Mode of Inheritance of Nitrogen Efficiency Traits in Wheat (*Triticum aestivum* L.) F_2 Diallel Crosses under Contrasting Nitrogen Environments

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Authors' contributions

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

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ABSTRACT

There is an increased interest worldwide in developing wheat cultivars that are more efficient in utilizing nitrogen (N) and better fitted to N limitations. The objective of this investigation was to study the effects of contrasting soil N levels on the genetic parameters controlling the nitrogen use efficiency (NUE) components in bread wheat. Parents of contrasting low-N tolerance and their diallel F_2 hybrids were evaluated in two seasons under varying levels of soil N, *i.e.* low-N (0 kg N/fed) and high-N (75 kg N/fed) using a randomized complete block design in three replications. Results of analysis of combining ability across seasons showed that variances due to both general (GCA) and specific (SCA) combining ability were significant for all studied nitrogen efficiency traits. Under low-N, the best general combiners were L25 and L26 for NUE and nitrogen uptake efficiency (NUPE)

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and L27 for NUE and the best F_2 cross for SCA effects was L25 x Gem 7 for two traits (NUE and NUPE), L25 x L27 and L26 x Gem 9 for NUPE. The magnitude of dominance in F_2's was much greater than that of additive variance for all studied traits under both high N and low N, suggesting that selection methods that eliminate masking non-additive effects and take advantage of the additive variance should be employed to improve NUE traits under low-N and high-N environments. The average degree of dominance in F_2's was in the range of partial dominance for all studied traits under the two levels of nitrogen, except for NUTE and nitrogen harvest index (NHI) under high N, which indicated over dominance and NHI under low-N, which indicated no dominance. Narrow-sense heritability (h^2_n) in F_2's ranged from 2.11% (NHI) to 42.64% (NUE) under high-N and from 6.80% (NHI) to 85.00% (NUE) under low-N, suggesting that it is better to practice selection for studied nitrogen efficiency traits under low-N conditions to obtain higher values of selection gain.

1. INTRODUCTION

Because of essential economic and ecological concerns, there is increased interest worldwide in cereal cultivars that are more efficient in utilizing soil resources and better fitted to water and nutrient limitations [1-8]. 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 favorable, 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) and plant adaptation to less favorable nutrition regimes is complex with various mechanisms involved [9-18]. Different characteristics, associated with both the uptake capacity (NUPE) 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 [19,20].

Although numerous reports on genotypic variation in components of N efficiency already suggest potential applications of this genetic knowledge for wheat improvements relatively fewer attempts have been made to breed wheat for these traits [21-24]. Progress in breeding bred wheat better adapted to less favorable fertilization regimes and/or low input/ organic agricultural systems is still restricted for several reasons. Wheat breeders are frequently skeptical not only because of the morpho-physiological complexity of the matter, but mainly due to limited data on both the variation among available wheat collections and the genetics of key characters involved. Hence, several important questions remain to be resolved, especially in regard to the most effective selection schemes, desirable plant ideotypes for low input ecosystems, appropriate selection criteria and features of the selection environment for such breeding programs [24-26]. Furthermore, modern Egyptian 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. On the contrary, beneficial plant characteristics for low-input ecosystems may be different from those present in modern, high-yielding wheats [1,27]. 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 components of N efficiency 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 [28-31], 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 [18]. In earlier investigations [32], both additive and non-additive genetic effects were crucial for agronomic NUE components in F_1 hybrids between modern French cultivars. In contrast, additive gene action was only important for NUE components among F_2 progenies of wheats of Turkish origin [33]. In Poland, Gorny et al. [18] reported that under high N-fertilization, the efficiency components were inherited in a manner favorable for wheat selection

(preponderance of additive effects). However, they found that 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. To the best of our knowledge, scarce information 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 and goals.

Thus, the objectives of this study were (i) to assess the modes by which nitrogen use efficiency (NUE) traits are inherited and (ii) to evaluate effects of varied nitrogen levels on combining ability, heritability and expected genetic advance from selection for NUE components.

2. MATERIALS AND METHODS

This study was carried out at Giza Research Station of the Agricultural Research Center(ARC), Giza Egypt (30º 02' N latitude and 31º 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 (30º 66' N latitude and 3º 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).

