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RESEARCH ARTICLE

Assessing genetic variability in maize inbred lines and hybrids for enhanced agronomic performance under high density planting conditions

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Abstract

Planting density plays an important role in enhancing maize productivity, but tolerance to high-density planting remains limited in several commercial hybrids. Therefore, developing hybrids with high-density tolerance is essential to meet global population increase and climate challenges. This study aimed to assess the combining abilities of newly developed maize lines, identify promising hybrids and investigate gene action controlling key traits under low and high-density planting conditions. Seven maize inbred lines were crossed using a half-diallel mating design to develop 21 F_1 hybrids, which were evaluated alongside a commercial hybrid (SC-10) over 2 seasons at low (57143 plants/ha) and high (95238 plants/ha) planting densities. Results showed significant differences in traits due to planting density and hybrid type. High-density reduced ear length, kernel number, ear diameter and kernel weight by 11.7, 18.2, 6.3 and 13.17 respectively compared to low-density. Otherwise, it increased plant height, days to silking and grain yield per ha by 11.2, 3.7 and 16.0% respectively, compared to low-density. Lines L1, L2, L5 and L6 exhibited strong general combining ability for improving grain yield under high-density conditions, while L1 and L3 were identified as good combiners for early maturity. Hybrids L2 × L6, L3 × L5, L4 × L7 and L6 × L7 demonstrated significant specific combining ability for increasing maize productivity under high-density. Additionally, L3 × L5 and SC-10, showed high tolerance to density stress. These hybrids are recommended for further testing for potential commercial cultivation, offering valuable insights for developing maize hybrids that adapted under dense planting and contribute to sustainable agriculture.

Keywords

gene action; high-density tolerance; high-yielding hybrids; hybrid performance; inbred lines; maize breeding; yield traits

Introduction

Maize (*Zea mays* L.) is an essential cereal crop worldwide, serving as a critical resource for food security (1). As a staple food, maize is integral to millions of people diets and is a vital component in animal nutrition due to its high energy and protein content (2). Besides, it is a crucial ingredient in various processed foods and industrial products such as ethanol and bioplastics (3). Maize is cultivated on approximately 203.47 million ha worldwide, producing 1.16 billion tons of grain annually (4). Despite the rising maize production, the world is projected to face significant food shortages in the coming decades due to the rapid increase in global population and adverse impacts due to climate change. In Egypt, maize is essential for food security, yet a considerable gap exists between consumption and production (5). Limited arable land, inefficient farming practices, inadequate crop densities and climate challenges contribute to this shortfall, increasing reliance on imports (6). Therefore, improving crop management practices and developing high-yielding maize hybrids are crucial to narrowing this gap.

Planting density is a crucial factor significantly influencing maize yield (7). Modern maize hybrids are designed to be more efficient in nutrient and water use and tolerate higher planting densities (8). However, the optimal planting density varies based different factors such as genetic traits, soil fertility, water availability and climatic conditions (9). Under low plant densities, maize plants generally have more access to resources such as light, water and nutrients, leading to increased individual plant growth and higher yield per plant (10). Conversely, high plant densities can lead to competition among plants for space, nutrients and light intensities, potentially resulting in reduced yields per plant (11). Increased lodging risk, prolonged anthesis-silking interval, weak kernel and more excellent rate of barrenness often cause this decline in yield (12, 13). However, higher planting densities can also increase number of ears per unit area, potentially boosting overall grain productivity (14). Previous studies have examined how modern hybrids respond to high planting densities, highlighting the importance of determining the optimal density for the newly developed maize hybrids (15-17).

Breeding efforts should focus on developing maize hybrids with enhanced tolerance to high planting densities. Understanding the combining ability of parent lines and the genetic factors influencing target traits is essential for developing hybrids that are both high-yielding and well-suited to dense planting conditions. General (GCA) and specific (SCA) combining abilities are pivotal for identifying effective parent lines and promising hybrids (18-20). The half-diallel mating design is frequently employed in maize breeding to evaluate SCA and GCA estimates (21-23). GCA is related to additive gene effects, while SCA refers to non-additive gene effects. Non-additive gene actions and additive play a pivotal role in inheritance of traits that impact grain yield (24-26). However, many studies suggest that non-additive effects influence these traits at low and high planting densities (27-29). Conversely, other research implies that additive gene action has more substantial role in grain yield inheritance (30, 31). These findings discrepancies may be due to variations in inbred lines utilized and plant densities applied during hybrid evaluations. This study aimed to (1) assess GCA of the parental lines and SCA of the developed hybrids under low and high plant density; (2) investigate gene action controlling grain yield contributing characters; investigate the interrelationship among the assessed traits and identify high-performing hybrids suitable for cultivation at elevated plant densities (3, 4).

Materials and Methods

Plant materials

Seven white maize lines were selected for their diversity in adaptive characteristics to high planting density and used as parental lines. Four inbreds were obtained from Agricultural Research Center in Egypt, while the remaining lines were sourced from CIMMYT. Detailed information regarding these lines is presented in Table 1. During summer of 2021, seeds of parental lines were divided and sown on 3 different dates (16, 23 and 30 May) to synchronize flowering times and ensure the production of adequate hybrid seeds. The parental lines were sown in rows 6 m long with a spacing of 0.70 m between rows. Within each row, 2 seeds were placed per hill 0.25 m apart. After the seedlings had fully emerged and before the initial irrigation, thinning was performed to leave one seedling per hill. All potential crosses between parental lines were performed using half diallel mating design, resulting in a total of 21 F_1 hybrids.

Field trail

The newly developed F_1 hybrids and check hybrid (SC-10, high-yielding commercial hybrid) were tested at low (57143 plants/ha) and high (95238 plants/ha) planting densities during the summer seasons of 2022 and 2023 at Kafr El-Sheikh Governorate, Egypt (31° 09'N, 30 °9'E). The soil analysis revealed that the soil profile comprised 52.08 % clay, 26.41 % silt and 21.51 % sand, with a 1.29 g/cm^3 bulk density. The pH and electrical conductivity were 7.9 of 2.14 dS/m. The organic matter was 1.45 % and the available nutrients were 29.3 mg N, 8.4 mg P and 423 mg K per kg of soil. The experimental site is arid, with high temperatures and a lack of rainfall during the summer seasons characterizes its climate. The meteorological data of experimental location are depicted in Table 2. Split plot design was utilized in 3 replicates. Main plots were designated for the 2 planting densities, while the subplots were allocated to different hybrids. Each subplot comprised 2 ridges, each 6 m long and 0.7 m wide. Two seeds were established per hill, with a spacing of 15 cm for high-density planting and 25 cm for low-density planting. Before the initial irrigation, the seedlings were thinned into a single plant per hill. Potassium, phosphorus and nitrogen fertilizers were added at 116 kg K_2O/ha, 76 kg P_2O_5/ha and 290 kg N/ha.

Table 1. Code, designation, pedigree and source of the seven maize inbred lines

Parent code	Designation	Pedigree	Source
L1	L4	G -13 AE	ARC- Egypt
L2	L17	G -268 Jellicarse (from R selection)	ARC- Egypt
L3	L53	Rg-8 g.s (Sanjuan x Ci 64) (SC.14)	ARC- Egypt
L4	L38	G-516 Improved by BC with (210 x K 61)	ARC- Egypt
L5	CML537	MAS [206/312]-23-2-1-1-B*5	CIMMYT- Mexico
L6	CML206	[EV7992#/EVPO44SRBC3]#BF37SR-2-3SR-2-4-3-BB	CIMMYT- Mexico
L7	CML211	[EV8449SR/POP62]#BF4SR-1-3SR-4-1-2-BB	CIMMYT- Mexico

Table 2. Monthly average minimum and maximum temperatures, relative humidity (R.H.) and precipitation (PERC.) in 2022 and 2023 seasons

Month	Minimum temperature (°C)	Maximum temperature (°C)	Relative humidity (%)	Precipitation (mm)
		First season (2022)		
May	16.93	32.95	53.85	0.0
June	21.33	36.62	53.04	0.0
July	22.28	37.72	53.53	0.0
August	23.42	37.58	55.52	0.0
September	22.40	36.35	55.36	0.0
		Second season (2023)		
May	17.28	32.86	52.17	0.0
June	21.01	36.39	52.28	0.0
July	23.38	39.78	52.53	0.0
August	23.74	38.08	55.29	0.0
September	23.51	37.78	54.20	0.0

Studied traits

Number of days from sowing until half of plants had visible silks was recorded as days to silking. The anthesis silking interval was scored as the period between 50% silking and 50% anthesis. Ear height was measured in centimetres from soil surface to base of highest ear while plant height was recorded in centimetres from soil to top of first tassel branch. Ten ears were randomly selected at harvest from each plot to assess ear length, number of kernels per row, ear diameter, number of rows per ear and weight of 1000 kernels. The plots were hand harvested and grain yield was estimated based on shelled grain weight, which was adjusted to a moisture content of 15.5 %. The grain yield per plot was then converted to tons per ha.

