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Assessment of N-efficiency and N-responsiveness of Six Wheat (Triticum aestivum L.) Genotypes and their F1 and F2 Diallel Crosses

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Authors' contributions

This work was carried out in collaboration between all authors. Author AMMA designed the study, wrote the protocol and wrote the first draft of the manuscript. Authors RS and MMAE managed the literature searches and author ZER managed the experimental process and performed data analyses. All authors read and approved the final manuscript.

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ABSTRACT

Screening wheat germplasm based on grain yield (GYPP) and nitrogen use efficiency (NUE) under contrasting N environments may be useful in identifying N-efficient (low-N tolerant) and responsive genotypes of great value in breeding programs. The main aim of the present study was to assess six wheat parents and their F_1 and F_2 diallel crosses for tolerance to low-N (N-efficiency) and responsiveness to high-N. A split plot design in a lattice arrangement with three replications was used in two-season experiment. Combined analysis across seasons indicated that mean squares due to genotypes (G), nitrogen levels (N) and G x N interaction were significant for most studied traits. In general, means of most studied traits 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 highest mean of GYPP under low-N was obtained from L26 × L27 followed by L25 x L26 and L25 x L27 in F₁ and L25 x L27 followed by L25 x L26 and L26 x Gz 168 in F₂ generation. Superiority of low-N tolerant (T) over sensitive (S) parents, F_1 's and F_2 's in GYPP

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(40.54%) under low-N was 40.54, 40.42 and 40.62%, respectively. Superiority in GYPP was associated with superiority in NUE and most studied traits. In general, T × T crosses had favorable (higher) values for GYPP and NUE traits than $S \times S$ and $T \times S$ crosses under low-N stress. Studied genotypes were classified into four groups, based on NUE, GYPP and tolerance to low-N. The parents L26 and L27, the F₁'s L26 \times L27 and L26 \times Gem7 and the F₂'s L25 \times L26 and L27 \times Gz168 occupied the first group in all classifications; they are N-efficient and high-yielding at low and high N, tolerant to low-N and responsive at high-N.

Keywords: Bread wheat; N-efficient; low-N tolerance; responsiveness; NUE.

1. INTRODUCTION

Wheat (Triticum aestivum L.) is one of the most important cereal crops of the world and provides over 20% of calories and protein for human nutrition for over 35% of the world's population in more than 40 countries including Egypt. Across the last five years, the average annual consumption of wheat grains in Egypt is about 14 million tons, while the average annual local production is about 8 million tons with an average grain yield of 18.0 ardab/feddan (6.43 t/ha) [1]. Therefore, the gap between annual local production and consumption is about 6 million tons. This gap could be narrowed by increasing local production of wheat via two ways. The first way is through vertical expansion, *i.e.* increasing wheat production per unit area through the development of new cultivars of high yielding ability, early maturity, resistance to biotic and abiotic stresses, and the adoption of abiotic stresses, and the adoption of recommended cultural practices for growing these cultivars. The second way is through the horizontal expansion, *i.e.* by increasing the area cultivated with wheat. Horizontal expansion in Egypt is available only in the desert, where the soil is deficient in nutrients and of low water holding capacity and thus needs improved wheat cultivars to tolerate such stresses.

Nitrogen (N) is one of the major inputs in wheat production systems. During the green revolution, plant breeding programs have released many Mexican type semi dwarf varieties with greater responses to high nitrogen input. Cultivation of these cultivars drastically increased wheat average yield in the world [2]. Thus the consumption of nitrogen fertilizers was increased tremendously in the world as well as in Egypt. Today, elevated nitrogen level in water, as result of leaching, is an important component of agricultural pollution [3], causing major problems in marine ecosystems and eutrophication of freshwater [4]. However, scientists try to release cultivars with low-input of manure and decrease of pollution risk to ecosystem [5].

