



Combining Ability and Gene Action for Grain Yield and Attributing Traits in Maize (*Zea mays* L.) Subjected to Drought Stress

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ABSTRACT

Background: Maize production is subdued by many impediments that cause yield minimization. Among various biotic and abiotic stress factors, one significant cause of yield reduction in maize is drought stress.

Methods: A set of 15 inbreds which were crossed with 3 narrow base testers in line × tester mating design and resulting 45 F₁s along with the parent inbreds and 3 commercial checks were then evaluated in RCBD, subjected to drought stressed and well-watered conditions to assess their genetic worth during *spring* 2021.

Result: The ANOVA unraveled significant mean sum of squares due to lines, testers and line × tester in pooled analysis for all the ten traits. The inbred EI-2188-2 followed by EI-2448 and EI-03-3 contained fair *per se* performance and significant high GCA effects over the environments for grain yield/plant, proline content and cob length whereas the cross EI-2448-1×EI-2156 was found most promising hybrid with significant and high SCA effects across the environments regarding grain yield/plant, proline content and cob girth. Prevalence of non-additive type of genetic variance in governing most of the traits suggests adoption of heterosis breeding will be rewarding for improving yield and drought tolerance. Heterotic pooling of the highlighted inbreds and utilization of the superlative hybrids in further breeding programmes for drought tolerance is proposed.

Key words: Drought, GCA, Grain yield, Maize, SCA.

INTRODUCTION

Maize (*Zea mays* L.) is a versatile crop possessing wider genetic variation and one of the most significant crops providing food, fodder and fuel worldwide covering tropical, sub-tropical and temperate agro-climatic conditions. Maize production is subdued by many impediments that cause yield minimization. Among various biotic and abiotic stress factors, one significant cause of yield reduction in maize is drought stress. When drought occurs during flowering of maize, it disrupts fertilization and diminishes availability of photosynthates to developing kernels, leading to kernel abortion, reduction in kernel number and a yield loss ranging from 17 per cent to 60 per cent (Edmeades *et al.*, 1999). Moreover, drought stress coinciding with both flowering and grain-filling stages of maize could result in yield losses of up to 90 per cent (Menkir and Akintunde, 2001). The unpredictability in rainfall pattern, ascending temperatures and intense changes in weather patterns linked with the issue of climate change will further upsurge the frequency and intensity of drought in many parts of India as well as the world. Therefore, strengthening of food security and alleviation in farmers' livelihood require concrete approach towards developing climate-smart crops and enhancing resilience of crops to drought stress.

Hence the current investigation was taken up to assess the available maize germplasm for its potential of adaptation to drought conditions. The combining ability analysis is of utmost importance in distinguishing excellent combiners and also assists in deciphering genetic basis of significant characters and their inheritance. Selection of

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appropriate breeding method for advancement of drought tolerance traits primarily depends upon the comparative significance of GCA and SCA variances. The additive gene action can be utilized for developing stress tolerant inbreds whereas non-additive gene action can be used for developing hybrids by involving the inbreds identified with good SCA effects for stress tolerance. Therefore, in the current investigation general combining ability effects of a set of inbreds and specific combining ability effects of the crosses were analyzed for grain yield and component traits under both well-watered and drought stressed conditions.

MATERIALS AND METHODS

The experiment was taken up at Instructional Farm, Rajasthan College of Agriculture, MPUAT, Udaipur (24°34' N latitude, 73° 42' E longitude), which comes under Zone

IVa (Sub-humid Southern Plains and Aravalli hills) of Rajasthan (India) with sub-tropical and humid climate. The type of soil at the experimental site was predominantly clay-loam and was alluvial in origin.

