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Role of additive and non-additive gene action effects inheritable economic traits of some wheat genotypes grown under various nitrogen levels

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دور الفعل الجينى المضيف والغير مضيف فى توريث الصفات الاقتصادية في بعض التراكيب الوراثية للقمح المنزرعة تحت مستويات مختلفة من النيتروجين

ABSTRACT

Improving grain yield and quality traits under low nitrogen (N) supply is a desirable goal for wheat breeders. Thus, genetic parameters in wheat crosses and use them in breeding programs under contrasting N environments were estimated during the 2020/21, 2021/22, and 2022/23 growing seasons at the Experimental Farm of the Faculty of Agriculture, Fayoum University. A total of 36 wheat genotypes consisting of six parents, fifteen F_1, and fifteen F_2 progeny generations were grown in two adjacent experiments, (*i.e.*, low level (50 kg N/feddan) represents the 1st environment; E_1 and recommended level (75 kg N/feddan) represent the 2nd environment; E_2. Each experiment was laid out in a randomized complete block design with three replications. Information on combining ability effects were estimated for physiological and grain yield and its components. The genetic analysis was performed using Griffing Method 2 and Model 1. The results revealed that mean squares due to N levels, genotypes, and genotypes × N interactions were significant for almost all studied traits. This indicates that variability that existed among these genotypes seems to provide a chance for the appearance of good new combinations that can be isolated in the following generations. The mean squares of general (GCA) and specific (SCA) combining ability were significant for almost all studied traits, indicating that additive and non-additive gene action are important to inheritance for these traits. The crosses Sakha 94 × Sakha 95, Sakha 94 × Giza171, Sakha 94 × Sids 14, Sakha 94 × Misr 1, Sakha 95 × Misr 1, Sakha 95 × Misr 3, Giza 171 × Misr 1, Sids 14 × Misr 1 and Misr 1 × Misr 3 had favorable SCA effects and had high mean performance for grain yield/plant and some of the other traits. The best general combiner's parents were Sakha 94, Giza 171, Sids 14, Misr 1, and Misr 3, who possessed high GCA effects for grain yield/plant and some of the other studied traits. It could be concluded that the use of a low nitrogen fertilizer level (50 Kg N/feddan); can minimize the chemical nitrogen and proved to be the best way to save about 30% of the chemical and avoid undesirable effects, then reduce the cost of production and pollution that could be accrued by the excessive use of chemical fertilizer.

Keywords: Wheat, Combining ability, Low nitrogen, Additive and non-additive

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1. INTRODUCTION

Bread wheat (*Triticum aestivum* L.) is one of the three important strategic cereal crops worldwide, together with maize and rice. Wheat is widely grown all over the world and its cultivated area is 216 million hectares, yielding about 766 million tons **(FAOSTAT, 2021)**. The total cultivated area of wheat in Egypt reached about 3.17 million feddan and produced 8.5 million metric tons with an average of 17.9 ardab/feddan **(Economic Affairs, 2020)**.

The concepts of general (GCA) and specific (SCA) combining ability defined by **Sprague and Tatum (1942)** are important genetic bases for crop improvement. Combining ability estimates is essential in wheat improvement not only in parents and crosses selection, but also in illustrating the relation between additive and non-additive portions of the genetic effects in the available germplasm. A half-diallel mating design developed by **Griffing (1956)** provides information on the GCA and SCA of parents and their crosses in applicable breeding programs. The design was widely used in wheat by many researchers (**Bayoumi, 2004; Abro *et al*., 2016; Verma *et al*., 2016; Motawea, 2017a; Motawea, 2017b; Askander *et al*., 2021; Mahmood and Al Hamdani, 2023)**.

Each genotype's performance behavior is influenced by the genotype and the production environment. There are relationships between the genotypic differences in the crop yield in the absence of stress that are greatly unrelated to differences in the presence of severe stress. This indicates that the differences in physiological mechanisms are tightly associated with production ability in normal conditions and high yield in abnormal conditions. Variations in quantitative traits under the control of polygenes and the contribution of the genes can differ under environmental conditions. Low-N stress is among the abiotic stresses, causing wheat yield reductions.

Although improving grain yield and its contribution, and quality under low N have been desirable objectives for wheat breeders. The available information regarding the relative contribution of GCA and SCA effects for different grain yield-related attributes under N-deficiency is limited. Further, the estimation of combining ability and genetic variance components is vital in the crop breeding program, being the right parent is the secret to success. One of the most important criteria in wheat breeding programs for the classification of crosses on a higher yield basis is knowing the parental genetic structure and information regarding their combining ability (**Mahmood and Al Hamdani, 2023; Al-Naggar *et al.*, 2015a, Al-Naggar *et al.*, 2015b; Al-Naggar *et al.*, 2015c; El-Seidy *et al.*, 2017; Kizilgeci, 2020; Abdel-Moneam *et al.*, 2021)**. It is widely known that wheat has a higher requirement for nutrients, particularly N. Thus, it is now more important than ever to develop wheat genotypes with enhanced adaptation to less ideal but more optimal N fertilization regimes. Such breeding strategies in Egypt are also justified by problems with N, which is a major constraint limiting wheat grain production.

The objectives of this current study were to estimate the relative importance of GCA and SCA in a set of six wheat cultivars and their crosses under two contrasting N environments.

2. MATERIALS AND METHODS

At the Experimental Farm of the Faculty of Agriculture, Fayoum. University, Fayoum, Egypt, during the three consecutive growing seasons (2020/21, 2021/22, and 2022/23), the present study was carried out to estimate the genetical parameters in wheat crosses under two contrasting N environments.

Plants grown from self-seeds of six different wheat genotypes, as shown in Table 1 were crossed in a half diallel mating design excluding reciprocal in the 2020/21 season. Artificial self-pollination was conducted for the resultant 15 F_1's to produce F_2's in the 2021/22 season. In the same season, crosses were carried out again to produce new F_1 seeds in the next season. In the following season of 2022/23, a total of 36 entries consisting of six parents, fifteen F_1 and fifteen F_2 progeny generations were grown in two separate and adjacent experiments on the 17th of November. The two different N fertilization levels [i.e., low level (50 kg N/feddan) represent the 1st environment; E_1 and recommended level (75 kg N/feddan) represent the 2nd environment; E_2]. The N fertilizer was added in the form of urea (46% N). The amount of each dose was divided into two applications; the first (1/3) was immediately applied before the first irrigation, while the second (2/3) was applied before the second irrigation. Pure bread wheat grains of six wheat varieties were obtained from the Agriculture Research Center.

