

***Per se* performance and combining ability of six wheat genotypes and their F₁ diallel crosses for NUE traits under contrasting-N conditions**

A. M. M. Al-Naggar¹ *, R. Shabana¹, M. M. Abd El-Aleem², Zainab A. El-Rashidy²

¹Department of Agronomy, Faculty of Agriculture, Cairo University, Giza, Egypt.

²Wheat Research Department, FCRI, Agricultural Research Centre (ARC), Giza, Egypt.

Abstract: Breeding wheat (*Triticum aestivum* L.) cultivars with improved adaptation to low-N fertilization has gained importance worldwide. This study aimed at investigating the *per se* performance of nitrogen use efficiency traits, the relative importance of general (GCA) and specific (SCA) combining ability in a set of wheat cultivars and promising lines and their F₁ diallel crosses. Parents (6) and F₁'s (15) were evaluated in two seasons in two separate experiments using randomized complete block design with three replications; each experiment under one level of N (0 or 75 kg N/fed). Results across seasons showed that the rank of crosses in F₁ generation for most studied traits was changed from one environment (N-level) to another, indicating a significant G x N interaction. 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 Gem 7, Gem 9 and Giza 168 under both high-N and low-N levels. Both GCA and SCA mean squares were significant, but the magnitude of GCA was higher than SCA, for all studied traits under the two levels of N, except GPC under low-N, suggesting the existence of a greater portion of additive than that of non-additive genetic variance in controlling the inheritance of these traits under the two levels of nitrogen. In general, the best general combiners in F₁'s for NUE and NUPE were L26 followed by L27 and L25 parents under both high-N and low-N. Under low-N conditions, the best SCA effects were shown by F₁'s L25 x Gz168 for NUE and NUPE, L2 x Gem9 and L27 x Gem9 for NUPE and L25 x L 26, L25 x L27 and L27 x Gem9 for NUTE trait. Results indicate that under both N-levels, the best performing parents for grain yield and nitrogen use efficiency and their components are also the best general combiners and *vice versa*. But under high-N only, the mean performance of a given F₁ cross could be considered an indication of its SCA effects.

Keywords: *Triticum aestivum*, NUE, N-uptake, N-utilization, N-harvest index, GCA, SCA

I. INTRODUCTION

Increased interest is being shown worldwide in cultivars that are more efficient in utilizing soil resources and better fitted to water and nutrient limitations (El Bassam 1998; Good et al. 2004; Fageria and Baligar 2005; Lammerts van Bueren et al. 2008; Sylvester-Bradley and Kindred 2009). Among cereals, bread wheat (*Triticum aestivum* L.) is commonly identified as a species with higher requirements for nutrients, especially nitrogen. Thus, breeding wheat cultivars with improved adaptation to less favourable, but more optimized N fertilization regimes has gained importance.

In Egypt, like in other developing countries, such breeding strategies are also justified by limited-nitrogen supply that is major constraint limiting grain production. The efficiency of nitrogen use (NUE; defined here as the grain yield per unit of the soil N) and plant adaptation to less favorable nutrition regimes is complex with various mechanism involved (Sattelmacher *et al.* 1994; Hirel *et al.* 2007). Different characteristics, associated with both the uptake capacity (NUPE; defined here as a proportion of total N uptake to N availability in the soil) and efficiency of nitrogen utilization in grain mass formation (NUTE; defined here as the grain mass formed per unit of N absorbed), appear to be critical components of NUE (Moll *et al.* 1982 and Huggins and Pan 2003).

Although numerous reports on genotypic variation in components of N efficiency already suggest potential applications of this genetic knowledge for wheat improvements (Dhugga and Waines 1989; Ortiz-Monasterio *et al.* 1997; El Bassam 1998; Le Gouis *et al.* 2000; Gorny *et al.* 2006a; Laperche *et al.* 2006a; Kichey *et al.* 2007; Baresel *et al.* 2008 and Barraclough *et al.* 2010), relatively fewer attempts have been made to breed wheat for these traits (Van Ginkel *et al.* 2001; Brancourt-Hulmel *et al.* 2005 and Wolfe *et al.* 2008).

