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General Combining Ability and Genetic Parameters for Grain Yield and Yield Components in Promising Lines of Maize

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Abstract

Khuzestan province lacks improved cultivars of maize adapted to its extreme heat and drought. The present study aimed to evaluate the genetic parameters and general combining ability of the promising lines of maize produced in Khuzestan using the top cross method. To identify traits influencing grain yield and improve local maize lines, 289 Khuzestan-bred lines were crossed with SC704 and evaluated over two cropping seasons (summer 2016 and spring 2017) at Dezful Agricultural Research Center. The experiment employed a 17×17 simple lattice design with two replications. Traits measured included plant height, ear length, ear diameter, grain depth, number of rows per ear, number of grains per row, 100-grain weight, grain yield, biological yield, and harvest index. Genetic parameters were estimated using ANOVA and general combining ability (GCA) analysis. Findings showed significant genetic diversity among maize lines for most traits except ear length, number of rows per ear, and grains per row. Combined analysis confirmed significant genotype effects for all traits ($P<0.01$), with significant genotype × season interactions, indicating differential responses between seasons. Broad-sense heritability ranged from 12.1% (ear diameter) to 97.7% (biological yield). The largest genetic advances were recorded for plant height (40.0 cm) in summer and biological yield (8,239.4 kg ha^{-1}) in spring, demonstrating ample additive genetic variation. Different lines were superior across seasons, confirming strong seasonal differentiation in trait expression and adaptive potential. Lines combining high yield and 100-grain weight with reduced plant height are promising parental candidates for developing stress-tolerant, high-yielding maize cultivars.

Keywords: additive variance, combining, heritability, GCA, grain yield and maize

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Capacidad combinatoria general y parámetros genéticos para el rendimiento de grano y componentes del rendimiento en líneas promisorias de maíz

Resumen

La provincia de Juzestán carece de cultivares mejorados de maíz adaptados a su calor extremo y sequía. Este estudio evaluó parámetros genéticos y la aptitud combinatoria general de líneas prometedoras de maíz desarrolladas localmente mediante el método top-cross. Se cruzaron 289 líneas de maíz desarrolladas en Juzestán con SC704 y se evaluaron en dos zafras (verano 2016 y primavera 2017) en el Centro de Investigación Agrícola de Dezful, usando un diseño de lattice simple 17×17 con dos repeticiones. Se midió altura de planta, longitud/diámetro de mazorca, profundidad de grano, filas/granos por fila, peso de 100 granos, rendimiento de grano, rendimiento biológico e índice de cosecha. Se estimaron parámetros genéticos mediante ANOVA y análisis de aptitud combinatoria general (ACG). Se detectó diversidad genética significativa en la mayoría de rasgos excepto longitud de mazorca, filas por mazorca y granos por fila. El análisis combinado confirmó efectos genotípicos significativos (P<0,01) para todos los rasgos, con interacciones genotipo×zafra significativas. La heredabilidad en sentido amplio varió de 12,1% (diámetro mazorca) a 97,7% (rendimiento biológico). Los mayores avances genéticos se registraron para altura de planta (40,0 cm, verano) y rendimiento biológico (8.239,4 kg ha^{-1}, primavera). Conjuntos diferentes de líneas destacaron en cada zafra. Líneas combinando alto rendimiento de grano, peso de 100 granos y baja estatura son candidatas parentales prometedoras para desarrollar cultivares de maíz tolerantes al estrés y de alto rendimiento adaptados a las condiciones extremas de Juzestán.

Palabras clave: varianza aditiva, combinación, heredabilidad, GCA, rendimiento de grano y maíz

Capacidade de combinação geral e parâmetros genéticos para o rendimento em grão e componentes de rendimento em linhagens promissoras de milho

Resumo

A província de Khuzestan carece de cultivares melhorados de milho adaptados ao calor extremo e seca. Este estudo avaliou parâmetros genéticos e capacidade geral de combinação de linhagens promissoras locais usando método top-cross. Foram cruzadas 289 linhagens de milho de Khuzestan com SC704 e avaliadas em duas safras (verão 2016 e primavera 2017) no Centro de Pesquisa Agrícola de Dezful, em delineamento lattice simples 17×17 com duas repetições. Avaliaram-se altura da planta, comprimento/diâmetro da espiga, profundidade do grão, fileiras/espigas, grãos/fileira, peso 100 grãos, rendimento de grãos, rendimento biológico e índice de colheita. Estimaram-se parâmetros genéticos via ANOVA e análise de capacidade geral de combinação (CGC). Observou-se diversidade genética significativa para maioria das características, exceto comprimento/fileiras da espiga e grãos/fileira. Análise combinada confirmou efeitos genotípicos significativos (P<0.01) para todos os caracteres, com interações genótipo×safra indicando respostas diferenciais. Herdabilidade em sentido amplo variou de 12,1% (diâmetro espiga) a 97,7% (rendimento biológico). Maiores avanços genéticos ocorreram para altura da planta (40,0 cm, verão) e rendimento biológico (8.239,4 kg ha^{-1}, primavera). Diferentes linhagens destacaram-se por safra. Linhagens combinando alto rendimento e peso 100 grãos com baixa altura representam parentais promissores para desenvolvimento de cultivares de milho tolerantes a estresse e alto rendimento adaptados às condições de Khuzestan.

Palavras-chave: variância aditiva, combinação, herdabilidade, GCA, rendimento em grão e milho

1. Introduction

Maize (*Zea mays* L.) is a vital cereal and multifunctional crop in the Poaceae family. It serves multiple purposes, including human food, animal and poultry feed, and various industrial applications such as maize starch, dextrose, maize syrup, and maize flakes (Gul et al., 2021). Maize thrives in diverse soil and climatic conditions and absorbs more nutrients than other crops like small grain cereals and legumes. It is cultivated for various purposes, including animal feed (silage and grains), poultry feed (grains), pig feed (grains), and human consumption in the form of grains, sweet corn, and grain maize (Gheith et al., 2022).