Stress tolerance indices and statistical analysis

Stress tolerance indices are quantitative measures used to evaluate the ability of studied genotypes to maintain productivity under stress conditions compared to optimal conditions, helping in identifying stress-tolerant genotypes. These indices were considered using grain yield means of hybrids under low planting density (Yp) and high planting density (Ys). The indices are defined as follows(32-34):

$$\text{Yield index} = \frac{\text{Ys}}{\text{Ys}}$$

$$\text{Geometric mean productivity} = \sqrt{Y_s \times Y_p}$$

$$\text{Mean productivity} = \frac{Y_s + Y_p}{2} \quad \text{Yield stability index} = \frac{Y_s}{Y_p}$$

$$\text{Stress tolerance index} = \frac{Y_s \times Y_p}{(Y_p)^2}$$

Hierarchical cluster analysis was performed using these indices to classify the assessed hybrids based on their tolerance level to high density. Variance analysis was applied using SAS software for split-plot design. Difference between means were explored using the Least Significant Difference (LSD) test at a 5 % significance level. GCA and SCA effects and their respective mean squares were estimated according to Griffing's Method 4, Model I (35). Principal component, cluster and heatmap analyses were applied using R statistical software version 4.2.2. The FactoMiner package was used for principal component analysis (PCA) and the heatmap package was used to perform heatmap (36, 37).

Results

Variance analysis

Variance analysis revealed that planting density, hybrids and their interaction (H × D) significantly affected all traits except for the interaction in the anthesis silking interval and number of rows per ear (Table 3). Additionally, most traits were significantly affected by the interactions among planting density and hybrids. Partitioning the hybrid effect into SCA and GCA components demonstrated that mean squares for both were significantly high across all analysed traits (Table 3). The GCA × D and SCA × D interactions were significant for most attributes, except for the anthesis-silking interval and the number of rows per ear. The GCA/SCA ratio was more than one for all traits, except for silking date, anthesis silking interval and 1000-kernel weight, revealing that additive gene effects mainly control the inheritance of these characters.

Performance of evaluated hybrids

Significant differences were detected among assessed maize hybrids across all measured traits under varying planting density conditions. High planting density caused a significant reduction in ear length, number of kernels per row, ear diameter, number of rows per ear and 1000-kernel weight by 11.7 %, 18.2 %, 6.3 %, 5.0 % and 13.2 %, respectively (Fig. 1). Conversely, it resulted in significant increases in days to silking, plant height, anthesis silking interval, ear height and grain yield per ha by 3.7 %, 11.2 %, 15.3 %, 12.3 % and 16.0 %, respectively compared to low-density conditions. The hybrids displayed significant genetic variation under low and high planting densities. Days to silking varied between 55.0 and 60.2 days (averaging 57.7 days) under low density and 56.2 to 63.5 days (averaging 59.8) under high density. Hybrids L1L1 × L3 and L2 × L3 showed the earliest flowering, while L2 × L6 and L4 × L5 were the latest under low and high planting densities respectively (Fig. 2A). Anthesis-silking interval fluctuated from 2.8 to 5.4 (average 3.9 days) under low density and from 3.16 to 5.57 (average 4.4 days) under high density. The lowest values of anthesis-silking interval were assigned for L2 × L6, L1L1 × L7, L1L1 × L5, L1L1 × L2, L3 × L5, L3 × L4, L3 × L6 and L5 × L6 under both densities. While the highest values were recorded by L4 × L6, L3 × L7, L2 × L4 and L5 × L7 under both densities (Fig. 2B). Plant height varied from 160.8 to 205.8 cm (average 178.1 cm) under low density and from 162.5 to 245.0 cm (average 198.0 cm) under high density. The tallest hybrids were L2 × L3 under low density and L5 × L6 under high density, whereas L3 × L7 was the shortest across both densities (Fig. 2C). Ear height followed a

Table 3. Mean squares and combining ability analysis for studied traits under both low and high plant density

Source of variation	DF	Days to silking	Anthesis-silking interval	Plant height	Ear height	Ear diameter
Year (Y)	1	38.89	16.83	2341	8610*	9.13
Replication/Y	4	3.23	2.58	113.3	55.02	1.88
Density (D)	1	250.0**	19.63*	26455**	10376**	6.44**
Y × D	1	12.89*	2.30	224.8**	5781**	0.18
Error a	4	0.88	2.04	8.66	28.08	0.19
Hybrid (H)	20	19.60**	5.39**	3323**	915.4**	0.77**
GCA	6	17.82**	4.09**	4092**	1231**	0.78**
SCA	14	20.37**	5.95**	2993**	779.9**	0.76**
H × Y	20	3.96**	0.22	3705**	447.0**	0.38**
GCA × Y	6	6.90**	0.08	6635**	495.9**	0.23**
SCA × Y	14	2.70	0.28**	2449**	426.1**	0.44**
H × D	20	4.04**	0.10	826.9**	192.9**	0.16**
GCA × D	6	1.76	0.10	698.2**	269.9**	0.19**
SCA × D	14	5.01**	0.11	882.0**	159. 9**	0.14**
H × D × Y	20	6.39**	0.26*	3448**	802.1**	0.12*
GCA × Y × D	6	5.98**	0.23	7354**	634.4**	0.08
SCA × Y× D	14	6.57**	0.27**	1773**	874.0**	0.14**
Error b	160	1.56	0.15	115.4	57.89	0.07
GCA/SCA		0.87	0.69	1.37	1.58	1.02
Source of variation	**DF**	**Ear length**	**Number of ows/ear**	**Number of kernels/row**	**1000-kernel weight**	**Grain yield**
Year (Y)	1	2.56	6.67	971.9*	169.4	131.0*
Replication/Y	4	6.82	1.06	124.1	2959	11.71
Densities (D)	1	260.4**	31.43**	3422**	130652**	148.9**
Y × D	1	11.33*	22.32**	302.7	155.6	29.07*
Error a	4	1.30	0.29	109.9	708.7	1.54
Hybrid (H)	20	27.15**	6.95**	53.89**	3479**	38.50**
GCA	6	35.52**	6.94**	74.26**	3299**	84.41**
SCA	14	23.56**	6.95**	45.16**	3556**	18.82**
H × Y	20	17.49**	6.46**	32.83**	419.4**	1.61**
GCA × Y	6	7.36**	9.70**	31.57**	280.9**	0.96**
SCA × Y	14	21.84**	5.07**	33.38**	478.7**	1.88**
H × D	20	10.05**	1.24	18.53**	3603**	0.63*
GCA × D	6	7.57**	1.11	22.02**	2923**	0.93**
SCA × D	14	11.12**	1.30	17.03**	3894**	0.50
H × D × Y	20	11.74**	4.61**	27.24**	1497**	1.36**
GCA × Y × D	6	11.35**	5.54**	24.76**	1679**	1.68**
SCA × Y × D	14	11.90**	4.21**	28.30**	1419**	1.22**
Error b	160	0.95	1.07	1.87	84.20	0.35
GCA/SCA		1.51	1.00	1.64	0.93	4.48

*and ** signify p value<0.05 and 0.01, in the same order .

similar trend, with averages of 101.1 cm under low density and 113.5 cm under high density, varying from 85.8 to 120.8 cm and 91.7 to 137.5 cm respectively (Fig. 2D). Hybrids L5 × L6 and L2 × L6 exhibited the uppermost ear placements, while L4 × L5 and L3 × L7 had the lowest under low and high densities respectively. Ear diameter averaged 5.1 cm under low density, fluctuating between 4.8 and 5.6 cm and 4.8 cm under high density, ranging from 4.1 to 5.5 cm (Fig. 2E). Hybrid L2 × L5 consistently exhibited the smallest ear diameter, while L1L1 × L4 had the largest across both densities (Fig. 2E). Ear length ranged from 14.1 to 20.9 cm under low density and 11.9 to 17.6 cm under high density, with hybrids L4 × L5 and L3 × L6 producing the extended ears under their respective conditions (Fig. 3A). Number of rows/ ear averaged 14.3 under low density and 13.6 under high density (Fig. 3B). Hybrids L6 × L7 and L3 × L5 displayed the highest row counts, while L3 × L7 and L2 × L4 had the lowest under their respective conditions. Number of kernels/row ranged from 32.0 to 43.7 (average 39.8) under low density and from 29.5 to 37.4 (average 32.5) under high density (Fig. 3C). Hybrid L5 × L7 produced the highest number of kernels/row, while L1L1 × L2 produced the lowest. The 1000-kernel weight ranged from 289.8 to 390.5 g (averaging 336.9 g) under low density and from 249.2 to 332.8 g (averaging 292.5 g) under high density (Fig. 3D). Hybrid L1L1 × L3 had the lowest 1000-kernel weight, while L6 × L7 had the highest across low and high density (Fig. 3D). Grain yield differed between 7.2 and 13.7 tons/ha (averaging 9.8 tons/ha) under low density and from 8.8 to 15.7 tons/ha (averaging 11.3 tons/ha) under high density (Fig. 3E). Hybrids L2 × L6 and L3 × L5 achieved the highest yields, while L3 × L7 and L4 × L6 recorded the lowest yields across both planting densities.

