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Unveiling hybrid potential and exploring combining ability for yield and related traits in maize (*Zea mays* L.) through line × tester mating design

Mohammad Ashraful Alam^{1,*}, Salahuddin Ahmed², Mohammad Alamgir Miah², Nasrin Jahan³,
Mohammad Marufur Rahman⁴, Mohammad Rafiqul Islam⁵

¹ Spices Research Centre, Bangladesh Agricultural Research Institute, Shibganj, Bogura 5810, Bangladesh

² Plant Breeding Division, Bangladesh Wheat and Maize Research Institute, Dinajpur 5200, Bangladesh

³ Plant Genetic Resources Centre, Bangladesh Agricultural Research Institute, Gazipur 1701, Bangladesh

⁴ Regional station, Bangladesh Institute of Research and Training on Applied Nutrition, Pirgonj, Rangpur 5470, Bangladesh

⁵ Agronomy Division, Regional Agricultural Research Station, Bangladesh Agricultural Research Institute, Ishwardi, Pabna 6620, Bangladesh

* **Corresponding author:** Mohammad Ashraful Alam, a.alam_83@yahoo.com

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Abstract: Combining ability analysis serves as an invaluable tool for evaluating the compatibility of parental lines and testers, as well as for elucidating the intricate genetic mechanisms at play within their hybrid progeny. This study was designed to ascertain the combining ability of maize lines when paired with testers, specifically focusing on yield-related traits through the utilization of a line × tester mating design. A total of fifteen advanced lines were systematically crossbred with three distinct testers to produce forty-five hybrid test crosses. The performance of these progenies was rigorously assessed across three distinct locations, thereby enhancing the robustness of the findings. The field trials were conducted using an alpha lattice design. Variance analysis, combining ability effects, and genetic components were estimated following a line × tester analysis. Employing variance analysis, significant variations were discerned in both general and specific combining abilities, underscoring the contribution of both additive and non-additive gene actions to the expression of the targeted traits. Notably, the magnitudes variance component indicated the prevalence of additive gene effects across the traits studied. Amidst the comprehensive exploration of parental lines and testers, it was evident that lines L10 and Tester T2 exhibited notable compatibility as general combiners, particularly in the context of maize grain yield. Additionally, Line L12 demonstrated favorable characteristics related to earliness. The superior performance of certain hybrid combinations emerged as a noteworthy outcome of this investigation. Specifically, the hybrid cross L10 × T2 displayed remarkable performance in terms of grain yield, while L12 × T1 demonstrated strong potential for the trait days to anthesis. Furthermore, in terms of specific combining ability, the cross L13 × T1 demonstrated the most pronounced effect, particularly concerning grain yield. Following closely were the combinations L5 × T1 and L2 × T2, each exhibiting significant potential for enhancing maize productivity. To conclude, this study underscores the indispensable role of combining ability analysis in elucidating the interplay between parental lines and testers, thus unraveling the intricate genetic dynamics within their hybrid offspring. The insights gathered hold promise for advancing maize production by employing judicious selection strategies, with a specific focus on the highlighted hybrid combinations.

Keywords: maize; general combining ability; line × tester analysis; specific combining ability; hybrid

1. Introduction

Maize (*Zea mays* L.), a prominent member of the Poaceae family, stands as a pivotal cross-pollinated cereal crop [1]. Notably, it is recognized as a significant C4 plant, offering a wide range of uses. This versatile crop capitalizes on solar energy with exceptional efficiency, rendering substantial contributions to global economies as a source of sustenance for humans, feed for animals, and raw materials for industrial applications [2,3]. However, the contemporary scenery portrays a demand for maize that outpaces its production, an issue observed in recent years [4]. Evidently, the worldwide average maize production hovers around 5.75 t/ha [5], and to effectively address the impending global demand for maize, a twofold increase in production is necessitated by the year 2050. A plausible avenue to fulfill this burgeoning demand lies in the development of high-yielding test cross varieties [6]. Yield is a complex polygenic trait that depends on different yield-contributing traits that are inherited in a quantitative pattern [7]. Gene action, inheritance pattern, and genetic control of yield-contributing traits are major factors for yield improvement [8]. Crucially, the propulsion of maize yield enhancement and heightened productivity finds its essence in the cultivation of high-yielding test crosses. This endeavor chiefly entails the discernment and selection of superior parent lines, facilitated through meticulous mating designs [9]. In this context, diverse crossing designs stand at the breeder's disposal. The line x tester mating design, underscored by combining ability analysis, emerges as an invaluable technique in breeding programs, wherein an array of diverse lines are interbred with a set of standardized parent entities known as testers [10]. In this mating scheme, testers conventionally operate as the male parents, while the advanced lines serve as the female contributors. As elucidated by Matzinger [11], the tester imparts a common platform for the lines, allowing their expected performances to manifest through the expression of their general combining ability (GCA) and specific combining ability (SCA). The capacity of inbred lines to seamlessly combine with a range of testers signifies strong GCA, while instances where enhanced performances manifest only within certain specific crosses signify robust SCA [12]. Moreover, the line x tester design not only unveils the genetic mechanisms governing yield and its correlated traits but also furnishes indispensable information regarding the effects of GCA and SCA on these attributes. Such insights prove invaluable for maize breeders in selecting optimal parent lineages for test cross development. Evidently, a numerous study has delved into assessing combining ability and gene action in maize populations through the prism of line x tester analyses, particularly concerning yield and its contributing traits [13–17]. There remains a gap in understanding the stability and adaptability of line \times tester combinations across diverse environments, highlighting the need for further research into gene action and yield-related traits under varying agro-ecological contexts. Thus, the aims of this investigation reside in estimating the combining ability of lines and testers and appraising the extent of gene action influencing yield and its affiliated attributes within the framework of a line \times tester mating design applied to maize across multiple environments.