More than 9.4 million tons of corn grain are consumed in Iran every year. According to official statistics, during the Iranian year 1400, more than 8.084 million tons of corn for animal feed from 14 different countries were imported into Iran, with a total value exceeding USD 3.269 billion (Statistical Center of Iran, 2022). On the other hand, only 1.4 million tons (14.8%) of the required corn has been produced in Iran this year. Due to this lack of production and also due to the need to change the cultivation pattern from high-water-intensive to low-water-intensive agriculture, the expansion of corn cultivation in Iran has become necessary. In the meantime, Khuzestan, with about 50,000 hectares under grain and fodder corn cultivation in 2022, as the most important corn-producing province of the country, lacks improved cultivars compatible with exceptionally hot and dry conditions and relies on foreign cultivars, including the old variety Single cross 704. In order to prepare suitable cultivars for Khuzestan, lines should be produced and evaluated in the region that can be used in the production of hybrid and open-pollinated cultivars (Statistical Center of Iran, 2022).

The use of agronomy methods will be less than 50% effective in solving the food shortage problem (Saeed et al., 2011), so it is necessary to pay attention to the genetic capacity and use this effective factor as much as possible, which can be done by using the science of plant breeding. The main pillar of any successful breeding program in crop plants is a rich and diverse germplasm collection (Saeed et al., 2011). Information and knowledge about the amount, type, and size of diversity in germplasm and genetic relationships of breeding materials can be valuable tools in the breeding strategy (Ramanappa et al., 2013; Saeed et al., 2011). To produce hybrid varieties, the main condition is to find a line or lines that have the best combination with a set of lines to produce hybrid, synthetic, or composite varieties (general combining ability; GCA) or the best combination between lines (specific combining ability; SCA). Also, the breeding of high-yielding varieties requires knowing the genetic structure of the crossed parents, as well as the combining ability of their desirable traits, which can be done through the use of quantitative genetic methods, such as bi-parental crosses, top-cross, poly Cross, North Carolina designs, diallel or line × tester crossing (Nduwumuremyi et al., 2013). Determining the combining ability and components of genetic variance is one of the most important tasks of any purebred program for cross breeding, and it helps breeders determine the mode of action of the gene or genes involved in the expression of quantitatively important traits and parents with positive general combining ability and identify hybrids with high private combining ability. Estimating public and private combinability helps breeders to make decisions about breeding programs and genotype selection strategies (Ahmadikhah, 2010).

One of the methods for estimating combining ability is the top-cross technique. In this method, the combining ability of a given line is evaluated by crossing it with a tester (Farshadfar, 1998), which may be a genotype with a broad genetic base. When a broad-based tester is used, the performance of the resulting crosses mainly reflects the general combining ability (GCA) of the evaluated lines, as it represents their average performance across a diverse genetic background. In contrast, specific combining ability (SCA), which is associated with non-additive genetic effects, is more effectively assessed through crosses between specific inbred lines (Okunlola et al., 2023). Knowledge of combining ability is essential for developing effective maize breeding programs aimed at hybrid production, as it enables the identification of superior parental lines with desirable additive genetic effects. Therefore, the present study was designed to evaluate the genetic parameters and general combining ability of promising maize lines developed in Khuzestan using the top-cross method.

2. Materials and Methods

2.1 Experimental Site

The study took place during two growing seasons (summer 2016 and spring 2017) at Safi-Abad Agricultural and Natural Resources Research Center, located 12 kilometers from Dezful city. The center is situated at 48 degrees

and 25 minutes East longitude, 32- and 16-minutes North latitude, and an altitude of 82 meters above sea level. The climate of the study area is classified as hot and arid according to the Köppen climate classification system (Köppen, 1936). The summary of weather parameters in two cropping seasons is given in Table 1. The analysis of the soil sample indicated phosphorus levels at 7.20 ppm, potassium at 110 ppm, and micronutrients iron, zinc, copper, and magnesium at 3.41, 0.37, 1.12, and 11.2 ppm, respectively, with a silt-loam texture and a pH of 7.28.

After Makhar (irrigation before plowing) and Gavvero soil, the land was first plowed with a plow. After the disks were perpendicular to each other twice, it was leveled with a leveler. The required basic fertilizers, including phosphate (100 kg/ha), potash (200 kg/ha) and urea (100 kg/ha), were applied in accordance with recommendations derived from soil test results and incorporated into the soil with a light disc harrow. After this stage, furrows with a width of 75 cm were created.

Table 1. Meteorological information of Safi Abad-Dezful Agricultural Research Station in two cropping seasons (2016-17)

Month	***Spring 2017***							
	Temperature				***Rainfall***		***Relative humidity***	
	Max.	**Min.**	**Absolute max.**	**Absolute min.**	**Daily max.**	**Monthly Total**	**Max.**	**Min.**
21 March-20 April	31.0	14.5	36.7	8.9	14.8	24.1	83	29
21 April-21 May	34.2	18.6	41.6	12.6	47.3	75.4	76	27
22 May-21 June	44.0	25.4	47.9	21.1	0.3	0.5	45	10
22 June-22 July	47.7	26.7	51.1	21.9	0.0	0.0	42	8
23 July-22 Aug.	47.0	25.9	49.9	23.0	0.0	0.0	50	10
23 Aug.-22 Sept.	44.7	25.4	47.7	22.3	0.0	0.0	56	14
23 Sept.-22 Oct.	38.2	21.1	43.3	17.4	8.1	8.9	66	22
23 Oct.-21 Nov.	25.7	15.1	32.6	10.3	38.6	119.9	96	56
22 Nov.-21 Dec.	20.6	10.9	26.4	6.4	60.1	139.3	100	65
22 Dec.-20 Jan.	16.9	7.2	21.7	0.4	23.4	96.1	100	65
21 Jan.-19 Feb.	18.8	7.4	23.6	2.2	47.3	88.7	97	53
20 Feb.-19 March	21.4	8.1	24.8	4.0	38.3	62.1	95	40
Annual	32.5	17.2	51.1	0.4	60.1	615.0	75.4	33.4
Month	***Summer 2016***							
	Temperature				***Rainfall***		***Relative humidity***	
	Max.	**Min.**	**Absolute max.**	**Absolute min.**	**Daily max.**	**Monthly Total**	**Max.**	**Min.**
21 march-20 April	29.3	14.9	38.6	8.6	25.7	25.7	79	31
21 April-21 May	39.4	20.0	44.4	14.2	1.4	1.4	57	12
22 May-21 June	44.9	22.3	49.6	15.7	0.0	0.0	40	7
22 June-22 July	48.0	26.9	51.2	20.3	0.0	0.0	39	9
23 July-22 Aug.	47.6	28.4	49.5	22.4	0.0	0.0	48	10
23 Aug.-22 Sept.	43.5	25.4	46.5	21.2	0.0	0.0	62	18
23 Sept.-22 Oct.	37.5	18.7	43.3	13.2	0.0	0.0	62	16
23 Oct.-21 Nov.	29.9	14.8	35.0	9.9	5.0	5.0	76	31
22 Nov.-21 Dec.	21.8	8.0	26.8	3.5	49.8	49.8	96	44
22 Dec.-20 Jan.	21.6	7.7	26.8	3.6	4.6	4.6	89	40
21 Jan.-19 Feb.	21.0	7.9	24.8	0.1	9.8	9.8	92	43
20 Feb.-19 March	25.4	11.1	31.0	7.4	40.6	40.6	94	43
Annual	34.2	17.2	51.2	0.1	49.8	215.1	69.4	25.3