¹ Corresponding Author: medhatalnaggar@gmail.com

Wheat breeders in Egypt have consistently targeted improved grain yield under high inputs of fertilizer, but nitrogen efficiency *per se* has never been a target. There is an extensive global literature on NUPE and NUTE in wheat. The small selection of papers cited here illustrates the points of agreement and conflict evident in the literature. Dhugga and Waines (1989) studied 12 varieties (3 tall) at 3 N-rates over 2 years in California, USA. There was genotypic variation in total-NUPE and grain-NUTE with total-NUPE being the dominant component of NUE (62–70%) at all N-rates. Ortiz-Monasterio *et al.* (1997) studied 10 varieties (2 tall) at 4 N-rates over 3 years in Mexico. NUE was found to track yield. There was genetic variation in total-NUPE and grain- NUTE between tall and short varieties and within short varieties. Total-NUPE contributed more to variation in NUE at low N, with equal contributions from NUPE and NUTE at medium N, and grain-NUTE contributed more at high N, the opposite of what Dhugga and Waines (1989) had found. There was a significant variety × N interaction for grain-NUTE, but not for total-NUPE. Le Gouis *et al.* (2000) studied 20 varieties (2 tall) at 2 N-rates over 2 years in France. They found genetic variation in total-NUPE and total-NUTE. The contribution of total-NUPE to the variation in NUE was 64% at low-N and 30% at high-N (in agreement with Ortiz-Monasterio *et al.* 1997). There was significant G×N interaction for total-NUPE but not for total-NUTE. The literature on N-efficiency in Egypt varieties is sparse. This study aimed at investigating the *per se* performance of nitrogen use efficiency traits, the relative importance of GCA and SCA in a set of wheat cultivars and promising lines and their F₁ diallel crosses and the correlations between *per se* performance and combining ability effects under contrasting N environments.

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 15.00 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-N, 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 promising lines and Egyptian cultivars of wheat used for making diallel crosses of this study

Designation	Pedigree	Tolerance to low-N
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 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 F₁ seeds of 15 crosses. In season 2007/2008, the half diallel of crosses was again done to increase quantity of F₁ seeds.

2.3. Field evaluation of 6 parents and 15 F1's

In the seasons 2007/2008, 2008/2009, parents (6) and F₁'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 (LN) and the high level was 75 kg Nitrogen/ feddan (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). Each parent or F₁ 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. 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. All other agricultural practices were followed according to the recommendations of ARC, Egypt. 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%), the pH is 8.93, the EC is 0.55 dSm⁻¹, the soluble cations in meq l⁻¹ are Ca²⁺ (5.30), K⁺ (0.70), Na⁺ (0.31), Mg²⁺ (2.60) and the soluble anions in meq l⁻¹ are CO₃²⁻ (0.00), HCO₃⁻ (2.10), Cl⁻ (5.30) and SO₃²⁻ (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 were estimated according to Moll *et al.* (1982).

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 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).

2.6. Genetic Analysis of F1 Crosses

Diallel crosses in F₁ 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_g^2) and specific (δ_s^2) 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 F₁'s; between *per se* performance of F₁ crosses and their SCA 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: $r_s = 1 - (6 \sum d_i^2) / (n^3 - n)$ 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.

III. RESULTS AND DISCUSSION

3.1. Mean Performance

Means of each parent, F1 cross and F2 cross for studied traits under two nitrogen fertilizer rates (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 Gem 7, Gem 9 and Giza 168 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 (Gem 7, Gem 9 and Giza 168) as low-N sensitive (N-inefficient) parents.

The rank of crosses in F1 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 L27 followed by L25 x L26 and L25 x L27 in F1 and L25 x L27 followed by L25 x L26 and L26 x Gz168 in F2 generation. These crosses were therefore considered tolerant (N-efficient) to low-N stress.