2. Materials and methods

The present study was conducted across three distinct geographical environments: Ishwardi in the northwestern region, Jessore in the southwestern region, and Barisal in the southern region of Bangladesh during the Rabi season of 2015–16. Detailed information pertaining to the prevailing weather conditions at these diverse locations is retrievable from a previous comprehensive investigation [18].

In this study, a compilation of fifteen advanced lines and three testers was engaged. This assemblage underwent deliberate crossing, culminating in the development of 45 F₁ test crosses, as previously documented [18]. For the present inquiry, both the lines, testers, and the F₁ test crosses were subjected to a comprehensive evaluation.

A meticulous alpha lattice design was implemented across all study locations, featuring two replications. At Ishwardi and Jessore, the test crosses were allocated single rows of 5 m length, while at Barisal, a row length of 4 m was adopted. Standardized row-to-row and plant-to-plant spacing of 75.0 cm and 20.0 cm, respectively, was upheld across all environments. Adherence to recommended intercultural practices was steadfastly observed to ensure optimal crop growth and development. The careful recording of observations relating to various traits was executed in accordance with established protocols. Specifically, days to anthesis (AD) were documented when 50% of plants commenced pollen shedding. The anthesis-silking interval (ASI) was determined as the temporal disparity between days to anthesis and silking. Thousand kernel weight (TKW) was recorded after shelling, while grain yield (GY) was deduced based on field weight adjusted to accommodate shelling percentage and maintain a moisture content of 15%, all executed on a whole plot basis. The data were statistically analyzed for combined analysis of variance (ANOVA) following the methodology described by as per [19], across locations for all studied traits. General combining ability (GCA) and specific combining ability (SCA) effects were estimated according to Kempthorne (1957) [20], implemented in ‘AGD-R’ version 5.0 software [21].

3. Results and discussion

3.1. Variance analysis

The analysis of variance for combining ability over locations demonstrated that maize genotypes exhibited noteworthy variations ($P < 0.01$) in relation to key traits, including AD, ASI, TKW, and GY (**Table 1**). Additionally, variance due to sites, interactions between sites and genotypes, as well as between sites and lines, testers, and their combinations, emerged as statistically significant for all the scrutinized traits, with the exception of the variance attributed to site, site vs lines, and site vs tester for the ASI. Significantly attributed variance was evident in respect to lines, testers, and the interaction between lines and testers, further emphasizing the appropriateness of the examined traits. The observed significant variation among maize genotypes for AD, ASI, TKW, and GY underscores the genetic diversity inherent in the population, providing valuable insights for trait selection and crop improvement strategies. Moreover, the statistically significant variance attributed to sites and their interactions

with genotypes, lines, testers, and their combinations emphasizes the influence of environmental conditions on trait expression.

The % TSS (Total Sum of Squares) in the ANOVA table delineates the proportion of overall variability ascribed to specific sources or interactions for each trait. Site elucidates 45.96% of total variability, signifying that nearly half of the discerned differences in flowering timing stem from variations between sites. Concurrently, it contributes to 10.31% of total variability in Grain Yield, indicating a moderate impact of site-specific conditions on observed yield disparities.

Genotype significantly contributes to the total variability in AD (23.33%), accentuating genetic influences on flowering timing (**Table 1**). Similarly, it accounts for 32.18% of the variability in ASI, emphasizing the substantial genetic impact on the interval between anthesis and silking. Additionally, Genotype significantly influences total variability in TKW at 43.83%, indicating a robust genetic influence on kernel weight. Consequently, Genotype has a considerable impact on GY, contributing 31.89% to the total variability. Within the genotype, the % SS values for Line, Tester, and Cross indicate noteworthy contributions to the overall variability.

Table 1. Combined analysis of variance for yield and yield components of maize evaluated across multiple environments.

Source	Df	AD			ASI			TKW			GY		
		MSS	% TSS	% SS	MSS	% TSS	% SS	MSS	% TSS	% SS	MSS	% TSS	% SS
Site	2	868.04**	45.96		0.33 ^{ns}	0.53		13287.63**	5.23		33.64**	10.31	
Rep (Site)	3	21.16**	1.68		0.13 ^{ns}	0.31		4150.10**	2.45		15.29**	7.03	
Gen	44	20.03**	23.33		0.92**	32.18		5058.51**	43.83		4.73**	31.89	
Line	14	43.36**		68.87	1.44**		49.58	9752.43**		61.34	7.30**		49.11
Tester	2	84.85**		19.25	3.59**		17.67	8759.77**		7.87	14.51**		13.96
Cross	28	3.76**		11.93	0.48*		32.78	2447.17**		30.79	2.74**		36.94
Site:Gen	88	10.82**	25.21		0.69**	47.84		1962.78**	34.01		2.64**	35.55	
Site:Line	28	23.22**		68.27	0.45*		21.06	1853.59**		30.05	4.47**		53.96
Site:Tester	4	28.95**		12.16	1.87**		12.39	6541.14**		15.15	3.46*		5.96
Site:Cross	56	3.33**		19.58	0.72**		66.55	1690.35**		54.80	1.66*		40.08
Residuals	90	1.60	3.82		0.27	19.14		816.77	14.48		1.10	15.21	

Df = Degrees of freedom, AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield, MSS = Mean sum of square, TSS = Total sum of square, SS = Sum of square, ** = Significant at 1% level, * = Significant at 5% level, ns = Not significant.