2.2 Plant Material

The 300 inbred lines used in this study were developed from improved maize germplasm varieties in the Khuzestan region. These inbred lines were not sourced from a single population but rather represent a diverse genetic pool from different local or regional sources, reflecting the genetic variability typically found in maize breeding programs. These lines were created through repeated self-pollination, ensuring a high level of homozygosity. Regarding the genetic relationship between the inbred lines and the hybrid SC704, the inbred lines were crossed with SC704 in the 2015 crop year to create the combinations for evaluation. SC704 is a well-established hybrid in maize breeding, and as a hybrid, it is genetically distinct from the inbred lines used in this study. The genetic distance between the inbred lines and SC704 would be influenced by the parental lines involved in the hybrid's development and the specific genetic makeup of the inbreds. However, further genetic analysis (e.g., molecular markers, SNPs, or genome-wide studies) would be required to precisely quantify the genetic distance between the inbred lines and SC704, as this would vary depending on the specific origin and breeding history of both the inbreds and the hybrid.

2.3 Sowing and Harvest Dates

Summer 2016: Sown June 15, 2016; harvested September 25, 2016 (102 days cycle); Spring 2017: Sown March 10, 2017; harvested June 20, 2017 (102 days cycle).

2.4 Experimental Layout

The experiment was carried out in the form of a simple lattice square design with two repetitions in the summer of 2016 and the spring of 2017 after randomizing the treatments. Each plot consisted of 4 planting rows, 4 m in length and spaced 75 cm apart, with 17 cm between plants within each row. The seeds were planted manually with the recommended density of 78,000 plants per hectare; irrigation was performed immediately, and subsequent irrigations were carried out according to the needs of the field. After the third irrigation, i.e. at the stage of about seven leaves, the soil of the fields was loosened and softened by the Cultivator and Lilystone machine, and after applying urea to the bottom of the fields, the soil was applied to the plants with a spade and irrigation was done immediately. During the growth of plants, micronutrient elements such as iron chelate in irrigation water and other nutrient solutions were used as foliar spraying on the leaves. Weeds between the lines were controlled by manual weeding, and empty spaces and irrigation ditches were controlled by non-selective herbicides such as paraquat. Due to the absence of pests, no chemical control measures were applied. Other agricultural operations were followed according to regional customs and recommendations of research centers.

During the growth period, five normal plants were randomly selected from each plot for trait measurement, and observations were recorded from emergence to physiological maturity. The measured traits included plant height, ear length, ear diameter, grain depth, number of rows per ear, number of grains per row, 100-grain weight, grain yield, biological yield, and harvest index. These measurements were carried out in accordance with the standard evaluation guidelines provided by the Maize and Fodder Plants Department of the Seed and Plant Improvement Institute (SPII), Iran (Ahmadikhah, 2010; Nduwumuremyi et al., 2013; Nematzadeh & Kiani, 2010). Grain yield (adjusted to 14% moisture content), along with other traits, was measured and calculated from the two central rows of each experimental plot.

The study of genetic parameters in this research, using expected value of mean square (EMS), was used in the form of the basic design of random complete blocks in the form of the following relationships (Nematzadeh & Kiani, 2010). The data was collected and analyzed for genotypic and phenotypic coefficients of variation, heritability (broad sense), and expected genetic advance as % of mean.

The genotypic and phenotypic coefficient of variation (GCV and PCV) was calculated according to the method suggested by Burton (1952), using the formulas:

$$\text{GCV } (\%) = \frac{\sqrt{\sigma_g^2}}{\bar{x}} \times 100$$

$$\text{PCV}(\%) = \frac{\sqrt{\sigma_p^2}}{\bar{x}} \times 100$$

Where, σ_g^2 and σ_p^2 are genotypic and phenotypic variances, respectively, and $\bar{x}$ is the trait mean.

Heritability in the broad sense h_b^2 was estimated according to the method indicated by Allard (1960).

$$h_b^2 = \frac{\sigma_g^2}{\sigma_p^2} \times 100$$

The genetic advance (GA) at 5% selection intensity was calculated for each character using the formula suggested by Johnson et al. (1955):

$$GA = k.h_b^2.\sigma_p$$

Where, k is the selection differential at 5% intensity, and σ_p is the phenotypic standard deviation.

Measurements were made on 10 random plants from each line in each repeat. The general combining ability analysis was done using the Savchenko method (Johnson et al., 1955; Savchenko, 1981). General combining ability variances were tested using their respective error variances obtained from the variance analysis table. The significance test of GCA effects was performed using the LSD test.