In order to enhance the efficiency of crop production system while reducing the agricultural pollutions, plant breeders would have to introduce varieties which minimize pollution risks and maximize yield potential. Therefore, development of cultivars that could absorb nitrogen more effective and use it more efficiently for grain production will lead to a significant reduction in nitrogen fertilizers [5]. Genetic variation for NUE has been studied on wheat [6- 8]. Recent studies have shown that it is possible to develop a framework for the analysis of genotypic variability for crop nitrogen uptake capacity across a wide range of genotypes [9,10]. There has been also a number of studies which show improvement in modern wheat varieties for NUE, based on nitrogen conditions [11].

Differences in NUE were primarily determined by greater yield, without any increasing concentrations of N in plant material [12]. NUE can be defined as the product of uptake efficiency (total N uptake/applied N through fertilizer) and utilization efficiency (grain yield/total N uptake). At low N rates, uptake efficiency is dominant as compared to utilization efficiency, whereas utilization efficiency is relatively more important than uptake efficiency at high nitrogen rates [6]. Breeding for NUE in wheat has produced good results in some European countries [12]. There has been a 56% decrease in total fertilizer use between 1987 and 2007, including a significant decrease in N application per hectare. Nitrogen use efficiency (NUE) has been defined as grain production per unit of available N [13].

Gorny et al. [14] categorized wheat parents and their F_2 progenies for yield potential under low-N and high-N conditions; the entries were classified into four groups, i.e. efficient and responsive, efficient and non-responsive, non-efficient and non-responsive and non-efficient and responsive. According to Fageria and Baligar [15,16] genotypes (progenies) belonging to the $1st$ group

"efficient and responsive" (above all) and 2nd group "efficient and non-responsive" (to a lesser extent) appear to be the most desirable materials for breeding programs that deal with adaptation to low-input agriculture.

The objectives of this study were (1) to assess the variation among six wheat genotypes and their F_1 and F_2 progenies in performance under contrasting N-environments, (2) to estimate the superiority of low-N tolerant over sensitive genotypes and (3) to classify studied genotypes into groups based on N- efficiency and Nresponsiveness to identify those of usefulness to breeding programs.

2. MATERIALS AND METHODS

This study was performed in 2006/2007, 2007/2008 and 2008/2009 seasons 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). Six bread wheat genotypes (Triticum aestivum L.) were chosen for their divergence in tolerance to low nitrogen, based on previous field screening carried out by Wheat Res. Dept., Field Crops Res. Inst., ARC, Egypt (Table 1).

2.1 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.

2.2 Field Evaluation of 6 Parents, 15 F1's and 15 F2's

In the seasons 2007/2008, 2008/2009, parents (6), F_1 's (15) and F_2 's (15) were sown on 17th of November each season in the field of Noubarya Res. Stat., under two levels of nitrogen fertilizer; 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 (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 split plot design in lattice (6×6) arrangement was used with three replications. The two levels of nitrogen were allotted to the main plots and the genotypes to the sup plots. Each parent or F_1 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 m² for parent or F_1 and 3.6 m² 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 I^1 are Ca²⁺ (5.30), K⁺ (0.70), Na⁺ (0.31) , $Mg²⁺$ (2.60) and the soluble anions in meq 1^1 are CO_3^2 (0.00), HCO₃ (2.10), Cl (5.30) and SO_3^2 (1.51).

2.3 Data Collection

The following characteristics were measured on a random sample of 10 plants of each genotype of parents and F_1 's and 30 plants of F_2 's. Days to 50% heading (DTH): Number of days from sowing date to of main peduncles/ plot have turned to yellow color (physical maturity). Plant height in cm (PH): Measured as plant length from

Designation	Pedigree	Tolerance to low nitrogen
Line25(L25)	MYNA/VUL//TURACO/3/TURACO/4/Gem7.	Tolerant
Line26(L26)	MUNIA/CHTO//AMSEL.	Tolerant
Line27(L27)	Compact-2/Sakha//Sakha61.	Tolerant
Gemeiza7(Gem7)	CMH74A.630/SX//Seri82/3/Agent.	Sensitive
Gemeiza9(Gem9)	Ald s"/HUC "s;;//CMH74A.630/SX.	Sensitive
Giza168 (Gz168)	MRL/BUC//Seri.	Sensitive