2.2 Making the F_1 and F_2 diallel Crosses

In the winter (normal) wheat 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 (off-season), a part of F_1 seeds was sown in greenhouse of Wheat Res. Dept. under controlled conditions to obtain the F_2 seeds. In the winter (normal) wheat season 2007/2008, the half diallel of crosses was again done to increase quantity of F_1 seeds and in summer 2007 (off-season), 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 F_2's

In the winter (normal) wheat 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., under two levels of nitrogen fertilizer; the low level was 0 kg N/fed (without fertilization) (LN) and the high level was 75 kg Nitrogen/ feddan (HN). This level of nitrogen fertilizer (in the form of Urea) was added in two equal doses, the first dose was added just before the sowing irrigation and the second dose just before the second irrigation (21 days after irrigation). Two separate experiments (one experiment for low-N and the other for high-N) were carried out using a randomized complete block design 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.

Table 1. 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
Gemmeiza7(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

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 (fed= feddan= 4200 m^2) in the winter (normal) 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

The following characteristics were measured on a random sample of 10 plants of each parents and 30 plants of each F_2. Grain yield/ plant (GYPP) was measured as weight of the grains of each individual plant. 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 70ºC 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. [34]. Total plant nitrogen (N_t) was calculated as follows: $N_t = N_g + N_{straw}$. The following traits were determined: **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. [19].

2.5 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 ® [35]. Combined analysis of variance across the two seasons was also performed if the homogeneity test was non-significant. 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. [36].

2.6 Genetic Analysis of F_2 Diallel Crosses

2.6.1 Griffing's approach

Diallel crosses in F_2 generations were analyzed to calculate general (GCA) and specific (SCA) combining ability variances and effects for studied traits according to Griffing [37] Model I (fixed effect) Method 2 as shown in Singh and Chaudhary [38].

2.6.2 Hayman's approach

Although Griffing's analysis was based on Model I (fixed effect) since parents of the diallels in this study were selected in purpose for the validity of diallel analysis, Hayman's approach (that assumes random model) was used to estimate genetic components and ratios. The conclusions obtained from Hayman's analyses will not be generalized, but will help us to characterize our genetic material for its proper use in the future breeding programs. The genetic parameters and ratios were calculated according to methods developed by Jinks and Hayman [39], Jinks [40] and Hayman [41,42] and described by Sharma [43].

Hayman's approach was performed for estimating variance components and ratios in F_2 generation, based on the same assumption proposed in F_1, but with the following modifications in F_2 for some genetic parameters (according to Sharma [43]. The following components of $\hat{E}$, D, H_1, H_2, h^2 and F were estimated in F_2: $\hat{E}$ = [(Errors S.S. + Reps S.S.)/r]/[(r-1) + (c-1) (r-1)]. **D** = $V_{0L0} - \hat{E}$. **F** = 4 $V_{0L0} - 8W_{0L01} - [2\hat{E} (n-2)/n]$. **$H_1$** =4 V_{0L0} + 16 W_{0L01}