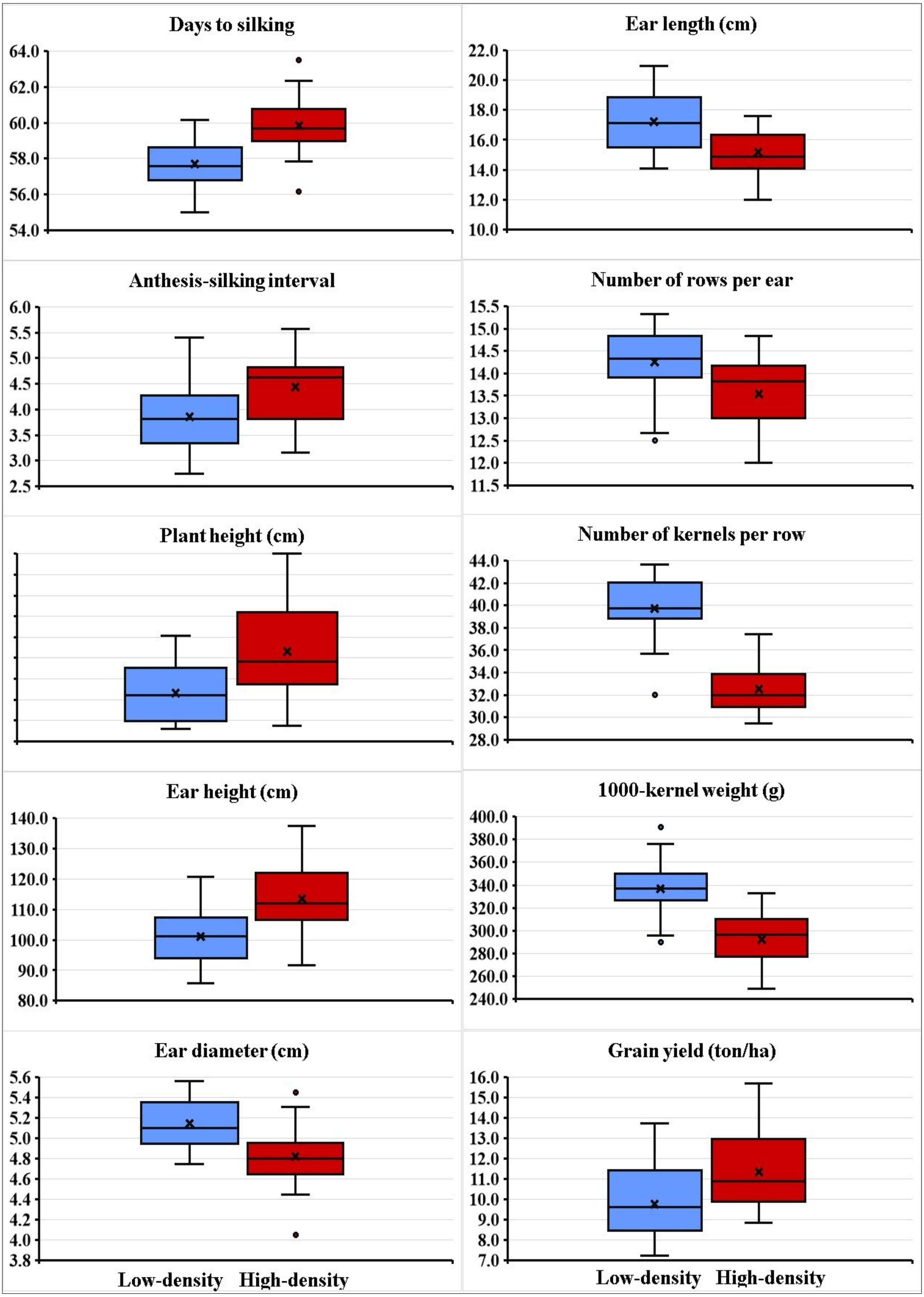

Fig. 1. Boxplots displaying the minimum, median, mean and maximum values for studied traits under low and high density.

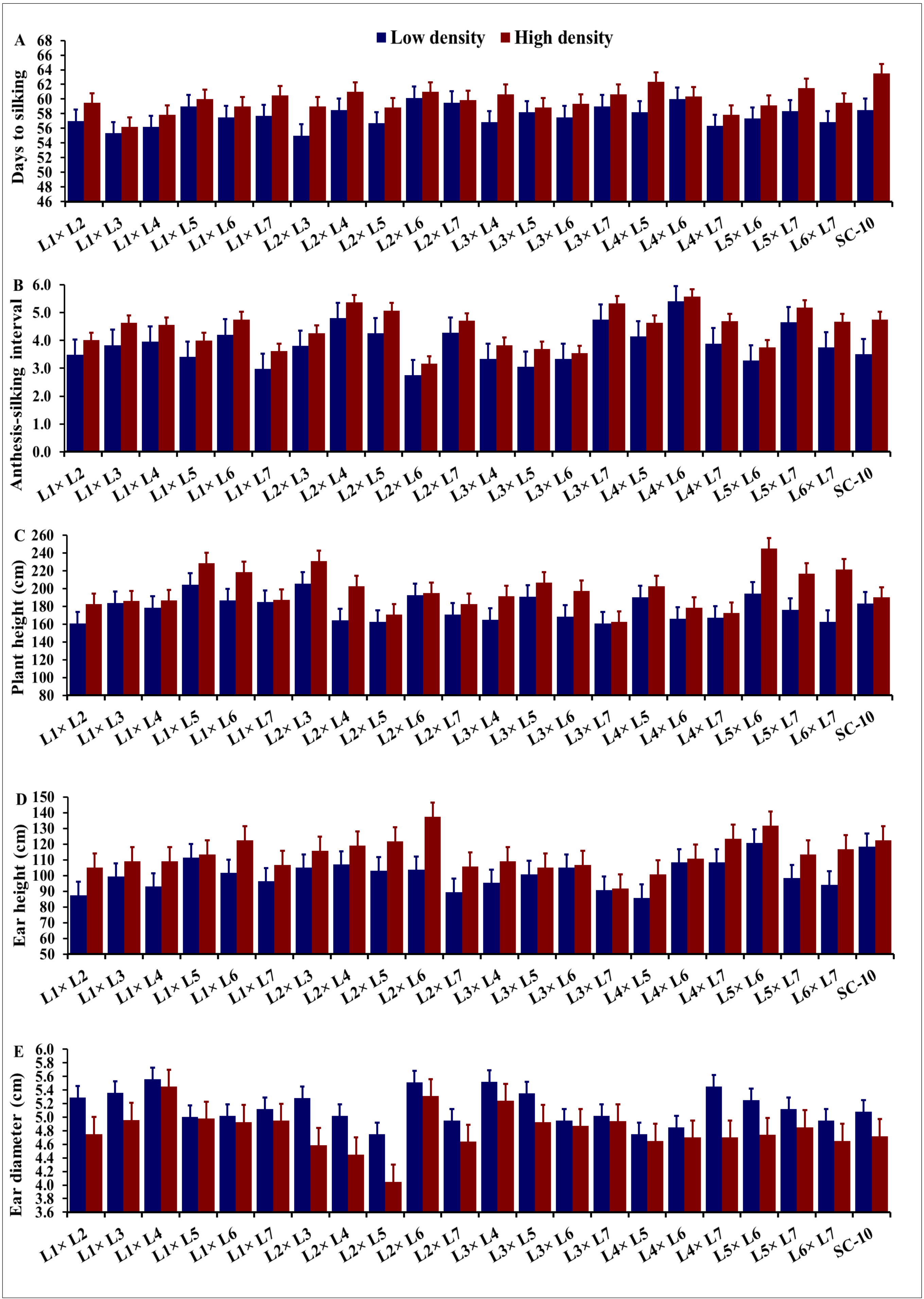

Fig. 2. Comparative performance of the assessed twenty-one hybrids and check hybrid under low and high density: Days to silking (**A**); anthesis silking interval (**B**); plant height (**C**); ear height (**D**); ear diameter (**E**). Least Significant Difference indicators at P<0.05 on the top of the columns.