Amongst various biometrical methods for evaluation of GCA and SCA of varying genetic material, the line $\times$ tester mating design was acquired in the present experiment wherein crossing of 15 inbred lines was performed with 3 narrow base testers during *rabi* 2019-20. The resulting 45 hybrids and 18 parent inbreds were further subjected to assess their genetic worth along with 3 commercial checks during *spring* 2021 by adopting Randomized Complete Block Design (RCBD) with three replications. The details of the inbreds, testers and commercial checks involved in the current experiment have been provided in Table 1. The experiment was executed over three different environments *i.e.* optimal environment with normal irrigation (E1), drought stress imposed at tasseling stage for 20 days (E2) and drought stress imposed at grain filling stage for 20 days (E3) by skipping irrigation at the desired crop growth stage for the mentioned period. A distance of 60 cm from row to row and 20 cm from plant to plant with a single row of 3 m length for each genotype was maintained in all the three environments and border rows were planted around the field in all the environments to check border effect. Each environment was separated from the other by 2 m wide channel in order to check the effect of lateral flow of moisture and the suggested

package of practices for Zone IVa was pursued in all the environments for getting a healthy crop stand.

Data was recorded on ten different traits in the current investigation out of which measurements were taken for each genotype in each replication on ten randomly selected competitive plants for total chlorophyll content (SPAD chlorophyll meter reading), leaf senescence score (0-10, where 0 for all green leaves and 10 for all dried leaves), cob length (cm), cob girth (cm), grain yield per plant (g) and drought tolerance index (%) and data was obtained on plot basis for days to 50 per cent tasseling, days to 50 per cent silking, anthesis-silking interval (ASI) and proline content ($\mu\text{g}/100$ mg fresh leaf tissue). The data were recorded in E1 and E2 during drought stress at tasseling stage and in E1 and E3 during drought stress at grain filling stage for total chlorophyll content, proline content and leaf senescence score. For computing drought tolerance index (DTI), observations were recorded in E2 and E3 environments only, by using following formula:

The analysis of variance (ANOVA) was executed with the collected data in each environment and over the environments for randomized complete block design by adopting the method advocated by Fisher (1954) and Panse and Sukhatme (1985). The general as well as specific

$$\frac{\text{Yield under normal condition} - \text{Yield under drought condition}}{\text{Yield under normal condition}} \times 100$$

Table 1: Details of parent inbreds, testers and commercial checks involved in the study on maize.

Symbol	Line code	Source of parental lines	Origin/Source of collection
L1	EI-11-3	UP-3	AICRP Maize, Udaipur
L2	EI-08	UP-3	AICRP Maize, Udaipur
L3	EI-2521	Late maturity GP	AICRP Maize, Udaipur
L4	EI-2448-1	Late maturity GP	AICRP Maize, Udaipur
L5	EI-2188-2	Late maturity GP	AICRP Maize, Udaipur
L6	EI-2449-2	Late maturity GP	AICRP Maize, Udaipur
L7	EI-01-2	UP-3	AICRP Maize, Udaipur
L8	EI-2448	Late maturity GP	AICRP Maize, Udaipur
L9	EI-2138-1	Medium maturity GP	AICRP Maize, Udaipur
L10	EIQ-212	QPM GP-3	AICRP Maize, Udaipur
L11	EI-561-1	UP-3	AICRP Maize, Udaipur
L12	EI-2188	Late maturity GP	AICRP Maize, Udaipur
L13	EI-2518-1	Late maturity GP	AICRP Maize, Udaipur
L14	EI-12-2	UP-3	AICRP Maize, Udaipur
L15	EI-03-3	UP-3	AICRP Maize, Udaipur
T1	EI-586-2	UP-3	AICRP Maize, Udaipur
T2	EI-2156	Late maturity GP	AICRP Maize, Udaipur
T3	EI-670-2	UP-3	AICRP Maize, Udaipur
C1	Pratap QPM Hybrid-1	DMR QPM 106 $\times$ HKI 193-1	MPUAT, Udaipur
C2	Pratap Hybrid Maize-3	EI-586-2 $\times$ EI-670-2	MPUAT, Udaipur
C3	Pratap Makka-9	Composite variety	MPUAT, Udaipur

Where, L: Lines; T: Testers; C: Checks; UP: Udaipur Gene Pool; GP: Gene Pool; AICRP: All India Coordinated Research Project; MPUAT: Maharana Pratap University of Agriculture and Technology.

combining ability effects in each environment and over the environments for line $\times$ tester mating design were computed (Software: BRR STATE) by using method propounded by Kempthorne (1957).