Table 1. 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

Source: wheat res. dept. field crops res. inst., ARC. Egypt

the soil surface to the tip of the spikes, excluding awns. Number of spikes/plant (SPP): Number of fertile spikes per plant. Numbers of grains\ spike (GPS): Number of grains per spike. 100 grain weight (100 GW) in g: Measured as weight of 100 grains taken from each guarded plant. Grain yield/ plant (GYPP) in g: Measured as weight of the grains of each individual plant. Biological yield/ plant (BYPP) in g: Measured as weight of the grains and stem of each individual plant. Harvest index (HI%) according formula: H= 100 (GYPP/ BYPP). 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_q) was determined using Kjeldahl procedure according to A.O.A.C. [17]. Total plant nitrogen (N_t) was calculated as follows: $N_t = N_g + N_{straw}$. Nitrogen use efficiency (NUE) $g/g =$ (GYPP / N_s). Nitrogen uptake efficiency (NUPE)% =100 (N_t / N_s). Nitrogen utilization efficiency (NUTE) $(g/g) = (GYPP/N_t)$. Grain protein content (GPC) was measured as follows: GPC%= N_q x 5.70 according to AACC [18]. 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_a is grain nitrogen content. Nitrogen efficiency parameters were estimated according to Moll et al. [13].

2.4 Biometrical Analysis

The analysis of variance (ANOVA) of the split plot design was performed on the basis of individual plot observation using the MIXED procedure of SAS ® [19]. Combined analysis of variance across the two seasons was also performed if the homogeneity test was nonsignificant. Moreover, each environment (HN and LN) was analyzed separately across seasons as lattice design 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. [20].

2.5 Tolerance Index

Low-N tolerance index (T), a general measure of stress intensity in the experiment, was calculated according to Fisher and Maurer [21] as follows: T= (Li/Hi) D, where: Li= Grain yield of ith genotype under low-N. Hi= Grain yield of ith genotype under high-N. D= Overall mean grain yield of L / overall mean grain yield of H.

3. RESULTS AND DISCUSSION

3.1 Analysis of Variance

Combined analysis of variance across years (Y) of the split plot design in lattice (6×6) arrangement across 2008/2009 and 2009/2010 seasons for the studied 36 wheat genotypes (6 parents, 15 F_1 's and 15 F_2 's) under two levels of nitrogen was performed (data not presented). Mean squares due to years were highly significant for nine studied traits, namely days to heading (DTH), plant height (PH), spikes/plant (SPP), grains/ spike (GPS), 100 grain weight (100GW), grain yield/ plant (GYPP), biological yield/ plant (BYPP) and nitrogen utilization efficiency (NUTE), indicating significant effect of climatic conditions on most studied traits. Results also exhibit that mean squares due to nitrogen levels (N) were highly significant for all studied traits, indicating that the N level has an obvious effect on all studied traits of studied wheat genotypes. Mean squares due to genotypes (G) were highly significant for all studied traits,

indicating that wheat genotypes used in this study were significantly (P≤ 0.01) different for all studied traits. Moreover, mean squares due to genotypes x nitrogen levels, *i.e.* $G \times N$ were significant ($P \le 0.01$ or 0.05) for all studied traits, indicating that genotypes ranks differently from one nitrogen level to another and that selection can be done under a specific soil nitrogen environment as proposed by Al-Naggar et al. [22- 30]. The significant G×N interaction for NUE was also a good evidence for varying responses of these wheat genotypes at various N levels [31,32]. The interactions $G \times Y$ and $G \times Y \times N$ were also significant (P \leq 0.01 or 0.05) for all studied traits, indicating that genotypes ranks differ from one combination of $Y \times N$ to another.

3.2 Performance of Genotypes under Low N and High N

Means of each parent, F_1 cross 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 GYPP, BYPP, GPS, GPC, 100GW, SPP, 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. 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, 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. 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_1 and 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 L26 \times L27 followed by L25 \times L26 and L25 \times L27 in F_1 and L25 x L27 followed by L25 x L26 and L26 \times Gz 168 in F₂ generation. These crosses also showed the lowest reduction due to low-N stress and the highest NUE means, and therefore were considered tolerant (N-efficient) to low-N stress.

