

Diallel Analysis of Wheat Grain Protein Content and Yield in F₁ and F₂ Generations under Contrasting Nitrogen Conditions

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Abstract: Grain yield and grain protein content (GPC) of bread wheat are crucial determinants of its profitability and product quality. In general, low levels of nitrogen fertilizer result in a lower protein content in wheat grains and lower grain yield. The main objective of this investigation was to get information on gene action, heritability and expected genetic advance from selection (GA) for GPC and grain yield/plant (GYPP) under contrasting soil-nitrogen conditions. Diallel crosses in F₁ and F₂ generations among six contrasting wheat parents in GPC and GYPP were evaluated in field experiments across two seasons in a split plot design under two N levels, *i.e.* low-N (0kg N/fed) and high-N (75kg N/fed). In both F₁'s and F₂'s, the magnitude of dominance (H₁) was much greater than that of additive (D) component for GPC under both high N and low N and GYPP under high-N, while the opposite was true for GYPP in F₁'s under low-N, where the additive was greater than dominance variance and GYPP in F₂'s under low-N, where the additive and dominance components were approximately equal. The average degree of dominance (H₁/D)^{1/2} in F₁'s was in the range of over-dominance, except for GYPP under low-N, which showed partial dominance, but in F₂'s was in the range of partial dominance for GYPP under both high and low N and GPC under high N, while GPC under low N showed no dominance. Narrow-sense heritability (h²_n) in F₁'s and F₂'s was generally of low magnitude; it ranged in F₁'s from 6.18% (GPC under low-N) to 20.41% (GYPP under high-N); the exception was GYPP under low-N, where h²_n was of high magnitude (67.14%) and ranged in F₂'s from 10.86% for GPC under low N to 46.90% for GYPP under low-N. The h²_n was higher under low-N for GYPP and under high-N for GPC. In F₁'s, the values of GA were higher under low-N than under high-N for GYPP, but were higher under high-N than low-N for GPC. In F₂'s, the values of GA for both traits were higher under low-N than under high-N, suggesting that it is better to practice selection in F₂'s for both traits under low-N conditions to obtain higher values of selection gain.

Keywords: *Triticum aestivum*, Grain protein content, Gene action, Heritability, Grain yield, Low-N

I. INTRODUCTION

Wheat (*Triticum aestivum* L.) is an important source of both carbohydrates and protein in human and livestock nutrition (Shewry, 2007). It is estimated to contribute as much protein as the total annual soybean crop, or 60 million tonnes of protein per year (Shewry, 2007). Grain yield potential and grain protein content (GPC) of a wheat crop are crucial determinants of its profitability and product quality.

Grain protein content is an important quality factor in wheat, as it helps to determine milling and baking quality (Bushuk 1977). Protein content of wheat is largely influenced by cultivar, available N, moisture and temperature conditions under which the crop is grown (Fowler et al. 1990 and Campbell et al. 1977). Changes in protein content with application of fertilizer N differ with cultivar (Clarke et al. 1989 and Fowler et al. 1990). Semi dwarf wheat cultivars show a smaller increase in grain protein with small applications of N fertilizer than do cultivars of conventional height due to greater yield potential of semi dwarf wheats (Campbell et al. 1971 and Clarke et al. 1989).

In general, high levels of nitrogen fertilizer result in a higher protein content in wheat grains and higher grain yield (Ortiz-Monasterio et al., 1997). Genotypic variability was found for wheat grain protein content and grain yield. Therefore a concomitant increase in grain yield and grain protein seems feasible (Bänziger et al., 1992). However, there are problems associated with N fertilizer use, because N can leach and cause eutrophication of water (Vitousek et al., 1997), and N fertilization increases emissions of the greenhouse gas nitrous oxide (N₂O) from agricultural soils (Bouwman et al., 2002).

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There is an increased pressure on plant breeders to improve grain protein and yield simultaneously. The feasibility of this simultaneous improvement, however, is a subject of controversy. Numerous genetic studies have shown the existence of major genes conferring enhanced grain protein concentration without adverse effects on yield (Stuber *et al.*, 1962; Johnson *et al.*, 1973 and Cox *et al.*, 1986). Nevertheless, plant breeders' experience shows that simultaneous selection of grain protein concentration and yield is only occasionally successful at enhancing both characters (Loffler and Busch, 1982).

While the observed variation in grain protein concentration in wheat is large (6-22%, Johnson and Lay 1974), much of this variation is environmental rather than genetic in origin. The protein concentration is determined by the genetic background, but also, to a large extent, by environmental factors such as nitrogen, water access, and temperature conditions. Consequently, selection for high grain protein concentration, especially in the early generations of a breeding program, is likely to be ineffective. Secondly, many studies have shown a negative correlation (r typically between -0.4 and -0.6) between grain protein concentration and overall yield (e.g. Grant and McCalla 1949; Halloran 1981 and Johnson *et al.* 1985).

The first step for starting a breeding program to improve grain protein content and grain yield is to determine the type of gene action that control expression of these traits. The type of gene action for grain yield in bread wheat under low-N and high-N conditions was studied by several investigators, who indicated the role of both additive and dominance gene effects under both low-N stress and non-stress conditions (Munir *et al.*, 2007, Abd El-Rahman and Hammad, 2009 and Jatoi *et al.*, 2012). Additive was more important than dominance variance under both conditions in controlling the inheritance of grain yield in wheat (Farshadfar *et al.*, 2008; Aboshosha and Hammad, 2009). On the other hand, non-additive variance was more important than additive variance under low-N stress in the inheritance of wheat grain yield (Bayoumi, 2004; Farhat, 2005 and Al-Naggar *et al.*, 2007b). Moreover, the overdominance type of gene action which controlled grain yield per plant under high-N changed into partial dominance under low-N stress as reported by Subhani and Chowdhry (2000). Literature on the gene action controlling inheritance of wheat grain protein content is scarce and of conflict results, probably due to different germplasm used and/or the environmental conditions prevailing at different studies.

The objectives of the present investigation were: (i) to assess the effect of low-N, genotype (G) and their interaction (G x N) on grain protein content (GPC) and grain yield/plant (GYPP) of wheat parents and their diallel F₁ and F₂ progenies, (ii) to estimate combining ability variances and effects of this material for the two characters and (iii) to determine gene action, heritability and expected genetic advance from selection for high values of GPC and GYPP under contrasting soil- nitrogen conditions.