- [$\hat{E}$ (3n-2)/n]. **H_2** = 16 V_{1L1} - 16V_{0L1} - 2$\hat{E}$ h^2 = 16$(M_{L1} - M_{L0})^2$ - [4$\hat{E}$ (n-1)/n²]. **h^2** = 4$(M_{L1} - M_{L0})^2$ - [4$\hat{E}$ (n-1)/n²]. Where: n = number of parents. $\hat{E}$ = expected environmental component of variance. D = variance due to additive effects of the genes. F = mean of the covariance of additive and dominance effects across all arrays. H_1= variance component due to dominance deviation. $H_{1=}[1-(u-v)^2]$, where, u and v are the proportions of positive and negative genes, respectively in the parents. h^2= algebraic sum of dominance effects across all loci in heterozygous phase in all crosses. **Average degree of dominance in F_2** is estimated as $1/4(H_1/D)^{1/2}$. If this ratio is zero, there is no dominance. If it is greater than zero, but less than one, there is partial dominance. If it is equal to 1, there is complete dominance. If it is greater than 1, it indicates over dominance. **The ratio of dominant genes with positive or negative effects in parents ($H_2/4H_1$)** was determined. The maximum theoretical value of 0.25 for this ratio arises when, p = q = 0.5 at all loci. A deviation from 0.25 would stem when p ≠ q Thus: if this ratio ≈ 0.25, it means symmetrical distribution of positive and negative dominant genes in parents, while if this ratio ≠ 0.25, it means asymmetry of distribution. **Ratio of dominant and recessive genes in the parents (K_D/K_R)** is estimated as follows: **K_D/K_R** = $[1/4(4DH_1)^{1/2}$+ F/2]/[1/4(4 DH_1)^{1/2}$ – F/2]. If K_D/K_R ≈1.0, it means nearly equal proportion of dominance and recessive alleles in parents, i.e. symmetrical distribution; p = q = 0.5. Any deviation from 1.0 indicates asymmetry of distribution (p # q). Thus: Ratio > 1 refers to excess of dominant alleles and minority of recessive alleles (p > q). Ratio < 1 means minority of dominant alleles and excess of recessive alleles (p < q). **Narrow-sense heritability (h^2_n) in F_2** was estimated using the following equation: $h^2_n = [1/4D / (1/4D + 1/16H_1 – 1/8F + \hat{E})]$. **Expected genetic advance from selection (GA)** The expected genetic advance (GA) from direct selection as a percentage of the mean (x) was calculated according to Singh and Narayanan [44] based on 1% selection intensity as follows: GA = $100[(k.h^2_n \delta_{ph})/x]$ Where: k = 2.64 (selection differential for 1% selection intensity), and δ_{ph}= square root of the dominator of the narrow sense heritability.

3. RESULTS AND DISCUSSION

3.1 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 (2) for high–N and Table (3) 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 under low-N conditions.

The ratio GCA/SCA mean squares was greater than unity for all studied traits of F_2 crosses under both high–N and low-N conditions, indicating that additive was larger in magnitude and more important than non-additive gene effects (dominance and epistasis) in controlling the inheritance of most studied traits under high-N and low N levels in the first segregating generation (F_2) 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 [45]. On the other hand, results of Gorny et al. [18] 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 [46-52].

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 in all studied nitrogen 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 under low-N, suggesting that SCA (non-additive variance) is more affected by year than GCA for most studied traits of F_2 crosses.

3.2 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 (4 and 5).

The best general combiners based on F_2 diallel analysis were considered those having the highest positive GCA effects for all studied F_2 traits.

Data in Table (4) indicate that under high-N the best general combiners based on F_2 diallel analysis were L27 for three out of four traits (NUE, NUPE and NUTE), L26 for two traits (NUPE and NUTE), L25 for one trait (NUTE) and Gz168 for two traits (NUE and nitrogen harvest index; NHI).

Under low-N (Table 5), the best general combiners were L25 and L26 for two traits (NUE and NUPE), L27 for one trait (NUE). L25, L26 and L27 are generally the best combiners for most nitrogen use efficiency traits based on diallel analysis of F_2 crosses. These parents are expected to have more additive genes for the respective characters.

Table 2. 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

Table 3. 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	6.14	0.01	11.85

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

Table 4. 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

3.3 8.c. SCA Effects

Specific combining ability (SCA) effects of the F_2 crosses under two levels of N are presented in Tables (6 and 7).

Under high-N, the best F_2 cross in SCA effects was L27 x Gem7 for two traits (NUE and NUTE), L26 x Gz168 for one trait (NUE), L26 x Gem7, L1 x Gem7, L25 x Gz 168, Gem7 x Gem9, L25 x Gz168 for NUPE and Gem9 x Gz168 for NUTE. Under low-N, the best F_2 cross for SCA effects was L25 x Gem7 for two traits (NUE and NUPE), L25 x L27 and L26 x 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.

Results of Gorny et al. [18] on wheat F_2 crosses appear to be in accord with similar N-Shortage – induced increases in the importance of non – additive effects for grain yield and components of NUE previously reported in maize [46-49,53] and those for NUE in grain sorghum [51,52].