On the contrary, the three crosses Gem7 x Gem9, Gem7 x Gz168 and L27 x Gem9 in F_1 and F_2 generations showed the lowest GYPP under low-N, the lowest NUE and high reduction due to 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, increased ability to accumulate protein in their grains, higher values of HI and PH and earlier DTH, suggesting transgressive effects in these characteristics. Gorny et al. [14] reported a similar conclusion for NUPE and grain dry weight produced per unit of N accumulated in grains (G_W/N_q) .

It is worthy to note that the magnitude of Ninduced 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 [5,33-36], barley [37-39] and maize [24-30,40-42], 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.[43], La Perche et al. [44], Dawson et al. [45], Wolfe et al. [46] and Al-Naggar et al. [24-30,47,48]. The rank of parents for GYPP was similar in the two Nenvironments, 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 \times L27 and L25 \times L27 in F₁ and L26 \times Gz168 in F₂ generation had the highest GYPP under high-N and are therefore considered responsive crosses.

3.3 Superiority of Tolerant (T) Over Sensitive (s) Genotypes

To describe the differences between tolerant (T) and sensitive (S) parents, F_1 's and F_2 's, data of selected characters were averaged for the two groups of parents, F_1 's and F_2 's differing in their tolerance by definition namely in grain yield/ plant under low-N (Table 3). The higher absolute GYPP and higher ratio of GYPP under low-N to yield under high-N were considered as an index of tolerance to low-N. Based on this index, the low-N tolerant (T) parents were L25, L26 and L27 and the low-N sensitive (S) parents were Gem7, Gem9 and Gz168. Moreover, the 3 F_1 crosses L25 \times L26, L25 \times L27 and L26 \times L27 and the 3 F_2 crosses L25 \times L26, L25 \times L27 and L26 \times Gz 168 were considered the most tolerant to low-N, while the 3 F_1 crosses Gem7 x Gem 9, Gem7 \times Gz168 and Gem9 \times Gz168 and the 3 F_2 crosses Gem7 x Gem9, Gem7 x Gz168 and L27 x Gem7 were considered as the most low-N sensitive crosses.

Continue Table 2.

Continue Table 2.

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

Traits	Parents			F_1 crosses			$F2$ crosses			
		S.	Superiority %	Т	S	Superiority %	Т	S	Superiority %	
GPS	82.30	57.30	43.63**	84.37	58.25	44.84**	76.36	49.91	53.00**	
100 GW (q)	4.62	3.48	32.76**	4.84	3.28	$50.30**$	3.46	1.84	88.04**	
SPP	10.87	7.35	47.80**	10.85	7.58	43.13**	10.77	5.08	$112.0**$	
GYPP(g)	26.19	18.63	40.54**	26.90	18.94	42.02**	25.03	17.80	40.62**	
BYPP(g)	60.33	49.44	22.01**	62.00	46.99	$31.94**$	58.84		42.46 38.58**	
HI%	43.44	38.02	$14.24**$		48.35 33.96	42.37**	49.93		34.45 44.93**	
NUE (g/g)	32.75	23.32	40.44**		33.62 23.88	40.79**	31.14		22.22 40.14**	
NUPE %	32.82	20.92	56.90**	36.67	21.66	69.30**	36.85	22.46	64.10**	
NUTE (g/q)	1.00	1.13	$-13.67**$	1.33	0.77	72.72**	1.21	0.76	59.21**	
GPC%	13.75	8.91	54.32**	13.75	10.19	$34.90**$	13.34	9.75	36.84**	
α Cunoriority $=$ 100 $\sqrt{(T - \mathcal{C})/\mathcal{C}^2}$										

Table 3. Superiority (%) in selected characters of the most three low –N tolerant (T) over the most three sensitive (S) parents, F1's and F2's under low–N (0 kg N/fed) across two seasons

% Superiority = $100 \times [(T - S)/S]$

Data averaged for each of the two groups (T and S) of parents, F_1 's and F_2 's differing in tolerance to low-N indicate that grain yield/ plant of low-N tolerant (T) was greater than that of the sensitive(s) parents, F_1 's and F_2 's by 40.54, 42.02 and 40.62%, respectively under low-N (0 kg N /fed) conditions. Superiority of low-N tolerant (T) over sensitive (S) parents in GYPP (40.54%) under low-N was due to their superiority in NUE (40.44%), NUPE (56.90%), SPP (47.80%), GPS (43.63%), GPC (54.32%) and 100 GW (32.76%), i.e. in most studied yield and NUE component traits.