Table 1. Pedigree and year release of the studied genotypes

Genotype	Cross/Pedigree and selection history	Year of release
Sakha 94	OPATA/RAYON//KAUZ CMBW90Y3180-0TOPM-3Y-010M-010M-010Y-10M-015Y-0Y-0AP-0S	2004
Sakha 95	PASTOR//SITE/MO/3/CHEN/AEGLLOPS SQUARROSA (TAUS)//BCN/4/WELL1 CMA01Y00158-040POY-040M-030ZIM-040SY26M-0Y-0B-0ET	2017
Giza 171	ROLF07*2/KIRITATI CGSS05B00123T-099TOPY-099M-099NJ-6WGY-0B-0EGY	2015
Sides 14	Bow "S"/Vee" S"/Bow" S"/TSI/Bani Sewef 1 SD293-1SD-2SD-4SD-0SD	2017
Misr 1	OASIS/SKAUZ//4*BCN/3/2*PASTOR CMSS00Y01881T-050M-030Y-030M-030WGY-33M-0Y-0S	2011
Misr 3	ATTILA*2/ABW65*2/KACHU CMSSO6Y00258 2T-099TOPM-099Y-099ZTM-099Y-099M-10WGY-0B-0EGY	2019

Each experiment was laid out in a randomized complete block design with three replications. Each replicate consisted of 36 rows, 2 m long and 30 cm apart with 15 cm between plants within row. All the other agronomic practices were performed based on the Agriculture Ministry recommendations for wheat production. Five individual random guarded plants were labelled to collect data.

Data of ten different traits were recorded and included the physiological traits, *i.e*., flag leaf area (FLA), chlorophyll *a* (CHLA), chlorophyll *b* (CHLB), carotenoids (CAROT), and yield and components traits; plant height (PH), number of spikes/plant (SPP), number of grains/spike (GPS), 1000-grain weight (TGW), grain yield/plant (GYPP) and harvest index (HI).

Statistical analysis

Estimates of both GCA and SCA were computed according to **Griffing (1956)** designated as method 2 (parents and one set of F_1's) are included without reciprocals i.e. [P (P+1)]/2 combinations, model 1 (fixed model). Forms of analysis for individual environments as given by **Griffing (1956)** and **Singh** and

Chaudhary (1979). The combined analysis was calculated across the two different environments to test the interactions of the different genetic components with the two environments as given by **Singh (1973)**.

3. RESULTS AND DISCUSSION

3.1. Variance analysis

3.1.1 Physiological traits

Variance analysis of the physiological traits; flag leaf area, chlorophyll *a*, *b*, and carotenoids are presented in Table 2. Results exhibited that mean squares due to wheat genotypes (G) and N levels (environments; E) were highly significant for all the studied traits. This suggests that the genotypes used in this investigation were significantly affected. Further, the genotypes × N levels (G × E) mean squares exhibited significant results for all parameters under study, indicating that parental and crosses of wheat in this study behaved differently at N levels (E). Moreover, results showed high and significant variation related to GCA in individual environments and combined data from 1st and 2nd generations for physiological traits. Also, significant variations due to SCA for the same traits were detected. The GCA/SCA ratios can be utilized as a measure to reveal the nature of the genetic variance involved *i.e.* additive versus non–additive effects.

When the variance associated with GCA is larger than the variance of SCA, a higher ratio indicates that additive genes comprise most of the genetic variance. The ratio of GCA/SCA was greater than unity in individual environments and the combined data of F_1 and F_2 generations were detected for flag leaf area and chlorophyll *b*. the obtained values were 2.00, 3.56, 1.15, and 2.71 in the combined data for F_1 and F_2, respectively. These results might be explained by the two prior characteristics' prevalence of additive gene effects.

Moreover, a low GCA/SCA ratio, which is less than unity was detected for chlorophyll *a* and carotenoid traits. Similar results were previously obtained by **Motawea (2017b), Abdallah *et al.* (2019), Din *et al.* (2020)**, and **Kumar *et al.* (2021)**.

3.1.2 Yield and yield components traits

The analysis of variance exerted significant and/or highly significant variation due to environments (E), parents (P), and genotypes (G) *viz* parents and their combinations and genotypes × environments (G × E) for most yield and its components traits. The substantial genetic variation suggests that the results are suitable for additional examination *via* the mating process, as recommended by **Griffing (1956)**. Further, results indicate the presence of adequate genetic variability in the genetic material. However, the interaction between N levels and genotypes (G × E) is highly significant for the same traits, indicating that the performance and the ranks of different wheat genotypes are moderately or highly affected by the N levels for investigated traits (Table 3). Other studies revealed significant interaction values between wheat genotypes and N stresses for one or more of these studies' traits as reported by **Emam *et al.* (2021)**.

Table 2. Analysis of variance of genotypes, general combining ability (GCA), specific combining ability (SCA) and GCA/SCA ratio for physiological traits (combined data)

Source of variance	Flag leaf area (cm^2)		Chlorophyll *a* (mg/g FW)		Chlorophyll *b* (mg/g FW)		Carotenoids (mg/g FW)	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Environ (E)	2478.87**	1064.10**	0.0077*	0.0092**	0.0005	0.0293	0.00023	0.01125**
Parents (P)	177.56**	177.56**	0.0045	0.0045*	0.0071**	0.0071**	0.00089	0.00117**
P × E	28.76**	28.76**	0.0145**	0.0145**	0.0012	0.0012	0.00042	0.00038**
Genotypes (G)	201.51**	134.09**	0.0120**	0.0026*	0.0026	0.0028**	0.00055	0.00091**
G × E	387.68**	146.24**	0.0063	0.0055**	0.0012	0.0008	0.00041	0.00034
GCA	76.76**	96.98**	0.0006**	0.0008	0.0010	0.0018	0.00012	0.00013*
SCA	38.41**	27.27**	0.0051	0.0009	0.0008	0.0006	0.00021*	0.00036**
GCA × E	34.65**	27.17**	0.003	0.0027**	0.0006	0.0002	0.00030	0.00011**
SCA × E	160.75**	111.50**	0.0017**	0.0015*	0.0003	0.0003	0.00008	0.00011**
Error	1.97	2.36	0.0021	0.0018	0.0010	0.0006	0.00013	0.00008
GCA/SCA	2.00	3.56	0.117	0.888	1.146	2.708	0.574	0.357