The interaction between Site and Genotype (Site:Gen) accounts for 25.21% of the total variability in AD, signifying a significant interplay between site-specific conditions and genotypic factors (**Table 1**). Analogously, Site:Gen interaction explains 47.84% of the total variability in ASI, underscoring the substantial influence of the interplay between site conditions and genotypic factors. Furthermore, Site:Gen interaction contributes 34.01% to the total variability in TKW, underscoring the significant role of site conditions and genotypic factors in kernel weight. Moreover, Site:Gen interaction contributes 35.55% to the total variability in Grain Yield, highlighting the significant interaction between site conditions and genotypic factors in determining grain yield. Within the Site:Gen Interaction, the % SS values for

Site:Line, Site:Tester, and Site:Cross indicate substantial contributions to the overall variability. Overall, the % TSS values provide insights into the relative importance of different sources and interactions in explaining the observed variability in each trait.

The ANOVA results underscore the significant impact of Site, Genotype, and their interactions on key yield components. The identified substantial variations among genotypes with regard to all studied traits aligns with analogous findings from prior investigations. Previous studies have also reported significant genotype-dependent variations in maize yield and yield-contributing attributes [22–28]. Past research has highlighted how genetic diversity among maize genotypes influences grain yield and kernel weight. This corroborative evidence reaffirms the genetic intricacies underlying these traits and underscores their modifiability for the purposes of crop improvement. The similarity of these findings with previous studies fortifies the understanding that genetic diversity profoundly shapes maize traits, reinforcing the potential for targeted enhancement and the selection of superior genotypes for achieving improved crop productivity. While our study identifies promising lines and crosses with better yield performance combining ability, the genotype-by-environment interaction (GEI) and its predictive modeling for multiple environmental contexts warrants further exploration.

3.2. Traits performances

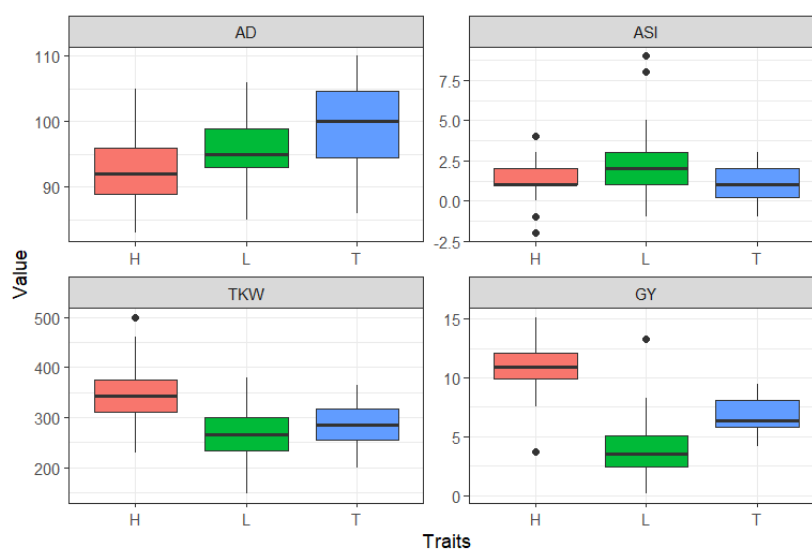


Figure 1. Boxplots represents the summary of performances by cross (H), line (L) and tester (T) for different traits of maize evaluated across multiple environments.

The phenotypic performances of the different lines, testers and crosses for the traits AD, ASI, TKW, and GY were depicted in boxplot (**Figure 1**) and presented in supplementary tables (Appendix). The presented boxplot visually summarizes the performance of lines, testers, and crosses across the studied traits, providing a comprehensive comparison (**Figure 1**). The crosses demonstrated superior performance in terms of AD, showcasing lower values compared to the lines and testers. This suggests a notable advantage in earliness for the crosses. Additionally, the testers exhibited more synchronized flowering than the maternal inbred lines, as

indicated by a reduced ASI, further emphasizing their potential in achieving optimal flowering synchronization. Similar to this the tester showed better performances for TKW and GY over most of the lines (Appendix).

Evident disparities in the mean performance of the traits under examination were discerned among the diverse entities, encompassing lines, testers, and the generated test crosses. Notably, the performances of the three testers exhibited a degree of uniformity across the range of studied traits (Appendix). Conversely, in the context of the lines, distinct trends emerged, with Line L10 registering the highest GY at 10.20 t/ha, while Line L1 displayed a propensity for producing grains with augmented size, characterized by a substantial TKW of 354.75 g. Moreover, Line L7 presented a notable minimum ASI of 0.54 days, suggestive of efficient synchrony between pollen shedding and silk emergence. In a parallel vein, Line L12 emerged as the harbinger of the lowest AD at 90.7 days. The resemblance in the performances exhibited by the three testers, underscored by similar trait values across the studied attributes, suggests a level of uniformity within this subgroup. Divergent trends within the lines' performance profiles not only emphasize the inherent variability in the germplasm but also delineate the distinct strengths of each line in relation to specific traits. Line L10's superior grain yield, Line L1's notable TKW, Line L7's synchronous reproductive timing, and Line L12's prompt anthesis all contribute to the rich diversity within the examined maize population. These findings resonate with the interplay of genetic factors and environmental influences that collectively shape trait expressions. The discerned divergences in performance underscore the potential of lines to exhibit specialized attributes, thereby highlighting the importance of such insights in the informed selection of parental material for crop improvement initiatives.