3. Results and Discussion

The mean ± standard deviation of grain yield and related traits for the summer and spring experiments are presented in Table 2. Grain yield was numerically higher in summer (12,447.3 ± 1,553.6) than in spring (11,632.8 ± 1,812.5), accompanied by a higher harvest index (55.72 vs. 50.61), indicating more efficient biomass partitioning under summer conditions. However, statistical significance of these differences was not assessed based on mean ± standard deviation alone. Biological yield was similar between seasons. Yield components differed between the two experiments, with grain depth, grains per row, and 100-grain weight higher in summer, while ear length and number of rows per ear were slightly higher in spring. These results suggest that grain filling contributed more to yield in summer, whereas grain number traits were relatively more important in spring. Accordingly, genotypes selected in summer were associated with superior grain weight and filling capacity, while those selected in spring were linked to greater ear size and grain number. This indicates the presence of distinct seasonal ideotypes.

Table 2. Mean ± standard deviation of grain yield and related traits across genotypes

Trait	Summer (Mean ± SD)	Spring (Mean ± SD)
Grain yield (kg/ha)	12,447.3 ± 1,553.6	11,632.8 ± 1,812.5
Biological yield (DM) (kg/ha)	22,486.9 ± 3,215.4	22,946.3 ± 2,967.7
Harvest index (kg/ha)	55.72 ± 4.21	50.61 ± 4.05
Plant height (cm)	223.8 ± 15.9	214.6 ± 18.7
Ear diameter (ED) (mm)	46.9 ± 2.9	45.0 ± 3.1
Grain depth (KD) (cm)	9.36 ± 0.86	8.23 ± 0.91
Ear length (EL) (cm)	17.87 ± 1.52	18.36 ± 1.68
Rows per ear (count)	14.9 ± 1.4	15.2 ± 1.6
Grains per row (count)	39.2 ± 4.8	36.8 ± 5.2
100-grain weight (g)	29.6 ± 2.9	27.9 ± 3.4

3.1 Analysis of Variance

The analysis of variance based on the simple lattice design showed that the relative efficiency of the design, compared with the random complete block design, was less than 100% for most yield and yield-component traits of the promising maize lines in the summer and spring cropping seasons; therefore, the analysis of variance of the data was performed based on the randomized complete block design. The significance of the interaction effect of genotype × season for all studied traits at the level of 1% indicates the different reaction of genotypes in summer and spring seasons; for this reason, the results for the summer and spring seasons were analysed separately.

According to the combined analysis in two cropping seasons, summer (2016) and spring (2017), it was found (Table 3) that the line effect in terms of yield and yield-components was significant at the 1% probability level, which indicates significant genetic diversity among the studied lines.

Table 3. Analysis of combined traits studied in two cropping seasons, summer and spring (2016-2017)

Traits	*Mean Square*					CV (%)
	Season	Rep(Season) (Ea)	Line	Line × Season	Eb	
Df	1	2	288	288	575	
Plant height (cm)	11581857**	199.65	435.32**	417.78**	16.60	3.63
Ear length (cm)	1259**	13.26	5.15**	6.53**	2.88	10.98
Ear diameter (mm)	395391**	217.79	11.61**	9.97**	6.86	10.13
Grain depth (cm)	21782**	14.54	5.69**	5.51**	0.86	7.18
Number of rows/ear (count)	93253**	11.07	83.71**	80.48**	4.25	8.76
Number of grain/row (count)	35946**	18.06	30.62**	28.63**	17.43	13.43
100 grain weight (g)	1422533**	128.90	40.11**	44.05**	16.87	6.63
Grain yield (kg/ha)	737580794**	45679877	12795482**	12566919**	3184579	19.49
Biological yield (kg/ha)	120728658**	163601078	32600027**	26258941**	10284382	17.14
Harvest index (kg/ha)	32600**	106.90	212.12**	193.02**	7.40	5.60

* , **, and ns: Significant at 5% and 1% levels of probability, and non-significant, respectively.

The variance analysis showed significant effects ($p \leq 0.01$) of maize promising lines in the summer cropping season (2017) for plant height, ear diameter, grain depth, 100-grain weight, grain yield, and biological yield, but not for ear length, number of rows per ear, number of grains per row, or harvest index. In the spring cropping season (2018), genotypic effects were significant ($p \leq 0.01$) for all 10 yield and yield-component traits studied. These results confirm sufficient genetic diversity among lines for selection and differential genotypic responses between cropping seasons. These patterns underscore pronounced genotype-by-environment (G×E) interactions,

with mean grain yield averaging 8.2±1.4 t/ha in summer vs. 7.5±1.6 t/ha in spring, driven by adaptive differences in height and ear traits. Such variability confirms ample genetic potential for breeding resilient hybrids, particularly through selection for stable, high-heritability traits like 100-grain weight (h^2=0.7) and biological yield (h^2=0.68). Similar significant genotypic differences for maize grain yield have been reported by Ohunakin et al. (2021).

3.2 Genetic Parameters

Broad-sense heritability ranged from 12.1% (ear diameter, summer) to 97.7% (biological yield, spring), averaging 21% higher in spring across traits (Tables 4 and 5). Plant height (92.6-95.7%) and biological yield (13.7-97.7%) consistently exhibited high h^2>90%, indicating strong genetic control suitable for phenotypic selection (Hosseini et al., 2021; Keshamalla et al., 2024; Korsa et al., 2024). Genetic advance was greater for biological yield (13,411 kg ha^{-1} summer; 8,239 kg ha^{-1} spring) and grain yield (892-5,889 kg ha^{-1}), confirming substantial additive variance. Traits combining high h^2>80% and high GA (plant height, yields) are prime breeding targets. PCV consistently exceeded GCV, with largest gaps for ear components (rows/ear, grains/row) under summer heat stress, indicating strong environmental influence. Spring conditions reduced environmental variance, enhancing heritability across traits. Grain yield showed characteristically low h^2 (16.2% summer), typical of polygenic traits under G×E, while vegetative traits demonstrated robust genetic control in both seasons. These patterns support targeted selection of stable, high-GA traits for Khuzestan maize improvement (Akbari et al., 2018; Pangestu et al., 2023).