II. MATERIALS AND METHODS

This study was carried out at Giza Research Station of the Agricultural Research Center(ARC), Giza Egypt (30° 02'N latitude and 31° 13'E longitude with an altitude of 22.50 meters above sea level), in 2005/2006 season and at Noubarya Research Station of the ARC, Noubarya, Egypt (30° 66'N latitude and 30° 06' E longitude with an altitude of 15.00 meters above sea level), in 2006/2007, 2007/2008 and 2008/2009 seasons.

III. MATERIALS

Six bread wheat genotypes (*Triticum aestivum* L.) were chosen for their divergence in grain protein content (GPC) and grain yield under low nitrogen, based on previous experiment carried out by Wheat Res. Dept., Field Crops Res. Inst., ARC, Egypt. Three parents (L25, L26 and L27) were of high GPC and tolerance to low-N and the other three parents (Gem7, Gem9 and Gz168) were of low GPC and tolerance to low-N.

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

3.2. Field Evaluation of 6 Parents, 15 F₁'s And 15 F₂'s

In the seasons 2007/2008, 2008/2009, parents (6), F₁'s (15) and F₂'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 (6x6) arrangement was used with three replications. The two levels of nitrogen were allotted to the main plots and the genotypes to the sub plots. Each parent or F₁ was sown in two rows and each F₂ 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 F₁ and 3.6 m² for F₂. All other agricultural practices were done according to the recommendation of Ministry of Agriculture for growing wheat in Noubarya region.

Available soil nitrogen in 30 cm depth was analyzed immediately prior to sowing and N application at the laboratories of Water and Environment Unit, ARC, Egypt in the two seasons. Soil nitrogen was found to be 55 and 57 kg N/ fed in the seasons 2007/2008, 2008/2009, respectively. Available soil nitrogen after adding nitrogen fertilizer was therefore 55 and 130 kg N/fed in the first season and 57 and 132 kg N/fed in the second season for the two treatments, i.e. LN and HN, respectively. The available nitrogen to each plant (including soil and added N) was calculated for each environment to be 0.79, 1.85 g/plant in 2007/2008 season and 0.81 and 1.89 kg/fed in 2008/2009 season, with an average across the two seasons of 0.80 and 1.87 g/plant for the two environments LN and HN, respectively.

The soil analysis of the experimental soil at Noubarya Research Station, as an average of the two growing seasons, indicated that the soil is sandy loam (67.86% sand, 7.00% silt and 25.14% clay), the pH is 8.93, the EC is 0.55 dSm⁻¹, the soluble cations in meq l⁻¹ are 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 SO₄²⁻ (1.51).

3.3. Data Recorded

The following grain characters were measured on a random sample of each entry each replicate. **1. Grain protein content (GPC)** measured as follows: $GPC\% = N_g \times 5.70$ according to AACC (2000), where N_g is grain nitrogen content. Grain samples were ground in powder and nitrogen of grains (N_g) was determined using Kjeldahl procedure according to A.O.A.C. (1990). **2. Grain yield/plant** measured on 10 guarded plants/plot for parents and F₁'s and 20 guarded plants/plot for F₂'s.

IV. BIOMETRICAL AND GENETIC ANALYSES

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 ® (Littell *et al.*, 1996). 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.* (1997).

4.1. Estimating Combining Ability In F₁'s And F₂'s

Diallel crosses in F₁ and F₂ generations were analyzed to estimate general (GCA) and specific (SCA) combining ability variances and effects for studied traits according to Griffing (1956) Model I (fixed effect) Method 2.

4.2. Estimating Genetic Components And Ratios In F₁'s

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 (1953), Jinks (1954) and Hayman (1954a and b) and described by Sharma (2003). The variance and covariance statistics across replications were used to obtain estimates of the components of variation and their respective standard errors. The validity of the assumptions of diallel analysis was tested by the following formula (Sharma, 2003): $t^2 = \frac{(n-2)/4[(MSS(Vr) - (MSS(Wr))^2] / \{MSS(Vr) \times [MSS(Wr) - MSP(Wr.Vr)^2]\}}{Where: Wr = covariance between parents and$

their off-spring and V_r = variance of each array in which a particular parent is involved. Significance of calculated "t" value was tested against the tabulated "F" value with 4 and (n-2) degrees of freedom. Significant value indicates failure of the assumptions (Hayman, 1954 a and b). Another test was done by estimating the regression coefficient "bWr.Vr" of Wr on Vr as follows: $b_{Wr,Vr} = [\text{cov}(Wr,Vr)/\text{var Vr}] = [\text{MSP}(Wr,Vr)/\text{MSS}(Vr)]$. The standard error (SE) for the regression coefficient (b) value was estimated as follows: $SE_b = [\text{MSS}(Wr) - b\text{MSP}(Wr,Vr)(n-2)]^{1/2}$ Where: n = number of parents. The significance of (b) different from zero (t_1) and from unity (=1) (t_2) can be tested by t-test as under: $t_1 = (b-0)/SE_b$ and $t_2 = (1-b)/SE_b$

The foregoing values were tested against the "t" tabulated value for (n-2) degrees of freedom according to (Jinks and Hayman, 1953). If all the assumptions were valid, the regression coefficient would be significantly different from zero but not from unity. Hayman (1954 a and b), derived the expectations for the statistics calculated from the F1 diallel table and the expected values of the component variations using least squares. The notations of Mather and Jinks (1971) are used and described as follows: V_{OL0} (V_p) (variance of the parents) = $D + \hat{E}$, $V_{IL1}(V_r)$ (mean of all the V_r values) = $1/4 D - 1/4 F + 1/4 H_1 + 1/4 H_2 + [\hat{E} + \hat{E} (n-2)/2n2]$, V_r (variance of all the progenies in each parental array) = $1/4 D + 1/4 H_1 - 1/4 H_2 - 1/4 F + (n+1)/2n2 \hat{E}$, $W_{OL01}(Wr)$ (mean of all the Wr. values) = $1/2 D - 1/4 F + \hat{E}/n$, $(M_{L1} - M_{L0})^2$ = dominance relationship = $1/4 h^2 + [(n-1) \hat{E}/n^2]$. The components of \hat{E} , D, H_1 , H_2 , h^2 and F were estimated in F_1 as follows: $\hat{E} = [(\text{Errors S.S.} + \text{Reps S.S.})/r]/[(r-1) + (c-1)(r-1)]$. $D = V_{OL0} - \hat{E}$, $F = 2 V_{OL0} - 4W_{OL01} - [2\hat{E} (n-2)/n]$, $H_1 = V_{OL0} + 4 V_{OL1} - 4W_{OL01} - [\hat{E} (3n-2)/n]$, $H_2 = 4 V_{IL1} - 4 W_{OL1} - 2\hat{E} h^2 = 4(M_{L1} - M_{L0})^2 - [4\hat{E} (n-1)/n^2]$ 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.

