain yield/ plant in gram, N_t is total nitrogen in the whole plant (grains and straw), N_s is available nitrogen in the soil for each plant, and N_g is grain nitrogen content. Nitrogen efficiency parameters No. 1, 2, and 3 were estimated according to Moll *et al.* (1982).

III. 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 Model I (fixed effect) Method 2. General (GCA) and specific (SCA) combining ability variances and effects were estimated according to Griffing (1956) model I (i,e the fixed model) method II. Estimates of both general (δ^2_g) and specific (δ^2_s) combining ability variances were calculated according to Griffing (1956) 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 ith 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.

IV. RESULTS AND DISCUSSION

4.1. Per Se Performance

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 (2). In general, means of NUE and NUPE of the three parents L25 , L26 and L27 were higher in magnitude than those of the three other parents Gem7, Gem9 and Giza168 under both high-N and low-N levels. The first three parents (L25, L26 and L27) were therefore considered as low-N tolerant (N-efficient) genotypes and the latter ones (Gem7, Gem9 and Giza168) as low-N sensitive (N inefficient) parents. These parents are therefore proper genetic material for diallel analysis for studying inheritance of nitrogen use efficiency traits 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 NUE under low-N was obtained from L26 x Gz 168 followed by L27 x Gem7, L26 x L27 and L25 x Gz168 in F_2 generation. These crosses were therefore considered tolerant (N-efficient) to low-N stress.

On the contrary, the three crosses Gem7 x Gz168, L25 x Gem9, Gem9 x Gz168 and L26 x Gem7 in F_2 generation showed the lowest NUE under low-N, and therefore were considered sensitive (N-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 N uptake efficiency, higher values of NHI, suggesting transgressive effects in these characteristics. Gorny *et al.* (2011) reported a similar conclusion for NUPE and 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 N-efficiency components 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, 2006, 2007, 2008, 2009, 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*. 2010, 2011, 2014, 2015 a, b, c), 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, c).

Table2. *Mean performance for nitrogen use efficiency traits of parents and F2's under high-and low- levels of nitrogen across two years.*

Genotypes	NUE(g/g)			NUPE(g/g)		
	High N	Low N	Red%	High N	LowN	Red%
	Parents					
L25	14.16	31.76	-124.3**	16.97	30.77	-81.30**
L26	16.80	33.64	-100.3**	18.88	36.87	-95.31**
L27	15.96	32.86	-105.9**	17.63	30.82	-74.79**
Gem7	13.89	22.99	-65.56**	15.26	22.30	-46.11**
Gem9	13.77	22.40	-62.65**	13.88	16.97	-22.30**
Giza168	13.74	24.57	-78.77**	13.38	23.48	-75.44**
				F₂ crosses		
L25 X L26	13.88	31.22	-125.0**	18.17	31.75	-74.73**
L25 X L27	12.80	32.61	-154.7**	19.38	34.27	-76.85**
L25 X Gem 7	12.47	29.82	-139.1**	20.74	31.18	-50.34**
L25 X Gem 9	12.28	19.95	-62.5**	15.20	32.79	-115.72**
L25 X Gz 168	14.48	27.27	-88.40**	17.09	32.30	-89.03**
L26X L27	15.49	25.33	-63.50**	19.89	30.22	-51.97**
L26X Gem 7	12.82	29.33	-128.9**	22.38	31.48	-40.66**
L26X Gem 9	13.63	27.49	-101.6**	19.30	37.29	-93.24**
L26X Gz 168	17.02	30.03	-76.50**	17.92	38.98	-117.52**
L27 X Gem 7	15.90	24.51	-54.10**	16.84	33.54	-99.23**
L27 X Gem 9	12.87	25.02	-94.4**	17.17	25.12	-46.29**
L27 X Gz168	14.01	29.16	-108.0**	18.40	23.75	-29.08**
Gem 7 X Gem 9	13.58	23.93	-76.20**	13.25	21.40	-61.47**
Gem 7 X Gz 168	11.74	22.79	-94.20**	11.82	23.28	-97.05**
Gem 9 X Gz 168	12.77	25.18	-97.20**	9.37	22.23	-137.32**
L.S.D.-0.05(G)	1.1	2.6		0.98	3.2	
(N)			3.2			8.15
(GN)			2.0			2.5