RESULTS AND DISCUSSION

Analysis of variance

The analysis of variance for individual environments revealed that all the genotypes were significantly different from each-other regarding all the ten traits involved in the study. The mean sum of squares estimated due to lines, testers and line $\times$ tester in pooled ANOVA for combining ability and components of genetic variance were noted significant for all the characters taken under investigation (Table 2). The significant mean sum of squares due to lines and testers for most of the characters indicated their significant contribution towards general combining ability. Likewise, significant mean sum of squares due to line $\times$ tester interaction for most of the characters indicated significant contribution of hybrids for specific combining ability effects. The line $\times$ environment interaction, tester $\times$ environment interaction and line $\times$ tester $\times$ environment interaction, all were noted significant for most of the characters except few traits under study, which indicated that maximum number of characters exhibited significant influence of environment on estimates of GCA and SCA effects. Analogous reports regarding ANOVA were cited by Annor *et al.* (2019); Keimeso *et al.* (2020); Chavan *et al.* (2022); Subba *et al.* (2022); Jebaraj *et al.* (2024) and Teja *et al.* (2024).

General combining ability (GCA) effects

Among the parent inbred lines, EI-2521 in E1, E2 and pooled basis and EI-11-3 in E3 consisted highest negative significant GCA effects for days to 50 per cent tasseling and days to 50 per cent silking whereas EI-08 for days to 50 per cent tasseling and EI-11-3, EI-2521 and EI-2188 for days to 50 per cent tasseling as well as silking displayed significant negative GCA effects in all the three environments as well as in pooled analysis, denoting consistency of their early tasseling and silking nature over the environments. Among the testers EI-2156 was found with significant negative GCA effects on pooled basis for days to 50 per cent tasseling and days to 50 per cent silking. For anthesis-silking interval, EI-2449-2 in all the environments and in pooled analysis followed by EIQ-212 in majority of the environments displayed high negative significant GCA effects, addressing their high-caliber in conveying genes preferable for minimum ASI. Among the testers, only EI-670-2 contained significant negative GCA effects in E2 and in pooled analysis. Alike findings for the above described traits were advocated by Geetha *et al.* (2019), Keimeso *et al.* (2020), Yu *et al.* (2020), Riache *et al.* (2021), Subba *et al.* (2022) and Teja *et al.* (2024). Hence the above described inbred lines should be incorporated in breeding programmes of maize proposed for early

Table 2: Mean sum of square over the environments for the ten traits involved in the study on maize.

Source	df	Days to 50% tasseling	Days to 50% silking	Anthesis-silking interval (ASI)	Total chloro-phyll content (SCMR)	Proline content (μ g/100 mg fresh leaf tissue)	Leaf sene-scence score	Cdb length (cm)	Cdb girth (cm)	Grain yield per plant (g)	Drought tolerance index (DTI)
Environment	2	130.29**	1317.44**	619.29**	7567.21**	538891.28**	771.67**	490.37**	28.20**	36776.98**	14781.31**
Rep./Env.	6	4.49	4.57	0.12	1.08	3.10	0.21	2.68	0.15	34.32	0.66
Genotype	5	126.57***+	124.88***+	1.77***+	140.23***+	10266.28***+	5.74**	30.41***+	1.20**	4570.74***+	662.44***+
G $\times$ E	130	6.94**	6.89**	0.75**	11.56**	2808.53**	4.63**	2.84**	0.15	348.88**	195.17**
Pooled error	390	3.51	3.45	0.12	1.80	2.00	0.14	1.97	0.12	77.14	1.12

**Significant at 1% level of significance. +,++ Significant against respective environmental interaction at 5% and 1% respectively.

flowering and maturity in stressed as well as non-stressed environments.