The following genetic parameters were also calculated: **Average degree of dominance** is estimated as $(H_1/D)^{1/2}$. 1. If the of this ratio is zero, there is no dominance. 2. If it is greater than zero, but less than one, there is partial dominance. 3. If it is equal to 1, there is complete dominance. 4. If it is greater than 1, it indicates over dominance. **Ratio of dominant and recessive genes in the parents (K_D/K_R)** is estimated as follows: $K_D/K_R = [(4DH_1)^{1/2} + F]/[(4 DH_1)^{1/2} - F]$ If $K_D/K_R \approx 1.0$, 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 ($p \neq q$). 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 ($p < q$). **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 $p \neq q$ Thus: if this ratio ≈ 0.25 , it means symmetrical distribution of positive and negative dominant genes in parents, while if this ratio $\neq 0.25$, it means asymmetry of distribution. **Narrow-sense heritability (h^2_n)** was estimated using the following equation: $h^2_n = [1/4D / (1/4D + 1/4H_1 - 1/4F + \hat{E})]$. **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 (2000) 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.

4.3. Estimating Variance Components And Ratios In F2's

Hayman's approach was performed for estimating variance components and ratios in F_2 generation of the same diallel crosses, based on the same assumption proposed in F_1 , but with the following modifications in F_2 for some genetic parameters (according to Sharma, 2003) as follows: $F = 4 V_{OL0} - 8W_{OL01} - [2\hat{E} (n-2)/n]$, $H_1 = 4 V_{OL0} + 16W_{OL01} - [\hat{E} (3n-2)/n]$, $H_2 = 16 V_{IL1} - 16V_{OL1} - 2\hat{E}$, $h^2 = 16(M_{L1} - M_{L0})^2 - [4\hat{E} (n-1)/n^2]$. Average degree of dominance in F_2 is estimated as $1/4(H_1/D)^{1/2}$. $K_D/K_R = [1/4(4DH_1)^{1/2} + F/2]/[1/4(4 DH_1)^{1/2} - F/2]$. Narrow-sense heritability (h^2_n) in F_2 was estimated using the following equation: $h^2_n = [1/4D / (1/4D + 1/16H_1 - 1/8F + \hat{E})]$.

V. RESULTS AND DISCUSSION

5.1. Analysis of Variance

Combined analysis of variance of a lattice design for studied traits under each environment (high N and low N) across two seasons is presented in Table (1). Mean squares due to genotypes, parents, F_1 's and F_2 's under the two levels of nitrogen were highly significant for the two studied traits. Significant differences among parents of diallel crosses in all studied traits are pre-requisite for performing the diallel analysis for estimating the inheritance of studied grain traits under different N- application rates. Mean squares due to parents vs. F_1 's and F_1 's vs F_2 's were

highly significant for both traits under the two levels of nitrogen, indicating the presence of significant heterosis inbreeding effects for the two studied grain traits. Mean squares due to the interaction G x Y were highly significant for both studied traits under the two levels of nitrogen, except for GPC under low N, which were not significant. Mean squares due to the interaction P x Y under high level of nitrogen were significant or highly significant for GYPP and non significant for GPC. Mean squares due to the interactions F₁'s x Y and F₂'s x Y under high-N were significant or highly significant for both studied traits.

Table1. Partitioning genotypes degrees of freedom and their interaction with years into their components under high N and low conditions.

S.V.	d.f.	M.S.			
		High-N		Low-N	
		GPC	GYPP	GPC	GYPP
Years (Y)	1	2919.1**	15.9**	112.7	61.6**
Error Y	4	56.01	1.1	54.9	2.2
Genotypes (G)	35	1375.8**	60.0**	1298.8**	57.2**
Parents (P)	5	1100.34**	36.7**	1837.2**	106.0**
F ₁ 's (F ₁)	14	1029.03**	52.6**	1072.2**	53.2**
F ₂ 's (F ₂)	14	2191.74**	8.2**	1302.4**	46.5**
P vs F ₁	1	245.46**	553.6**	538.4**	172.7**
F ₁ vs F ₂	1	346.8**	100.2**	226.6**	94.1**
G x Y	35	164.1**	7.9**	28.6	22.7**
P x Y	5	10.57	4.6*	68.1**	3.1
F ₁ x Y	14	120.7**	5.4**	14.7	3.9
F ₂ x Y	14	366.61**	12.5**	54.2**	8.2**
P vs F ₁ x Y	1	153.53**	52.4**	39.5	39.3**
F ₁ vs F ₂ x Y	1	44.0**	98.8**	13.9	521.9**
Error	140	18.4	1.9	37.3	1.8

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

Mean squares due to the interactions F₂'s x Y were significant or highly significant for both studied traits under low N. Mean squares due to the interactions P's vs F₁'s x Y and F₁'s vs F₂'s x Y under the two levels of nitrogen were significant and highly significant for both studied traits, except GPC for F₁'s vs. F₂'s x Y.

VI. MEAN PERFORMANCE

6.1. Effects of low N on grain characters

A comparative summary of means of the two studied traits across all 36 genotypes (6 parents, 15 F₁'s and 15 F₂'s) subjected to two levels of nitrogen conditions and across two years is presented in Table (2). In general, low N caused a significant reduction in both studied traits, namely GYPP and GPC). Mean grain yield/plant (GYPP) was significantly decreased due to low-N by an average of 18.96, 21.17, and 15.40% for parents, F₁'s and F₂'s, respectively. Reduction in grain yield of wheat due to low soil nitrogen was reported by several investigators. A positive relationship between N application levels and the grain yield has already been shown in many studies (Austin *et al.*, 1980 and Desai and Bahatia, 1978). In general, high levels of nitrogen fertilizer result in a higher protein content in wheat grains (Ortiz-Monasterio *et al.*, 1997).

Table2. Means of studied grain traits under low-N (0 Kg N/fed) and high-N (75 Kg N/fed) and relative reduction compared to high-N combined across parents, F₁'s and F₂'s across two seasons.