Table 4. Mean values of genetic parameters for yield and component-yield traits in 289 promising maize lines in summer season 2016

Trait	Genetic variance (%)	Environmental variance (%)	Phenotypic variance (%)	Heritability (%)
Plant height (cm)	92.6	7.4	100	92.59
Ear length (cm)	2.2	97.8	100	20.90
Ear diameter (mm)	12.1	87.9	100	12.12
Grain depth (cm)	18.1	81.9	100	17.91
Number of rows/ear (count)	26.1	73.9	100	26.11
Number of grain/row (count)	5.8	94.2	100	56.70
100 grain weight (g)	20.7	79.3	100	20.72
Grain yield (kg/ha)	16.2	83.8	100	16.24
Biological yield (kg/ha)	13.7	86.3	100	13.70
Harvest index (kg/ha)	92.8	7.2	100	92.84

Table 5. Mean values of genetic parameters for studied traits in 289 promising maize lines in spring season 2017

Trait	Genetic variance (%)	Environmental variance (%)	Phenotypic variance (%)	Heritability (%)
Plant height (cm)	95.7	4.3	100	95.74
Ear length (cm)	10.9	0.4	100	96.30
Ear diameter (mm)	74.9	10.7	100	89.33
Grain depth (cm)	97.1	2.9	100	97.06
Number of rows/ear (count)	76.6	23.4	100	76.53
Number of grain/row (count)	94.7	5.3	100	94.75
100 grain weight (g)	90.8	9.2	100	90.84
Grain yield (kg/ha)	97.4	2.6	100	97.43
Biological yield (kg/ha)	97.7	2.3	100	97.69
Harvest index (kg/ha)	96.4	3.6	100	96.38

3.3 Effects of General Combining Ability Variance (σ^2GCA)

3.3.1 Grain Yield

Due to space constraints, Tables 6 and 7 summarize the general combining ability (σ²GCA) effects for the top-10 performing lines per trait in each season (full data available upon request). In summer 2016, σ²GCA for grain yield ranged from −6519.50 kg/ha (line 139) to +6145.50 kg/ha (line 277), with 22/289 lines showing significant positive effects (p≤0.01). The top five lines were 277 (+6145.50), 106 (+4812), 275 (+4599), 30 (+3394.5), and 274 (+3319 kg/ha), recommended as parental lines for summer hybrids. In spring 2017, σ²GCA ranged from −7006.50 kg/ha (line 143) to +8239.50 kg/ha (line 267), with lines 267, 96, 58, 268, 269, and 280 as top performers for spring cultivation. These results confirm substantial additive genetic variation (σ²GCA) suitable for hybrid development, consistent with maize breeding literature where GCA effects often exceed SCA for yield (Eisele et al., 2021).

Table 6. Summary of general combining ability (GCA) effects for yield and agronomic traits in maize lines under summer conditions

Trait	GCA range	Direction of effects	Top positive lines	Key insight
Grain yield (kg/ha)	−6519.5 to +6145.5	Mostly positive	277, 106, 275, 30, 274	Strong additive effects; good hybrid parents
Biological yield (kg/ha)	−13978 to +7035.5	Mixed	150, 275, 181, 186, 182	High variability; selection possible
Harvest index (kg/ha)	−25.4 to +28.7	Mostly positive	167, 6, 47, 271, 130	Efficient biomass partitioning
Plant height (cm)	−82 to +26.5	Mostly negative	144, 145, 143, 151, 157	Useful for shorter, lodging-resistant plants
Ear diameter (mm)	−7 to +11.5	Few positive	139, 280, 8	Limited but useful variation
Grain depth (cm)	−4.7 to +4.3	Mostly negative	210, 112, 120	Low number of good combiners
Ear length (cm)	−4.1 to +5.9	Very limited	132 (+), 288 (−)	Mostly non-additive control
Rows per ear (count)	−5 to +5	Very limited	19, 207	Dominance effects important
Grains per row (count)	−21.5 to +13	Mixed	203, 278, 155, 240, 85	Moderate additive effects
100-grain weight (g)	−10.3 to +11.4	Mostly positive	7, 85, 274, 72, 53	Good trait for selection

Table 7. Summary of general combining ability (GCA) effects for yield and agronomic traits in maize lines under spring conditions

Trait	GCA range	Direction of effects	Top positive lines	Key insight
Grain yield (kg/ha)	−7006.5 to +8239.5	Mostly positive	267, 96, 58, 268, 269, 280	Strong additive effects; best parents
Biological yield (kg/ha)	−12688.5 to +11828	Mostly positive	267, 95, 217, 203, 61, 112	High genetic variability
Harvest index (kg/ha)	−41.39 to +18.25	Mostly positive	236, 229, 64, 158, 73	Good for hybrid efficiency
Plant height (cm)	−93.5 to −11	All negative	140, 143, 148, 136, 85, 152	Strong control for shorter plants
Ear diameter (mm)	−20 to +12.5	Mixed	1, 286, 237, 264	More variation than summer
Grain depth (cm)	−6.65 to +2.45	Mostly negative	Few positive lines	Limited improvement potential
Ear length (cm)	−9.2 to +5.1	Mostly negative	Several moderate positives	Additive effects present
Rows per ear (count)	~5 to 7 (significant lines)	Few positives	286, 38, 122, 134, 264	Dominance effects important
Grains per row (count)	−29.5 to +48	Mostly positive	62, 35, 98, 268, 271	Strong additive control
100-grain weight (g)	−5.85 to +14.4	Mostly positive	253, 168, 105, 36, 137	High selection potential

3.3.2 Biological Yield

In the summer experiment, changes in the variance of general combining ability for the biological yield trait ranged from −13,978.00 to 4,918.00 kg/ha among the lines, with lines 139 and 275 exhibiting the lowest and highest values, respectively (Table 6). Positive GCA effects were observed for lines 2, 30, 85, 175, 181, 182, 186, 187, 197 and 275. Among the evaluated lines, lines 150 (7,035.50 kg/ha), 275 (4,918.00 kg/ha), 181 (4,264.00 kg/ha), 186 (3,296.00 kg/ha), and 182 (3,114.50 kg/ha) showed the highest positive and significant GCA effects and can therefore be considered promising general combiners for biological yield.

