

Effect of moisture stress on combining ability and gene action for polygenic traits in maize

Sumalini Katragadda^{1*}, Pradeep Tekale², Manjulatha Guddeti¹

¹Maize Research Scheme, Agricultural Research Station, PJTSAU, Karimnagar, Telangana state, India - 505 001

²Maize Research Centre, Agricultural Research Institute, PJTSAU, Rajendranagar, Hyderabad, Telangana state, India, 500 030

*Corresponding author: E-mail: sumaliniKatragadda@gmail.com

Abstract

Present study was carried out to assess the general combining ability effects of parents and specific combining ability effects of hybrids for yield and yield related traits purely under rainfed situations. Incidentally, it mimicked mid season drought conditions i.e. moisture stress at flowering stage for a period of 22 days. Combining ability analysis using Line \times Tester design was conducted in maize (*Zea mays* L) inbred lines by growing 135 F₁'s generated by crossing fifteen lines with nine testers at ARS, Karimnagar, PJTSAU during rainy season, 2011. Female lines were derived from the recurrent selection cycle carried out in the drought tolerant population «Tuxpeno Sequia», procured from CIMMYT in 1996. Males were developed using pedigree breeding. Analysis of variance showed highly significant genotypic differences for all the traits studied indicating wide range of variability among the genotypes. The ratio of gca /sca was less than unity indicating the preponderance of non-additive gene action in the expression of all the characters studied except flowering traits. Moderate narrow sense heritability was observed for majority of the characters. Three lines KMLD-3, KMLD-11, and KMLD-19 and one tester, KML-9 were good general combiners for grain yield and one or more yield contributing characters. The crosses KMLD-3 \times KML-99, KMLD-5 \times BML-7, KMLD-5 \times KML-801, KMLD-6 \times KML-36, and KMLD-11 \times KML-29 showed significant positive sca, standard heterosis and high mean values for grain yield plant⁻¹ and two or more yield components. These hybrids were found to be early in flowering with significant negative heterosis providing some clue about their usefulness under drought conditions. Therefore further testing of these new inbred lines for use in a crossing program is recommended to combine major yield components with high yield to derive climate resilient hybrids.

Keywords: maize, moisture stress, combining ability, line \times tester, standard heterosis, narrow sense heritability

Introduction

Drought is estimated to cause average annual yield losses in maize of about 17% in the tropics (Edmeades et al, 1989), and this figure is expected to increase in the future as a large population of the crop is being shifted to marginal lands. Indian agriculture is dominated by rain fed farming and so even after development of large irrigation infra structure, still 63% area is rain fed. In India, Maize is grown on 6 mha area mainly as rain fed crop during rainy (kharif) season. Telangana state is one of the major maize producing states in the country and maize is cultivated mainly as a rain fed crop in kharif season.

Maize is particularly sensitive to water stress in the period one week before to two weeks after flowering (Grant et al, 1989). Drought during this period results in increased anthesis-silking interval (ASI) (Edmeades et al, 2000) and consequently in grain abortion (Boyle et al, 1991). Hence, development of maize cultivars with high and stable yields under drought is most important particularly in Northern Telangana Zone where mid season and terminal droughts during kharif are common. Keeping this constraint in view an attempt has been made in the present investigation

to study the gca and sca effects of parents and hybrids respectively in crosses where drought tolerant lines were used.

Materials and Methods

The experimental material comprised of fifteen lines, viz. KMLD-3, KMLD-5, KMLD-6, KMLD-11, KMLD-18, KMLD-19, KMLD-21, KMLD-61, KMLD-65, KMLD-66, KMLD-68, KMLD-70, KMLD-71, KMLD-73, and KMLD-82. These lines were derived from the recurrent selection cycle carried out in the population «Tuxpeno Sequia», procured from CIMMYT in 1996. Nine testers viz. BML-7, KML-9, KML-29, KML-36, KML-55, KML-99, KML-224, KML-801, and KML-802 were developed using pedigree breeding. These parents were crossed in line \times tester fashion during rabi season of 2011-12 at Agricultural Research Station, Karimnagar to generate 135 F₁'s. During kharif season of 2012, all the single crosses were evaluated in a randomized block design with two replications with row-to-row and plant-to-plant spacing of 75 cm \times 20 cm, respectively purely under rain fed situation against DHM-117, the popular check. Crop was sown on July 25th and at flowering stage crop was under

severe moisture stress in the month of September. Incidentally, it mimicked mid-season drought condition for a period of 22 days. Rainfall at vegetative stage i.e. in the month of August was 10.5% deficit (217.8 mm) over the normal rainfall (246.52 mm) and at flowering stage i.e. in the month of September was 103.52% deficit (97 mm) over the normal rainfall (172.66 mm). The data were recorded on five selected plants for 11 yield and yield contributing characters. Combining ability analysis was done according to the model given by Kempthorne (1957).