Traits	Parameter	Parents		F ₁ crosses		F ₂ crosses	
		High-N	Low-N	High-N	Low-N	High-N	Low-N
GYPP(g)	Average	27.53	22.41	29.12	22.83	25.65	21.54
	Reduction%	---	18.96**	----	21.17**	---	15.40**
GPC(%)	Average	14.35	11.33	14.61	12.64	14.86	12.91
	Reduction%	-----	21.3**	-----	14.71**	-----	13.12**

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

Moreover, low nitrogen caused a significant reduction in grain protein content (GPC) by 21.3, 14.71 and 13.12% for parents, F₁'s and F₂'s, respectively. Reduction in grain protein content due to low soil-N is predicted due to the important role of N in protein synthesis. This conclusion was previously reported by previous investigators (e.g Fowler *et al.* 1990).

6.2. Effect of genotypes

Ranges of means of the two studied traits of 6 wheat parents and their 15 F₁ and 15 F₂ diallel crosses across studied N levels and across two seasons are presented in Table (3). In general, parents varied in both studied traits, especially in grain protein content (GPC), indicating their usefulness as parents of diallel crosses for studying inheritance of these traits. The parental line L26 showed the highest means for GPC and GYPP (16.45% and 29.16 g, respectively).

Table3. Means and ranges of studied traits of wheat parents and their diallel F₁ and F₂ crosses across two N levels and two seasons.

Genotypes	GPC %		GYPP(g)	
	Mean	Range	Mean	Range
Parents	12.84	9.96 – 16.45	24.97	21.83 – 29.16
F ₁ crosses	13.67	11.17 – 16.96	25.97	21.33 – 29.84
F ₂ crosses	13.90	9.41 – 16.72	23.60	19.47 - 27.93
LSD _{0.05(G)}	4.00		2.05	

On the contrary, the parent Gemmeiza 9 showed the lowest mean for GYPP (21.83g) and GPC (96%). In general, the first three parents L25, L26 and L27 show significantly higher means than the second three parents Gem7, Gem 9 and Gz168 for GYPP, and GPC traits. Such significant differences among wheat parents in this study are prerequisite for the validity of using them as parents of diallel crosses to study the inheritance of both traits. Several investigators reported genotypic variation in grain yield and grain protein content in wheat (Van Sanford and MacKown, 1986, Ortiz-Monasterio *et al.* 1997; Le Gouis *et al.* 2000; Austin *et al.* 1977; Foulkes *et al.*, 2006 and Barraclough *et al.* 2010) and in maize (Al-Naggar *et al.* 2010 a, b and 2011a,b).

The studied diallel crosses varied greatly in both studied traits either in F₁ or F₂ generation (Table 3). The cross Gem 7 x Gem 9 exhibited the lowest means in F₁ for GYPP and in F₂ for GPC. The cross L25 x Gem 9 exhibited the lowest GYPP in F₂. On the contrary, the highest means were exhibited by the cross L26 x L27 for GYPP and GPC in the F₁, L2 x Gz 168 for GYPP, in F₂ and L1 x Gz 168 for GPC in F₂. It is interesting to mention that the rank of crosses for GYPP and GPC differed from F₁ to F₂ generation.

In general, F₁ crosses showed higher means for GPC and GYPP than their parents (Table 3), indicating that heterozygotes exhibit better (more favorable) values for these two traits than homozygotes, which is logic and may be attributed to heterosis phenomenon.

On the contrary, F₂ crosses exhibited lower means than their corresponding F₁ crosses for GYPP, indicating the role of inbreeding depression in this trait, while for GPC trait, the F₂'s were higher than both F₁'s and parents, indicating appearance of transgressive segregants for grain protein content trait. Thus, selection in F₂ could improve grain protein content in wheat.

6.3. Genotype x nitrogen interaction

Means of each parent, F₁ cross and F₂ cross for studied traits under two nitrogen levels (0 and 75 kg N /Fed) across two seasons are presented in Table (4). In general means of GYPP and GPC 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 and GPC, 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.

Table4. Mean performance of all genotypes under high-and low- levels of nitrogen across two years for studied traits.

Genotype	GPC(%)			GYPP(g)		
	High N	Low N	Red%	High N	Low N	Red%
Parents						
L25	14.96	12.87	13.97**	26.48	25.39	4.1**
L26	17.27	15.62	9.55**	31.42	26.91	14.35**
L27	15.73	12.76	18.88**	29.86	26.28	11.99**
Gem7	13.53	9.46	30.08**	25.96	18.37	29.22**
Gem9	12.43	7.48	39.82**	25.76	17.89	30.53**
Giza168	12.21	9.79	19.82**	25.71	19.65	23.57**
F₁ crosses						
L25 X L26	15.07	12.65	16.06**	30.86	26.94	12.71**
L25 X L27	14.74	11.77	20.15**	25.78	26.23	-1.75
L25X Gem 7	15.18	12.54	17.39**	25.62	24.50	4.40**
L25 X Gem 9	15.51	13.64	12.06**	26.79	20.06	25.13**
L25 X Gz 168	16.94	14.74	12.99**	27.65	25.46	7.94**
L 26X L 27	17.05	16.83	1.29	32.16	27.52	14.41**
L26 X Gem 7	14.96	12.87	13.97**	29.49	22.68	23.11**
L 26 X Gem 9	13.97	14.41	-3.15	30.81	21.00	31.84**
L 26 X Gz 168	12.65	13.75	-8.70**	33.55	22.07	34.23**
L 27X Gem 7	11.66	10.67	8.49**	34.32	24.16	29.60**
L 27 X Gem 9	14.19	15.62	-10.08**	29.74	20.56	30.85**
L27 X Gz168	13.97	10.78	22.83**	30.59	23.74	22.40**
Gem 7 X Gem9	13.75	9.13	33.60**	24.88	17.78	28.56**
Gem 7 X Gz 168	12.21	11.88	2.70**	28.56	18.99	33.51**
Gem 9 X Gz 168	17.49	9.57	45.28**	26.09	20.73	20.55**
F₂ crosses						
L25 X L26	18.15	13.2	27.27**	25.96	24.97	3.81**
L25 X L27	13.2	13.97	-5.83*	23.94	26.09	-9.02**
L25X Gem 7	15.29	13.42	12.23**	23.33	23.88	-2.36
L25 X Gem 9	17.16	13.75	19.87**	22.97	15.97	30.49**
L25 X Gz 168	19.69	13.75	30.17**	27.08	21.75	19.71**
L 26X L 27	17.71	12.87	27.33**	28.97	20.25	30.09**
L26 X Gem 7	16.17	14.08	12.93**	23.95	23.51	1.84
L 26 X Gem 9	15.51	16.94	-9.22**	25.45	22.04	13.42**
L 26 X Gz 168	15.18	17.49	-15.22**	31.84	24.03	24.52**
L 27X Gem 7	15.84	13.64	13.89**	29.74	19.62	34.04**
L 27 X Gem 9	12.65	11.11	12.17**	24.07	20.07	16.61**
L27 X Gz168	11	10.45	5.00*	26.21	23.39	10.77**
Gem 7 X Gem9	9.13	9.68	-6.02*	25.41	19.18	24.50**
Gem 7 X Gz 168	12.43	9.9	20.35**	21.97	18.25	16.93**
Gem 9 X Gz 168	13.97	9.68	30.71**	23.88	20.16	15.57**
L.S.D. _{.05} (G)	4.41	5.47		2.1	2	
(N)		6.78			2.5	
(GN)		4.31			2.04	