Table2. Mean performance of all genotypes under high-and low- levels of nitrogen across two years for studied traits

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**
Gizal68	13.74	24.57	-78.77**	13.38	23.48	-75.44**
F₁ crosses						
L25 X L26	16.50	33.68	-104.2**	17.81	30.46	-71.05**
L25 X L27	13.79	32.80	-137.9**	16.86	28.24	-67.47**
L25X Gem 7	13.71	30.62	-123.4**	16.52	30.47	-84.41**
L25 X Gem 9	14.32	25.06	-74.98**	16.40	30.37	-85.26**
L25 X Gz 168	14.80	31.84	-115.2**	16.85	34.67	-105.8**
L 26 X L 27	17.20	34.39	-99.98**	19.37	39.32	-102.99**
L26 X Gem 7	15.76	28.35	-79.86**	19.47	31.36	-61.07**
L 26 X Gem 9	16.47	26.26	-59.46*	16.78	33.92	-102.08**
L 26 X Gz 168	17.94	27.59	-53.75	15.81	30.65	-93.85**
L 27 X Gem 7	18.35	30.19	-64.54**	13.84	25.00	-80.62**
L 27 X Gem 9	15.89	25.68	-61.59	12.92	36.03	-178.80**
L27 X Gz168	16.36	29.65	-81.29**	16.16	24.11	-49.19**
Gem 7 X Gem9	13.31	22.22	-66.9**	15.41	20.92	-35.77**
Gem 7 X Gz 168	15.27	23.74	-55.45**	14.59	25.96	-77.89**
Gem 9 X Gz 168	13.95	25.91	-85.65**	13.31	19.96	-49.97**
L.S.D. _{0.05} (G)	1.1	2.6		0.98	3.2	
(N)			3.2			8.15
(GN)			2.0			2.5

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
Gizal68	1.04	1.06	-2.15**	57.04	55.98	1.87
F₁ crosses						
L25 X L26	0.93	1.11	-19.20**	53.14	55.66	0.28

L25 X L27	0.82	1.16	-42.14**	56.01	55.36	-4.75
L25X Gem 7	0.84	1.01	-20.82**	55.88	55.21	1.17
L25 X Gem 9	0.88	0.83	5.30**	57.92	59.87	1.19
L25 X Gz 168	0.88	0.92	-5.08**	57.52	56.86	-3.37
L 26X L 27	0.89	0.88	1.41**	54.61	57.62	1.15
L26 X Gem 7	0.81	0.91	-11.51**	54.92	54.88	-5.51
L 26 X Gem 9	0.99	0.78	21.19**	55.84	56.87	0.08
L 26 X Gz 168	1.14	0.90	20.76**	55.37	60.03	-1.85
L 27X Gem 7	1.33	1.22	8.00**	57.27	56.79	-8.42
L 27 X Gem 9	1.23	0.71	42.15**	56.57	57.95	0.85
L27 X Gz168	1.02	1.23	-21.31**	54.83	59.79	-2.43
Gem 7 X Gem9	0.86	1.08	-25.26**	56.85	58.97	-9.04**
Gem 7 X Gz 168	1.05	0.92	11.91**	59.02	61.59	-3.73*
Gem 9 X Gz 168	1.05	1.31	-24.31**	57.40	63.78	-4.35*
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

On the contrary, the three crosses Gem 7 x Gem 9, Gem 7 x Gz168 and L27 x Gem 9 in F1 and F2 generations showed the lowest NUE under low-N, and therefore were considered sensitive (inefficient) to low-N stress.

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 and other 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. 2012), 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. 2008, 2009, 2010, 2011b, 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. (2006a) , Dowson et al. (2008), Wolfe et al. (2008) and Al-Naggar et al. (2006, 2007b, 2009, 2010, 2011, 2012, 2015 a, b, c). The rank of parents for NUE was similar in the two N- environments, indicating less effect of interaction between parent and nitrogen level on nitrogen use efficiency.

The three tolerant parents showed the highest NUE under high-N and were therefore considered responsive parents. Moreover, L26 x L27 and L25 x L27 in F1 and L26 x Gz168 in F2 generation had the highest NUE under high-N and are therefore considered responsive crosses.