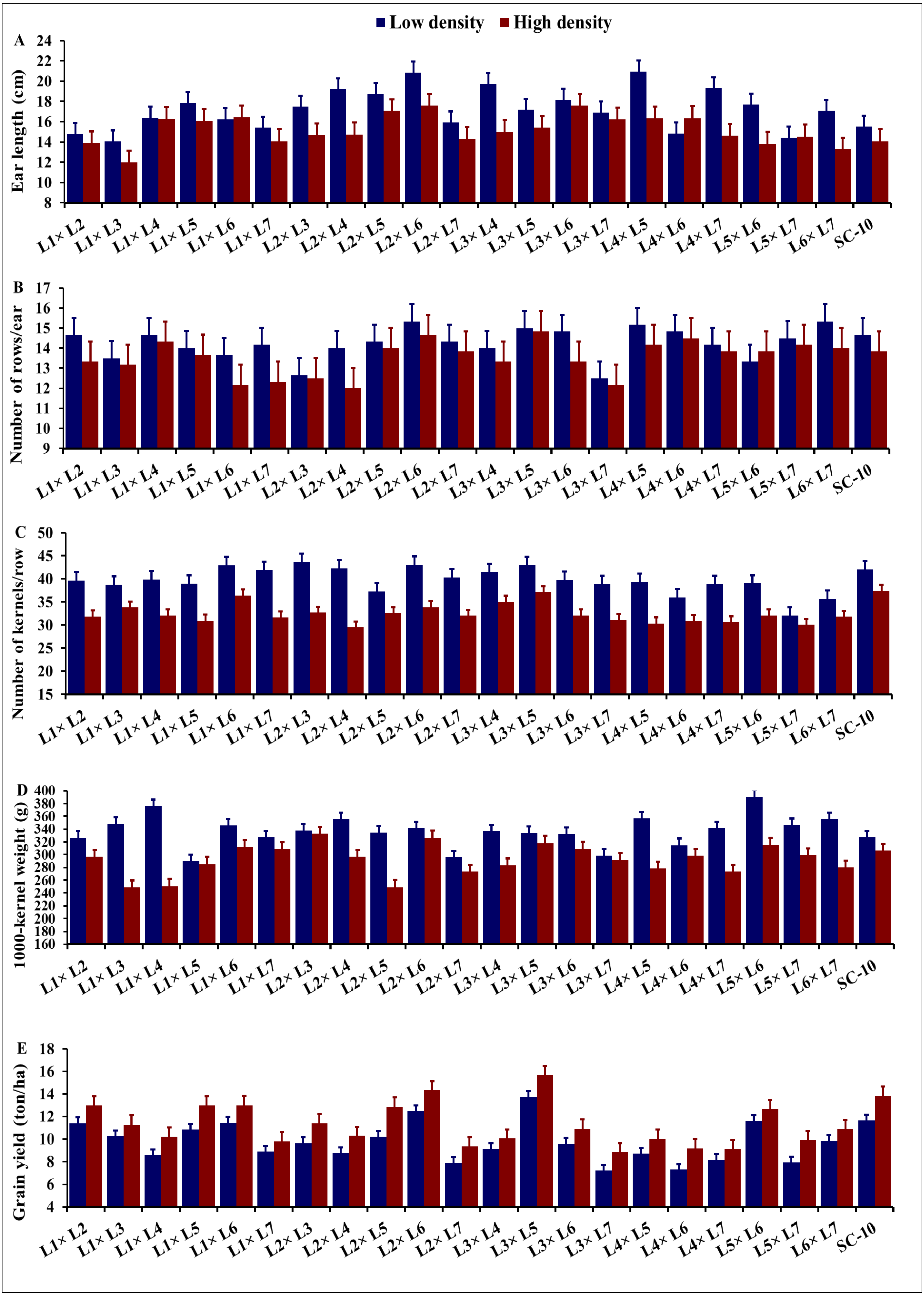

Fig. 3. Comparative performance of the assessed twenty-one hybrids and check hybrids under low and high density: Ear diameter (**A**); number of rows per ear (**B**); number of kernels per row (**C**); 1000-kernel weight (**D**); grain yield (**E**). Least Significant Difference indicators at P<0.05 on the top of the columns.

Stress tolerance indices and hybrids Classification

The responses of the developed hybrids to high plant density were evaluated using stress indices, including yield index, mean productivity, stress tolerance index, geometric mean productivity and yield stability index (Table 4). Based on these indices, the assessed hybrids and the commercial hybrid were grouped into 5 clusters as illustrated in Fig. 4. Group A consisted solely of L3 × L5, which exhibited the highest tolerance indices under high plant density conditions. Group B included 7 hybrids (L2 × L6, SC-10, L5 × L6, L1 × L2, L1 × L6, L1 × L5 and L2 × L5) which also demonstrated high tolerance indices. Group C comprised 4 hybrids (L3 × L6, L6 × L7, L1 × L3 and L2 × L3) with moderate tolerance indices. In contrast, Group D (L2 × L4, L1 × L4, L4 × L5, L1 × L7 and L3 × L4) and Group E (L3 × L7, L4 × L6, L5 × L7, L2 × L7 and L4 × L7) contained 10 hybrids with the lowest tolerance indices. Besides, the hybrids L3 × L5 (13), L2 × L6 (10) and SC-10 (22) were the least affected by high plat density because they had small numbers of average rank (blue color) in the heatmap (Fig. 5).

Table 4. Stress tolerance indices of newly developed 21 maize hybrids and commercial check hybrids evaluated under low and high density

Hybrid	Geometric mean productivity	Mean productivity	Stress tolerance index	Yield index	Yield stability index
L1 × L2	12.18	12.21	1.55	1.14	1.14
L1 × L3	10.75	10.77	1.21	0.99	1.10
L1 × L4	9.36	9.40	0.92	0.90	1.19
L1 × L5	11.86	11.91	1.47	1.14	1.20
L1 × L6	12.20	12.23	1.56	1.15	1.14
L1 × L7	9.33	9.35	0.91	0.86	1.10
L2 × L3	10.49	10.53	1.15	1.01	1.18
L2 × L4	9.49	9.52	0.94	0.91	1.18
L2 × L5	11.45	11.53	1.37	1.13	1.26
L2 × L6	13.36	13.39	1.87	1.26	1.15
L2 × L7	8.57	8.61	0.77	0.82	1.19
L3 × L4	9.57	9.59	0.96	0.89	1.10
L3 × L5	14.68	14.71	2.25	1.38	1.14
L3 × L6	10.23	10.25	1.09	0.96	1.14
L3 × L7	7.99	8.03	0.67	0.78	1.22
L4 × L5	9.35	9.37	0.91	0.88	1.15
L4 × L6	8.18	8.24	0.70	0.81	1.26
L4 × L7	8.62	8.63	0.78	0.80	1.12
L5 × L6	12.11	12.12	1.53	1.12	1.09
L5 × L7	8.86	8.92	0.82	0.87	1.25
L6 × L7	10.34	10.35	1.12	0.96	1.11
SC-10	12.70	12.75	1.69	1.22	1.19