* and ** Significance at 5% and 1% levels, respectively.Fresh weight (FW)

Table 3. Analysis of variance of genotypes, general combining ability (GCA), specific combining ability (SCA) and GCA/SCA ratio for yield and yield components traits (combined data)

Source of variance	Plant height (cm)		Number of spikes/plant		Number of grains/spike		1000-grain weight (g)		Grain yield/plant (g)		Harvest index (%)	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Environ (E)	1369.30**	2584.00**	54.29**	108.69**	2715.92**	5934.52**	954.25**	79.37**	2013.25**	3758.33**	21.68**	357.27**
Parents (P)	142.21**	142.21**	2.79**	2.79**	209.48**	209.48**	71.14**	71.14**	87.31**	87.31**	35.11**	35.11**
P × E	34.73**	34.73**	1.11**	1.11**	49.27**	49.27**	44.18**	44.18**	15.94**	15.94**	284.51**	284.51**
Genotype	112.55**	47.12**	4.08**	22.41**	330.36**	154.37**	179.10**	43.70**	132.42**	103.34**	283.21**	242.15**
G × E	31.61**	31.85**	1.50	11.76	146.68**	127.45**	99.49**	46.35**	60.10**	86.77**	258.21**	93.62**
GCA	34.68**	15.66**	0.30**	3.64**	136.33**	40.77**	15.33**	17.05**	30.51**	22.35**	105.87**	18.88**
SCA	38.46**	15.72**	1.72**	8.75**	101.38**	55.02**	74.49**	13.74**	48.68**	38.48**	90.58**	101.33**
GCA × E	8.13**	13.57**	0.18	3.73**	87.23**	21.22**	8.07**	16.62**	27.39**	9.85**	74.76**	42.63**
SCA × E	11.34**	9.63**	0.61	3.98**	36.11**	49.57**	41.53**	15.06**	17.58**	35.28**	89.84**	27.40**
Error	2.96	3.53	0.03	0.14	1.17	3.27	4.53	7.79	0.63	1.15	4.28	15.03
GCA/SCA	0.90	1.00	0.17	0.42	1.34	0.74	0.21	1.24	0.63	0.58	1.17	0.19

* and ** Significance at 5% and 1% levels, respectively.

3.2. Combining ability

3.2.1. Physiological traits

To estimate GCA effects for parental genotypes for physiological traits; (flag leaf area, chlorophyll *a*, *b*, and carotenoids) in the two environments, their combined data were determined, and the results are illustrated in Table 4. The results indicated that the two wheat varieties Giza 171 (P_3) and Sids 14 (P_4) exhibited highly significant GCA effects for the flag leaf area trait, while the two varieties Misr 1 (P_5) and Misr 3 (P_6) had highly significant or significant GCA effects, meaning that these genotypes could be useful combiners in breeding programs for the improvement of the flag leaf area trait. While the reminder varieties exhibited a negative GCA effect for most studied cases for the same trait. These results agreed with those obtained by **Bayoumi (2004), Ali (2019)** and **Mahmood and Al Hamdani (2023)**.

With respect to chlorophy11 a trait, the wheat varieties; Sids 14 (P_4) and Misr 3 (P_6) showed significant GCA effects E_1 F_1 and E_2 F_2, suggesting that these could be considered useful combiners in breeding programs of wheat improvement for chlorophy11 a trait. On the other hand, the rest of the varieties showed undesirable and/or insignificant GCA effects in individual environments and their combined effects in the two generations for the previous trait, suggesting that these varieties could be considered poor combiners for this trait under study. This conclusion was drawn by **Bayoumi (2004)** and **Singh *et al.* (2018)**.

Concerning the chlorophy11 b trait, the variety Misr 3 (P_6) showed a highly significant GCA positive effect at individual environments and their combined of two F_1 and F_2, indicating that the previous variety was found to be an effective combiner for this trait. These results were noted by **Bayoumi (2004), Abdallah *et al*. (2019),** and **Ali (2019).** The other genotypes of parental wheat showed a negative GCA effect for the same trait and were considered poor combiners.

Regarding the carotenoids trait, the wheat variety Misr 3 (P_6) demonstrated significant positive and effective GCA effects. While the reminder varieties showed negative GCA effects, consequently, they could be considered good combiners for this trait under study. These results were reported by **Abro *et al*. (2016)** and **Mahmood and Al Hamdani (2023)**.

SCA for physiological characteristics was calculated for 15 parental combinations, *via* flag leaf area, chlorophy11 a, chlorophy11 b, and carotenoids and the recorded values are given in Table 5. Out of 15 crosses combinations, two crosses $P_1 \times P_5$ and $P_2 \times P_3$ obtained positive SCA effects and exhibited the highest values. Concurrently, the crosses, $P_1 \times P_6$, $P_2 \times P_4$, $P_2 \times P_5$, $P_3 \times P_4$ and $P_5 \times P_6$ exhibited significant positive SCA effects in most cases studied. The previous hybrids that showed significant positive SCA originated from good × good, good × low, and low × low and can be considered promising hybrids for this trait. These results were obtained by **Bayoumi (2004), Ali (2019)** and **Mahmood** and **Al Hamdani (2023)**.

Concerning the chlorophyll *a* trait, out of 15 hybrids combinations, seven hybrid combinations ($P_1 \times P_2$, $P_1 \times P_4$, $P_1 \times P_5$, $P_1 \times P_6$, $P_2 \times P_3$, $P_3 \times P_4$ and $P_3 \times P_6$ showed either significant or significant positive specific combining ability. While the remainder of the hybrid's combinations exhibited either negative or insignificant SCA effects for the previous trait. These results obtained by **Bayoumi (2004)** and **Kajla *et al*. (2022)**.