Among the test cross combinations, a notable observation pertains to the prevalence of sixteen test crosses that exhibited earlier AD compared to their respective parent lines (Appendix). Remarkably, the test cross combination L3 × T1 emerged as the frontrunner in terms of the shortest AD (88.77), while the test cross L7 × T2 showcased the lengthiest AD (96.24). Evidently, the anthesis-silking interval (ASI) values across the test crosses exhibited a range spanning from 0.17 to 3.50. Specifically, the test cross L7 × T2 demonstrated the minimal ASI value, while the test cross L1 × T1 showcased the maximal ASI value. Of dominant significance is the identification of test crosses characterized by earliness and favorable yield performance, a profile that holds promise for the development of short-duration varieties. Particularly, the test cross L3 × T1, distinguished by its early anthesis and potential for enhanced yield, signifies a promising candidate. These findings hold not only implications for the cultivation of short-duration varieties but also illuminate the prospective avenues for integration into future breeding programs tailored to the development of such varieties. The observed variation in anthesis timing among the test crosses can be attributed to the intricate interplay of genetic factors underlying the trait, encompassing both additive and non-additive components. Moreover, the potential yield advantages of the early maturing test crosses underscore their potential utility in addressing specific cultivation and market demands, reinforcing the importance of such insights in crop improvement strategies.

Clear variations became apparent in the context of TKW across the range of test cross combinations. The lowest TKW was observed in the test cross L4 × T1 (290.66),

followed by L8 × T2 (298.89) and L11 × T1 (299.62) (Appendix). In contrast, the highest TKW values materialized in the test crosses L1 × T2 (413.79), L3 × T3 (393.17), L12 × T3 (386.71), L3 × T2 (379.76), L1 × T3 (376.02), L13 × T2 (372.41), and L6 × T3 (372.34). It is noteworthy that twenty test crosses surpassed the TKW values of their parental lines. Such heightened TKW values notably contribute to the ultimate grain yield of maize, underlining their significance in crop productivity enhancement. Furthermore, the test cross L10 × T2 emerged as the pinnacle performer in terms of grain yield (GY), recording 12.53 t/ha (Appendix). This was trailed by L14 × T3 (12.51 t/ha) and L3 × T2 (12.21 t/ha). Conversely, the test cross L7 × T1 exhibited the lowest GY output at 8.55 t/ha, followed by T15 × L1 (8.92 t/ha). Intriguingly, a substantial twenty-six test crosses surpassed the parental grain yield values. This abundance of heterotic effects manifesting predominantly in grain yield denotes their crucial role in shaping the crop's productivity potential. Noteworthy are the superior performances exhibited by specific test cross combinations, as discerned across an array of traits. Exemplary cases include L3 × T3, L5 × T1, L8 × T1, L12 × T3, and L15 × T3, which not only outperformed their parental values but also demonstrated superior performances in terms of AD, TKW, and GY. This trend illuminates the diverse potential within the examined test cross combinations for fostering desirable trait expressions. The observed variations in mean values across lines, testers, and crosses underscores the distinctiveness characterizing each entity, thereby affording prospects for the identification and selection of desirable test crosses. Comparable investigations involving maize inbred lines and crosses have yielded analogous outcomes i.e., how specific line × tester interactions contribute to heterotic responses and yield advantages, as documented by various researchers [24,29–31]. These findings collectively reinforce the significance of genotype interactions and the potential inherent in test cross combination for tailored breeding strategies aimed at enhancing maize traits and yield. Future research directions should aim to integrate high-throughput phenotyping and multi-environment trials to better characterize the stability and adaptability of test cross combinations across diverse agro-climatic zones.

3.3. General combining ability (GCA) effects

The estimates pertaining to the GCA effects of both lines and testers for the studied traits—AD, ASI, TKW, and GY combined across the three study locations, were presented in **Table 2**. Regarding GY, the GCA unveiled positive effects within eight out of the fifteen inbred lines. Notably, Line L10 showcased the highest GCA effect (1.1), while Line L2 demonstrated the lowest and negative GCA effect (−0.08). Thus, the lines manifesting positive GCA effects hold promise as potent candidates for facilitating grain yield enhancement through effective combination in maize breeding initiatives. As for the testers, Tester T1 exhibited a favorable positive GCA effect for grain yield. In contrast, Testers T2 and T3 demonstrated negative GCA effects. These findings are congruent with earlier studies that reported a spectrum of both positive and negative combining ability effects in maize, thereby reinforcing the present observations [32–36].

Table 2. General combining abilities (GCA) effects of yield and yield components of maize evaluated across multiple environments.

Code	AD	ASI	TKW	GY
Line				
L1	-1.00	0.29	34.50	0.15
L2	1.37	0.68*	2.86	-0.01
L3	-1.92	-0.23	29.90	1.02
L4	-1.43	-0.05	-39.60 ⁺	-1.12 ⁺
L5	-1.01	-0.26	8.28	0.26
L6	-1.81	-0.10	26.50	-0.68
L7	1.15	-0.85**	-21.10	-0.74
L8	0.72	0.25	-29.90	0.11
L9	0.69	-0.19	-16.80	0.29
L10	2.12	0.02	2.50	0.99
L11	1.96	0.27	-16.00	-0.10
L12	-2.91 ⁺	0.23	26.40	-0.14
L13	0.77	-0.01	11.70	0.00
L14	1.89	-0.12	1.39	0.75
L15	-0.52	0.11	-20.80	-0.79
Tester				
T1	-0.85	0.24	-11.30	-0.46
T2	1.11	-0.15	6.64	0.25
T3	-0.25	-0.09	4.70	0.21

AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield ** = Significant at 1% level, * = Significant at 5% level, + = Significant at 10% level.