Superiority of T over S for F_1 hybrids in GYPP under low-N (40.42%) was due to their superiority of 40.79, 69.30, 43.13, 44.84, 34.90, 50.30, 72.72, 42.73 and 31.94 (%) for NUE, NUPE, SPP, GPS, GPC, 100GW, NUTE, HI and BYPP, respectively than sensitive F_1 crosses (Table 3). Likewise, under low-N, the tolerant $F₂$ hybrids showed 40.62% higher GYPP, 40.14% higher NUE, 64.10% higher NUPE 59.21% higher NUTE, 112.00% higher SPP, 88.04% higher 100 GW, 53.00% higher GPS, 65.50% higher GPC, 36.84% higher HI and 38.58% higher BYPP than sensitive $F₂$ crosses (Table 3).

The superiority of T over S under low-N for crosses was greater than that for parents. This might be attributed to the high nitrogen use efficiency traits of the hybrids due to heterosis as compared to their parents. These results are in agreement with those reported by Al-Naggar et al. [29]. CIMMYT breeders found that maize grain yield under low-N was closely related to some secondary traits such as improved Nuptake, high plant nitrate content, high-specific leaf-N content and late leaf senescence [49,50]. These results are in consistency with those reported by Al-Naggar et al. [24-27,29,30,47,48].

3.4 Differential Response of T x T, T x S and S x S Crosses

Mean performance of traits were averaged across three groups of F_1 and F_2 crosses, *i.e.*, T \times T, T \times S and S \times S groups based on grain yield / plant of their parents under low-N stress and non- stress conditions, i.e. parental tolerance to low-N stress and presented in Table (4). Number of crosses was 3, 9 and 3 for $T \times T$, $T \times S$ and S \times S group, respectively in both F₁ and F₂ crosses.

In general, $T \times T$ crosses had favorable (higher) values for grain yield and its attributes and nitrogen use efficiency traits than $S \times S$ and $T \times$ S crosses under low-N stress. Low-N T×T crosses (in F_1 and F_2 generations) were generally superior in most studied traits over other groups of crosses; where $S \times S$ crosses were the most inferior under low-N stress conditions (Table 4). This indicates that the tolerant F_1 and F_2 cross to low-N should include two tolerant parents and assure that low-N tolerance trait is quantitative in nature, so the tolerant cross accumulates additive genes of low-N tolerance from both parents. Superiority of low-N TxT crosses (in F_1 and F_2 generations) over T×S and S×S crosses was more pronounced under high-N conditions, indicating that those T×T crosses are tolerant to low-N and responsive to high-N conditions.

Grain yield per plant of low-N $T \times T$ was greater than that of T×S by 18.55 and 10.15 % and S×S by 50.84 and 23.80% for F_1 's and F_2 's,

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respectively. Superiority of low-N T×T over T×S and S × S crosses in GYPP under low-N conditions was due to their superiority in SPP by 21.64 and 34.28% for F_1 's and 65.44 and 72.04% For F_2 's, GPS by 15.77 and 29.04% for F_1 's and 7.69 and 14.81% for F_2 's, 100GW by 30.98 and 43.88% for F_1 's and 19.17 and 59.07% For F_2 's, NUE by 18.55 and 40.32 % for F_1 's and 10.28 and 23.99% For F_2 's, and NUPE by 6.31 and 46.63% for F_1 's and 0.82 and 43.86% For F_2 's, respectively (Table 4).