3.2. Combining Ability Variances

Variances estimates for general (GCA) and specific (SCA) combining ability of the F₁ diallel crosses of wheat for combined data across two years under high and low levels of nitrogen are presented in Table (3 and 4). Mean squares due to genotypes were highly significant for all studied traits under the two levels of N. Mean squares due to GCA and SCA were also highly significant for all studied traits, except NHI for SCA under low-N, indicating that both additive and non-additive gene effects play an important role in the inheritance of most studied 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 N, except 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 these traits under the two levels of nitrogen.

Table3. Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied traits in F₁'s under high N conditions across two years

SOV	df	MS			
		NUE	NUPE	NUTE	NHI
Genotypes (G)	20	14.06**	22.94**	0.11**	10.87**
GCA	5	33.28**	64.84**	0.15**	16.95**
SCA	15	7.65**	8.98**	0.10**	8.84**
GCA x Y	5	1.81*	0.68	0.01**	13.24**
SCA x Y	15	1.24*	2.81**	2.28**	13.97**
GCA/SCA		4.35	7.22	1.52	1.92
GCA x Y/SCA x Y		1.46	0.24	0.01	0.95
error	80	0.51	0.36	0.003	1.70

* 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 F₁ diallel crosses under low N conditions across two years

SOV	df	MS			
		NUE	NUPE	NUTE	NHI
Genotypes (G)	20	99.87**	291.41**	3.87**	41.32**
GCA	5	352.82**	674.51**	5.97**	120.84**
SCA	15	15.56**	163.71**	3.17**	14.81
GCA x Y	5	7.39**	9.40**	4.71**	27.0*
SCA x Y	15	7.73**	21.45**	2.29**	38.74**
GCA/SCA		22.67	4.12	1.88	8.15
GCA x Y/SCA x Y		0.95	0.43	2.05	0.70
error	80	2.72	3.832	0.012	9.73

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

The greater importance of GCA relative to SCA variance as observed in this study was also reported by Larik *et al.* (1995) and Al-Naggar *et al.* (2006, 2007, 2012, 2014 and 2015 a, b, c) for (GYPP) and its components. Le Gouis *et al.* (2002) reported that in N-limited diallel F₁ 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. A similar preponderance of GCA effects for N uptake and NUTE was identified in F₂ and F₃ progenies of factorial hybrids between modern and exotic cultivars of barley grown under reduced N fertilization (Gorny and Ratajezak, 2008).

Results in Tables (3 and 4) 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 GPC and NHI 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 NUPE under high-N and GPC under low-N, which were not significant, indicating that additive variance for most 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 NHI and NUE under high-N, suggesting that SCA (non-additive) variance (in most cases) is more affected by year than GCA (additive) variance.

3.3. 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 traits.

Table5. Estimates of general combining ability effects (g_i) of all traits in F_1 's under high N conditions across two seasons

Parents	NUE	NUPE	NUTE	NHI
L25	-0.74*	0.71*	-0.10*	-0.22
L26	1.27*	1.79*	-0.03*	-0.31
L27	0.77*	0.21	0.04*	-0.76*
Gem 7	-0.39*	-0.29	-0.01	-0.12
Gem 9	-0.73*	-1.27**	0.04*	0.75*
Giza 168	-0.19	-1.15*	0.05*	0.66
SE _{gi}	0.38	0.32	0.03	0.70
SE _{gi-gj}	0.59	0.50	0.05	1.08

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

In general, the best general combiners in F_1 's for NUE and NUPE were L26 followed by L27 and L25 parents under both high-N and low-N. For NUTE, the best combiners were L27, Gem9 and Gz168 under high-N and Gem9 under low-N. However, for NHI, the best combiners were Gem9 under high-N and Gem9 and Gz 168 under low-N. On the contrary, the worst general combiners in F_1 's were Gem 9, Gem 7 and Giza 168 for NUE and NUPE traits under both high-N and low-N environments.