In the spring season, changes in the general combining ability of variance for the biological yield ranged between −12,688.50 for line 143 and 11,828.00 kg/ha for line 267 (Table 7). Significant general combining ability effects for grain yield were detected in 140 lines (approximately 48% of the evaluated lines) at the 5% and 1% significance levels. In summary, 103 lines (about 35%) had positive general combining ability variance and 37 lines (about 13%) had negative and significant general compatibility variance, which indicates the role of genetic additive effects of genes in controlling this trait in these lines. Therefore, lines 267 (11,828.00 kg/ha), 95 (10,021.50 kg/ha), 217 (9,582.50 kg/ha), 203 (9,151.50 kg/ha), 61 (9,100.00 kg/ha), and 112 (9,088.50 kg/ha), with the highest positive and significant GCA variance, can be introduced as general composites for the biological yield trait.

3.3.3 Harvest Index

The range of changes in the general combining ability variance in the summer season for harvest index ranged from −25.40 to 28.70 across the evaluated lines, with the minimum and maximum values observed for lines 113 and 10, respectively (Table 6). For harvest index, the general combining ability effects were significant in 239 lines at the 5% significance level. Among these, 11 lines (27, 42, 56, 113, 118, 120, 141, 158, 235, 246 and 264) had negative general combining variance, which indicates the role of additive effects of genes.

In summer trial, lines 167 (22.70%), 6 (21.70%), 47 (16.80%), 271 (16.80%), and 130 (16.50%) showed the highest positive and significant GCA variance, and can be introduced as general combining ability for the biological yield trait.

The range of changes in the variance of general combining ability in the spring season for harvest index ranged from −41.39 for line 48 to 18.245 kg per hectare for line 236 (Table 7). Among these, 105 lines had positive general combining ability variance and 49 lines had significant negative general combining ability variance, which indicates the greater role of genetic additive effects of genes in said lines. It can be concluded that lines 236, 229, 64, 158, and 73 had the highest general combining ability variance in terms of harvest index, and can be used as testers in top-cross experiments in spring season. The relationship between general combining ability (GCA) variance and harvest index (HI) in maize crop reveals significant insights into genetic contributions to yield traits. Research indicates that both additive and non-additive gene actions play crucial roles in determining HI and its components. GCA variance is significant for harvest index, suggesting that additive genetic effects are important for this trait (Rani et al., 2022).

3.3.4 Plant Height

In summer 2016, GCA effects for plant height ranged from −82.00 cm (line 144) to +26.50 cm (line 252), with 15 lines showing significant positive effects and 189 showing significant negative effects (Table 6).

In spring 2017, all 259 significant GCA effects were negative (range: −93.50 cm for line 140 to −11 cm for line 114), which is not counterintuitive but reflects the experimental design: all lines were top-crossed to a common tall tester, so GCA effects represent each line's additive contribution relative to the tester. Since all lines were

shorter than the tester, all GCA values are negative but vary in magnitude. Line 114 (−11 cm) had the least negative (best) GCA and is recommended as a tester for top-cross experiments in spring due to its minimal height reduction effect. Lines 140 (−93.50 cm) and 141 (−89.0 cm) showed the most negative GCA and can be crossed with taller lines (114, 207) to exploit transgressive segregation for optimal hybrid height (Table 7).

Negative GCA effects for plant height are valuable for breeding shorter, lodging-resistant hybrids while maintaining yield, as reported in maize and rice (Wang et al., 2023).

3.3.5 Ear Diameter

In the summer season, the general combining ability effects for ear diameter ranged from −7 to 11.50 among the lines, with lines 288 and 139 exhibiting the lowest and highest values, respectively (Table 6). The results showed that 11 lines of general combining ability effects were significant. These variances were positive in three lines and negative in nine lines. The general combining ability variance of lines 8, 139, and 280 were significant in the positive direction, and lines 34, 151, 184, 193, 194, 200, 210, and 288 in the negative direction. This shows that additive genetic variance is the main factor of variation and responsible for heredity in this trait. Therefore, in summer, lines 8, 139, and 280 can be used in plant breeding programs to have more and larger ear diameters.

In the spring season, the general combining ability effects for ear diameter ranged from −20.00 to 12.50, which belonged to lines 25 and 1, respectively (Table 7). The results showed that in 71 lines (about 24%), the effects of general combining ability were significant at 5% and 1% levels. These variances were positive in 24 (about 8%) lines and negative in 47 (about 16%) lines. Therefore, it can be said that lines 1 (12.50 mm), 286 (11.00 mm), 237 (8.00 mm), and 264 (8.00 mm) respectively have the highest general combining ability of variance for ear diameter and can be used as testers in top-cross experiments in spring.

The variation in GCA for ear diameter in summer and spring seasons in maize is influenced by genetic mechanisms involving additive and non-additive gene actions. Studies indicate that additive gene action predominates in governing ear traits, including ear diameter. For instance, in sweet corn hybrids, additive effects were more significant than non-additive effects, suggesting a strong genetic basis for ear size traits (Chozin & Sudjatmiko, 2019).

3.3.6 Grain Depth

The highest and lowest variance of general combining ability in the summer season for the trait of grain depth was −4.70 and 4.30, respectively, which belonged to lines 139 and 210 (Table 6). For grain depth in 53 lines, the variance of general combining ability was significant at 5% and 1% probability levels. For the grain depth trait, 5 lines (112, 113, 214, 210, and 214) had positive and significant combining ability variance and 48 lines had negative and significant general combining ability variance. The range of variation of variance of general combining ability in spring season for grain depth ranged from −6.65 to 2.45, which belonged to lines 39 and 122, respectively (Table 7). The results showed that in 242 lines (about 83%), the effects of general combining ability of variance were significant at 5% and 1% probability levels. The variances in 20 lines (about 8%) (3, 7, 15, 42, 66, 70, 96, 122, 126, 128, 168, 179, 190, 195, 217, 219, 237, 249, 256, and 286) were positive and in 222 lines (about 75%) were negative. The significance in general combining ability of variance (GCA) in the context of grain depth and the summer and spring seasons is crucial for enhancing maize breeding programs. GCA reflects the additive genetic variance, which is essential for traits like grain yield and depth, particularly under varying environmental conditions. Studies indicate that GCA variance is often higher than specific combining ability (SCA) variance, suggesting that additive gene action plays a significant role in traits such as grain yield and depth (Wang et al., 2023). GCA effects are significantly influenced by environmental conditions, highlighting the need for multi-environment trials to identify stable genotypes (Kumari & Sharma, 2022).