The GCA effects for ASI and AD revealed that eight and nine lines, respectively, indicates the ability of these lines to confer early maturity. Conversely, concerning TKW, seven lines manifested positive GCA effects. This distribution of negative GCA effects for ASI and AD, alongside positive GCA effects for TKW, aligns with desired outcomes. Particularly, Line L2 demonstrated a commendable, significant GCA for anthesis-silking interval. In contrast, Line L4 presented a significant negative GCA effect for thousand kernel weights. Among the testers, all exhibited positive combining ability for ASI and TKW. Notably, the range of estimates for lines' GCA effects for AD spanned from -2.92 (Line L12) to +2.19 (Line L10). Noteworthy is the observation that ten out of the fifteen lines exhibited negative GCA effects for AD, while Testers T1 and T3 similarly manifested negative GCA effects for AD. Comparable studies have also highlighted the coexistence of positive and negative GCA effects for traits such as maize days to tasseling and silking [37]. The comprehensive assessment yielded the insight that none of the parents emerged as an optimal combiner across all traits. The presence of both positive and negative GCA effects for AD and ASI reflects the potential for the production of offspring characterized by both early and late trait expressions. This variance in GCA effects aligns with the diverse genetic influences underlying these traits, as illustrated by prior research endeavors in maize [38–41]. Studies in maize have demonstrated that hybrids

developed from parents with high GCA values tend to perform consistently across environments, while those with strong SCA effects excel under specific conditions [38–41]. Future studies should aim to include a broader spectrum of parental germplasm, encompassing genetically diverse and underutilized lines. This would provide a more comprehensive understanding of genetic interactions and heterosis patterns.

3.4. Specific combining ability (SCA) effects

The outcomes of SCA effects, examined across the three study locations for the 45 test crosses, are detailed in **Table 3**. Among these, it is noteworthy that the cross $L7 \times T1$ exhibited negative and significant SCA effects for GY, which is not expected given their tendency toward poorer yields. Conversely, the cross combination $L15 \times T3$ and $L13 \times T1$ manifested significant and positive SCA effects for grain yield. Such significant and positive SCA estimates hold potential as promising candidates for selection in breeding endeavors. Notably, twenty-five test crosses in the present study exhibited negative SCA effects for GY, possibly due to the influence of parents with similar genetic backgrounds. On the contrary, twenty test crosses revealed positive SCA effects for GY, suggestive of improved performance when parents with diverse genetic backgrounds were combined [42]. The cross $L15 \times T3$ emerged with the highest SCA effect for GY (1.28), followed by $L13 \times T1$ (1.05). These findings reinforce the observation that crosses characterized by higher grain yield tend to exhibit elevated SCA values. Similar insights have been reported by previous researchers, where specific combining ability effects served as predictors for various traits in test cross performance [42,43]. The study that focuses only on specific crosses, which, while informative, may not capture the full genetic diversity available for hybrid development. The incorporation of high-throughput phenotyping and stress simulation platforms could also help disentangle the contributions of SCA under complex stress scenarios, such as combined drought and heat stress.

Regarding TKW, twenty-two crosses displayed negative SCA effects, while twenty-three crosses exhibited positive SCA effects. Notably, the cross $L8 \times T1$ and $L15 \times T3$ demonstrated significant positive SCA effects for TKW, whereas cross $L15 \times T2$ manifested higher negative SCA effects for TKW. Comparable studies have highlighted the coexistence of both significant positive and negative SCA effects for TKW, underscoring the multifaceted genetic interaction underlying this trait [44]. The occurrence of significant and positive SCA effects for TKW suggests the compatibility of these crosses in augmenting maximum TKW and thereby enhancing grain yield [45,46].

For ASI, twenty crosses displayed negative SCA effects, while twenty-three crosses exhibited positive SCA effects (**Table 3**). Specifically, cross $L1 \times T2$, $L5 \times T1$ and $L9 \times T2$ evidenced significant negative SCA effects for ASI, while cross $L3 \times T1$ and $L14 \times T1$ demonstrated noteworthy significant positive SCA effects. Among the test crosses, twenty-eight out of forty-five exhibited negative SCA effects for AD. However, cross $L4 \times T3$ and $L7 \times T2$ exhibited significant positive SCA effects for AD, in contrast, cross $L3 \times T1$ and $L13 \times T2$ showed significant negative SCA effects for AD. Analogous observations of both positive and negative SCA effects for days to

anthesis have been documented in prior studies [37]. These findings underscore the intricate genetic interactions that contribute to the observed specific combining ability effects across the diverse traits examined in this study. The disparities between positive and negative SCA effects accentuate the potential for tailored breeding strategies aimed at leveraging favorable genetic interactions to enhance desired trait expressions.

Table 3. Specific combining ability (SCA) effects of yield and yield components of maize evaluated across multiple environments.