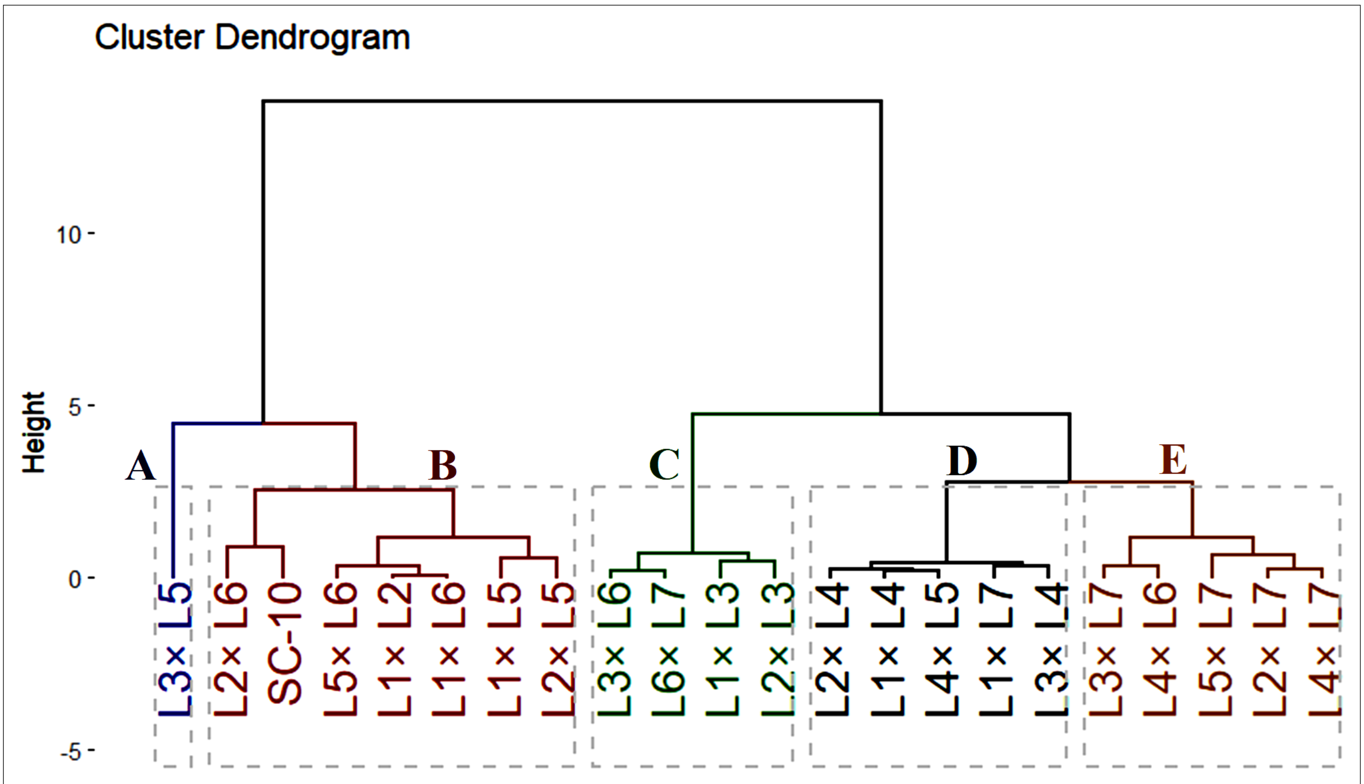

Fig. 4. Dendrogram depicting phenotypic distances among 21 hybrids and commercial check hybrids based on stress tolerance indices.

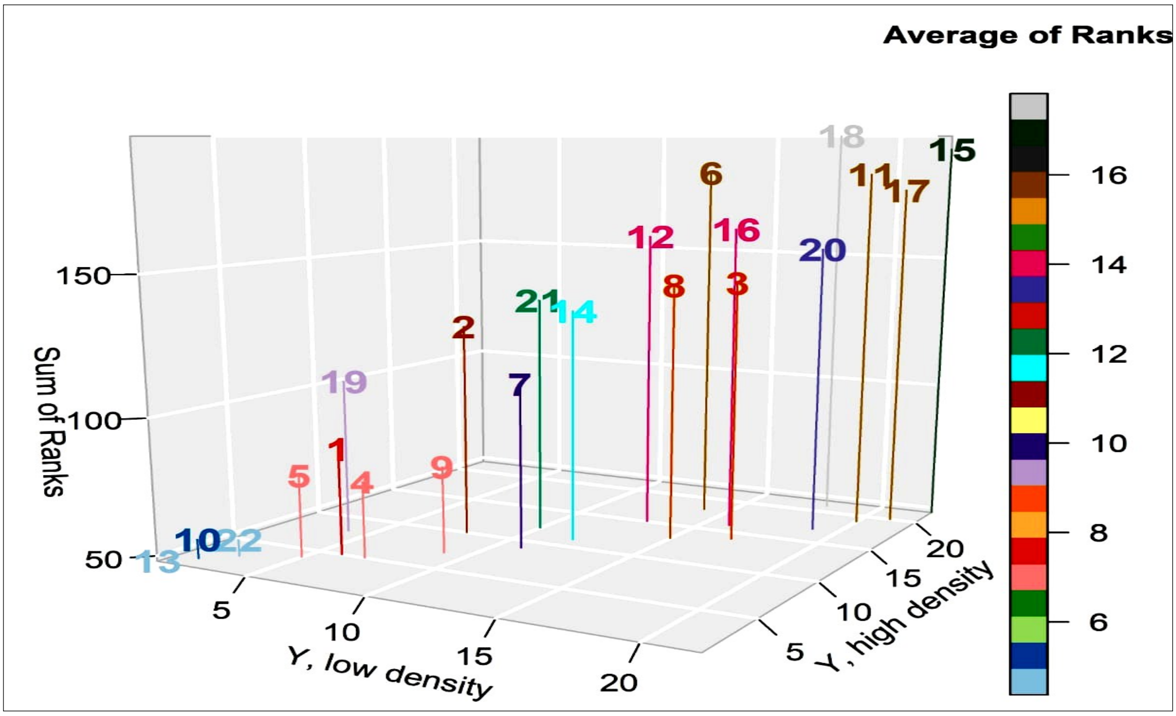

Fig. 5. Ranking of maize hybrids by tolerance to high density based on tolerance indices. Small numbers of average ranks mean less affected by late sowing (near graph bottom). **1:** L1 × L2, **2:** L1 × L3, **3:** L1 × L4, **4:** L1 × L5. **5:** L1 × L6, **6:** L1 × L7, **7:** L2 × L3, **8:** L2 × L4, **9:** L2 × L5, **10:** L2 × L6, **11:** L2 × L7, **12:** L3 × L4, **13:** L3 × L5, **14:** L3 × L6, **15:** L3 × L7, **16:** L4 × L5, **17:** L4 × L6, **18:** L4 × L7, **19:** L5 × L6, **20:** L5 × L7, **21:** L6 × L7 and **22:** SC10.

General combining ability

The GCA effects are illustrated in Fig. 6 & 7. For most traits studied, high positive GCA values are preferred, except for days to silking, anthesis-silking interval, ear height and plant height where high negative values are more desirable from a breeding perspective. The inbred lines L1 and L3 displayed negative and significant GCA effects for anthesis silking interval and days to silking under the 2 plant densities (Fig. 6). Likewise, L4 and L7 were identified as excellent combiners for plant height, showing negative GCA effects under low and high density. In addition, L7 had the highest negative GCA estimates for ear height. In contrast, positive and significant GCA estimated for ear diameter were noted for L3 under low density, while L1 under high density. Additionally, L2, L4 and L5 under low density and L6 under high density_showed significant and positive GCA estimates for ear length (Fig. 7). L5 showed advantageous GCA effects for number of rows/ear under high density. The inbreds L2 under low density while L6 under high density and L1 and L3 under both conditions exhibited the most substantial GCA effects for number of kernels/row. The highest GCA effects for the 1000-kernel weight were attributed to L4, L5 and L6 under low density and to L2, L3 and L6 under high density. Moreover, L1, L2, L5 and L6 exhibited the highest GCA effects and were identified as excellent combiners for grain yield across both plant densities.

Specific combining ability

The hybrid L2 × L3 documented the superior significant and negative SCA effects for days to silking and L6 × L7 under low density, while L1 × L3 and L1 × L4 under high density and L2 × L5, L4 × L7 and L5 × L6 across both plant densities (Table 5). For anthesis silking interval, the hybrids L1 × L7, L2 × L6, L3 × L4, L3 × L5 and L4 × L7 displayed the most significant negative effects. Likewise, favourable negative SCA estimates for plant height were attributed to L1 × L2, L2 × L5 and L3 × L6 under low density while L1 × L2, L2 × L5, L2 × L6, L3 × L7 and L4 × L6 under high density. Negative and significant SCA estimates for ear height were noted in the hybrids L1 × L2, L4 × L5 and L6 × L7 under low density conditions, while L1 × L2, L2 × L6, L3 × L6, L3 × L7, L4 × L5 and L4 × L6 exhibited similar effects high density conditions. On the other hand, the highest significant positive SCA effects for ear diameter were detected in L1 × L4 and L2 × L5 across the low and high plant densities respectively. The highest positive effects for ear length were noted in hybrids L1 × L5, L2 × L6 and L4 × L5 under low density, whereas in hybrids L1 × L4, L1 × L5, L1 × L6, L2 × L5 and L3 × L6 under high density. Furthermore, L3 × L5 under low density and L1 × L4, L2 × L6 and L3 × L5 displayed the strongest SCA effects for number of rows per ear. Regarding the number of kernels per row, the cross combinations L1 × L6, L1 × L7, L2 × L6 and L3 × L5 achieved the highest values under low density, while L1 × L6, L2 × L7, L3 × L4, L3 × L5 and L3 × L6 under high density. The hybrids L1 × L3, L1 × L4, L5 × L6 and L6 × L7 exhibited superior positive significant SCA effects for 1000-kernel weight under low density. The hybrids L1 × L2, L1 × L6, L1 × L7, L2 × L6 and L3 × L5 achieved similar effects under high density.

Additionally, hybrids L2 × L3, L2 × L4 and L5 × L7 displayed the uppermost significant positive SCA estimates for 1000-kernel weight across both densities. Furthermore, positive and significant SCA effects for grain yield were detected in L2 × L6, L3 × L5, L4 × L7 and L6 × L7 across the 2 plant densities. None of the assessed hybrids demonstrated ideal SCA estimates across all traits. Nevertheless, certain hybrids showed advantageous effects for grain yield and contributing attributes. Specifically, hybrids L2 × L6 and L3 × L5 stood out with their favourable SCA effects for number of rows per ear, number of kernels per row, 1000-kernel weight and grain yield, demonstrating their effectiveness as specific combiners under both low and high plant densities.