For total chlorophyll content, the inbred line EI-561-1 was recorded with highest significant positive GCA effects followed by EI-2188 on pooled basis as well as over the environments. Among the testers, only EI-2156 contained significant positive GCA effects on pooled basis. For proline content, EI-03-3 on pooled basis was recorded with highest significant positive GCA effects while the lines, EI-2448 and EI-Q-212 displayed significant positive GCA effects over the environments as well as in pooled analysis. Among the testers, EI-670-2 on pooled basis contained significant positive GCA effects. For leaf senescence score, EI-2448 on pooled basis was recorded with significant highest negative GCA effects while the lines, EI-08 and EI-2518-1 displayed significant negative GCA effects over the environments as well as in pooled analysis. Among the testers, only EI-670-2 on pooled basis contained significant negative GCA effects. It thus addresses that the above pointed lines can be chosen for carrying forward genes admissible for higher chlorophyll and proline and lower leaf senescence score. Alike findings were advocated by Khandagale (2017), Patil *et al.* (2020), Kamphorst *et al.* (2022), Subba *et al.* (2022) and Teja *et al.* (2024) for total chlorophyll content; Annor *et al.* (2019), Rahimi (2021) and Osuman *et al.* (2022) for proline content and leaf senescence score.

For cob length, EI-2449-2 on pooled basis was recorded with significant and highest positive GCA effects and the lines, EI-2449-2 and EI-03-3 displayed significant positive GCA effects over the environments and in pooled analysis. Among the testers, only EI-2156 on pooled basis contained significant positive GCA effects. For cob girth, EI-2521 on pooled basis was recorded with significant and highest positive GCA effects and the line EI-2521 displayed significant positive GCA effects over the environments and in pooled analysis. Among the testers, only EI-2156 on pooled basis contained significant positive GCA effects. It disclosed that the above stated parent inbred lines were excellent in delivering beneficial genes for greater cob length and girth and must be involved in breeding programmes proposed for enhancing maize yields. Alike outcomes for cob length and cob girth were backed by Khandagale (2017), Geetha *et al.* (2019), Chavan *et al.* (2022) and Jebaraj *et al.* (2024).

The highest positive GCA effects for grain yield per plant were demonstrated significantly by the line EI-2188-2 in E1, EI-2448 in E3 and EI-03-3 in E2 as well as on pooled basis for grain yield per plant, thus these lines were considered the best in their respective environments for higher grain yield. Among all the lines, EI-2188-2, EI-2448 and EI-03-3 held significant positive GCA effects in all the three environments and in pooled analysis, which addressed about their consistency in performance over stressed and non-stressed environments and greater proficiency in conveying genes preferable for higher grain

yield to their next generation. Among the testers, only EI-2156 in E1, E2, E3 and on pooled basis attained significant positive GCA effects. Alike outcomes were reported by Annor *et al.* (2019), Ramadan *et al.* (2021), Subba *et al.* (2022), Osuman *et al.* (2022) and Jebaraj *et al.* (2024) for grain yield per plant. The top outstanding inbreds and testers for grain yield per plant have been listed in Table 3. Since drought tolerance index is drought stress relevant index, it was recorded only in the stressed environments *i.e.* E2 and E3. Among all the lines, EI-2521, EI-2449-2, EI-01-2, EI-Q-212, EI-2188, EI-2518-1, EI-12-2 and EI-03-3 displayed significant negative GCA effects in the two environments and in pooled analysis, indicative of their preeminence in delivering genes admissible for lower DTI and higher drought tolerance. Among the testers, EI-670-2 and EI-2156 on pooled basis contained significant negative GCA effects. Alike findings were recited by Adebayo and Menkir (2014).

Specific combining ability (SCA) effects

Out of all hybrids, EI-01-2 × EI-2156 on pooled basis as well as in all the environments and EI-12-2 × EI-670-2 in majority of the environments had registered significant high SCA effects in preferable direction for days to 50 per cent tasseling and silking, indicating their early flowering nature. For ASI, EI-Q-212 × EI-586-2 on pooled basis and in each environment, followed by EI-2188 × EI-2156 and EI-2138-1 × EI-670-2 in majority of the environments, had registered significant SCA effects in preferable negative direction. Findings kin to the above results for days to 50 per cent tasseling as well as silking and ASI were advocated by Amegbor *et al.* (2020), Yu *et al.* (2020), Riache *et al.* (2021), Subba *et al.* (2022) and Teja *et al.* (2024).