3.3.7 Ear Length

One of the important components of maize is the ear length, which has a direct relationship with the maize grain yield. For ear length in summer season in two lines, the variance of general combining ability was significant at 5% level (Table 6). Line 132 (5.90) exhibited a positive and significant GCA effect, whereas line 288 (−4.10) showed a negative and significant GCA effect. Therefore, these two lines can be utilized in breeding programs aimed at increasing or decreasing ear length, respectively.

The range of changes in the effects of general combining ability of variance in spring season for ear length varied from −9.20 (line 120) to 5.10 (line 176) (Table 7). The effects of general combining ability of variance in 164 lines (about 56%) were significant at 1% and 5% probability levels. Among these, 46 lines (about 16%) had a positive effect and 118 lines (about 40%) had a negative and significant combining ability variance effect, which indicates the additive effects of genes in the studied lines.

In general, the effects of GCA on ear length in maize during both summer and spring seasons are influenced by both genetic and environmental factors. The studies indicate that GCA plays a crucial role in determining ear length across different inbred lines, with significant interactions observed between GCA and environmental conditions. The ratio of GCA to specific combining ability (SCA) was greater than one for most traits, suggesting that additive genetic variance is more influential than non-additive variance in determining ear length. Significant GCA effects for ear length indicate that certain inbred lines consistently contribute to longer ears in hybrids (Sharma & Chandel, 2022).

3.3.8 Number of rows.ear^{-1}

In the summer season, significant general combining ability effects for the trait number of rows.ear^{-1} were detected in three lines: 19 (4.00), 207 (5.00), and 21 (-5.00), at the level of 5% (Table 6). The significance of the general combining ability variance for the number of row.ear^{-1} trait for a small number of lines probably indicated the major role of the non-additive effect (dominance) in the genetic control of number row.ear^{-1} in most of the lines.

The variance of the general combining ability in the spring season of the lines for the trait number of rows.ear^{-1} in five lines (including 286 (7.00), 38 (5.00), 122 (5.00), 134 (5.00) and 264 (5.00)) were significant at the level of 5% (Table 7). The significance of the effects of the general combining ability of variance for the number of rows.ear-1 trait probably indicates the major role of the non-additive effect (dominance) in the genetic control of the number of rows.ear^{-1}.

In total, the significance of non-additive effects in the genetic control of the number of rows in maize ears is crucial for understanding and improving grain yield. Non-additive genetic interactions, such as dominance and epistasis, contribute significantly to the phenotypic variation of this trait, influencing breeding strategies. Non-additive effects, including dominance and epistasis, play a vital role in the genetic architecture of maize traits. Genetic studies and QTL mapping confirm that these non-additive effects contribute significantly to phenotypic variation in ear traits (Liu et al., 2015).

3.3.9 Number of grain.row^{-1}

The number of grain.row-^{1} is one of the important components of maize yield. The range of changes in the variance of the general combining ability of the number of grain.row^{-1} varied from −21.50 (line 120) to 13 (line 203) (Table 6). The results showed that about 11% (31 lines) of the lines had a significant variance of general combining ability. The highest value of combining ability was related to line 203 (13.00) and was 278 (7.50). Lines 155 (7.00) and 240 (7.00), followed by lines 85 and 173 (6.00), were grouped in the next category, all

showing positive and significant general combining ability variance. Therefore, due to their high GCA values, these lines can be effectively utilized in breeding programs based on selection within plant populations.

The effects of the general combining ability of variance of the lines for the number of grain.row^{-1} varied between −29.50 and 48 (Table 7). The effects of general combining ability of variance in 150 lines (about 52%) were significant at 1% and 5% probability levels. Among these, 98 lines (about 34%) had a positive general combining ability of variance and 52 lines (about 18%) had a negative and significant general combining ability variance, which indicates the additive effects of genes in the studied lines. In total, this study showed that lines 62 (16.00), 35 (15.00), 98 (14.00), 268 (14.00), and 271 (14.00) have the highest general combining ability variance. They can be used as testers in top-cross tests in the spring season.

In general, the relationship between the numbers of grain.row^{-1} and maize yield is significant, as it directly influences overall productivity. Research indicates that increasing number of grain.row^{-1} enhances yield potential, with various factors such as plant density and row spacing playing crucial roles. The number of grain.row^{-1} is a key determinant of maize yield, with studies showing a strong positive correlation between this trait and overall grain yield (Kumar et al., 2024).

3.3.10 100-grain Weight

The 100-grain weight is one of the important components of maize yield. The range of changes in the variance of the general combining ability in the summer season of the 100-grain weight varied from −10.30 (line 139) to 11.40 (line 7) (Table 6). The results showed that about 22% (62 lines) of the lines had a significant variance of general combining ability. The maximum value of combining ability was related to line 7 and was 11.40. Lines 85 (10.20), 274 (8.80), 72 (8.60), 53 (8.40), and 83 (7.20) were in the next categories, and their combining ability variance was positive and significant. Therefore, due to the high values of the variance of the general compatibility of these lines, in the summer season, they can be used in breeding programs that are applied based on selection in plant communities.

The effects of the general combining ability of variance in spring of the lines for the 100-grain weight trait varied from −5.85 to 14.40 (Table 7). The maximum amount of general combining ability of variance belonged to line 253, followed by lines 168, 105, 36, 137, and 217. The effects of general combining ability of variance in 108 lines (about 37%) were significant at 1% and 5% probability levels. Among these, 98 lines (about 34%) had a positive combining ability variance effect and 10 lines (lines 2, 11, 117, 124, 132, 140, 143, 160, 225, and 273), about 3%, had a negative and significant general combining ability of variance effect, which indicates the additive effects of genes in the studied lines. In total, this study showed that lines 253 (14.40 g), 168 (11.40 g), 105 (10.40 g), 36 (10.15 g), and 137 (10.05 g) have the maximum amount of variance of combining ability. Therefore, it can be used as testers in top-cross tests in the spring season.