For the chlorophy11 b trait, the results revealed that highly significant and positively specific combining abilities were obtained in some hybrids at the combined data analysis. Four hybrid combinations, *i.e.* $P_1 \times P_2$, $P_1 \times P_3$, $P_1 \times P_4$, and $P_2 \times P_3$, showed highly significant and positive SCA effects for this trait. It is worth mentioning that the excellent combinations were obtained from crossing between good by good, good by low or low × low combiners. This conclusion was also drawn by **Bayoumi (2004)** and **Abdallah *et al*. (2019)**.

Regarding the carotenoids, two out of fifteen hybrid combinations $P_1 \times P_2$ and $P_2 \times P_3$ showed significant positive SCA effects. It is worth mentioning that, the negative significance of SCA or insignificant was observed by many hybrid combinations across the individual environments and combined analysis. These results are like those obtained by **Bayoumi (2004)**.

3.2.2. Yield and yield components traits

Estimates of GCA effects for six wheat varieties in yield and its component traits are shown in Table 6. For the plant height trait, the data indicated that these varieties Sakha (94) P_1 and Sids 14 (P_4) exhibited highly significant or significant GCA effects for the same trait, as well as the two wheat varieties; Misr 1 (P_5) and Misr 3 (P_6) recorded positive significant GCA effect for this trait, demonstrating that these varieties may be useful combiners in breeding programs since GCA effects are attributed to additive and additive × additive gene effects.

Regarding the number of spikes/plant trait, data revealed that four out of six parental genotypes; Sakha 94 (P_1), Giza 171 (P_3), Sids 14 (P_4) and Misr 1 (P_5) exhibited positive and significant general combining ability effects, while the reminder varieties exhibited undesirable and/or insignificant GCA effects for the previous trait, suggesting that these varieties could be considered poor combiners for this trait. These findings are in harmony with those obtained by **Bayoumi (2004), Ali (2019), Akram *et al*. (2011)**, and **Kajla *et al*. (2022)**.

Regarding the grains number/spike trait, the results of general combining ability effects two varieties, Giza 171 (P_3) and Misr 3 (P_6) were determined to have a positive effect on the effect of GCA. These varieties are thought to have the potential to be used as a parent in recombination studies to increase this trait, indicating that this trait was under additive gene effect. **Kajla *et al*. (2022)** reported that the grains number/plant was under the effect of the additive gene action. On the other hand, the reminder genotypes exerted insignificant GCA effects for the same trait.

For the 1000-grain weight trait, the parental genotypes Giza 171 (P3) and Sids 14 (P_4) illustrated highly significant and significant GCA effects. This would indicate that the above parental genotypes are good combiners for a heavier 1000-grain weight. Moreover, the varieties *i.e.* Sakha 94 (P_1), Misr 1 (P_5), and Misr 3 (P_6) showed desirable GCA, suggesting that these genotypes could be considered good combiners for this trait.

Combining ability for grain yield/plant refers to a parent's ability to generate progenies when crossed with another parent. Information on combining ability provides hints about the nature of gene action in breeding programs, for parents of Misr 3 (P_6) expressed highly significant (gi) values for grain yield/ plant. Further, varieties of Sakha 94 (P_1) and Giza 171 (P_3) show desirable and significant GCA, so these parents may be used in the breeding program for improvement of this trait, generally the parental variety Misr 3 (P_6) seemed to be a good combiner for grain yield/plant. These results were also obtained by **Al-Mafarji and AL-Jubouri (2023)**.

Table 4. Estimates of general combining ability effects for physiological traits of six parental genotypes (combined data)

Parent	Flag leaf area (cm^2)		Chlorophyll *a* (mg/g FW)		Chlorophyll *b* (mg/g FW)		Carotenoids (mg/g FW)	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Sakha 94	-0.46	-2.59**	-0.008*	-0.0137**	-0.0038	-0.0087**	-0.0042**	-0.0054**
Sakha 95	-0.10	-2.68**	-0.007	0.0008	-0.0021	-0.0048	-0.0005	0.0011
Giza 171	2.67**	2.62**	0.004	0.0013	-0.0023	-0.0049	0.0005	-0.0002
Sids 14	0.73**	2.44**	0.003	0.0028	-0.0060*	-0.0050	-0.0015	0.0009
Misr 1	-1.26**	1.44**	0.001	0.0039	-0.0012	0.0038	0.0028**	0.0007
Misr 3	-1.60**	-1.24**	0.007	0.0048	0.0155**	0.0196**	0.0029**	0.0029
LSD at 5% (g_i)	0.25	0.27	0.008	0.0081	0.0055	0.0053	0.0020	0.0032
LSD at 1% (g_i)	0.33	0.36	0.011	0.0108	0.0073	0.0070	0.0027	0.0043

* and ** Significance at 5% and 1% levels, respectively. Fresh weight (FW)

Table 5. Estimates of general combining ability effects for yield and yield components traits of six parental genotypes (combined data)

Parent	Plant height (cm)		Number of spikes/plant		Number of grains/spike		1000-grain weight (g)		Grain yield/plant (g)		Harvest index (%)	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Sakha 94	-0.04	-1.10**	0.165**	0.809**	-2.443	-1.676**	-1.39**	-0.20	-0.951**	0.819**	-3.99**	-0.85*
Sakha 95	0.94**	-0.69**	-0.098**	-0.055	-1.682	-0.646*	-0.36	-0.40	-1.094**	-0.436**	-1.80**	-0.01
Giza 171	0.70**	-0.66**	0.023	0.060	2.849	0.053	-0.15	0.74**	1.489**	0.103	-0.54**	1.20**
Sids 14	1.75**	1.54**	0.121**	-0.179**	-1.323	-0.427	-0.28	1.16**	-0.465**	-0.450**	2.20**	-0.42
Misr 1	-2.31**	0.34*	-0.009	-0.666	-1.907	-0.341	0.67**	-1.79**	-0.986**	-1.737**	1.70**	1.26**
Misr 3	-1.04**	0.56**	-0.202**	0.031	4.506**	3.036**	1.49**	0.26	2.007**	1.701**	2.43**	-1.42**
LSD at 5% (g_i)	0.31	0.33	0.056	0.113	0.387	0.555	0.38	0.50	0.244	0.329	0.37	0.69
LSD at 1% (g_i)	0.40	0.44	0.075	0.150	0.513	0.736	0.50	0.66	0.323	0.436	0.49	0.91

* and ** Significance at 5% and 1% levels, respectively.