Positive significant SCA effects for total chlorophyll content were showcased by the crosses EI-2448-1 × EI-586-2, EI-2449-2 × EI-586-2, EI-2448 × EI-586-2, EI-Q-212 × EI-586-2, EI-01-2 × EI-2156, EI-08 × EI-670-2 and EI-2188 × EI-670-2 in all the environments and in pooled analysis. For proline content, EI-2449-2 × EI-670-2 on pooled basis evinced highest SCA effects while the crosses EI-2521 × EI-586-2, EI-2188-2 × EI-586-2, EI-01-2 × EI-586-2, EI-561-1 × EI-586-2, EI-03-3 × EI-586-2, EI-2448-1 × EI-2156, EI-08 × EI-670-2, EI-2448 × EI-670-2, EI-Q-212 × EI-670-2 and EI-2518-1 × EI-670-2 had registered significant SCA effects in acceptable positive direction over the environments. For leaf senescence score, EI-03-3 × EI-670-2 on pooled basis evinced significant highest negative SCA effects whereas the crosses EI-2521 × EI-586-2, EI-2448 × EI-2156, EI-12-2 × EI-2156, EI-561-1 × EI-670-2 and EI-2188 × EI-670-2 had registered significant SCA effects in acceptable negative direction in majority of the environments. Similar reports were backed by Khandagale (2017), Patil *et al.* (2020), Kamphorst *et al.* (2022), Subba *et al.* (2022) and Teja *et al.* (2024) for total chlorophyll content; Annor *et al.* (2019), Rahimi (2021) and Osuman *et al.* (2022) for proline content and leaf senescence score.

Table 3: Five best parent inbreds and hybrids identified based on their GCA and SCA effects, respectively, on pooled basis for grain yield per plant in maize.

	Inbreds/Hybrids	Grain yield per plant (g)	GCA/SCA effect
Inbred lines			GCA effect
	EI-03-3	135.66	21.78**
	EI-2448	97.52	20.50**
	EI-2188-2	104.58	15.43**
	EI-561-1	89.27	11.22**
	EI-2448-1	45.73	7.16**
Tester			GCA effect
	EI-2156	91.31	8.74**
Hybrids			SCA effect (Parental GCA status)
	EI-2448-1 × EI-2156	138.58	22.96** (G × G)
	EI-08 × EI-586-2	121.06	21.64** (A × P)
	EI-2518-1 × EI-670-2	95.92	19.13** (P × P)
	EI-2138-1 × EI-670-2	82.03	17.37** (P × P)
	EI-12-2 × EI-586-2	101.68	16.05** (P × P)

**Significant at 1% level of significance.

For cob length, the cross EIQ-212 × EI-670-2 on pooled basis and in each environment followed by EI-01-2 × EI-586-2 and EI-01-2 × EI-2156 in majority of the environments had registered significant SCA effects in acceptable positive direction. For cob girth, EI-2448-1 × EI-670-2 on pooled basis and in each environment followed by EI-01-2 × EI-2156 in majority of the environments had registered significant SCA effects in preferable positive direction. Alike outcomes were backed by Geetha *et al.* (2019), Keimeso *et al.* (2020), Chavan *et al.* (2022) and Jebaraj *et al.* (2024).