Table 5. Estimates of general combining ability effects (ĝ$_i$) 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

Table 6. 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
L25X 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
L 26X L 27	-0.18	-0.30	0.03	1.52
L26 X Gem 7	-1.77*	3.61**	-0.22**	-1.49
L 26 X Gem 9	-0.75	2.22*	-0.17*	-3.31*
L 26 X Gz 168	2.03*	0.93	0.02	-1.72
L 27X Gem 7	1.74*	-0.87	0.13*	-0.06
L 27 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 X Gz 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

3.4 Gene Action, Heritability and Expected Selection Gain in F_2 Progenies

Genetic parameters and ratios for studied traits in F_2's under high- and low-N environments across two years are presented in Table (8). Additive genetic variance (D) was highly significant for NUE and NUPE under high-N and low-N and NHI (nitrogen harvest index) under low-N, indicating that the additive gene effects in F_2's of this experiment are important for the inheritance of NUE and NUPE traits both environments and NHI under low-N only in the first segregating generation of the studied cross populations of wheat. It is observed that the magnitude of additive variance was much higher under low-N than that under high-N conditions in most studied nitrogen use efficiency traits.

The dominance genetic component of variation (H_1) was highly significant for all studied traits under both high and low-N environments, except for NHI under low-N, indicating that the dominance gene effects in F_2's of this experiment are important for the inheritance of most studied traits under low-N and high-N. It is also observed that the magnitude of dominance variance was much higher under low-N than under high-N conditions in all studied traits, except nitrogen harvest index (NHI).

The magnitude of dominance (H_1) in F_2's was much greater than that of additive (D) variance for all studied traits under both high N and low N, except for NHI trait under low-N, where the opposite was true, i.e. the additive was greater than dominance variance. This indicates that the dominance gene effects are more important than additive in F_2's and plays the major role in the inheritance of most studied nitrogen efficiency traits.

The preponderance of dominance (non-additive) effects in F_2 generation of this study suggest that selection methods that eliminate masking non-additive effects and take advantage of the additive variance should be employed to improve nitrogen use efficiency traits under low-N and high-N environments. Thus, selection should be postponed to later segregating generations under low-N conditions to develop N-efficient genotypes of wheat. In this respect, Le Gouis et al. [32] reported that in N-limited diallel F_1 hybrids between modern French cultivars found markedly preponderance of additive variance 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 additive 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 [45].

Table 7. Estimates of specific combining ability effects ($\hat{s}_{ij}$) 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
L25X 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
L 26X L 27	-5.87*	-9.09**	0.10	-2.16
L26 X Gem 7	1.37	3.32	-0.07	1.49
L 26 X Gem 9	0.78	11.02**	-0.30*	-1.93
L 26 X Gz 168	1.18	3.43	-0.07	0.11
L 27X Gem 7	-2.40	1.44	-0.10	2.34
L 27 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

Table 8. Estimates of genetic parameters and ratios for studied traits under high and low-N in F$_2$ populations of 15 diallel crosses across two seasons

Variance components	NUE	NUPE	NUTE	NHI
High-N				
E	0.17	0.16	0.00	0.67
D	1.58**	4.60**	0.01	0.14
H$_1$	5.44**	20.94**	0.09**	14.97**
H$_2$	5.23**	17.95**	0.08**	14.45**
F	-0.17	-7.56**	-0.02	-0.10
h^2	2.69**	3.43**	0.03*	0.86**
(H$_1$/D)$^{1/2}$	0.46	0.53	1.08	2.61
H$_2$/4H$_1$	0.24	0.21	0.22	0.24
K$_D$/K$_R$	0.94	0.44	0.38	0.93
h^2/H$_2$	0.51	0.19	0.31	0.06
h^2_b%	81.64	95.03	91.83	59.53
h^2_n%	42.64	33.37	20.41	2.11
GA%	7.70	9.52	6.80	0.12
Low-N				
E	0.89	2.05	0.003	3.95**
D	26.66**	50.19**	0.01	1.27**
H$_1$	28.28**	64.78**	0.08**	-6.97
H$_2$	25.78**	61.65**	0.07**	-4.41**
F	11.85**	11.30**	0.01	-6.25**
h^2	2.95*	25.43**	0.02	6.30**
(H$_1$/D)$^{1/2}$	0.26	0.28	0.58	0.00
H$_2$/4H$_1$	0.23	0.24	0.21	0.16
K$_D$/K$_R$	1.55	1.22	1.43	0.00
h^2/H$_2$	0.11	0.41	0.27	1.43
h^2_b%	88.60	88.10	67.57	14.30
h^2_n%	85.00	72.80	27.00	6.80
GA%	23.10	27.43	6.80	6.70

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

On the other hand, results of Gorny et al. [18] 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 [48,49] and those for NUTE in barley [52]. Gorny et al. [18] 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 effects and take advantage of the additive variance should be employed to improve those traits. Results of the present study assure the conclusion of Gorny et al. [18].