Concerning the harvest index trait (Table 6), the parental genotypes Misr 3 (P6) exhibited highly significant and significant GCA effects, further the varieties, *i.e.* Giza 171 (P_3), Sids 14 (P_4), and Misr 1 (P_5) showed significant GCA effects in most cases studied for the harvest index trait, these parental genotypes had favorable genes and considered a good combiner for this trait. These findings agreed with those obtained by **Motawea (2017a),** and **Al-Mafarji and AL-Jubouri (2023),** and **Burdak *et al*. (2023)**. While the reminder parental genotypes exhibited undesirable and/or insignificant GCA effects for the same trait.

Estimates of SCA for yield and yield components are presented in Table 7. Results showed that the crosses; ($P_1 \times P_4$, $P_1 \times P_6$, $P_2\times P_5$, $P_2\times P_6$, and $P_3\times P_5$) had positive significance SCA for plant height; Moreover, two crosses; $P_4\times P_5$ and $P_5 \times P_6$ exserted significant SCA effects for the same trait. These results indicated that a considerable part of the genetical variance could be attributed to the non-additive gene effects. While the reminder crosses showed negative SCA effects or failed to reach the level of significance for the studied trait. These results are in line with the results of **Nada *et al.* (2017)** and **Abdallah *et al.* (2019)**.

Concerning the number of spikes/plant, the results showed that most of the fifteen crosses: ($P_1 \times P_2$, $P_1 \times P_3$, $P_1\times P_4$, $P_1\times P_5$, $P_1\times P_6$, $P_2 \times P_3$, $P_2 \times P_4$, $P_2\times P_5$, $P_4\times P_5$, $P_4\times P_6$ and $P_5\times P_6$) were positive and significant for this trait. This indicated that these crosses had desirable non-additive gene effects. While the rest of the crosses had undesirable SCA effects for this trait. These results were obtained by **El-Sayed and Mosheef (2005)**.

The results of grains number/spike trait showed that eight out of fifteen wheat crosses; ($P_1 \times P_3$, $P_1\times P_4$, $P_2 \times P_4$, $P_2 \times P_5$, $P_2 \times P_6$, $P_3\times P_5$, $P_3 \times P_6$ and $P_5 \times P_6$) showed positive (desirable) and highly significant and significant SCA effects. While, the reminder crosses exhibited either negative significant or insignificant SCA effects for the previous trait. This conclusion was also drawn by **Askander *et al*. (2021)** and **Mahmood and Al Hamdani (2023)**.

Regarding the 1000-grain weight trait, positive and significant SCA effects were recorded by crosses $P_3\times P_5$, $P_3\times P_6$, $P_4\times P_5$, $P_4\times P_6$, and $P_5\times P_6$, indicating a tendency for heavier 1000-grain weight; Therefore, these crosses are considered good cross combinations for this trait. Also, many crosses showed desirable SCA effects in most studied cases. These results agreed with those obtained by **Abdallah *et al.* (2019), Ali (2019), Din *et al.* (2020)** and **Askander *et al*. (2021)**.

For the grain yield/plant trait the result showed that many crosses were significant positive SCA; ($P_1 \times P_2$, $P_1\times P_3$, $P_1 \times P_4$, $P_2 \times P_4$, $P_2 \times P_5$, $P_2\times P_6$, and $P_3 \times P_6$), these results revealed that they had a considered non- allelic gene effect in these combinations for grain yield/ plant and could be used in the segregating generations to produce lines that have high grain yield/plant. Comparable outcomes were attained by **Hamada (2002), Mostafa (2002), Abdel-Majeed *et al*. (2004),** and **El-Sayed and Mosheef (2005).**

For the harvest index trait, results from Table 6 showed that highly significant and positive SCA effects were obtained by numerous hybrids; $P_1\times P_3$, $P_1\times P_5$, $P_2\times P_3$, $P_2\times P_5$, $P_2\times P_6$, $P_3\times P_4$, and $P_3\times P_5$. As well as the three hybrids *i.e.* $P_4\times P_5$, $P_4\times P_6$, and $P_5\times P_6$ obtained significant and positive SCA effects for this trait. Meanwhile, the reminder parental combinations exhibited significantly and negatively specific combining ability effects in some studied cases. Similar results were obtained by **Hamada (2002)**.

Table 6. Estimates of specific combining ability effects for physiological traits of 15 wheat crosses in F_1 and F_2 generations (combined data)

Cross	Flag leaf area (cm^2)		Chlorophyll *a* (mg/g FW)		Chlorophyll *b* (mg/g FW)		Carotenoids (mg/g FW)	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
P1 × P2	-2.81**	-5.46**	0.0333*	0.0158	0.0220*	0.0119	-0.0097*	0.0082
P1 × P3	-1.91**	-4.59**	0.0108	0.0078	0.0132	0.0034	0.0011	0.0050
P1 × P4	-2.57**	0.74	0.0626**	-0.0022	0.0150	-0.0064	0.0024	-0.0029
P1 × P5	3.22**	0.52	0.0411*	0.0070	-0.0125	-0.0011	0.0005	-0.0181**
P1 × P6	1.33*	-0.10	0.0308	0.0248	-0.0108	-0.0090	-0.0022	-0.0013
P2 × P3	9.18**	-1.12*	0.0582**	0.0484**	0.0016	0.0148	0.0024	0.0084
P2 × P4	-4.04**	-2.92**	0.0105	0.0060	0.0135	0.0015	0.0015	-0.0013
P2 × P5	3.42**	0.70	0.0023	-0.0080	-0.0202	-0.0233*	-0.0003	-0.0077
P2 × P6	-2.13**	1.90**	0.0062	-0.0249	-0.0109	-0.0183	-0.0106*	-0.0143*
P3 × P4	0.06	-2.61**	0.0175	0.0069	-0.0001	-0.0084	0.0001	-0.0053
P3 × P5	-10.29**	0.94	0.0330	-0.0184	-0.0048	-0.0126	-0.0046	-0.0092
P3 × P6	-4.20**	2.05**	0.0431*	0.0033	-0.0152	-0.0215*	-0.0108*	-0.0103
P4 × P5	-12.22**	0.09	0.0014	0.0090	-0.0099	0.0042	-0.0022	-0.0073
P4 × P6	0.58	-0.85	0.0080	-0.0224	-0.0289*	-0.0059	-0.01166**	-0.0079
P5 × P6	1.63**	-2.50**	0.0037	-0.0003	-0.0169	-0.0200	-0.01392**	-0.0120
LSD at 5% (S_{ij})	1.01	1.11	0.0332	0.0330	0.022	0.022	0.0080	0.0130
LSD at 1% (S_{ij})	1.34	1.47	0.0440	0.0438	0.030	0.029	0.0110	0.0170

* and ** Significance at 5% and 1% levels, respectively. Sakha 94 (P1), Sakha 95 (P2), Giza 171 (P3), Sids 14 (P4), Misr 1 (P5), and Misr 3 (P6). Fresh weight (FW).