Table6. Estimates of general combining ability effects (g_i) of all traits in F_1 's diallel crosses under low N conditions across two years

Parents	NUE	NUPE	NUTE	NHI
L25	2.35**	2.21*	-0.14*	-1.82*
L26	2.35**	5.17**	-0.23*	-0.89
L27	2.46**	2.03**	-0.11*	-0.55
Gem 7	-2.20**	-2.47*	-0.13*	-0.55
Gem 9	-3.60**	-4.94**	0.71*	1.38*
Giza 168	-1.36**	-2.00*	-0.10*	2.43**
SE _{gi}	0.83	1.05	0.06	1.66
SE _{gi-gj}	1.37	1.62	0.09	2.57

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

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 NUE traits under both high and low-N environments.

3.4. SCA effects

Estimates of specific combining ability (SCA) effects of the F_1 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_1 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 was the F_1 cross L26 x Gz 168 followed by the F_1 L27 x Gem7 in two traits (NUE and NUTE), the F_1 L25 x L26 for NUTE and the F_1 L25 x Gz 168, L26 x L27, and L26 x Gem7 for NUPE and L27 x Gem9 for NUTE. These F_1 's include at least one parent of high GCA effects under high N.

Table7. Estimates of specific combining ability effects (\hat{s}_{ij}) of F_1 's under high N conditions across two seasons

Crosses	NUE	NUPE	NUTE	NHI
L25 X L26	0.63	-0.79	0.09*	1.52
L25 X L27	-1.58*	-0.16	-0.09*	0.55
L25 X Gem 7	-0.49	0.004	-0.03	-0.30
L25 X Gem 9	0.46	0.85	-0.03	-0.45
L25 X Gz 168	0.39	1.19*	-0.05	0.41

L26 X L27	-0.18	1.27*	-0.09*	0.91
L26 X Gem 7	-0.44	1.87*	-0.12*	0.12
L26 X Gem 9	0.60	0.16	0.01	1.29
L26 X Gz 168	1.53*	-0.92	0.14*	0.97
L27 X Gem 7	2.64*	-2.18*	0.33*	-0.36
L27 X Gem 9	0.52	-2.13*	0.19*	-0.32
L27 X Gz168	0.44	1.00*	-0.05	-0.70
Gem 7 X Gem9	-0.90	0.87	-0.13*	-0.24
Gem 7 X Gz 168	0.52	-0.06	0.03	-1.89
Gem 9 X Gz 168	-0.46	-0.37	-0.01	-0.10
SE _{Sij}	1.05	0.89	0.09	1.91
SE _{Sij-Sik}	1.57	1.32	0.10	2.16
SE _{Sij-Skl}	1.45	1.23	0.12	2.85

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

Under low-N conditions, the best SCA effects were shown by F₁'s L25 x Gz168 for NUE and NUPE, L2 x Gem9 and L27 x Gem9 for NUPE and L25 x L 26, L25 x L27 and L27 x Gem9 for NUTE trait. Again these F₁'s include at least one parent of high GCA effects under low-N.

Table8. Estimates of specific combining ability effects (\hat{s}_{ij}) of F₁'s under low N conditions across two years

Crosses	NUE	NUPE	NUTE	NHI
L25 X L26	0.59	-5.22**	0.30**	1.75
L25 X L27	-0.40	-4.31**	0.24*	0.39
L25X Gem 7	2.09	2.43	0.10	1.36
L25 X gem 9	-2.08	4.81**	-0.92*	2.11
L25 X Gz 168	2.46*	6.15**	-0.01	-2.11
L26 X L27	1.19	3.80*	0.04	-0.66
L26 X Gem 7	-0.19	0.36	0.09	-0.81
L26 X Gem 9	-0.88	5.42**	-0.88**	1.90
L26 X Gz 168	-1.79	-0.8	0.06	-2.15
L27 X Gem 7	1.54	-2.88	0.28**	-1.48
L27 X Gem 9	-1.57	10.63**	-1.07**	-1.42
L27 X Gz168	0.16	-4.22**	0.27*	0.67
Gem 7 X Gem9	-0.37	0.04	-0.68**	-0.35
Gem 7 X Gz 168	-1.09	2.12	-0.02	0.43
Gem 9 X Gz 168	-1.09	-1.41	-0.42*	0.29
SE _{Sij}	2.43	2.88	0.16	4.58
SE _{Sij-Sik}	3.63	3.25	0.24	5.16
SE _{Sij-Skl}	3.36	3.98	0.22	6.84

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

Results of Gorny *et al.* (2011) on wheat 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 and Al-Naggar *et al.* 2008, 2011, 2015a) and those for NUE in grain sorghum (Al-Naggar *et al.* 2006, 2007 b). Gorny *et al.* (2011), who 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.