Line	Tester	AD	ASI	TKW	GY
L1	T1	0.28	0.16	-18.50	0.78
L1	T2	0.17	-0.59**	27.10 ⁺	-0.02
L1	T3	-0.46	0.42 ⁺	-8.56	-0.76
L2	T1	0.79	-0.04	23.40	-0.51
L2	T2	0.10	0.14	-15.10	0.72
L2	T3	-0.90	-0.11	-8.31	-0.22
L3	T1	-1.05 ⁺	0.46*	-10.70	0.26
L3	T2	0.38	-0.05	-2.47	-0.01
L3	T3	0.66	-0.42 ⁺	13.10	-0.26
L4	T1	-0.49	0.17	-3.86	0.23
L4	T2	-0.96	0.08	10.30	0.20
L4	T3	1.43*	-0.26	-6.40	-0.43
L5	T1	0.45	-0.46*	26.40 ⁺	0.69
L5	T2	0.10	0.16	-4.75	-0.74
L5	T3	-0.56	0.29	-21.60	0.05
L6	T1	0.91	-0.17	-16.70	-0.29
L6	T2	-0.88	0.20	20.60	0.35
L6	T3	-0.04	-0.04	-3.95	-0.06
L7	T1	-0.65	0.00	-4.89	-1.22*
L7	T2	1.41*	-0.01	21.20	0.45
L7	T3	-0.78	0.01	-16.30	0.77
L8	T1	-0.38	0.24	36.40*	0.85
L8	T2	0.38	-0.15	-23.00	-0.05
L8	T3	-0.02	-0.09	-13.40	-0.81
L9	T1	-0.16	0.44 ⁺	-2.36	-0.38
L9	T2	0.58	-0.41 ⁺	-1.58	0.17
L9	T3	-0.44	-0.03	3.94	0.21
L10	T1	-0.39	-0.07	15.90	0.08
L10	T2	-0.21	0.06	1.53	0.32
L10	T3	0.59	0.00	-17.50	-0.40
L11	T1	0.16	-0.14	-17.90	-0.16
L11	T2	0.12	0.09	7.31	-0.12
L11	T3	-0.28	0.04	10.60	0.28

Table 3. (Continued).

Line	Tester	AD	ASI	TKW	GY
L12	T1	0.18	-0.22	3.98	-0.21
L12	T2	-0.24	0.01	-15.00	-0.13
L12	T3	0.05	0.20	11.00	0.34
L13	T1	0.02	-0.14	-12.90	1.05*
L13	T2	-1.06 ⁺	-0.09	9.14	-0.48
L13	T3	1.03	0.21	3.74	-0.57
L14	T1	-0.54	-0.14	-7.39	-0.41
L14	T2	0.63	0.44*	-9.19	-0.18
L14	T3	-0.10	-0.31	16.60	0.59
L15	T1	0.81	-0.14	-11.00	-0.79
L15	T2	-0.58	0.09	-26.10	-0.49
L15	T3	-0.24	0.05	37.10*	1.28*

AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield ** = Significant at 1% level, * = Significant at 5% level, + = Significant at 10% level.

3.5. Genetic components estimates

The investigation into genetic components yields invaluable insights into the underlying mechanisms driving the variation in the studied traits. The findings, as summarized in **Table 4**, provide a comprehensive overview of the contributions from various sources to the trait variances. The insights assembled from the genetic components analysis (**Table 4**) serve to elucidate the respective contributions of lines, testers, and line \times tester interactions to the overall variances observed.

Table 4. Genetic component estimates of the studied traits across multiple environments.

Estimates	AD	ASI	TKW	GY
$\sigma^2\text{GCA}_L \times \text{Env}$	2.20	0.05	406.00	0.25
$\sigma^2\text{GCA}_T \times \text{Env}$	0.90	0.03	70.10	0.13
$\sigma^2\text{SCA} \times \text{Env}$	0.36	0.03	272.00	0.27
σ^2_g	1.66	0.05	266.00	0.20
σ^2_a	6.64	0.18	1060.00	0.81
σ^2_d	1.44	0.14	1090.00	1.09
σ^2_e	4.14	0.32	927.00	1.25
h^2_b	0.66	0.50	0.70	0.60
h^2_n	0.54	0.29	0.35	0.26

AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield, $\sigma^2\text{GCA}_L \times \text{Env}$ = GCA (line) \times environment variance, $\sigma^2\text{GCA}_T \times \text{Env}$ = GCA (tester) \times environment variance, $\sigma^2\text{SCA} \times \text{Env}$ = SCA \times environment variance, σ^2_g = Genotype variance, σ^2_a = Additive variance, σ^2_d = Dominance variance, σ^2_e = Environmental variance, h^2_b = Heritability in broad sense, h^2_n = Heritability in narrow sense.

Notably, the contribution of testers to total variance surpassed that of lines and line vs. tester interactions in the context of TKW and GY. Intriguingly, the contribution of lines was overshadowed by interactions to total variance in the context

of TKW and GY. This nuanced observation underscores the substantial influence of the male parent in contributing to the overall variance observed in maize. This result diverges from the findings of prior studies [47–49], which reported a comparatively lower contribution of testers to total variance. This discrepancy might be attributed to variations in the genetic makeup of the studied populations and the specific experimental conditions.

The F_1 test crosses consistently exhibited higher values for the assessed traits compared to their parental lines. This phenomenon aligns with the concepts of allele frequencies within parental populations, a factor that can contribute to the observed trait expressions [50–54]. Many studies, focus predominantly on additive effects, potentially overlooking non-additive interactions that could further enhance trait performance. Further analysis uncovered the dominance of additive and non-additive gene effects in driving the expression of grain yield. Specifically, additive variance outpaced dominant genetic variance across the dimensions of AD, TKW, and GY. The intricate interaction between these genetic components is known to influence the precision of selection, thereby establishing a link between the observed patterns and the concept of narrow sense heritability. Notably, the medium to high heritability observed for the studied traits within the present investigation reinforces the presence of additive genetic variance and augments the feasibility of effective selection strategies. These results underscore the multifaceted interplay of genetic and environmental factors shaping the studied traits. The shades uncovered through the genetic components analysis reinforce the complex genetic interactions underlying the traits examined. This understanding enhances the potential for informed breeding practices tailored to harness the inherent genetic variations and their contributions to trait expressions. The substantial influence of additive genetic effects on traits like thousand kernel weight and grain yield supports the prospect of targeted breeding strategies aimed at trait enhancement. The outcomes of this genetic components analysis lay the foundation for informed and effective breeding program in maize improvement.