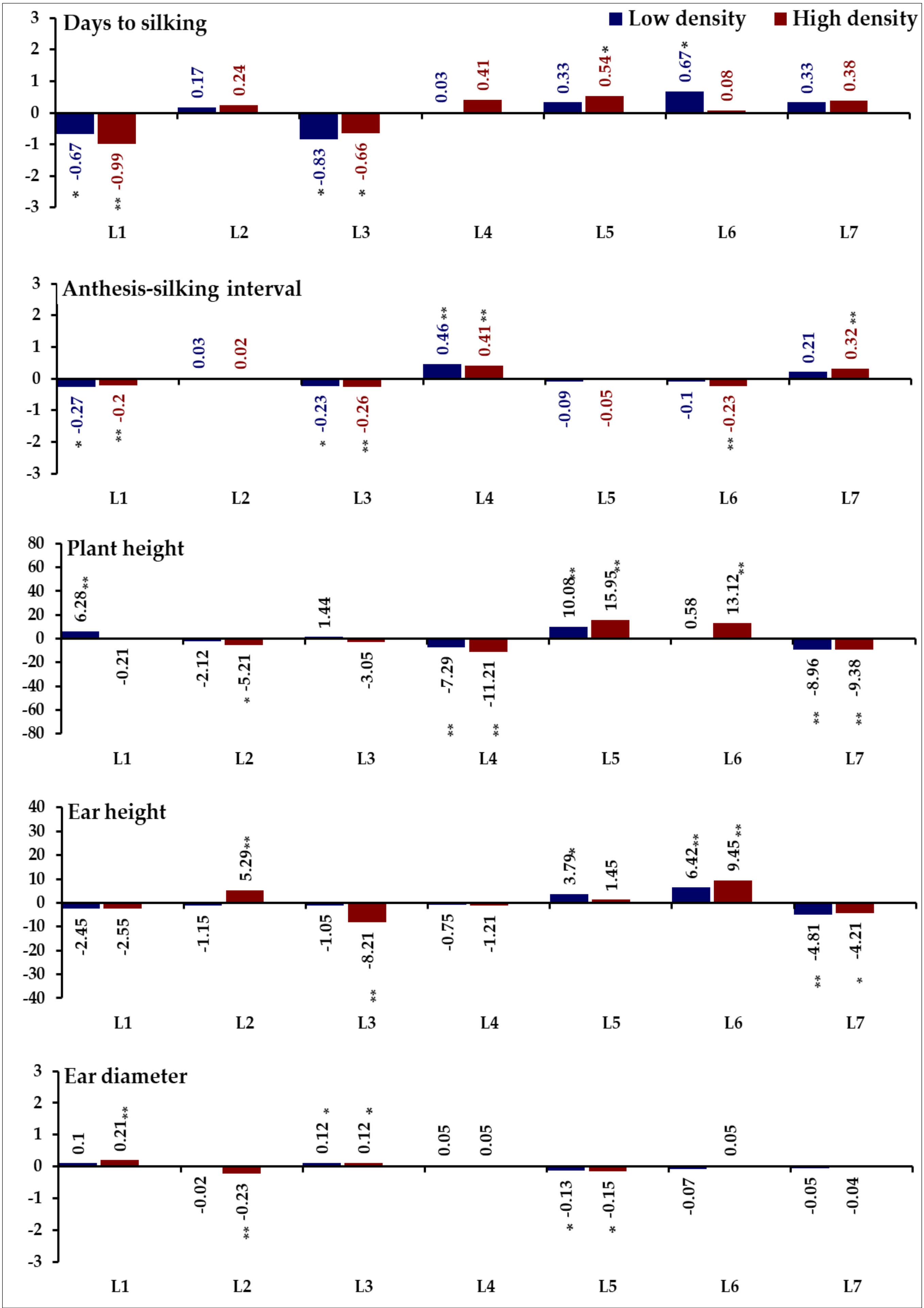

Fig. 6. General combining ability effects of the evaluated lines for days to silking, anthesis-silking interval, plant height, ear height and ear diameter.
*and ** signify p-value < 0.05 and 0.01 respectively.

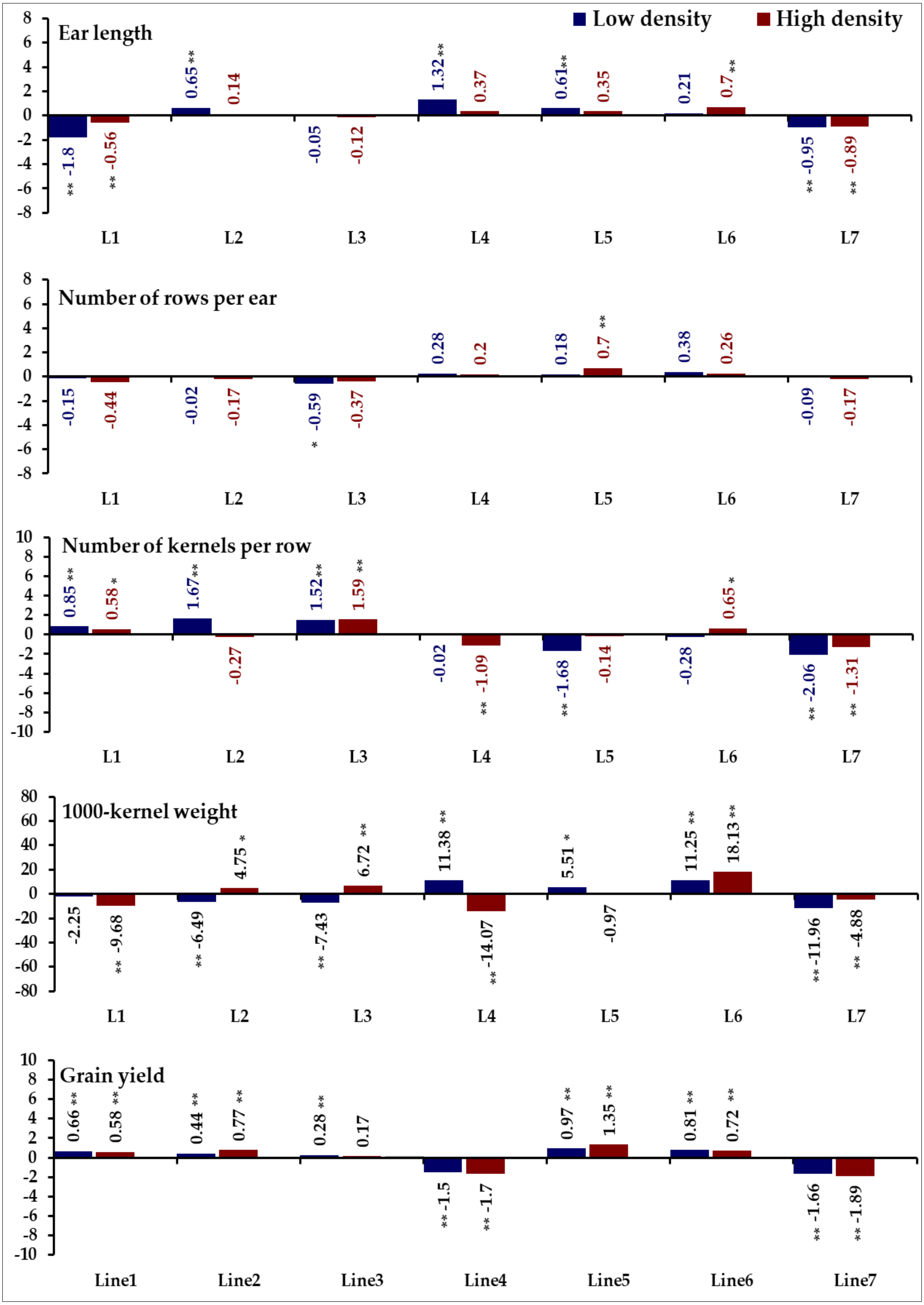

Fig. 7. General combining ability effects of the evaluated lines for ear length, number of rows per ear, number of kernels per row, 1000-kernel weight and grain yield. *and ** signify p-value < 0.05 and 0.01 respectively.