For grain yield per plant, EI-2448-1 × EI-2156 in E1, EI-2138-1 × EI-670-2 in E2, EI-08 × EI-586-2 in E3 and EI-2448-1 × EI-2156 on pooled basis contained highest SCA effects for grain yield per plant while the crosses EI-08 × EI-586-2, EI-12-2 × EI-586-2, EI-2448-1 × EI-2156 and EI-2521 × EI-670-2 in all the environments and in pooled analysis followed by EI-2448-1 × EI-2156 and EI-2448-1 × EI-670-2 in majority of the environments had registered significant SCA effects in admissible positive direction. It points towards notability of SCA effects and non-additive component of gene action in hybrid development for higher yield. The outcomes kin to these results were backed by Annor *et al.* (2019), Ramadan *et al.* (2021), Osuman *et al.* (2022) and Jebaraj *et al.* (2024). The top outstanding hybrids for grain yield per plant have been listed in Table 3. Negative significant SCA effects in all the environments for lower DTI were held by EI-11-3 × EI-586-2, EIQ-212 × EI-586-2, EI-561-1 × EI-586-2, EI-03-3 × EI-586-2, EI-08 × EI-2156, EI-2188-2 × EI-2156, EI-01-2 × EI-2156, EIQ-212 × EI-2156, EI-2188 × EI-2156, EI-2518-1 × EI-2156, EI-2521 × EI-670-2, EI-2449-2 × EI-670-2, EI-2138-1 × EI-670-2 and EI-2188 × EI-670-2. Alike findings were recited by Adebayo and Menkir (2014) whereas contrasting reports by Ribaut *et al.* (1997).

The analysis of contribution of lines, testers and line × tester interaction towards expression of all the characters revealed that contribution of lines was greater than testers for all the characters whereas line × tester interaction had greater contribution than the parents for the characters viz. ASI, proline content, cob length, cob girth and drought tolerance index on pooled basis. It also unraveled that the good × poor general combiners or good × average general combiners combination of parents representing high SCA effects in their crosses remarked the role of additive × dominance type of gene interaction, while the poor × poor general combiners' combination evinced importance of complementary gene action with over-dominance effects.

CONCLUSION

The present investigation addressed the fact that both the additive type (fixable) and non-additive (non-fixable) type of gene actions have played a crucial role in the inheritance of the characters considered in this study but the non-additive type of genetic variance was prevalent in governing most of the traits, which suggests that adopting heterosis breeding will be rewarding. It was ascertained from the study that the three hybrids, out of the top five hybrids for grain yield per plant, had both the parents as poor general combiners that indicates combination of two poor general combiners or one poor with other average/good general combiner could also lead to production of a superlative hybrid. However, it would be beneficial if any one parent of the two possesses good or average GCA for giving rise to a high yielding hybrid.

The analysis of data evinced that the lines, EI-2188-2 for grain yield per plant followed by EI-2448 and EI-03-3 for grain yield per plant as well as cob length and proline content, were promising in all the three environments as

well as in pooled analysis. Among other inbreds, EIQ-212 for ASI, proline content and DTI and EI-2188 for days to 50 per cent tasseling, days to 50 per cent silking, total chlorophyll content and DTI were spotted as excellent inbreds. Among the testers, only EI-2156 emerged out as good general combiner for grain yield per plant across the environments and also for days to 50 per cent tasseling, days to 50 per cent silking, total chlorophyll content, cob girth and DTI in pooled analysis. Therefore these inbreds might be considered for the breeding plans proposed for alleviating grain yield and drought tolerance under stressed and non-stressed environments. The hybrid, EI-2448-1 × EI-2156 was noted outstanding regarding grain yield per plant and for proline content and cob girth whereas EI-08 × EI-586-2 also excelled for grain yield per plant along with days to 50 per cent tasseling, days to 50 per cent silking and leaf senescence score. Therefore, the present investigation confirmed the potential perks of hybrid breeding and exploitation of heterosis to improve maize production in such environmental conditions of moisture stress or scanty rainfall. Incorporating the above stated potential inbreds to heterotic pools based on their combining ability may prove as a promising approach in breeding for drought stress. The recognized superlative hybrids may also be utilized for further construction of double crosses, three-way crosses, etc. in drought stress breeding programmes. Nonetheless multi-location as well as multi-year trials will be of perforce to endorse the presented findings and to support the expression of genes.

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Conflict of interest

All the authors declare that they have no conflicts of interest.

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