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

The rank of crosses in F₁ and F₂ 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 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 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. The highest mean of GPC under low-N was shown in L26 x L27 (16.83%) and L27 x

Gem9 (15.62%) in F₁ and L26 x Gz168 (17.49%) followed by L26 x Gem9 (16.94%) in F₂ generation. It is observed that the cross L26 x L27 in the F₁ showed the highest GYPP and the highest GPC. This means that it is possible to improve both traits (GYPP and GPC) simultaneously. Several authors described the negative relationship between the percentage of grain protein and grain yield (Cox *et al.*, 1985a and Löffler and Busch, 1982). Implications to overcome the negative correlation between the percentage of grain protein and grain yield were reviewed by Feil (1997). Increased efficiency of N utilization is realized when the nitrogen concentration in the kernels increases and grain yield remains stable (Kramer, 1979). Genotypic variability was found for N accumulation and/or N remobilization. Therefore a concomitant increase in grain yield and grain protein seems feasible (Bänziger *et al.*, 1992).

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 GYPP under low-N, and high reduction due to low-N and therefore were considered sensitive (N-inefficient) to low-N stress. Changes in protein content with application of fertilizer N differ with cultivar (Clarke *et al.* 1989 and Fowler *et al.* 1990). Semidwarf wheat cultivars show a smaller increase in grain protein with small applications of N fertilizer than do cultivars of conventional height due to greater yield potential of semidwarf wheats (Campbell *et al.* 1971 and Clarke *et al.* 1989).

The rank of parents for GYPP and GPC was similar in the two N- environments, indicating less effect of interaction between parent and nitrogen level on these traits. The three tolerant parents showed the highest GYPP under high-N and therefore were considered responsive parents. Moreover, L26x L27 and L25 x L27 in F₁ and L26 x Gz 168 in F₂ generation had the highest GYPP under high-N and are therefore considered responsive crosses.

VII. COMBINING ABILITY VARIANCES

7.1. In F₁'s

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 (5). Mean squares due to GCA and SCA were highly significant, for the two studied traits, indicating that both additive and non-additive gene effects play an important role in the inheritance of both 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 both studied traits under the two levels of N.

Table5. 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 and low N conditions across two years.

S.V.	d.f.	M.S.			
		High-N		Low-N	
		GPC	GYPP	GPC	GYPP
Genotypes (G)	20	707.29**	49.29**	1325.14**	63.99**
GCA	5	1590.41**	116.77**	1844.74**	226.07**
SCA	15	412.92**	26.80**	1152.0**	9.97**
GCA xY	5	39.93*	6.70**	21.0	4.96**
SCA xY	15	63.88**	4.38*	7.50	4.97**
GCA/SCA		3.85	4.36	0.72	22.68
GCA xY /SCAxY		0.62	1.53	2.80	0.99
error	80	16.14	1.78	29.0	1.74

* 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), Riaz and Chaudry (2003a and b) and Al-Naggar *et al.* (2007b, 2014 and 2015) 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 and grain N yield than in those grown under high N nutrition.

Results in Table (5) indicate that mean squares due to SCA x year interaction were significant ($P \leq 0.01$) for both studied traits under the two levels of N, except GPC under low N, indicating that non-additive variance was affected by years. Mean squares due to the GCA x year interaction were significant ($P \leq 0.05$ or 0.01) for GYPP under low and high N and GPC under high N, indicating that additive variance for these cases differs from one year to another.

The mean squares due to GCA x year was higher than those due to SCA x year for both studied traits, except for GPC under high-N, suggesting that GCA (non-additive) variance is more affected by year than SCA (additive) variance in most studied cases.

7.2. In F₂'s

Analysis of variance of general (GCA) and specific (SCA) combining ability of F₂ crosses of wheat for combined data across two years under high and low levels of nitrogen are presented in Table (6). Results of F₂ crosses also show highly significant estimates of GCA and SCA mean squares under both high-N and low-N for both studied traits.

Table6. Mean squares due to general (GCA) and specific (SCA) combining ability and their interactions with years (Y) for studied traits in F₂'s under high and low N conditions across two years.

S.V.	M.S.				
	d.f.	High-N		Low-N	
		GPC	GYPP	GPC	GYPP
Genotypes (G)	20	1917.10**	45.54**	1516.3**	60.04**
GCA	5	5830.25**	79.92**	2450.8**	150.04**
SCA	15	612.73**	34.08**	1204.8**	17.59**
GCA xY	5	468.05**	7.53**	59.08	14.87**
SCA xY	15	162.17**	10.80**	32.8	39.84**
GCA/SCA		9.52	2.35	2.03	8.53
GCA xY /SCAxY		2.88	0.70	1.80	0.37
error	80	19.81	1.78	43.14	1.71

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

The ratio GCA/SCA mean squares was greater than unity for both studied traits of F₂ crosses under both high-N and low-N conditions. These observations are in partial conflict with data reported by Le Gouis *et al.* (2002) who 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. More recently, 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). On the other hand, results of Gorny *et al.* (2011) on wheat appear to be in accord with similar N-shortage- induced increases in the importance of non-additive effects for grain yield previously reported in maize (Di Fonzo *et al.*, 1982; Medici *et al.*, 2004; and Al-Naggar *et al.* 2010 a,b) and those for NUTE in barley (Gorny and Sodikiewicz 2001).