Table 5. Specific combining ability effects of twenty-one hybrids for all measured traits under low and high plant density

Cross	Silking date		Anthesis-silking interval		Plant height		Ear height		Ear diameter	
	Low D	High D	Low D	High D	Low D	High D	Low D	High D	Low D	High D
L1 × L2	-0.17	0.59	-0.14	-0.21	-21.20**	-10.44*	-9.17*	-10.83**	0.06	-0.06
L1 × L3	-0.83	-1.84**	0.46*	0.66**	-1.93	-9.28	2.57	6.83	0.00	-0.19
L1 × L4	-0.83	-1.24*	-0.10	-0.09	1.47	-0.28	-4.07	-0.17	0.27*	0.36*
L1 × L5	1.67*	0.79	-0.10	-0.18	9.93	14.22**	9.90**	1.33	-0.11	0.09
L1 × L6	-0.17	0.26	0.71**	0.75**	1.93	7.06	-2.57	2.50	-0.16	-0.16
L1 × L7	0.33	1.46**	-0.84**	-0.93**	9.80	-1.28	3.33	0.33	-0.06	-0.04
L2 × L3	-2.00**	-0.24	0.13	0.09	28.63**	40.72**	6.93*	5.67	0.03	-0.12
L2 × L4	0.67	0.69	0.44	0.52**	-4.30	20.56**	8.63*	2.00	-0.17	-0.19
L2 × L5	-1.50*	-1.61**	0.45	0.69**	-23.33**	-38.28**	0.27	1.83	-0.25*	-0.39**
L2 × L6	1.67*	1.02	-1.04**	-1.05**	16.17**	-11.28*	-1.87	9.67*	0.45**	0.67**
L2 × L7	1.33*	-0.44	0.17	-0.05	4.03	-1.28	-4.80	-8.33*	-0.13	0.09
L3 × L4	0.00	1.26*	-0.77**	-0.76**	-7.03	7.56	-3.13	5.50	0.20	0.25
L3 × L5	1.00	-0.71	-0.51*	-0.42**	1.43	-4.61	-2.17	-1.33	0.21	0.14
L3 × L6	0.00	0.26	-0.20	-0.40**	-11.57*	-10.94*	-0.63	-7.67*	-0.25*	-0.12
L3 × L7	1.83**	1.29*	0.89**	0.83**	-9.53	-23.44**	-3.57	-9.00*	-0.19	0.04
L4 × L5	0.17	1.72**	-0.10	-0.16	9.33	-0.61	-17.47**	-12.50**	-0.32**	-0.07
L4 × L6	1.67*	0.19	1.17**	0.96**	-5.33	-21.94**	2.40	-10.50**	-0.28*	-0.23
L4 × L7	-1.67*	-2.61**	-0.64**	-0.48**	5.87	-5.28	13.63**	15.67**	0.30**	-0.13
L5 × L6	-1.33*	-1.11*	-0.40	-0.41**	5.80	17.56**	10.37**	7.67*	0.30**	0.02
L5 × L7	0.00	0.92	0.66**	0.48**	-3.17	11.72*	-0.90	3.00	0.16	0.22
L6 × L7	-1.83**	-0.61	-0.24	0.15	-7.00	19.56**	-7.70*	-1.67	-0.07	-0.18
LSD $Sij_{0.05}$	1.27	1.07	0.45	0.22	10.57	9.55	6.92	7.34	0.22	0.28
LSD $Sij_{0.01}$	1.68	1.42	0.60	0.30	14.02	12.66	9.18	9.73	0.29	0.38

Cross	Ear length (cm)		Number of rows/ear		Number of kernels/row		1000-kernel weight (g)		Grain yield (ton/ha)	
	Low D	High D	Low D	High D	Low D	High D	Low D	High D	Low D	High D
L1 × L2	-1.36**	-0.95*	0.60	0.41	-2.53**	-0.77	-2.14	9.55*	0.65**	0.40
L1 × L3	-1.36**	-2.60**	0.00	0.44	-3.29**	-0.64	20.46**	-39.72**	-0.38	-0.69*
L1 × L4	-0.41	1.23*	0.30	1.04*	-0.58	0.25	29.66**	-17.09**	-0.26	0.10
L1 × L5	1.73**	1.03*	-0.27	-0.12	0.17	-1.82**	-50.80**	4.31	-0.49*	-0.17
L1 × L6	0.52	1.02*	-0.80	-1.19*	2.77**	2.86**	-0.68	11.55*	0.28	0.48
L1 × L7	0.87	0.27	0.17	-0.59	3.46**	0.11	3.50	31.38**	0.20	-0.11
L2 × L3	-0.40	-0.60	-0.97	-0.49	0.82	-0.95	14.37**	29.52**	-0.77**	-0.75*
L2 × L4	-0.08	-1.02*	-0.50	-1.56**	0.97	-1.45**	13.23**	13.81**	0.13	-0.01
L2 × L5	0.19	1.32**	-0.07	-0.06	-2.40**	0.70	-1.89	-46.29**	-0.91**	-0.48
L2 × L6	2.70**	1.47**	0.73	1.04*	2.03**	1.20*	-0.47	11.78**	1.52**	1.60**
L2 × L7	-1.05*	-0.21	0.20	0.64	1.11	1.27*	-23.10**	-18.38**	-0.62**	-0.76*
L3 × L4	1.15*	-0.50	0.07	-0.02	0.36	2.20**	-4.83	-1.16	0.65**	0.35
L3 × L5	-0.69	-0.06	1.17*	0.98*	3.51**	3.36**	-1.46	20.74**	2.79**	2.94**
L3 × L6	0.71	1.76**	0.80	-0.09	-1.11	-2.49**	-9.03*	-7.36	-1.20**	-1.19**
L3 × L7	0.59	2.00**	-1.07*	-0.82	-0.29	-1.47**	-19.52**	-2.03	-1.10**	-0.65
L4 × L5	1.73**	0.37	0.47	-0.26	1.32	-0.71	2.24	1.54	-0.44*	-0.86*
L4 × L6	-3.99**	0.03	-0.07	0.51	-3.36**	-1.00	-45.00**	2.44	-1.70**	-1.07**
L4 × L7	1.60**	-0.11	-0.27	0.28	1.29	0.72	4.71	0.44	1.62**	1.49**
L5 × L6	-0.44	-2.49**	-1.47**	-0.66	1.33	-0.74	36.34**	6.34	0.12	-0.65
L5 × L7	-2.52**	-0.17	0.17	0.11	-3.93**	-0.78	15.58**	13.34**	-1.07**	-0.78*
L6 × L7	0.51	-1.78**	0.80	0.38	-1.65*	0.16	18.84**	-24.76**	0.98**	0.82*
LSD $Sij_{0.05}$	0.89	0.94	1.02	0.91	1.47	1.06	8.37	8.83	0.42	0.66
LSD $Sij_{0.01}$	1.18	1.24	1.36	1.21	1.95	1.41	11.10	11.72	0.56	0.88

*and ** signify p value<0.05 and 0.01, in the same order

Association among developed hybrids and yield attributes

The association between developed maize hybrids and the evaluated characters was examined using principal component (PC) analysis. The first 2 PCs accounted for a substantial portion of the total variance, with the first principal component explaining 44.73 % and the second principal component capturing 15.22 % of the variance, as depicted in the PCA biplot (Fig. 8). The first principal component exhibited greater variation, effectively distinguishing hybrids with positive and negative values along this axis.

The hybrids positioned on the positive side of first principal component, such as L3 × L5, L2 × L6, L1 × L6, SC-10 and L5 × L6 were associated with superior yield traits under high density. In contrast, hybrids located on the negative side, including L3 × L7, L4 × L7 and L4 × L6 showed lower agronomic performance. The close proximity of the vectors suggested a strong positive association between grain yield and most traits, particularly number of kernels per row and 1000-grain weight, while a negative association with anthesis -silking interval, ear height and plant height.

Discussion

Under high-density planting, individual plants face competition for essential resources such as light, nutrients and water (38, 39). This competition negatively impacts yield -attributing traits, including kernel weight, ear length and the number of kernels per ear, as the limited availability of resources restricts the growth potential of each plant (40). However, despite these individual plant-level reductions, the increased plant population per ha compensates for the diminished traits (41). The effect of increased number of plants per unit area exceeds individual reductions, leading to a considerable increase in grain yield per hectare. This highlights the trade-off between individual plant performance and population-level productivity, emphasizing the importance of optimizing planting density to achieve maximum yield. Consequently, exploring genetic variations and combining abilities is vital for developing maize hybrids that perform well under high plant density conditions. The significant variations observed among the assessed hybrids highlighted substantial diversity within the tested hybrids offering the potential to select those with excellent performance (42-44). Likewise, there were several reports on significant genetic variability in newly developed maize hybrids for multiple agronomic attributes under different plant densities (16, 45-47). The significant interaction between hybrids and densities suggests hybrid performance and ranks varied across the 2 planting densities. This interaction revealed that certain hybrids are resilient under high-density planting due to traits such as erectile leaf architecture, which optimizes light capture and compact root systems that reduce competition for water and nutrients. These hybrids also exhibit enhanced stress tolerance, maintaining yield stability under environmental stresses. Their phenotypic resilience including balanced biomass allocation, ensures efficient resource use and reduces lodging risks. These traits display the importance of breeding programs focusing on resource efficiency, stress tolerance and adaptability to enhance yield potential in high-density maize production systems. This result is in consonance with several other studies, who determined significant interaction between maize hybrids and plant density for yield attributes (9, 14, 30, 48, 49).