The overall dominance effects of heterozygous loci in Hayman's model (h^2) controlling all studied traits of F$_2$'s under both high- and low-N environments were significant (P< 0.01 or 0.05), except NUTE under low-N; that could be due to the presence of a considerable amount of dominant genes for most studied traits in the parental genotypes.

The average degree of dominance (H$_1$/D)$^{1/2}$ in F$_2$'s was in the range of partial dominance (smaller than unity) for all studied traits under the two levels of nitrogen, except for NUTE and nitrogen harvest index (NHI) under high N, which indicated over dominance and NHI under low-N, which indicated no dominance (Table 8).

Lower ratio (H$_2$/4H$_1$) than 0.25 (Table 8) indicated symmetrical distribution of positive dominant genes in parents for all studied traits of F$_2$'s under both high- and low-N environments.

Under low-N, the ratio (K_D/K_R) in F_2's was greater than unity for NUE, NUPE and NUTE traits, indicating excess of dominant alleles and minority of recessive alleles (p>q) for most studied nitrogen efficiency traits. The exception under low-N was nitrogen harvest index (NHI) of F_2's, where the ratio (K_D/K_R) was less zero, indicating minority of dominant alleles and the excess of recessive alleles (p<q).

However, under high-N, the ratio (K_D/K_R) in F_2's was less than unity for all studied traits, indicating minority of dominant alleles and the excess of recessive alleles (p<q) (Table 8).

Number of genes or groups of genes controlling the inheritance of a given trait (h^2/H) was one gene or group of genes for most studied traits of F_2's under both high-N and low-N environments (Table 8). The exception was nitrogen harvest index (NHI) under low-N which was controlled by two genes or groups of genes.

Broad-sense heritability (h^2_b) in F_2's for all studied traits (except NHI under low N) in this experiment was of high magnitude and ranged from 59.53% (NHI) to 95.03% (UPEN) under high-N and from 14.30% (NHI) to 88.60% (NUE) under low-N environments (Table 8), indicating that environment had a small effect on the phenotype of F_2's for most studied nitrogen efficiency traits. Nitrogen harvest index (NHI) trait under low-N (14.30%) showed very small h^2_b value, indicating a large effect of this environment on this trait.

Narrow-sense heritability (h^2_n) in F_2's (Table 8) was generally of low to high magnitude and ranged from 2.11% (nitrogen harvest index; NHI) to 42.64% (NUE) under high-N and from 6.80% (NHI) to 85.00% (NUE) under low-N.

The big difference between broad- and narrow-sense heritability estimated from F_2's in this experiment could be attributed to the high estimates of non-additive (dominance and epistasis) as compared to additive component.

It is observed that narrow-sense heritability (h^2_n) in F_2's of the present study was generally higher in magnitude under low-N than under high-N for all studied traits. This increase in h^2_n under low-N compared to high-N was more pronounced in NUE and NUPE; i.e. the most important component of nitrogen use efficiency in wheat.

The F_2 results are in agreement with one group of researchers, e.g. [16,17,54-59] who support the idea that heritability is higher under stressed than non-stressed environment. On the contrary, other group of investigators reported that heritability is higher under non-stressed environments [60-63].

Expected genetic advance (GA) from selection (based on 1% selection intensity) across two years ranged from 0.12% for NHI to 9.52% for NUPE under high-N and from 6.70% for nitrogen harvest index (NHI) to 27.43% for NUPE under low-N. In general, the values of GA were higher under low-N than under high-N (for 3 out of 4 studied traits). The traits NUE, NUPE and NHI showed much higher estimates of GA (23.10, 27.43 and 6.70%, respectively) under low-N than those under high-N (7.70, 9.52 and 0.12%, respectively). It is therefore expected that to improve nitrogen use efficiency components in the present germplasm, it is better to practice selection for these traits under low-N conditions to obtain higher values of selection gain.