Table 7. Estimates of specific combining ability effects for yield and yield components traits of 15 wheat crosses (combined data)

Cross	Plant height (cm)		Number of spikes/plant		Number of grains/spike		1000-grain weight (g)		Grain yield/plant (g)		Harvest index (%)	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
P1 × P2	-4.37**	-6.01**	1.371**	1.525**	-7.110**	7.427**	0.06	0.11	-2.009**	7.253**	-7.66**	-9.93**
P1 × P3	-4.92**	-1.47*	0.216	-0.690**	8.720**	0.744	3.19**	-1.24	5.353**	-1.700	1.34	7.67**
P1 × P4	-3.91**	2.84*	0.751**	0.633**	8.631**	4.958**	4.85**	3.88**	7.060**	4.992**	-5.23**	2.08
P1 × P5	-2.47**	-3.85**	0.648**	2.436**	-0.677	-1.381	-3.03**	0.96	0.765	3.920**	-0.72	13.41**
P1 × P6	0.08	2.76**	0.800**	0.706**	-2.626**	-4.421**	-4.45**	-2.89**	0.316	-1.050	-9.10**	-3.02*
P2 × P3	-0.96	-1.57*	0.246*	3.549**	-2.986**	-1.502	6.05**	3.78**	-1.238*	5.998**	-3.78**	3.61*
P2 × P4	-5.52**	-0.63	0.381**	-2.887**	10.536**	7.167**	2.74**	-0.38	6.778**	-2.725**	-3.09**	1.54
P2 × P5	0.04	1.53*	0.278*	-3.033**	5.979**	4.483**	1.87*	3.24**	3.901**	-3.385**	-6.07**	2.97*
P2 × P6	0.75	4.23**	0.055	1.603**	10.507**	0.815	1.08	0.33	5.749**	3.515**	-0.25	7.12**
P3 × P4	-3.73**	0.94	-0.074	-2.191**	2.378**	1.246	-14.79**	2.42*	0.912	-3.006**	-6.89**	5.66**
P3 × P5	-1.51*	2.08**	-0.302*	-0.557*	0.953	-0.320	7.74**	0.10	-0.056	-2.017**	-5.84**	2.35
P3 × P6	1.82**	-0.57	-0.067	-1.695**	4.368**	-0.600	1.79*	-2.09*	2.303**	-2.700**	-1.33	-9.82**
P4 × P5	3.73**	0.14	0.726**	1.025**	-2.055*	2.065	7.60**	-1.19	0.315	3.368**	2.02**	-10.86**
P4 × P6	3.88**	-0.78	-1.248**	1.005**	-3.810**	1.147	0.91	-2.24*	-4.773**	2.570**	2.11**	-1.01
P5 × P6	-4.64**	-2.06**	0.804**	-2.094**	2.771**	5.708**	1.84*	-1.43	3.394**	-1.724*	1.81*	0.54
LSD at 5% (Sij)	1.24	1.35	0.229	0.459	1.571	2.254	1.53	2.01	0.989	1.335	1.49	2.79
LSD at 1% (Sij)	1.64	1.80	0.304	0.609	2.083	2.989	2.03	2.67	1.312	1.770	1.98	3.70

* and ** Significance at 5% and 1% levels, respectively. Sakha 94 (P1), Sakha 95 (P2), Giza 171 (P3), Sids 14 (P4), Misr 1 (P5), and Misr 3 (P6).

3.3. Mean performance of genotypes

3.3.1. Physiological traits

The mean performance of the studied physiological traits, *i.e.* flag leaf area, chlorophyll *a* and *b*, and carotenoids for genotypes including parental varieties and their crosses are shown in Table 8.

The average flag leaf area for parental genotypes showed significantly higher values, and differences were observed among genotypes. In this respect, the variety Sides 14 (P_4) showed significantly higher values than all parental varieties regarding this trait. The obtained value was 54.87 cm^2. The GCA effects corresponded to the performance of the parental varieties themselves. While the varieties Misr 3 (P_6) and Sakha 95 (P_2) showed the lowest values for the same trait. At the same time, the remainder of the genotypes gave comparable values.

It could be noticed that the F_1` hybrids $P_3 \times P_4$, $P_3 \times P_5$, $P_3 \times P_5$, $P_4 \times P_5$ and $P_4 \times P_6$ exerted significantly higher values than their parents. The rest of the crosses exerted comparable values in the individual environments and combined analysis.

Concerning the chlorophyll *a* trait, the variety Misr 3 (P_6) showed the highest value, while Sakha 94 (P_1) was the lowest parent in the same order. This result showed that the performance of Sakha 94 (P_1) and Misr 3 (P_6) corresponded to their GCA effects. The mean performance of hybrids, *i.e.* $P_3 \times P_5$ and $P_3 \times P_6$ showed the highest values compared to their parents, which corresponded to their specific combining ability (Table 6). The highest chlorophyll values were 0.36 and 0.39 for the two previous hybrids, reflecting the superiority of these crosses in this trait. The F_2 generations mean values were generally lower than their corresponding F_1 hybrids for this trait. On the other hand, there are insignificant differences (parents and their hybrids) for this trait. Similarly, **Dewdar *et al.* (2008)** found that variations between varieties and levels of N are essential for chlorophyll measurements, while **Vidal and Hètier (1999)** reported that chlorophyll *a* and *b* had the minimum values in the event of a severe N deficiency of the flag leaf area, but these values also increased in parallel with the increase in high N level.