Determining diverse inbred lines with beneficial alleles is crucial for ensuring their progeny inherits these advantageous traits (50-52). The favorable GCA effects observed for inbreds L1 and L3 concerning silking date and anthesis-silking interval highlight their potential for improving earliness in maize. Inbreds L4 and L7, conversely, are identified as promising parents for diminishing plant and ear height, which is essential for increasing lodging resistance, particularly under high plant density. Furthermore, inbreds L1, L2, L5 and L6 demonstrated highly favorable GCA effects for yield-related traits under high plant density, suggesting their value as genetic resources for improving maize yield in environments with intense plant competition. Consequently, if these inbred lines are crossed with other lines under high plant density stress will likely generate superior progeny to enhance productivity and resilience (53). Moreover, SCA analysis identified several promising hybrids. Hybrids such as L2 × L6, L3 × L5, L4 × L7

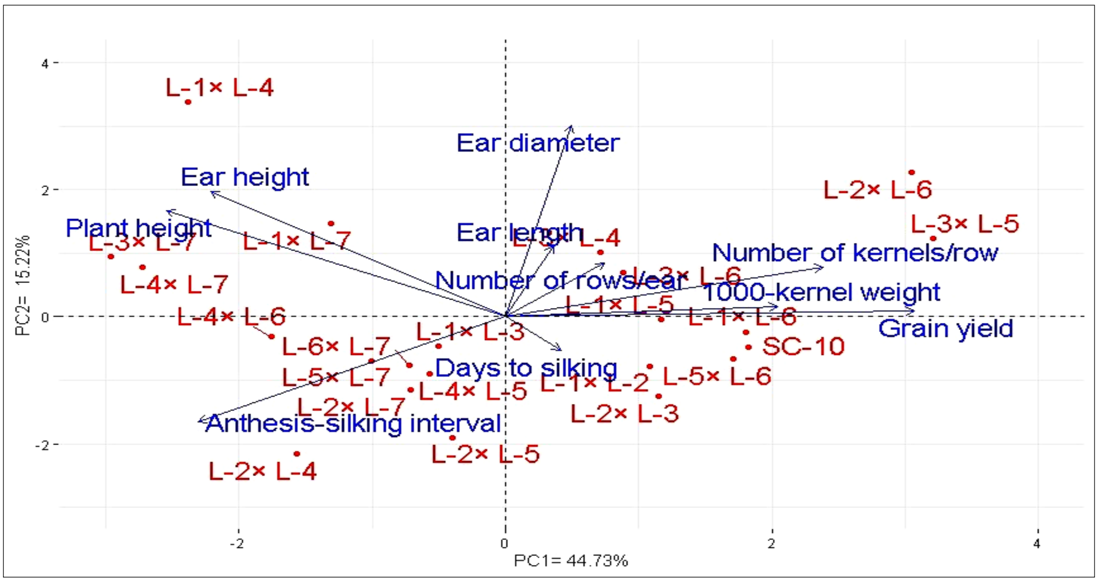

Fig. 8. PC-biplot explores the relationship between studied traits and the evaluated hybrids under high density.

and L6 × L7 exhibited positive SCA effects under both low and high plant density. These promising hybrids could be exploited effectively to enhance productivity and yield potential under different high plant densities. These hybrids resulted from crosses of parents exhibited both strong and weak GCA where one parent contributes substantial additive effects while the other provides advantageous epistatic interactions (54). None of hybrids displayed substantial SCA effects across all studied traits. However, hybrids such as L2 × L6 and L3 × L5 were identified as specific substantial combiners for multiple traits, including a short anthesis-silking interval, enhancing kernel number/row and rows/ear. Due to their complementary traits, these hybrids are promising candidates for enhancing maize grain yield under high plant density conditions.

Utilizing tolerance indices and cluster analysis to identify tolerant genotypes offers valuable insights and enhances classification accuracy (55-57). This approach enables breeders to make more informed decisions, increasing the likelihood of selecting hybrids that perform well under stressful conditions, such as high plant density (58-60). The evaluated hybrids were categorized into 5 groups (A-E) in the current study, ranging from highly tolerant to highly sensitive to dense planting conditions. Notably, the hybrids L3 × L5, L2 × L6, SC-10, L5 × L6, L1 × L2, L1 × L6, L1 × L5 and L2 × L5 were identified as tolerant to high density and exhibited superior agronomic performance under high density than the sensitive hybrids. These hybrids showed excellent resilience and improved yield under high density conditions; hence, further evaluation is recommended for commercial cultivation. Understanding the association between grain yield and agronomic attributes is essential for improving maize breeding for high plant density tolerance (61-63). The PC-biplot analysis reveals that enhancing one trait can positively affect others due to their strong correlations. Grain yield was notably associated with number of kernels/row and 1000-kernel weight, highlighting the importance of these characters for indirect selection to boost yield under high plant densities (64).

Non-additive and additive gene actions substantially impacted inheritance of examined attributes, as indicated by significant GCA and SCA effects (65, 66). The ratio of GCA/SCA surpassed the unity of most traits signifying that additive gene action had a dominant role in controlling inheritance of such characteristics. As a result, hybridization proves to be an efficient approach for enhancing these traits and utilizing heterosis. These findings are consistent with other studies (30, 31), who similarly found that additive genetic variance was the predominant factor influencing grain yield expression across different plant densities. However, these results contrast with studies of others (28, 29), which emphasized the prominence of non-additive gene action in genetic regulation of grain yield under comparable conditions. The observed significant GCA × D and SCA × D interactions for most traits suggest that GCA and SCA effects varied notably across different plant densities.

The results of the present study have significant practical implications for both maize breeders and farmers. Breeders could exploit the identified inbred lines with superior general combining ability for yield contributing traits (L1, L2, L3 and L5) to improve maize productivity under high-density conditions. These inbred lines can be attributed to their superior genetic makeup and the expression of traits that enhance resource efficiency, stress tolerance and adaptability. These lines have important implications for maize breeding programs, particularly in regions where land availability necessitates high-density planting. Furthermore, breeders should focus on traits such as erect leaf architecture, compact root systems, efficient resource use and stress tolerance in maize breeding programs. By focusing on developing hybrids with these traits, breeders can optimize yield potential and ensure sustainability in intensive maize production systems. In addition, the findings revealed that both non-additive and additive gene actions significantly influenced the inheritance of key traits, with additive gene action playing a dominant role, as indicated by a GCA/SCA ratio exceeding unity for most traits. These results emphasized the efficiency of hybridization in enhancing traits and utilizing heterosis. On the other hand, for farmers, cultivating these high-performing hybrids can lead to substantial yield improvements in high-density planting systems. Farmers can mitigate the risks associated with resource competition by utilizing hybrids with demonstrated tolerance to environmental stresses. Additionally, farmers can maximize returns by optimizing planting densities to suit the specific hybrid potentiality, ensuring a balance between yield potential and resource availability. These strategies are particularly critical in regions with limited arable land and high demand for maize production.

Conclusion

This study demonstrated considerable genetic variability among assessed maize hybrids in response to different planting densities. High-density planting significantly reduced ear length, kernel number, ear diameter and kernel weight by 11.7 %, 18.2 %, 6.3 % and 13.17 % respectively, while increased plant height, days to silking and grain yield per ha by 11.2 %, 3.7 % and 16.0 % respectively, compared to low-density planting. The inbred lines L1, L2, L3 and L5 demonstrated superior general combining ability effects for crucial yield contributing attributes, making them excellent candidates for integration into breeding programs to improve yield under high-density conditions. Consequently, maize breeders can exploit these inbred lines to develop hybrids optimized for regions with limited arable land. Despite the challenges posed by high-density planting on reducing certain yield components certain hybrids such as L3 × L5 and L2 × L6 exhibited superior agronomic performance and yield resilience, indicating their strong potential for high-density environments. Stress tolerance indices further categorized the evaluated hybrids into 5 groups based on tolerance to high density. Groups A and B comprised 8 hybrids that showed the highest tolerance indices and robust agronomic performance under dense planting conditions (L3 × L5, L2 × L6, SC-10, L5 × L6, L1 × L2, L1 × L6, L1 × L5 and L2 × L5). The principal component analysis confirmed these findings by effectively differentiating these hybrids based on their performance on the positive side. The farmers can utilize these hybrids adapted to planting densities to balance yield potential and resource availability. These newly developed hybrids displayed potential to enhance maize productivity under high-density planting conditions. The principal component analysis highlighted the positive relationship between grain yield and specific traits, such as 1000 kernel weight and number of kernels/row under high planting density. The results highlighted the dominance of additive gene action in trait inheritance, supported by significant GCA/SCA ratios and interactions across planting densities, reinforcing the efficiency of hybridization and heterosis utilization for trait improvement.

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Authors' contributions

NMA and MMK participated in the design of the study and performed the statistical analysis. NMA and MMK conceived of the study and participated in its design and coordination. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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