3.5 Graphical Approach of Diallel Analysis

The graphical analysis of diallel crosses purposed by Hayman (1954 a and b) will be illustrated on the following bases according to Singh and Narayanan (2000): (1) The parabola marks the limits within which the variance-covariance points (V_r, W_r) should lie, (2) If the regression coefficient (b) of (V_r, W_r) is not different from unity, the genetic control system may be deduced to be additive without the complications of gene interactions, (3) Complementary gene effects (epistasis) generally reduces the covariance (W_r) disproportionally more than the variance (V_r) causing the slope of the regression line (b) to be less than unity, (4) When dominance is complete, the regression line with b = 1 would pass through the origin, (5) Over dominance causes the regression line to intercept the (W_r) axis below the origin, while partial dominance causes the regression line to intercept the (W_r) axis above the origin point, (6) The closeness of the regression line or (V_r, W_r) points to the limiting parabola indicates little dominance and (7) The order of the array points on the regression line is a good indicator of the dominance order of parents. The parents with more dominant genes are located nearer to the origin, while those with more recessive genes fall farther from the origin. The parents with equal frequencies of dominant and recessive genes occupy an intermediate position.
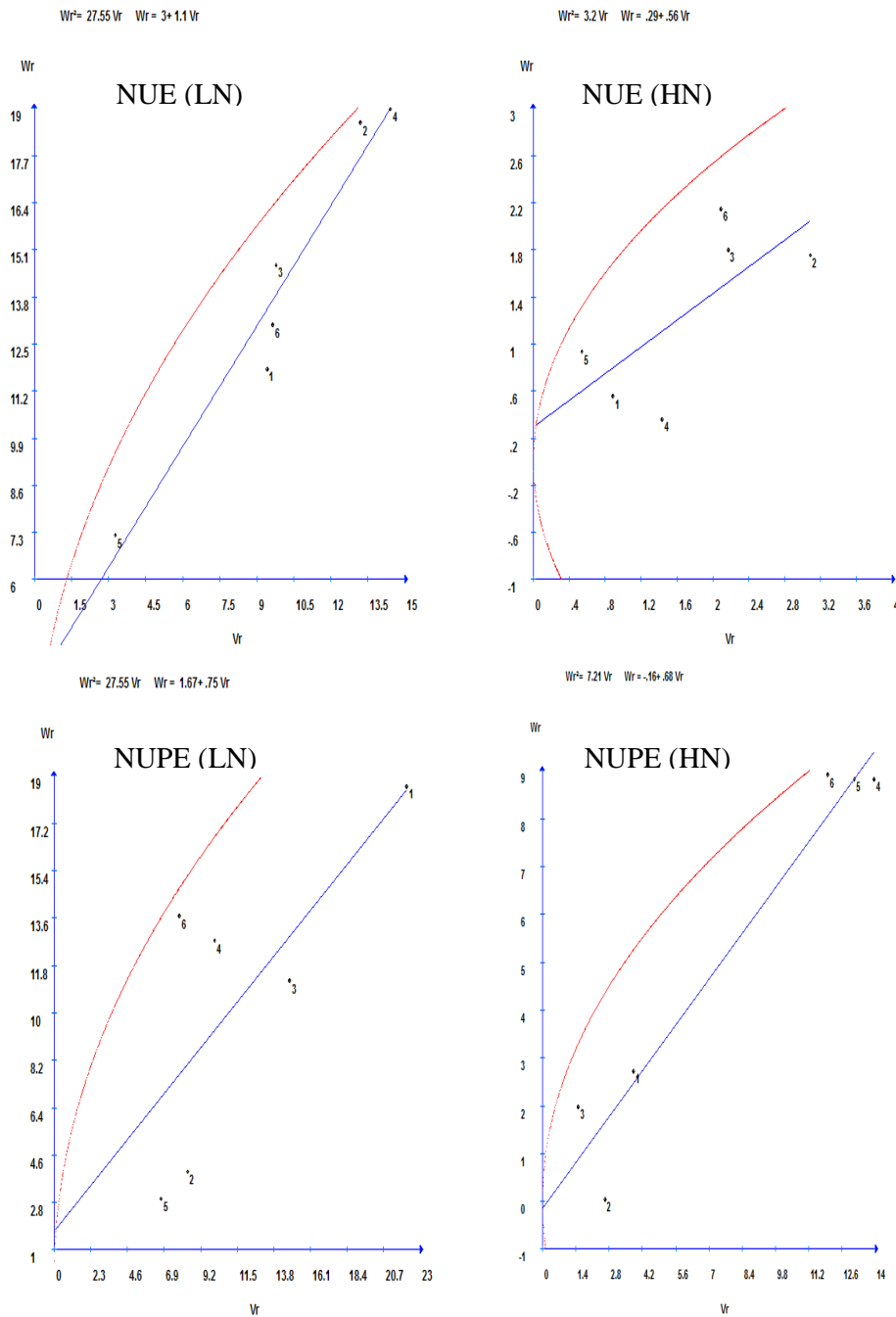
$Wr^2= 27.55 \ Vr \quad Wr = 3+1.1 \ Vr$