Regarding the chlorophyll *b* trait, the variety Misr 3 (P_6) showed the highest mean performance. On the contrary, the variety Sakha 94 (P_1) gave the lowest value in the same order; the obtained values were 0.20 and 0.11 for the two previous parents P6 and P_1, respectively. The mean performance of F_1 was higher than the respective parents for the crosses *i.e*. $P_1 \times P_2$, $P_1 \times P_6$, $P_2 \times P_3$, $P_4 \times P_6$, and $P_5 \times P_6$ while the F_2 generation values were lower than their corresponding F_1 hybrids.

Concerning the carotenoids trait, significant differences were observed among genotypes for this trait. In this respect, the variety Misr 3 (p_6) showed the highest values for the same trait. It could be noticed that the F_1 hybrids exerted significantly higher values than their parents in most crosses.

Table 8. Mean performance of parental genotypes and their cross in F_1 and F_2 generations in combined data for physiological traits (combined data)

Genotype	Flag leaf area (cm²)			Chlorophyll *a* (mg/g FW)			Chlorophyll *b* (mg/g FW)			Carotenoids (mg/g FW)		
	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2
P1	121.25			0.1875			0.1082			0.0716		
P2	120.43			0.2244			0.1221			0.0835		
P3	119.57			0.2200			0.1274			0.0831		
P4	119.80			0.2484			0.1225			0.0781		
P5	111.33			0.2546			0.1590			0.0920		
P6	110.50			0.2607			0.2016			0.1065		
P1 × P2		40.36	27.30		0.2545	0.3186		0.1018	0.1451		0.0724	0.0431
P1 × P3		46.06	31.43		0.2393	0.3194		0.1091	0.1207		0.0661	0.0688
P1 × P4		45.28	34.74		0.2490	0.3993		0.0875	0.1225		0.0603	0.0737
P1 × P5		51.89	30.73		0.2750	0.3051		0.0939	0.1442		0.0564	0.0882
P1 × P6		43.36	33.73		0.2767	0.3264		0.1013	0.1526		0.0561	0.0734
P2 × P3		55.44	36.87		0.2800	0.3284		0.1027	0.1575		0.0644	0.0796
P2 × P4		47.90	27.27		0.2395	0.2909		0.1072	0.1263		0.0594	0.0787
P2 × P5		45.58	38.38		0.2568	0.2590		0.0849	0.1165		0.0594	0.0714
P2 × P6		45.21	32.60		0.2470	0.2975		0.0982	0.1450		0.0594	0.0614
P3 × P4		56.44	28.58		0.2794	0.3521		0.0998	0.1138		0.0594	0.0796
P3 × P5		45.02	33.80		0.2480	0.3601		0.1023	0.1205		0.0594	0.0841
P3 × P6		49.30	34.80		0.2835	0.3885		0.0904	0.1462		0.0594	0.0766
P4 × P5		43.82	29.23		0.2793	0.2959		0.1069	0.1492		0.0594	0.0855
P4 × P6		49.08	31.87		0.2280	0.2914		0.1097	0.1579		0.0594	0.0584
P5 × P6		47.92	27.81		0.2793	0.3277		0.1040	0.1531		0.0594	0.0661
LSD at 5%		2.41	2.33		0.0599	0.082		0.0246	0.0611		0.0085	0.0182
LSD at 1%		3.22	3.12		0.0801	0.1097		0.0329	0.0817		0.0114	0.0243

Sakha 94 (P1), Sakha 95 (P2), Giza 171 (P3), Sids 14 (P4), Misr 1 (P5), and Misr 3 (P6). Fresh weight (FW).

3.3.2. Yield and yield components traits

For plant height trait, the mean values for parental genotypes ranged from 105.27 to 131.17 cm for Misr 3 (P_6) and Sakha 94 (P_1), while the values ranged from 104.33 to 130.07 cm for hybrids; $P_5 \times P_6$ and $P_1 \times P_4$. Also, the means of crosses were slightly lower than those of parents under N stress (Table 9). Results indicated that for the highest plant height was recorded by the variety Sakha 94 (P_1) with a value (131.17 cm). The crosses $P_1\times P_4$, $P_1\times P_5$, $P_1 \times P_6$, $P_2 \times P_4$, $P_2\times P_6$, $P_3\times P_4$, $P_3 \times P_6$, $P_4\times P_5$, and $P_4 \times P_6$) recorded the highest plant height values in the studied most cases. On the other side, the rest of the genotypes gave comparable values of plant height. The average values of F_2 hybrids under low and high N levels were lower than those of F_1 hybrids. These results were found to agree with those by **Kizilgeci (2020)**. The long stem length in wheat is an undesirable characteristic, particularly; excessive use of N in cereal crops may significantly increase the risk of crop lodging, resulting in a loss of yield.

Regarding grains number/spike characteristic means of each parent, F_1 and F_2 cross under two N levels of 50 and 75 kg/feddan. In general, the values of two parents Giza 171 and Sids 14 were generally larger in magnitude than those of the other parents. As a result, these parents provide suitable genetic material for diallel analysis, which is used to investigate how wheat develops an adaptive low-N tolerance. The rank of hybrids F_1 and F_2 generations for this trait was changed from one environment (N-level) to another, indicating that these genotypes as low-N sensitive as compared to F_1 and F_2 under high-N levels and therefore were considered tolerant (N-efficient) to low-N stress. These differences may be due to varietal performance which is corrected by genetic makeup effects. These results agree obtained by **Le Gouis *et al*. (2000), Le Gouis *et al*. (2002)**, and **Al-Naggar and Shehab-El-Deen (2012)**. At the same time, the remainder of the genotypes under study gave comparable values.

For average values of grains number/spike trait in Table 9, data revealed that genotypes had a significant effect on this trait. The highest values obtained were 57 and 55 for the two parents Giza 171 and Misr 3. On the contrary, the four parents Sakha 94, Sakha 95, Sides 14, and Misr 1 showed the lowest grain number/spike and therefore were considered sensitive (N-inefficient) to low-N stress. The average efficiency of F_1 and F_2 hybrids, these genotypes were similar in general in the two N environments, indicating less effect of interaction between these crosses and N levels on the grains number/spike. These crosses; ($P_1 \times P_2$, $P_1 \times P_3$, $P_1 \times P_4$, $P_2 \times P_6$, $P_3 \times P_4$, $P_3 \times P_6$ and $P_5 \times P_6$) showed the highest values. These results were reported by **Tran and Tremlay (2000), Emam *et al.* (2021), Mohamed *et al.* (2021)**, and **Ranjan and Yadav (2021).**

Concerning the 1000-weight grain trait Table (9), the data analysis mean values ranged from 56.40 to 63.20 for Sakha 95 and Sids 14 varieties under LN, 57.20 to 68.53 for Sakha 95 and Misr 3 varieties, respectively. While the trait means showed a significant difference for F_1 and F_2, indicating a greater effect of interaction between these crosses (F_1 and F_2) and the N level on this trait, it also observed that some crosses had a high 1000-grain weight; the same trend was obtained by **Koumber *et al.* (2006)**.