Results indicate that mean squares due to GCA x year and SCA x year interactions in F₂'s were significant or highly significant in the two levels of N, except for GPC under low-N, indicating that the additive and non-additive gene effects in most cases were affected by years. The mean squares due to GCA x year were higher in magnitude than those due to SCA x year for GPC of F₂ crosses, under both high and low N and, suggesting that GCA (additive variance) is more affected by year than SCA for GPC of F₂ crosses. The opposite was true for GYPP of F₂'s.

VIII. GCA EFFECTS

8.1. GCA Effects In F₁'s

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 7. In general, the best general combiners in F₁'s for GYPP and GPC attributes were L27 followed by L26 parents under both high-N and low-N, L25 under low-N and Gem.7 under high-N. On the contrary, the worst general combiners in F₁'s were Giza 168, Gem9 and Gem7 and for the two studied traits under both high-N and low-N environments. 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 two studied traits under both high and low-N environments.

Table7. Estimates of general combining ability effects (g_i) of studied traits in F_1 's under high and low N conditions across two seasons.

Parents	High-N		Low-N	
	GPC	GYPP	GPC	GYPP
L25	-0.10	-1.38*	-4.12**	1.87**
L26	5.87**	2.38*	5.56**	1.88**
L27	8.05**	1.45*	9.96**	1.97**
Gem 7	-3.72*	1.45*	-2.91*	-1.76*
Gem 9	-4.18**	-1.38*	-3.74**	-2.88**
Giza 168	-5.91**	-0.35	-4.74**	-1.08*
SE _{gi}	3.43	0.71	2.87	0.71
SE _{gi-gj}	2.14	1.11	4.91	1.09

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

8.2. GCA Effects Of Parents In F2 Crosses

Estimates of general combining ability (GCA) effects calculated from the analysis of F_2 diallel crosses under the two levels of N are presented in Table (8). Data in Table (8) indicates that under low-N and high-N, the best general combiners based on F_2 diallel analysis for both traits were L27 followed by L26 and then L25 for GYPP under low-N and Gem7 for GPC under high-N. The best combiners identified from both F_1 and F_2 diallel analyses under high-N and low-N are more or less similar in most cases under low-N conditions. L25, L26 and L27 are generally the best combiners for grain protein content and grain yield traits based on diallel analyses of both F_1 and F_2 crosses. These parents are expected to have more additive genes for the studied grain quantity and quality characters.

Table8. Estimates of general combining ability effects (\hat{g}_i) of all traits in F_2 's under high N conditions across two years

Parents	High-N		Low-N	
	GPC	GYPP	GPC	GYPP
L25	-4.21**	-0.88*	-4.91*	1.36*
L26	9.01**	1.96**	7.25**	2.01*
L27	13.04**	1.17**	10.44**	1.18*
Gem 7	6.13**	-0.87*	-1.27	-1.42*
Gem 9	-9.41**	-1.25*	-6.61**	-2.42
Giza 168	-14.55**	-0.11	-4.89*	-0.71*
SE _{gi}	2.37	0.71	3.50	0.70
SE _{gi-gj}	3.68	1.11	5.44	1.08

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

IX. SCA EFFECTS

9.1. In F_1 's

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 Table (9). The rank of F_1 crosses for SCA effects was changed from high-N to low-N conditions. The best cross for SCA effects of GPC was the F_1 cross L25 x L26, L27 x Gem7 and Gem7 x Gem9 under high-N and L25 x L26, L26 x Gz168 and Gem7 x Gem9 under low-N. For GYPP, the best combiner was L27 x Gem7 under high-N and L25 x Gz168 under low-N. These F_1 's include at least one parent of high GCA effects.

Table9. Estimates of specific combining ability effects (δ_{ij}) of F_1 's under high and low N conditions across two seasons.

Crosses	High-N		Low-N	
	GPC	GYPP	GPC	GYPP
L25 X L26	13.21**	1.20	18.43**	0.48
L25 X L27	0.64	-2.96*	-3.12	-0.33
L25X Gem 7	-2.26	-0.93	-10.74**	1.68
L25 X Gem 9	-9.21**	0.85	-21.52**	-1.65
L25 X Gz 168	-9.11**	0.71	-6.38	1.96*
L 26X L 27	-9.47**	-0.34	-19.29**	0.95
L26 X Gem 7	0.17	-0.82	-1.02	-0.15
L 26 X Gem 9	3.37	1.12	5.94	-0.71
L 26 X Gz 168	7.12*	2.86*	13.84**	-1.44
L 27X Gem 7	13.42**	4.94*	-3.68	1.24
L 27 X Gem 9	-0.17	0.97	6.69	-1.24
L27 X Gz168	-5.13	0.82	3.72	0.14
Gem 7 X Gem9	10.45**	-1.69	26.47**	-0.29
Gem 7 X Gz 168	7.87*	0.98	-1.81	-0.87
Gem 9 X Gz 168	5.61	-0.84	6.01	1.99
SE _{Sij}	5.91	1.96	7.91	1.94
SE _{Sij-Sik}	6.65	2.93	8.93	2.90
SE _{Sij-Skl}	8.81	2.71	11.82	2.68

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

9.2. In F₂'s

Specific combining ability (SCA) effects of the F₂ crosses under two levels of N are presented in Table (10). The best F₂ cross in SCA effects for GPC was L25 x L25, L27 x Gem7, L27 x Gem9, L27 x Gz168 and Gem7 x Gz168 under high-N and L25 x L26, L27 x Gem9 and L27 x Gz168 under low-N. For GYPP, the best F₂ cross was L27 x Gem9 and L27 x Gz168 under high-N and L25 x Gem7 under low-N.

Table10. Estimates of specific combining ability effects (δ_{ij}) of F_2 's under high and low N conditions across two years.