3.5 Classifying the Parents and Hybrids

Mean grain yield per plant across seasons of studied wheat genotypes (6 parents + 15 F_1 's + 15 F_2 's) under low-N was plotted against same trait of the same genotypes under high-N (Figs. 1, 2 and 3) where numbers from 1 to 6 refer to parent names No $1 = L25$, No $2 = L26$, No 3 = L27 , No 4 = Gem 7 , No 5 = Gem 9 and No 6=Gz 168, numbers from 1 to 15 refer to F_1 and F_2 crosses names No 1= L25 \times L26, No 2 = L25 \times L27, No 3 = L25 \times Gem 7, No 4= L25 \times Gem 9 , No 5= L25 × Gz 168 , No 6= L26 × L27 , No 7= L26 × Gem 7, No 8= L26 × Gem 9, No 9= L26 x Gz 168, No 10= L27 x Gem 7, No 11= L27 x Gem 9, No 12= L27 x Gz 168, No 13=Gem 7 × Gem 9, No 14= Gem 7 × Gz 168, and No 15= Gem $9 \times$ Gz168. This made it possible to distinguish between efficient and nonefficient genotypes on the bases of aboveaverage and below- average grain yield under low-N and responsive and non-responsive genotypes on the bases of above- average and below-average grain yield under high-N [27,29,48-51]. Similarly, means of NUE under low-N were plotted against means of the same trait for the same genotypes under high-N (Figs. 6, 7 and 8) according to Worku et al. [52] and Al-Naggar et al. [27,29,47,48].

According to tolerance to low-N and responsiveness to high-N, studied genotypes were classified into four groups, i.e, N efficient and high N responsive, N-efficient and nonresponsive, N-non-efficient and responsive and N-non-efficient and non-responsive based on GYPP (Figs. 4, 5 and 6) and NUE (Figs. 7, 8 and 9) traits.

The wheat parent No. 2 (L26) and No. 3 (L27), the F_1 crosses No 10 (L27 \times Gem 7), No 6 (L26 × L27), No 1 (L25 × L26) and No 12 (L27 × Gz 168) and the F_2 crosses No 9 (L26 \times Gz 168), No 1 (L25 x L26) and No 12 (L27 x Gz 168) and No. 5 (L25 \times Gz 168) had the highest NUE and GYPP under high-N and low-N, i.e., they could be considered as the most N efficient and the most responsive genotypes in this study (Fig.1 through 6) . On the contrary, the parents No 4. (Gem 7), No 5. (Gem 9) and No.6 (Gz 168), the F_1 crosses No 13 (Gem 7 \times Gem 9), No 14 (Gem7 ×Gz 168) and No 15 (Gem 9 × Gz 168) and No 4 (L25 \times Gz 168) and the F₂ crosses No 11 (L27 × Gem 9), No 13 (Gem 7 × Gem 9) , No 14 (Gem 7 × Gz 168), No 15 (Gem 9 × Gz 168) and No 4 (L25 \times Gem 9) had the lowest GYPP and NUE under both high-N and low-N and therefore could be considered in-efficient and non-responsive (Fig. 1 through 6). The 2^{nd} group (efficient and non-responsive) included parent No. 1(L25), F_1 crosses No. 2,3 and 5 and F_2 crosses No. 2,3,7 and 8 based on both GYPP and NUE. Based on both NUE and GYPP traits, the F_1 crosses No.7, 8, 9 and 11 and the F_2 crosses No 6 and 10 were classified as inefficient but responsive.

Classification of the studied genotypes in the previously- mentioned groups based on grain yield/ plant (Figs. 1 through 3) was similar to that based on NUE (Fig. 4 through 6). According to Fageria and Baligar [15,16] genotypes (progenies) belonging to the $1st$ group "efficient" and responsive" (above all) and $2nd$ group "efficient and non-responsive" (to a lesser extent) appear to be the most desirable materials for breeding programs that deal with adaptation to low-input agriculture.

Based on GYPP under low and high-N, the four groups, efficient and responsive, efficient and non-responsive, inefficient and responsive and in-efficient and non-responsive (Figs. 1 to 3) could also be considered efficient at low-N and efficient at high-N, efficient – inefficient, inefficient – efficient and inefficient – inefficient based on NUE at low-N and High-N (Figs. 7 to 9).