The grain harvest from a single plant is of unique importance among the traits of plants because it plays a very important role in raising the economy of the farmers and the country. A comparative analysis of means for grain yield/plant trait is presented in Table 9 across 21 genotypes: 6 parents and 15 F_1. The two parents Giza 171 and Misr 3 were higher in magnitude than those of four other parents; Sakha 94, Sakha 95, Sids 14 and Misr 1, where the values obtained were 27.41, 29.39 and 28.40 g for Giza 171, 27.49, 31.66 and 29.58 g for Misr 3, respectively. Therefore, the genetic material from these parents is suitable for diallel analysis, which studies the inheritance of an adaptation trait for low-N tolerance in wheat. The rank of crosses in the F_1 and F_2 generations was changed from one environment to another. The highest mean was obtained from, ($P_1 \times P_4$, $P_2 \times P_6$, and $P_3 \times P_6$) While the rest of the crosses of the F_1 and F_2 crosses gave comparable mean values. The same trend of results obtained by **Al-Naggar *et al.* (2015a), Al-Naggar *et al.* (2015b), Al-Naggar *et al.* (2015c), Rajan *et al.* (2019)**, and **Ranjan and Yadav (2021)**. Concerning harvest index trait Table (9), data analysis for HI ranged from 28.62 for Sids 14 to 42.62 for Giza 171 varieties and 35.37 for Sakha 94 to 42.78 for Sids 14. Harvest index values for F_1 and F_2 crosses exhibited highly significant differences among genotypes.

Finally, it can conclude that N fertilization and the large differences between low and normal values for the previously mentioned attributes have the greatest effects on wheat grain yield and its major components, namely the number of spikes/plant, number of grains/spike, 1000-grain weight, and grain yield/plant. Consequently, this demonstrates how crucial N fertilization is for raising wheat grain yield.

Table 9. Mean performance of parental genotypes and their crosses for yield and yield components (combined data)

Genotype	Plant height (cm)			Number of spikes/plant			Number of grains/spike			1000-grain weight (g)		
	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2
P1	121.25			12.47			43.13			60.33		
P2	120.43			12.67			39.66			56.80		
P3	119.57			14.07			50.47			61.13		
P4	119.80			14.00			41.00			62.20		
P5	111.33			12.93			44.19			56.73		
P6	110.50			13.45			54.89			65.80		
P1 × P2		110.07	112.79		15.47	15.43		40.25	55.25		61.73	60.53
P1 × P3		109.28	117.36		14.43	13.33		60.61	49.27		65.07	60.33
P1 × P4		111.33	123.86		15.07	14.42		56.35	53.00		66.60	65.87
P1 × P5		108.71	115.97		14.83	15.73		46.46	46.75		59.67	60.00
P1 × P6		112.53	122.80		14.79	14.70		50.92	47.08		59.07	58.20
P2 × P3		114.20	117.67		14.20	16.71		49.67	48.05		68.95	65.13
P2 × P4		110.70	120.80		14.43	10.03		59.02	56.24		65.52	61.40
P2 × P5		112.20	121.76		14.20	9.40		53.88	53.64		65.59	62.07
P2 × P6		114.17	124.68		13.78	14.73		64.82	53.35		65.62	61.20
P3 × P4		112.24	122.40		14.10	10.84		55.39	51.02		48.20	65.33
P3 × P5		110.41	122.33		13.74	11.99		53.38	49.54		71.67	60.07
P3 × P6		114.99	119.92		13.78	11.55		63.21	52.63		66.53	59.93
P4 × P5		116.70	122.59		14.87	13.33		46.20	51.44		71.40	59.20
P4 × P6		118.11	121.90		12.70	14.01		50.86	53.90		65.53	60.20
P5 × P6		105.54	119.41		14.62	10.43		56.86	58.55		67.40	58.07
LSD at 5%		2.79	3.05		14.43	13.33		40.25	55.25		3.46	4.54
LSD at 1%		3.71	4.05		15.47	15.43		60.61	49.27		4.59	6.01

Sakha 94 (P1), Sakha 95 (P2), Giza 171 (P3), Sids 14 (P4), Misr 1 (P5), and Misr 3 (P6).

Table 9. (continue)

Genotype	Grain yield/plant (g)			Harvest index (%)		
	P	F_1	F_2	P	F_1	F_2
P1	21.41			35.54		
P2	20.28			39.66		
P3	28.40			40.00		
P4	22.98			42.78		
P5	22.93			40.64		
P6	29.58			41.06		
P1 × P2		25.01	34.12		19.38	31.44
P1 × P3		34.95	25.70		29.64	50.25
P1 × P4		34.70	31.84		25.82	43.04
P1 × P5		27.89	29.49		29.82	56.04
P1 × P6		30.43	27.95		22.17	36.94
P2 × P3		28.22	32.15		26.72	47.02
P2 × P4		34.28	22.87		30.15	43.32
P2 × P5		30.88	20.92		26.66	46.43
P2 × P6		35.72	31.26		33.21	47.91
P3 × P4		31.00	23.13		27.61	48.66
P3 x P5		29.51	22.83		28.16	47.02
P3 × P6		34.86	25.59		33.39	32.19
P4 × P5		27.92	27.66		38.76	32.19
P4 × P6		25.83	30.30		39.57	39.38
P5 × P6		33.47	24.72		38.77	42.59
LSD at 5%		25.01	34.12		3.36	6.30
LSD at 1%		34.95	25.70		4.46	8.35

Sakha 94 (P1), Sakha 95 (P2), Giza 171 (P3), Sids 14 (P4), Misr 1 (P5), and Misr 3 (P6).

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