$Wr^2= 3.2 \ Vr \quad Wr = .29+.56 \ Vr$

NUE (LN)

NUE (HN)

$Wr^2= 27.55 \ Vr \quad Wr = 1.67+.75 \ Vr$

$Wr^2= 7.21 \ Vr \quad Wr = -.16+.68 \ Vr$

NUPE (LN)

NUPE (HN)

Fig. 1. Wr-Vr graph of nitrogen use efficiency (NUE) and uptake efficiency (NUPE) of F$_2$'s for combined data across two seasons under low-N (LN) and high-N (HN)

Based on the above information, in the F$_2$ diallel crosses**,** it is clear from Figs. (1 and 2) for 4 studied traits, that the regression line intercepted the Wr-axis below the origin, *i.e* cutting the Wr-axis in the negative region (intercept= a < 0 (negative)) or D (additive variance) < H$_1$ (dominance variance), indicating the presence of overdominance for 2 out of 8 cases, namely

NUPE (Fig.1) and NHI (Fig. 2) trait under low-N and high-N.

The regression line passed through the origin (D = H$_1$), indicating complete dominance for 3 out of 8 cases in F$_2$'s, namely NUTE (Fig.2) under low-N and high-N and NUPE under high-N.
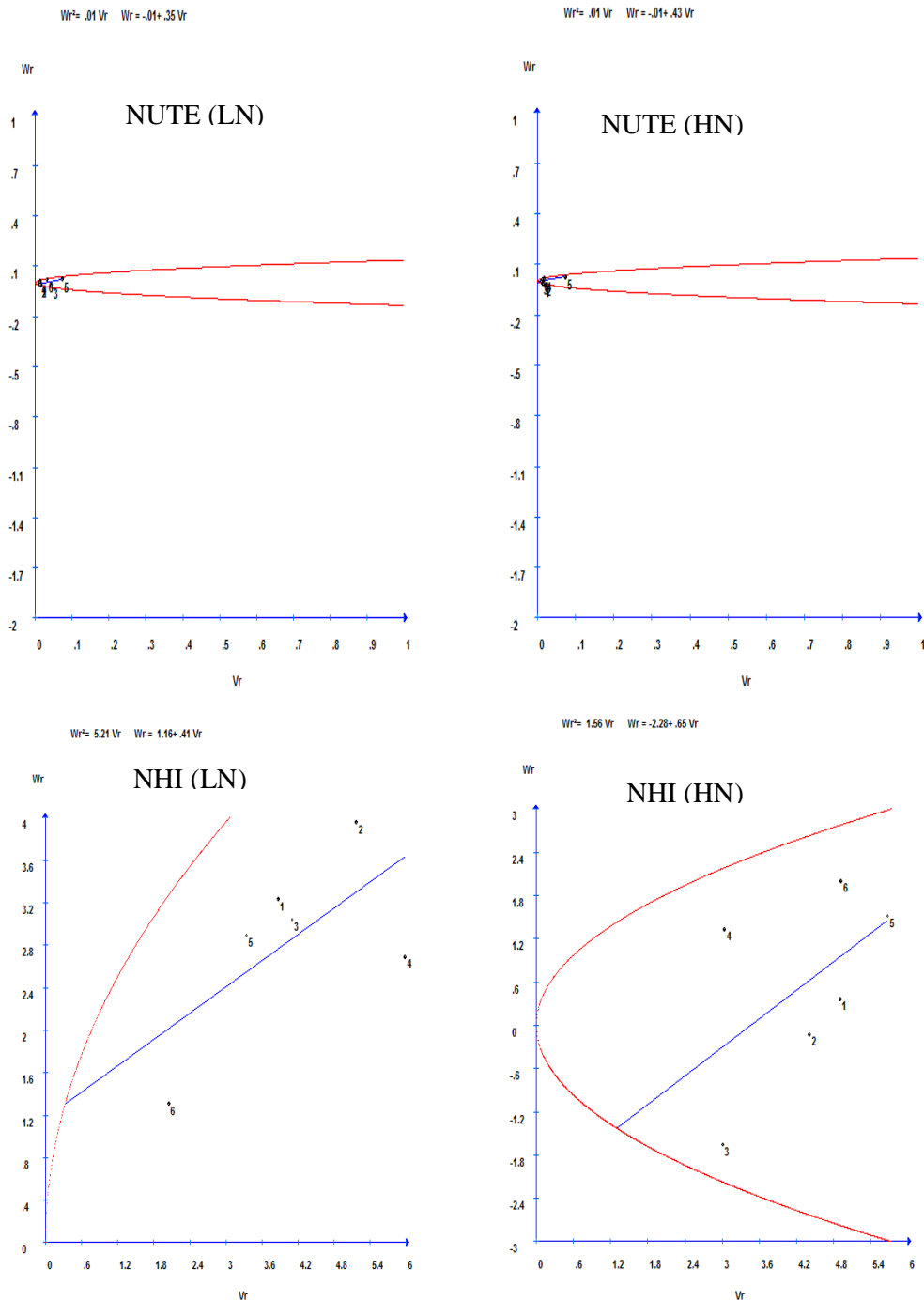
11