3.6. Selection of lines based on specific criteria

The results of combining ability analyses for various traits were meticulously examined to identify optimal lines demonstrating favorable performances across multiple trait combinations. The selection process considered both the mean and GCA effects of traits, focusing on specific criteria like days to anthesis ($AD < 91$ days), anthesis-silking interval ($ASI \leq 1$ day), thousand kernel weight ($TKW > 345$ g), and grain yield ($GY > 11$ t/ha). The majority of the chosen lines exhibited characteristics aligning with the reference values for these traits (**Table 5**).

Lines L1, L2, L10, and L13 were selected for their combination of TKW and GY, showcasing bold-seeded and high-yielding characteristics. On the other hand, lines L3, L5, L6, L12, and L14 were chosen for traits related to earliness and synchronized flowering, with L3 standing out for being selected based on four traits: earliness, synchronized flowering, bold seeding, and high yield. Additionally, L5, L9, and L14 were chosen for a combination of ASI, TKW, and GY, highlighting synchronized flowering, bold-seeded traits, and high yield. Lines L7 and L8 were each selected for

a single trait (ASI and GY, respectively), emphasizing specific focuses on synchronized flowering or high yield. While some lines (e.g., L1, L2, L10, L13) focused on the combination of TKW and GY, there was variability in the number of traits selected, indicating diversity in breeding goals for these lines.

The boxplot offered a visual summary of trait performance across lines used in crosses, illustrating data distribution patterns (**Figure 2**). Blue dots on the boxplot highlighted selected lines that met specified selection criteria (threshold values) for each trait.

In summary, these findings suggest a targeted and strategic selection of lines to achieve specific trait combinations. This precision in line selection indicates a strategic approach to expressing particular trait combinations, aiming for a balance of earliness, synchronized flowering, bold-seeded characteristics, and high grain yield. The inclusion of trait thresholds further emphasizes a detailed and precise selection criterion for certain lines. Lastly, breeding programs should explore hybrid designs that combine high-performing testers with diverse genetic backgrounds to maximize heterotic potential. These insights can guide future studies and decision-making in crop breeding and agricultural research, enhancing the potential for achieving desired crop characteristics.

Table 5. Selected lines with trait combinations and corresponding features.

LINE	Selected for (traits)	Number (traits)	Feature	Reference
L1	TKW + GY	2	Bold seeded; High yielding	
L2	TKW + GY	2	Bold seeded; High yielding	
L3	AD + ASI + TKW + GY	4	Earliness; Synchronized flowering; Bold seeded; High yielding	
L5	ASI + TKW + GY	3	Synchronized flowering; Bold seeded; High yielding	
L6	AD + ASI + TKW	3	Earliness; Synchronized flowering; Bold seeded	AD <91 days; ASI ≤1 days; TKW > 345 g; GY > 11 t/ha
L7	ASI	1	Synchronized flowering	
L8	GY	1	High yielding	
L9	ASI + GY	2	Synchronized flowering; Bold seeded	
L10	TKW + GY	2	Bold seeded; High yielding	
L12	AD + TKW	2	Earliness; Bold seeded	
L13	TKW + GY	2	Bold seeded; High yielding	
L14	ASI + TKW + GY	3	Synchronized flowering; Bold seeded; High yielding	

AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield.

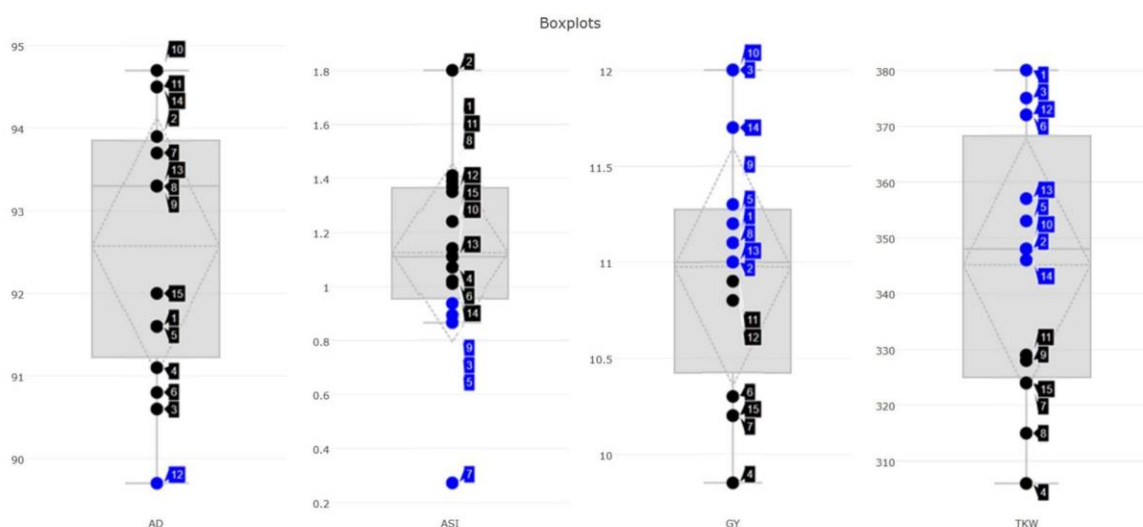


Figure 2. Boxplots represent the performances by different lines and are selected from GCA.

The blue dot represents the best genotypes for different traits as indicated by the GCA effects. Overall, this study provides valuable insights into the combining ability of maize genotypes and their interactions across diverse traits. Significant variations, diverse performances among lines and testers, and the identification of promising hybrid combinations offer valuable information for future breeding perspectives. These findings contribute to a deeper understanding of the genetic mechanisms influencing trait expressions and guide targeted breeding strategies for maize improvement.