3.5. Correlations between XP vs GCAF1 effects and XF1 vs SCAF1 effects

Rank correlation coefficients calculated between mean performances of parents (X_p) and their GCA effects of F_1 's for studied characters are presented in Table (9). Significant ($P \leq 0.05$ or 0.01) and positive correlations between X_p and GCA_{F_1} effects existed for all studied traits under both high-N and low-N. In general, the magnitude of correlation coefficient between X_p and GCA_{F_1} effects was very high (> 0.91 in 7 out of 10 cases) and was higher at low-N than high-N in all studied traits, except NHI. The highest correlation coefficient under low-N between X_p and GCA was observed for NUPE (1.00) followed by 0.98 for NUE and 0.95 for NUTE. These results indicate that the best performing parents for grain yield and 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.*, (2008, 2015 a, b, c) 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 means performance of parents (X_p) and their GCA effects for F_1 's and between X_{F_1} and SCA_{F_1} effects under high and low-N environments across two seasons

Traits	X_p vs GCA		X_{F_1} vs SCA_{F_1}	
	HN	LN	HN	LN
NUE	0.95**	0.98**	0.79**	-0.02
NUPE	0.95**	1.00**	0.70**	-0.08
NUTE	0.83**	0.95**	0.90**	-0.09
NHI	0.61**	0.38*	0.03	-0.12

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

For F_1 crosses, under low-N, all studied traits showed very low in-magnitude values of negative and non-significant correlation coefficients between X_{F_1} and SCA_{F_1} effects ranging from $r = -0.02$ to $r = -0.12$ (Table 9). All studied NUE traits did not show significant correlation coefficients between X_{F_1} and SCA_{F_1} effects under low-N environment. Therefore, it could be concluded that under low-N, the mean performance of a given F_1 cross of wheat is not an indication of its specific combining ability. This conclusion was previously reported by Al-Naggar *et al.* (2014, 2015 a, b).

On the contrary, under high-N, there were significant and positive correlation coefficients (ranging from 0.70 to 0.90) between X_{F_1} and SCA_{F_1} effects for the three nitrogen use efficiency traits NUE, NUPE and NUTE, indicating that under high-N, the mean performance of a given F_1 cross could be considered as an indication of its specific combining ability, especially for NUE, NUPE and NUTE.

Summarizing the above mentioned results, it could be concluded that low-N stress affects on the associations between mean performance of F_1 's and their SCA effects 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. 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. But under high-N only, the mean performance of a given F_1 cross could be considered an indication of its SCA effects.

IV. CONCLUSIONS

This study 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 all studied nitrogen use efficiency traits under the two levels of nitrogen. In general, the best general combiners in F_1 's for NUE and NUPE traits were L26 followed by L27 and L25 parents under both high-N and low-N. For NUTE, the best combiners were L27, Gem9 and Gz168 under high-N and Gem9 under low-N. However, for NHI, the best combiners were Gem9 under high-N and Gem9 and Gz 168 under low-N. Under low-N conditions, the best SCA effects were shown the by F_1 's L25 x Gz168 for NUE and

NUPE, L2 x Gem9 and L27 x Gem9 for NUPE and L25 x L 26, L25 x L27 and L27 x Gem9 for NUTE trait. These F_1 's include at least one parent of high GCA effects under low-N. The study concluded that under either low-N or high-N, the mean performance of a given parent could be considered an indication of its general combining ability effects. But under high-N only, the mean performance of a given F_1 cross could be considered an indication of its SCA effects in F_1 generation.

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