Wr²= .01 Vr   Wr = -.01+ .35 Vr

Wr²= .01 Vr   Wr = -.01+ .43 Vr

Fig. 2. Wr-Vr graph of nitrogen utilization efficiency (NUTE) and nitrogen harvest index (NHI) of F$_2$'s for combined data across two seasons under low-N (LN) and high-N (HN)

For 3 out of 8 cases in F$_2$'s, namely NUPE (Fig. 1) and NUE (Fig. 1) under low-N and NUE (Fig. 1) under high-N, the regression line intercepted the Wr-axis above the origin (D > H$_1$), indicating partial dominance and the predominance of additive variance in these cases.

The dispersion of parents (1 = L25, 2 = L26, 3 = L27, 4 = Gem7, 5 = Gem9 and 6 = Gz168) around the regression line for NUE trait (Fig. 1), under low-N, the dispersion of parents around the regression line reveals that parent 5 is close to the origin of the coordinate, and accordingly

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

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

With respect of NUTE trait (Fig. 2), all parents, except 5 under both low-N and high-N environments located very close to the origin of coordinate, and accordingly have > 75% of dominant genes, while parent 5 is little far from the origin, therefore has < 75% of dominant genes.

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

4. CONCLUSIONS

Analysis of combining ability indicated that under low-N, the best general combiners were L25 and L26 for NUE and NUPE and L27 for NUE and the best F_2 cross for SCA effects was L25 x Gem 7 for two traits (NUE and NUPE), L25 x L27 and L26 x Gem 9 for NUPE. These genotypes could

be used in the future breeding programs for improving NUE traits. The preponderance of dominance (non-additive) effects in F_2 generation of this study suggests that selection methods that eliminate masking non-additive effects and take advantage of the additive variance should be employed to improve nitrogen efficiency traits under low-N environment. Therefore, selection should be postponed to later segregating generations under low-N conditions to develop N-efficient genotypes of wheat. In general, the values of heritability and genetic advance from selection (GA) were higher under low-N than under high-N. It is therefore expected that to improve nitrogen use efficiency components in the present germplasm, it is better to practice selection for studied nitrogen efficiency traits under low-N conditions to obtain higher values of selection gain.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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