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

Continu. Table (2)

Genotypes	NUTE(g/g)			NHI (%)		
	High N	Low N	Red%	High N	LowN	Red%
	Parents					
L25	0.84	1.03	-23.25**	54.87	52.07	5.11
L26	0.89	0.91	-2.31**	57.17	56.51	1.14
L27	0.91	1.07	-18.31**	55.75	55.49	0.47
Gem7	0.92	1.03	-12.43**	55.52	56.46	-1.68
Gem9	1.03	1.32	-27.92**	56.25	59.15	-5.15
Giza168	1.04	1.06	-2.15**	57.04	55.98	1.87
	F₂ crosses					
L25 X L26	0.76	1.03	-34.22**	60.07	55.37	7.83**
L25 X L27	0.67	0.90	-34.60**	58.04	54.41	6.26**
L25 X Gem 7	0.61	0.93	-51.08**	54.92	57.53	-4.75*
L25 X Gem 9	0.81	0.75	7.83**	54.44	55.92	-2.73
L25 X Gz 168	0.86	1.07	-24.72**	56.39	56.97	-1.04
L26X L27	0.79	1.03	-30.65**	54.01	56.62	-4.84*
L26X Gem 7	0.57	0.85	-47.71**	55.03	59.84	-8.75**
L26X Gem 9	0.72	0.67	7.49**	57.32	60.74	-5.97**
L26X Gz 168	0.95	0.90	4.77**	56.43	60.03	-6.37**
L27 X Gem 7	0.95	0.92	2.75**	57.50	54.14	5.83**

L27 X Gem 9	0.75	1.00	-32.88**	55.38	58.91	-6.37**
L27 X Gz168	0.76	1.18	-54.27**	53.86	58.47	-8.56**
Gem 7 X Gem 9	1.03	1.22	-19.00**	59.42	61.01	-2.68
Gem 7 X Gz 168	1.00	1.09	-8.54**	58.22	57.35	1.50
Gem 9 X Gz 168	1.38	1.22	11.70**	60.71	58.63	3.43
L.S.D.$_{-0.05}$(G)	0.09	0.15		0.76	1.75	
(N)			0.24			2.16
(GN)			0.15			3.87

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

The rank of parents for NUE was similar in the two N- environments, indicating less effect of interaction between parent and nitrogen level on NUE. The three tolerant parents showed the highest NUE under high-N and therefore were considered responsive parents. Moreover, L26 x L27 and L25 x L27 in F_1 and L26 x Gz168 in F_2 generation had the highest GYPP under high-N and are therefore considered responsive crosses.

4.2. Combining Ability Variances

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 (3) for high–N and Table (4) 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, except SCA mean squares for NUTE and NHI under low-N conditions.

Table3. *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			
		NUE	NUPE	NUTE	NHI
Genotypes (G)	20	13.02**	59.32**	3.82**	22.24**
GCA	5	22.92**	144.31**	0.33**	28.41**
SCA	15	9.72**	30.99**	0.14**	20.19**
GCA xY	5	2.21**	8.76**	0.03**	11.95**
SCA xY	15	3.05**	7.54**	0.89**	23.85**
GCA/SCA		2.36	4.66	2.30	1.41
GCA xY /SCAxY		0.72	1.16	0.04	0.50
error	80	0.51	0.48	0.004	2.00

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

Table4. *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			
		NUE	NUPE	NUTE	NHI
Genotypes (G)	20	93.84**	243.31**	0.15**	32.05**
GCA	5	235.46**	547.07**	0.17**	69.18**
SCA	15	46.63**	142.05**	0.002	19.67
GCA xY	5	40.79**	21.22**	2.96**	92.64**
SCA xY	15	61.92**	53.79**	0.07**	32.82**
GCA/SCA		5.05	3.85	86.00	3.51
GCA xY /SCAxY		0.66	0.39	42.41	2.82
error	80	2.68	6.138	0.01	11.85

* 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 nitrogen use efficiency 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 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. More recently, a similar preponderance of GCA effects for N uptake and NUTE 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 and components of NUE previously reported in maize (Di Fonzo *et al.*, 1982; Medici *et al.*, 2004 and Al-Naggar *et al*. 2015 a, b) and those for NUTE in barley (Gorny and Sodkiewicz 2001).