When the entries were classified according to low-N tolerance and GYPP under low-N (Figs. 7 to 9), it was apparent that the tolerant and highyielding under low-N genotypes included the parents No.1,2 and 3 the F_1 's No. 1, 2, 3, 5 and 6 and the F_2 's No. 1, 2, 3,7, 8 and 12. The 2^{nd} group "non-tolerant but high-yielding under low-N" included the F_1 's No. 10 and 12 and the F_2 's No. 5 and 9.

Classification based on tolerance to low-N and NUE under low-N (Figs. 13 to 15) grouped the entries into four groups, i.e., tolerant and efficient

at low-N, non-tolerant and efficient, tolerant and inefficient and non-tolerant – inefficient at low-N which included the same entries in the classification based on tolerance and GYPP at low-N (Figs. 10 to 12).

Based on tolerance to low-N and GYPP under high-N (responsiveness) (Figs. 13 to 15), entries were classified into four groups, i. e., tolerant and responsive (parents No. 2 and 3, F_1 's No. 1 and 6 and F_2 's No. 1 and 12), tolerant and nonresponsive (parent No.1 F_1 's No. 2,3,5 and 15 and F_2 's No. 2,3,7,8 and 15), non-tolerant but responsive (F_1 's No. 7, 8, 9, 10, 11, and 12 and $F₂$'s No. 5, 6, 9, and 10) and non-tolerant and non-responsive (parents No. 4, 5, and 6, and F_1 's No. 4.13 and 14 and F_2 's No.4, 11, 13 and 14).

Fig. 1. Relationships between grain yield/ plant (GYPP) of 6 parents under high-N and low-N across two seasons. broken line represent mean of GYPP. Numbers from 1 to 6 refer to parent name

Fig. 2. Relationships between grain yield/ plant (GYPP) of 15 F1 wheat crosses under high-N and low-N across two seasons. Broken line represent mean of GYPP. Number from 1 to 15 refer to F1 cross name

Fig. 3. Relationships between grain yield/ plant (GYPP) of 15 F2 wheat crosses under high-N and low-N across two seasons. Broken line represent mean of GYPP. Numbers from 1 to 15 refer to F2 cross name

Summarizing the above-mentioned classifications, it is apparent that the the two parents L26 and L27, the F_1 's No. 6 (L26 \times L27) and No.7 (L26 \times Gem7) and the F₂'s No.1 (L25 \times L26) and No.12 (L27 \times Gz168) occupied the first group in all classifications; they are efficient, at low-N and high-N, tolerant to low-N, responsive at high-N and high-yielding at low-N. The parent L25, the F₁'s No.2 (L25 x L27), 3 (L27 x Gem7) and 5 (L25 \times Gz168) and F₂'s No. 2 (L25 \times L27), 3 (L25 × Gem7), 7 (L26 × Gem7) and 8 (L26 × Gem9) are tolerant to low-N, high-yielding at lowN and N efficient. The F_1 's No.10 (L27 \times Gem7) and 12 (L27 \times Gz168) and F₂'s No. 5 (L25 \times Gz168) and 9 (L26 ×Gz168) are N efficient and responsive. The F_1 's No. 10 (L27 \times Gem7) and 12 (L27 × Gz168) are high-yielding and efficient at low-N, No. 2 (L25 ×L27),3 (L25 × Gem7) and 5 (L25 × Gz168) are efficient and tolerant to low-N and No.15 (Gem9 \times Gz168) is tolerant to low-N. The F_2 's No. 5 (L25 x Gz168) and 9 (L26 x Gz168) are high-yielding and efficient at low-N, No, 2 (L25 × L27), 3 (L25 × Gem7), 7 (L26 × Gem7) and 8 (L26 \times Gem9) are efficient and tolerant and No. 15 (Gem9 \times Gz168) is tolerant to low-N.