4. Conclusion

The effectiveness of a successful breeding program hinges upon the extent of genetic variability inherent within lines, testers, and their collective combining abilities. Within the scope of this investigation, the discerned combining ability effects pertaining to AD, ASI, TKW, and GY underscore a substantial potential for the development of high-yielding maize test crosses. Significant variability was observed for the studied traits. The competence of line L10 and L3, coupled with tester 2, emerges as a promising combination for elevating grain yield. Similarly, the exceptional combining ability of lines L3 and L6 encompasses earliness, synchronized flowering, and the production of bold-sized kernels. Delving deeper into specific test cross performance, the dynamic $L15 \times T3$ and $L13 \times T1$ emerge as a dominant choice for optimal grain yield, while the $L3 \times T1$ and $L13 \times T2$ crosses resonate as the epitome of reduced days to anthesis. The cross $L1 \times T2$ and $L5 \times T1$ showed potential for synchronized flowering. The pronounced specific combining ability effect within the $L15 \times T3$ test cross for the trait TKW manifests as a pivotal avenue for enhancing grain yield. The study identified promising lines exhibiting desirable traits, including earliness, synchronized flowering, bold seeding, and high yield, meeting specific thresholds and reflecting diverse breeding goals. Moreover, the manifestation of additive gene action intensely underscores the scope for targeted selection, thus underscoring the prospect of breeding advancements. As we navigate the ground of

lines, testers, and test crosses, the identified candidates herein—lines, testers, and combinations—possess distinct potential for strategic integration within the breeding program. In agreement, they converge towards the cultivation of high-yielding maize varieties, which stands as evidence of meticulous research and genetic insights.

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Appendix

Trait wise Means of all genotypes (lines, testers and test cross hybrids) and standard errors were presented as appendices.

Table A1. Performances of different lines and testers with respect to studied traits.

Code	AD (days)	ASI (days)	TKW (g)	GY (t/ha)
Line				
L1	91.6	1.41	380	11.1
L2	93.9	1.8	348	11
L3	90.6	0.89	375	12
L4	91.1	1.07	306	9.85
L5	91.6	0.87	353	11.2
L6	90.8	1.02	372	10.3
L7	93.7	0.27	324	10.2
L8	93.3	1.37	315	11.1
L9	93.3	0.94	328	11.3
L10	94.7	1.14	348	12
L11	94.5	1.39	329	10.9
L12	89.7	1.35	372	10.8
L13	93.3	1.11	357	11
L14	94.5	1.01	346	11.7
L15	92	1.24	324	10.2
SE	1.5	0.27	22.5	0.62
Tester				
T1	91.7	1.36	334	10.5
T2	93.7	0.98	352	11.2
T3	92.3	1.04	350	11.2
SE	0.79	0.16	8.06	0.33

AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield, SE = Standard error.

Table A2. Performances of different test cross hybrids with respect to studied traits.

Line	Tester	AD (days)	ASI (days)	TKW (g)	GY (t/ha)
L1	T1	92.90	1.28	327.00	11.70
L1	T2	92.70	0.54	372.00	10.90
L1	T3	92.10	1.54	337.00	10.20
L2	T1	93.40	1.08	368.00	10.50
L2	T2	92.70	1.27	330.00	11.70
L2	T3	91.70	1.01	337.00	10.70
L3	T1	91.50	1.58	334.00	11.20
L3	T2	93.00	1.07	343.00	11.00
L3	T3	93.20	0.70	358.00	10.70
L4	T1	92.10	1.30	341.00	11.20
L4	T2	91.60	1.20	355.00	11.20

Table A2. (Continued).

Line	Tester	AD (days)	ASI (days)	TKW (g)	GY (t/ha)
L4	T3	94.00	0.86	339.00	10.50
L5	T1	93.00	0.67	371.00	11.70
L5	T2	92.70	1.28	340.00	10.20
L5	T3	92.00	1.42	323.00	11.00
L6	T1	93.50	0.96	328.00	10.70
L6	T2	91.70	1.32	366.00	11.30
L6	T3	92.50	1.08	341.00	10.90
L7	T1	91.90	1.12	340.00	9.74
L7	T2	94.00	1.11	366.00	11.40
L7	T3	91.80	1.13	329.00	11.70
L8	T1	92.20	1.36	382.00	11.80
L8	T2	93.00	0.97	322.00	10.90
L8	T3	92.60	1.03	332.00	10.20
L9	T1	92.40	1.56	343.00	10.60
L9	T2	93.20	0.71	344.00	11.10
L9	T3	92.10	1.09	349.00	11.20
L10	T1	92.20	1.06	361.00	11.00
L10	T2	92.40	1.18	347.00	11.30
L10	T3	93.20	1.13	328.00	10.60
L11	T1	92.70	0.99	327.00	10.80
L11	T2	92.70	1.21	352.00	10.80
L11	T3	92.30	1.16	356.00	11.20
L12	T1	92.70	0.90	349.00	10.80
L12	T2	92.30	1.13	330.00	10.80
L12	T3	92.60	1.33	356.00	11.30
L13	T1	92.60	0.99	332.00	12.00
L13	T2	91.50	1.04	354.00	10.50
L13	T3	93.60	1.33	349.00	10.40
L14	T1	92.00	0.98	338.00	10.60
L14	T2	93.20	1.57	336.00	10.80
L14	T3	92.50	0.81	362.00	11.50
L15	T1	93.40	0.98	334.00	10.20
L15	T2	92.00	1.21	319.00	10.50
L15	T3	92.30	1.17	382.00	12.20
SE		0.62	0.22	15.90	0.53

AD = Days to anthesis, ASI = Anthesis-silking interval, TKW = Thousand kernel weight, GY = Grain yield, SE = Standard error.