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, indicating that the additive and non–additive gene effects controlling studied nitrogen use efficiency traits 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 NUPE under high–N and NUTE and NHI under low-N, suggesting that SCA (dominance and epistasis variance) is more affected by year than GCA (additive variance) for most studied traits of F_2 crosses.

4.3. GCA Effects of Parents in F_2 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 (5 and 6). The best general combiners based on F_2 diallel analysis were considered those having the highest positive GCA effects for all studied nitrogen use efficiency traits.

Table5. *Estimates of general combining ability effects ($\hat{g}_i$) of all traits in F_2's under high N conditions across two years*

Parents	NUE	NUPE	NUTE	NHI
L25	-2.97*	-0.47*	0.86**	-0.57
L26	1.10	1.05*	2.22**	0.62
L27	1.56*	0.62*	1.16**	-0.69
Gem 7	0.10	-0.47*	-0.26	-0.80*
Gem 9	-1.64*	-0.668*	-1.95*	0.54
Giza 168	1.86*	-0.063*	-2.04**	0.90*
SE$_{gi}$	1.22	0.38	0.37	0.75
SE$_{gi-gj}$	1.88	0.59	0.58	1.62

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

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

Parents	NUE	NUPE	NUTE	NHI
L25	1.72**	2.22*	-0.04	-1.60
L26	2.51**	5.32*	-0.09*	-1.05
L27	1.46*	0.64	0.01	0.40
Gem 7	-1.78**	-1.94*	0.001	-0.12
Gem 9	-3.03	-3.37**	0.05	1.69
Giza 168	-0.88*	-2.87*	0.07	0.69
SE$_{gi}$	0.88	1.33	0.06	2.85
SE$_{gi-gj}$	1.36	2.06	0.09	1.72

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

Data in Table (5) indicate that under high-N the best general combiners based on F_2 diallel analysis were L27 for three traits (NUE, NUPE and NUTE), Gz 168 for two traits (NUE and NHI), L26for two traits (NUPE and NUTE), L25 for one trait (NUTE).

Under low-N (Table 6), the best general combiners were L25 and L26 for two traits (NUE and NUPE) and L27 for one trait (NUE). L25, L26and L27 are generally the best combiners for nitrogen use efficiency traits based on diallel analyses of F_2 crosses, especially under low-N conditions. These parents are expected to have more additive genes for the respective characters.

4.4. SCA Effects in F_2'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 two traits (NUE, NUTE),L26x Gz168 for NUE and L26x Gem 7, L25 x Gem 7, L25 x Gz 168 and L26x Gem9 for NUPE.

Under low-N, the best F_2 cross for SCA effects was L25 x Gem 7 for two traits (NUE, NUPE), L25 x L27 and L26x Gem 9 for NUPE. 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.

Table7. *Estimates of specific combining ability effects (ŝ$_{ij}$) of F_2's under high N conditions across two years.*

Crosses	NUE	NUPE	NUTE	NHI
L25 X L26	-0.70	-1.72*	0.04	0.53
L25 X L27	-1.35	0.55	-0.07	0.43
L25 X Gem 7	-0.59	3.33*	-0.16*	0.31
L25 X Gem 9	-0.58	-0.52	-0.06	0.29
L25 X Gz 168	1.01	1.46*	-0.04	0.12
L26X L27	-0.18	-0.30	0.03	1.52
L26X Gem 7	-1.77*	3.61**	-0.22**	-1.49
L26X Gem 9	-0.75	2.22*	-0.17*	-3.31*
L26X Gz 168	2.03*	0.93	0.02	-1.72
L27 X Gem 7	1.74*	-0.87	0.13*	-0.06
L27 X Gem 9	-1.09*	1.15*	-0.16*	0.88
L27 X Gz168	-0.55	2.47*	-0.18*	-0.37
Gem 7 X Gem9	0.78	-1.34*	0.09	-0.94
Gem 7 XGz 168	-1.74*	-2.69*	0.03	-2.83*
Gem 9 x Gz 168	-0.50	-3.46*	0.30*	0.18
SE$_{Sij}$	1.05	1.02	0.10	2.05
SE$_{Sij}$-$_{Sik}$	1.57	1.52	0.15	3.01
SE$_{Sij}$-$_{Skl}$	1.45	1.41	0.14	2.87

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

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 components of NUE previously reported in maize (Di Fonzo *et al*., 1982, Medici *et al*., 2004, Al-Naggar *et al*. 2015 a, b) and those for NUE in grain sorghum (Al-Naggar *et al*., 2008). Gorny *et al*. (2011) reported that under high N-fertilization, the efficiency 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.