Crosses	High-N		Low-N	
	GPC	GYPP	GPC	GYPP
L25 X L26	9.49**	-1.31	16.62**	-0.19
L25 X L27	4.92	-2.53*	-3.73	1.76
L25X Gem 7	-12.7**	-1.1	-12.50**	2.15**
L25 X Gem 9	-4.56	-1.08	-18.77**	-4.77*
L25 X Gz 168	-1.05	1.90	-6.34	-0.70
L 26X L 27	-3.20	-0.40	-8.61	-4.73**
L26 X Gem 7	4.94	-3.32	-0.11	1.13
L 26 X Gem 9	-12.32**	-1.44	7.09	0.65
L 26 X Gz 168	6.22	3.80*	5.73	0.94
L 27X Gem 7	11.19**	3.26*	0.82	-1.93*
L 27 X Gem 9	13.27**	-2.04*	23.47**	-0.48
L27 X Gz168	8.38**	-1.03	25.36**	1.13
Gem 7 X Gem9	3.69	1.35	-0.59	1.23

Gem 7 X Gz 168	12.9**	-3.23*	-6.50	-1.41
Gem 9 X Gz 168	-3.70	-0.94	-3.96	1.50
SE_{Sij}	6.54	1.96	9.66	1.92
SE_{Sij}-sik	9.76	2.93	14.40	2.87
SE_{Sij}-skl	9.04	2.71	13.34	2.66

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

These F₂ crosses and especially those showing high SCA effects and including one parent of high GCA effects are expected to release more transgressive segregants if additive gene effects existed in the high general combiner parent and epistasis acts in the cross in the same direction for decreasing the undesirable characters and increasing the desirable traits. Results of Gorny *et al.* (2011) on wheat F₂ crosses appear to be in accord with similar N-Shortage – induced increases in the importance of non – additive effects for grain yield previously reported in maize (Di Fonzo *et al.*, 1982, Medici *et al.*, 2004, Al-Naggar *et al.* 2015) and in grain sorghum (Al-Naggar *et al.*,2006 and 2007a).

X. GENE ACTION, HERITABILITY AND EXPECTED SELECTION GAIN

10.1. In F₁'s

Estimates of genetic components and ratios for studied traits in F₁'s under high-N and low-N environments across two years are presented in Table (11). The dominance genetic component of variation (H₁) was highly significant for both studied traits under both high and low-N environments, indicating that the dominance gene effects in F₁'s of this experiment are important for the inheritance of GPC and GYPP traits under low-N and high-N. The additive component of variation (D) was also significant (P≤ 0.01 or 0.05) for both traits in F₁'s under both high- and low-N, indicating that selection may be efficient for improving most studied traits.

Table11. Estimates of genetic parameters and ratios for studied traits under high and low-N in F₁'s across two seasons.

Parameter	High-N		Low-N	
	GPC	GYPP	GPC	GYPP
E	6.60**	0.59	9.67**	0.58
D	3.31*	5.52**	2.63*	17.12**
H₁	24.28**	15.18**	30.23**	4.63**
H₂	3.61**	13.52**	1.89*	3.98*8
F	0.97**	-3.99**	-22.59**	-1.43**
h²	-4.24**	6.68**	-9.72**	0.10*
(H₁/D)^{1/2}	2.71	1.66	3.39	0.52
H₂/4H₁	0.20	0.22	0.19	0.21
K_D/K_R	0.40	0.64	0.30	0.85
h²/H₂	0.22	0.49	0.08	0.02
h²_b%	80.55	91.27	77.26	91.00
h²_n%	9.66	20.41	6.18	67.14
GA%	10.12	5.11	8.39	19.70

However, in F₁'s the magnitude of dominance (H₁) was much greater than that of additive (D) component for GPC under both high N and low N and GYPP under high-N, while the opposite was true for GYPP under low-N, where the additive was greater than dominance variance. This indicates that the dominance gene effects are more important than additive in F₁'s and plays the major role in the inheritance of most studied cases, the exception was GYPP under low-N, where additive plays the major role in their inheritance. The grain yield trait of F₁'s under low-N showed more importance for additive than dominance variance. Selection for high values of GYPP in the segregating generations of the studied diallel crosses under low-N would be efficient for obtaining improved high yielding wheat genotypes.

The overall dominance effects of heterozygous loci in Hayman's model (h^2) controlling both studied traits of F_1 's under both high- and low-N environments, were significant ($P < 0.01$ or 0.05); that could be due to the presence of a considerable amount of dominant genes for GPC and GYPP in the parental genotypes.

The average degree of dominance (H_1/D)^{1/2} in F_1 's was in the range of over-dominance (greater than unity) for both studied traits under the two levels of nitrogen, except for GYPP trait under low-N, which showed partial dominance.

Lower ratio of ($H_2/4H_1$) than 0.25 (Table 11) indicated symmetrical distribution of positive dominant genes in parents for both studied traits of F_1 's under both high- and low-N environments.

The ratio (K_D/K_R) in F_1 's was less than unity for both traits under the two levels of nitrogen, indicating minority of dominant alleles and the excess of recessive alleles ($p < q$).

Number of genes or groups of genes controlling the inheritance of a given trait (h^2/H_2) was one group of genes for both studied traits (GPC and GYPP) of F_1 's under both high-N and low-N environments (Table 11).

Broad-sense heritability (h^2_b) in F_1 's for both studied traits in this experiment was of high magnitude and ranged from 77.26% (GPC under low-N) to 91.27% (GYPP under high-N) (Table 11), indicating that environment had a small effect on the phenotype of F_1 's for both studied traits. Grain protein content (GPC) trait showed smaller h^2_b value under both high and low N environments than GYPP, indicating a larger effect of environment on this trait (GPC).

Narrow-sense heritability (h^2_n) in F_1 's (Table 11) was generally of low magnitude and ranged from 6.18% (GPC under low-N) to 20.41% (GYPP under high-N). The exception was GYPP under low-N, where h^2_n was of high magnitude (67.14%). The big difference between broad- and narrow- sense heritability estimated from F_1 's in this experiment could be attributed to the high estimates of dominance as compared to additive component, except GYPP under low-N. It is observed that narrow-sense heritability (h^2_n) in F_1 's of the present study was generally higher in magnitude under low-N than under high-N for both studied traits. This increase in h^2_n under low-N compared to high-N was more pronounced in GYPP.

Our results are in agreement with some researchers, e.g. Blum (1988 a and b), Hefny (2007), Al-Nagggar *et al.* (2008, 2009, 2011a,b, 2014 and 2015), who support the idea that heritability is higher under stressed than non-stressed environment. On the contrary, other investigators reported that heritability is higher under good (non-stressed) environment (Rosielle and Hamblin, 1981, Atlin and Frey, 1990, Banziger and Laffite, 1997, Banziger *et al.*, 1997 and Worku, 2005).

Expected genetic advance (GA) from selection (based on 1% selection intensity) across two years ranged from 5.11% for GYPP under high-N to 19.70% for GYPP under low-N. In general, the values of GA were higher under low-N than under high-N for GYPP, but were higher under high-N than low-N for GPC. These results indicated that to improve grain yield in the present germplasm, it is better to practice selection under low-N conditions to obtain higher values of selection gain.