Fig. 4. Relationships between nitrogen use efficiency (NUE) of 6 parents under high-N and low-N across two seasons. Broken line represent mean of NUE. Number from 1 to 6 refer to parent name

Fig. 5. Relationships between nitrogen use efficiency (NUE) of 15 F1 wheat under high-N and low-N across two seasons. Broken line represent mean of NUE. Numbers from 1 to 15 refer to F1 cross name

NUE under high N

Fig. 6. Relationships between nitrogen use efficiency (NUE) of 15 F2 wheat under high-N and low-N across two seasons. Broken line represent mean of NUE. Numbers from 1 to 15 refer to F2 cross name

Fig. 7. Relationships between tolerance to low-N and (GYPP) of 6 parents under low-N across two seasons. Broken line represent mean of GYPP tolerance. Numbers from 1 to 6 refer to parent name

Fig. 8. Relationships between tolerance to low-N and (GYPP) of F1 crosses under low-N across two seasons. Broken line represent mean of GYPP and tolerance. Numbers from 1 to 15 refer to F1 cross name

Fig. 9. Relationships between tolerance to low-N and (GYPP) of F2 crosses under low-N across two seasons. Broken line represent mean of GYPP and tolerance. Number from 1 to 15 refer to F2 cross name

Fig. 10. Relationships between tolerance to low-N and (NUE) of 6 parents under low-N across two seasons. broken line represent mean of NUE tolerance. Numbers from 1 to 6 refer to parent name

Fig. 11. Relationships between tolerance to low-N and (NUE) of F1 crosses under low-N across two seasons. Broken line represent mean of NUE tolerance. Number from 1 to 15 refer to F¹ cross name

Fig. 12. Relationships between tolerance to low-N and (NUE) of F2 crosses under low-N across two seasons. Broken line represent mean of NUE tolerance. Numbers from 1 to 15 refer to F² cross name

Fig. 13. Relationships between tolerance to low-N and (GYPP) of parents under high-N across two seasons. Broken line line res represent mean of GYPP and tolerance. Numbers from 1 to 6 refer to F1 cross name

Fig. 14. Relationships between tolerance to low-N and (GYPP) of F1 crosses under high-N across two seasons. Broken line represent t mean of GYPP and tolerance. Number from 1 to 15 refer to F1 cross name

Fig. 15. Relationships between tolerance to low-N and (GYPP) of F2 crosses under high-N across two seasons. Broken line represent t mean of GYPP and tolerance. Numbers from 1 to 15 refer to F2 cross name

The lowest stress-induced depression in grain yield occurred in some wheat parents and their hybrids in F_1 and F_2 generations may at least partly be associated with excellent rooting capacities of these entries [14]. These entries exhibited high GYPP under both low-N and highN, i.e., more stable yielding capacity. Other wheat entries in the present study, tended to produce relatively high grain yields under low-N conditions, but gave lower yields with high N nutrition, confirming that the highest yielding entries tended to be less tolerant to N shortage as demonstrated in Figs.(8 and 9) (F_1 's No. 12 and 10 and F_2 's No. 5 and 9). These observations imply that selection for high yield in favorable environments might lead to identification of wheat genotypes with greater stress-induced yield depression, i.e., forms less adapted to low-N input agriculture [14].

4. CONCLUSIONS

Results of this study indicates that the tolerant F_1 and $F₂$ cross to low-N should include two tolerant parents and assure that low-N tolerance trait is quantitative in nature, so the tolerant cross accumulates additive genes of low-N tolerance from both parents. Superiority of low-N T×T crosses (in F_1 and F_2 generations) over TxS and S×S crosses was more pronounced under high-N conditions, indicating that those T×T crosses are tolerant to low-N and responsive to high-N conditions. This study concluded that the two parents L26 and L27, the F_1 's L26 \times L27 and L26 \times Gem7 and the F₂'s L25 \times L26 and L27 \times Gz168 occupied the first group in all classifications; they are efficient, at low-N and high-N, tolerant to low-N, responsive at high-N and high-yielding at low-N. The parent L25, the F_1 's L25 x L27, L27 x Gem7 and L25 x Gz168 and F_2 's L25 x L27, L25 x Gem7, L26 x Gem7 and $L26 \times$ Gem9 occupied the second group; they are tolerant to low-N, high-yielding at low-N and N efficient, but they are non-responsive to high-N. These genotypes (progenies) that belong to the 1st group "efficient and responsive" (above all) and 2^{nd} group "efficient and non-responsive" (to a lesser extent) appear to be the most desirable materials for breeding programs that deal with adaptation to low-input agriculture.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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