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

Crosses	NUE	NUPE	NUTE	NHI
L25 X L26	-0.24	-5.01**	0.15	1.95
L25 X L27	2.19	5.80*	-0.09	-0.52
L25 X Gem 7	2.65*	3.91*	-0.04	0.96
L25 X Gem 9	-5.97*	0.91	-0.28*	1.83
L25 X Gz 168	-0.80	-2.19	0.04	-0.33
L26X L27	-5.87*	-9.09**	0.10	-2.16
L26X Gem 7	1.37	3.32	-0.07	1.49
L26X Gem 9	0.78	11.02**	-0.30*	-1.93
L26X Gz 168	1.18	3.43	-0.07	0.11

L27 X Gem 7	-2.40	1.44	-0.10	2.34
L27 X Gem 9	-0.64	0.001	-0.08	1.42
L27 X Gz168	1.34	-1.20	0.09	1.71
Gem 7 X Gem9	1.51	-2.91	0.16	0.12
Gem 7 X Gz 168	-1.78	-2.05	0.01	0.68
Gem 9 X Gz 168	1.86	-0.31	0.09	-2.25
SE$_{Sij}$	2.41	3.65	0.16	5.06
SE$_{Sij}$-$_{Sik}$	3.60	5.44	0.23	7.55
SE$_{Sij}$-$_{Skl}$	3.33	5.04	0.22	6.98

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

4.5. Correlations between X_P and GCA_{F2} and between X_{F2} and SCA_{F2}

Rank correlation coefficients calculated between mean performances of parents (Xp) and their GCA effects of F$_2$'s for studied characters are presented in Table (9). Significant (P≤ 0.05 or 0.01) correlations between Xp and GCA$_{F2}$ effects existed for all studied traits under both high-N and low-N, except for NHI under low-N. In general, the magnitude of correlation coefficient between Xp and GCA$_{F2}$ effects was higher at low-N than high-N for most studied traits. The highest correlation coefficient under low-N between Xp and GCA was observed for NUE (0.98) followed by NUPE (0.96). On the contrary, the lowest correlation coefficient between Xp and GCA$_{F2}$ effects was shown under high-N for NUE (0.44). These results indicate that the best performing parents for nitrogen use efficiency and their 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* (2013) and Al-Naggar *et al*., (2015 a, b) 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 and nitrogen use efficiency were positively correlated with GCA effects of themselves at N0 level; this can be used to obtain high N use efficient lines.

Table9. *Rank correlation coefficients among mean performance of parents (Xp) and their GCA effects for F$_2$'s (GCA$_{F2}$) and between means 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**
NUE	0.44**	0.98**	0.83**	0.66**
NUPE	0.73**	0.96**	0.83**	0.50**
NUTE	0.86**	0.70**	0.89**	0.90**
NHI	0.78**	0.61**	0.02	0.14

* 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 SCA$_{F2}$ effects for all studied nitrogen use efficiency traits, except HNI were highly significant and positive; with little higher estimate under high-N than low-N in most studied traits (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, either under high-N or under low-N. This conclusion was also reported by Le Gouis *et al*., (2000) and Yildirim *et al*. (2007) under low-N conditions.

V. CONCLUSIONS

This study identified wheat genotypes (the lines L25, L26 and L27 and their F$_2$ crosses L26 x Gz168, L27 x Gem7, L26 x L27 and L25 x Gz168) of highest mean performance and combining ability effects of nitrogen use (NUE),nitrogen uptake (NUPE) and nitrogen utilization (NUTE) efficiencies. 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 nitrogen efficiency component 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 NUE component traits.

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