10.2. In F_2 's

Genetic parameters and ratios for studied traits in F_2 's under high- and low-N environments across two years are presented in Table (12). Additive genetic variance (D) was highly significant for both studied traits under both high and low-N environments, indicating that the additive gene effects in F_2 's of this experiment are important for the inheritance of both studied traits under low-N and high-N, and that selection may be practiced in this segregating generation of the studied cross populations of wheat for improving GPC and GYPP traits. It is observed that the magnitude of additive variance was higher under low-N than under high-N conditions in both studied traits.

The dominance genetic component of variation (H_1) in F_2 's was highly significant for both studied traits under both high and low-N environments, indicating that the dominance gene effects in F_2 's of this experiment are important for the inheritance of GPC and GYPP 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 GPC trait.

The magnitude of dominance (H_1) in F_2 's was much greater than that of additive (D) variance for GPC under both high N and low N and GYPP under high-N, while for GYPP under low-N, the additive and dominance components were approximately equal. This indicates that the dominance gene effects are generally more important than additive in F_2 's and play the major role in the inheritance of GPC and GYPP under the two levels of nitrogen.

Table 12. Estimates of genetic parameters and ratios for studied traits under high and low-N in F₂'s across two seasons.

Parameter	High-N		Low-N	
	GPC	GYPP	GPC	GYPP
E	6.60**	0.59	14.38**	0.57
D	3.31*	5.52**	7.35**	17.13**
H₁	17.39**	19.11**	45.61**	18.25**
H₂	-13.46**	18.35*	-33.84**	16.65**
F	-13.33**	-0.57	-17.94**	7.72*
h²	1.39*	9.44**	6.76**	1.74**
(H₁/D)^{1/2}	0.57	0.47	0.00	0.26
H₂/4H₁	0.01	0.24	0.19	0.23
K_D/K_R	0.01	0.95	0.34	1.56
h²/H₂	0.10	0.51	0.001	0.10
h²_b%	75.82	97.66	78.65	98.44
h²_n%	12.12	21.88	10.86	46.90
GA%	17.48	7.70	18.11	23.14

The preponderance of dominance (non-additive) effects in F₂ generation of this study suggest that it is preferable to postpone the selection for high grain protein and grain yield/plant, either under high or low N environments, to later segregating generations, until completing the homozygosity process and eliminating masking non-additive influences in order to take advantage of the additive variance to improve these traits.

In this respect, Le Gouis *et al.* (2002) reported that in N-limited, diallel F₁ 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 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). On the other hand, results of Gorny *et al.* (2011) on wheat appear to be in accord with similar N-shortage- induced increases in the importance of non-additive effects for grain yield previously reported in maize (Al-Naggar *et al.*, 2015) and in barley (Gorny and Sodikiewicz 2001). Gorny *et al.* (2011) reported that under high N-fertilization, the efficiency components were incanted in a manner favorable for wheat selection (preponderance of additive effects) however the enhanced contribution of non-additive gene effects and increased dominance under N-limited conditions could impede wheat selection to improve the N efficiency and adaptation to less luxurious fertilization regimes. They concluded that selection methods that eliminate masking non-additive 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.* (2011).

The overall dominance effects of heterozygous loci in Hayman's model (h²) controlling all studied traits of F₂'s under both high- and low-N environments were significant (P < 0.01 or 0.05), 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 (H₁/D)^{1/2} in F₂'s was in the range of partial dominance (smaller than unity) for GYPP under both high and low N and GPC under high N, while GPC under low N showed no dominance, *i.e.* additive (Table 12).

Lower ratio (H₂/4H₁) than 0.25 (Table 13) indicated symmetrical distribution of positive dominant genes in parents for both studied traits of F₂'s under both high- and low-N environments.

The ratio (K_D/K_R) in F₂'s was greater than unity, indicating excess of dominant alleles and minority of recessive alleles (p > q) for GYPP under low-N. However, for GPC under low and high N and GYPP under high N in F₂'s, the ratio (K_D/K_R) was less than unity, indicating minority of dominant alleles and the excess of recessive alleles (p < q).

Number of genes or groups of genes controlling the inheritance of a given trait (h²/H) was one group of genes for both studied traits of F₂'s under both high-N and low-N environments (Table 12).

Broad-sense heritability (h^2_b) in F_2 's for both studied traits under both environments in this experiment was of high magnitude and ranged from 75.82% for GPC under high N to 98.44% for GYPP under low N (Table 12), indicating that environment had a small effect on the phenotype of F_2 's for both studied traits.

Narrow-sense heritability (h^2_n) in F_2 's (Table 12) was generally of low to medium magnitude and ranged from 10.86% for GPC under low N to 46.90% for GYPP under low-N. It is observed that GPC trait recorded lower h^2_n than GYPP under both high- and low- N and that h^2_n for GYPP was higher under low-N than under high-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 dominance 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 GYPP trait, while the opposite was true for GPC. In this aspect, Blum (1988 a and b), Hefny (2007) , Al-Naggar *et al.* (2008, 2009, 2014 and 2015), supported 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 (Rosielle and Hamblin, 1981, Atlin and Frey, 1990, Banziger and Laffite, 1997, Banziger *et al.*, 1997 and Worku, 2005).

Expected genetic advance (GA) from selection in F_2 's (based on 1% selection intensity) across two years ranged from 7.70% for GYPP under high-N to 23.14% under low-N. In general, the values of GA were higher under low-N than under high-N. It is therefore expected that to improve grain yield and grain protein content in the present germplasm, it is better to practice selection in F_2 's for both traits under low-N conditions to obtain higher values of selection gain.

XI. CONCLUSIONS

This investigation concluded that under low-N, there were great differences among genotypes in grain protein content (GPC) and grain yield/plant (GYPP) that permit for successful selection for high values of these traits. The parent L26, the F_1 (L26 x L27) and the F_2 (L26 x Gz168) showed the highest means of both GPC and GYPP under low-N, indicating that it is possible to improve both traits simultaneously under limited N environment and these genotypes could be useful in future breeding programs. In both F_1 's and F_2 's, the magnitude of dominance (H_1) was much greater than that of additive (D) component for GPC under both high N and low N and GYPP under high-N, while the opposite was true for GYPP in F_1 's under low-N, where the additive was greater than dominance variance and GYPP in F_2 's under low-N, where the additive and dominance components were approximately equal. The results of this study concluded that selection in early segregating generations would be effective in improving grain yield/plant under low-N, while for grain protein content, selection would be more effective if it is postponed to the later segregating generations, when additive variance is released due to complete homozygosity by more selfing generations.

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