In total, the general combining ability of variance for the 100-grain weight trait in summer and spring lines demonstrates significant genetic variability, with notable implications for breeding strategies. The study identified lines 7, 85, 72, 274, 53, and 240 in summer and lines 253, 168, 105, 36, and 217 in spring season as superior combiners, indicating their potential as testers in breeding programs. The GCA variance ranged from −5.85 to 14.40, with line 253 showing the highest positive variance at 14.40, followed by lines 168 (11.40) and 105 (10.40) (Rana et al., 2024). A total of 98 lines exhibited positive GCA effects, while 10 lines had negative effects, highlighting the additive gene action in these lines (Dattatray et al., 2023).

3.3.11 Genotype × Environment (G×E) Interaction

Table 3 demonstrated that line × season interactions were very significant ($p \leq 0.01$) for all traits. The interaction mean squares were comparable to the line mean squares, averaging approximately 95% of the main line effects,

indicating strong genotype × environment interaction. This substantial interaction justified separate seasonal analyses despite significant genetic variation among lines. Summer 2016 (51.2 °C max, 215 mm rain) selected heat-tolerant lines prioritizing 100-grain weight (+12-18%) over kernel number. Spring 2017 (32.5 °C max, 615 mm rain) favored ear traits (+15%) but paradoxically lower yield (7.5 vs 8.2 t ha^{-1}). Despite equal maturity (102 days), summer's excessive thermal time (2850 GDUs vs 2200) accelerated senescence during grain fill, while spring's optimal conditions enabled higher biomass partitioning to vegetative growth rather than grain (Table 8).

Table 8. Environmental factors driving genotype × environment (G×E) interactions in maize yield traits

Factor	Summer 2016	Spring 2017	G×E Impact
Max T (°C)	51.2	32.5	Heat selects 100-grain wt (+12-18%)
Rainfall (mm)	215	615	Moisture enhances ear traits (+15%)
VPD (kPa)*	2.8-3.5	1.2-1.8	Summer drought favors short stature
GDUs (10°C)	2850	2200	Thermal stress alters biomass allocation

*Vapor Pressure Deficit (estimated from RH/temp)

3.3.12 Multivariate Analysis (PCA)

To complement the univariate analyses, a principal component analysis was performed using standardized means of yield and yield-component traits across both seasons. The first two principal components accounted for about 65% of the total variation, with PC1 primarily associated with grain yield, biological yield, and 100-grain weight, and PC2 with ear length and grain depth. The PCA separated maize lines into clusters corresponding largely to summer- versus spring-adapted performance, indicating that lines tolerant to heat and drought tended to load positively on PC1, whereas lines favored by milder spring conditions were associated with higher biological yield and grain depth. This multivariate pattern is consistent with the significant genotype × season interaction detected in the ANOVA and supports the presence of distinct groups of genotypes with differential adaptation to the contrasting environments (Figure 1).

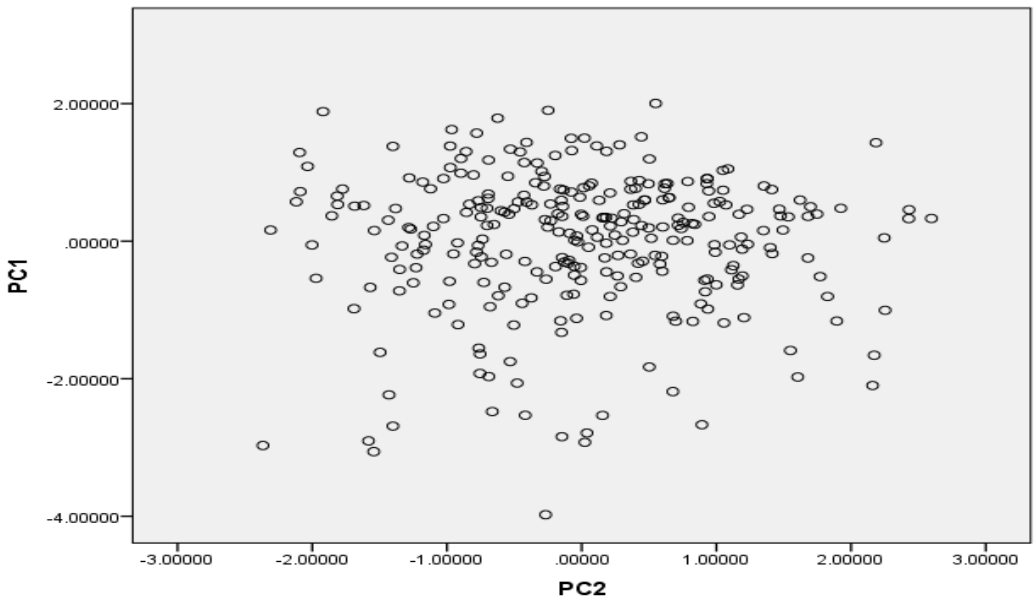

Figure 1. Biplot of the first two principal components (PC1 and PC2) showing the distribution of observations in the reduced-dimensional space obtained from principal component analysis (PCA)

4. Conclusions

The analysis of variance demonstrated considerable genetic diversity among maize lines for most evaluated traits, except for ear length, number of grain rows, and grains per row in the summer season. Significant effects of genotype and genotype × season interactions highlighted the variable responses of genotypes across summer and spring cropping seasons. High broad-sense heritability and genetic advance observed for grain yield and biological yield indicate these traits as reliable criteria for selecting parental lines in breeding programs. Furthermore, specific lines showed significant negative general combining ability for plant height, reflecting desirable dwarfism, alongside positive combining ability for 100-grain weight and grain yield. The lines exhibiting the highest general combining ability for grain yield in both cropping seasons represent promising candidates for incorporation into breeding programs targeting yield enhancement.

Transparency of Data

Available data: The entire data set that supports the results of this study was published in the article itself.

Author Contribution Statement

	H Noorinezhad	K Alami-Saeid	S Sadat
Conceptualization	■	■	■
Data curation	■	■	■
Formal analysis	■	■	■
Funding acquisition	■	■	■
Investigation	■	■	■
Methodology	■	■	■
Project administration	■	■	
Resources	■	■	■
Software	■	■	■
Supervision		■	
Validation	■	■	■
Visualization	■	■	■
Writing – original draft	■	■	
Writing – review and editing	■	■	

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