Results and Discussion

In the present investigation, the analysis of variance for all the yield and yield component traits showed that, variance due to hybrids was highly significant for all the traits studied indicating the manifestation of parental genetic variability in their crosses (Table 1). The mean squares for hybrids were partitioned into three components viz., due to lines, due to testers and due to line \times tester interactions. The differences among hybrids due to the lines, testers and line \times tester interaction were significant for all the characters except number of ears plant⁻¹ in lines and testers, ear length, number of kernels row⁻¹ and grain yield plant⁻¹ in lines and ear height and ear girth in testers, suggesting that the experimental material possessed considerable variability and that both gca and sca were involved in genetic expression of these traits. A higher proportion of sca variance than gca variance was noticed for all the traits except days to 50% pollen shed and days to 50% silk emergence indicating significantly higher non-additive interactions among the hybrids, which could be exploited. Higher sca variance than the gca variance exhibiting preponderance of non-additive gene effects has also been earlier reported by Aminu and Izge (2013). However, the results contradict the view reported by Sharma et al (2004), who found the preponderance of additive genetic effects in the control of most traits in maize.

Estimates of gca effects (Table 2) indicated that the lines KMLD-3 KMLD-11, and KMLD-19 were good general combiners for grain yield plant⁻¹. Lines KMLD-19 and KMLD-21 were good general combiners for 100 grain weight and number of kernels

row⁻¹, respectively. Lines KMLD-5 and KMLD-6 were good combiners for kernel rows and ear girth. For ear length, KMLD-71 and KMLD-73 were good general combiners and for days to 50% silking, KMLD-19, KMLD-65, KMLD-68 and KMLD-71 were good general combiners. KMLD-3, KMLD-5, KMLD-19, and KMLD-61 were good general combiners for plant height. Among testers, KML-9 was a good general combiner for grain yield plant⁻¹, ear girth and number of kernels row⁻¹. BML-7 was a good general combiner for plant height, ear height, ear girth and 100 grain weight and KML-224 was a good general combiner for plant height, ear length and 100 grain weight. KML-55, KML-801, and KML-802 were good general combiners for days to 50% pollen shed and days to 50% silking.

Among the hybrids, KMLD-5 \times KML-801 was the best specific combiner for grain yield followed by KMLD-6 \times KML-36 and KMLD-11 \times KML-29 (Table 3). The lines KMLD-5, KMLD-18 and KMLD-68 with tester BML-7 were good specific combiners for grain yield plant⁻¹. KMLD-70 \times KML-801 was the only combination with significant positive sca for grain yield plant⁻¹ coupled with significant negative sca for days to 50% silking desirable for early maturity. Line KMLD-5 with testers BML-7 and KML-9 showed significant positive sca for plant height, ear height, ear length, and ear girth, lines KMLD-19 and KMLD-65 with the same testers showed significant positive sca for plant height and ear girth. In most of the hybrids that had the highest sca effects for grain yield plant⁻¹, one of the parents was KMLD-3 or BML-7 or KML-9. These are the best general combining parents either for grain yield plant⁻¹ and yield attributing characters and therefore, the combination of favorable genes from the parents for the corresponding traits could have resulted in high and desirable sca effects. In the present study, some of the superior hybrids were from either one of the parents with high gca effect or parents that are low \times low general combiners, indicating that the parents with either high gca or low gca would have a higher chance of having excellent complementarity with other parents. This is in similarity with that of earlier findings of Premliatha and Kalamani (2010).

Table 1 - Analysis of variance for combining ability.

Source	df	Grain yield plant ⁻¹	Days to 50% pollen shed	Days to 50% silking	Plant height	Ear height	Number of ears plant ⁻¹	Ear length	Ear girth	Kernel rows	Number of kernels row ⁻¹	100 grain weight
Replications	1	1217.73**	0.00	0.37	607.50**	0.53	0.01	2.60	8.22**	0.03	529.20**	44.00**
Hybrids	134	241.83**	7.35**	7.31**	379.74**	187.65**	0.03**	2.67**	1.55**	3.67**	14.93**	16.18**
Lines 14	358.24	19.00**	16.26**	1381.65**	956.56**	0.04	3.82	3.62**	10.57**	19.20	26.24**	
Testers	8	432.98*	42.77**	36.58**	902.46**	175.22	0.03	6.49**	2.24	9.72**	41.08**	65.60**
Lines \times Testers	112	213.62**	3.36**	4.09**	217.16**	92.43**	0.03**	2.26***	1.24**	2.38**	12.53**	11.39**
Error 134	61.43	1.97	2.45**	80.46	34.35	0.01	0.69	0.39	1.18	8.07	3.88	
gca variance		7.58*	1.15**	0.93**	38.54**	19.73**	0.00	0.12**	0.07	0.32**	0.73*	1.44**
sca variance		76.09**	0.69**	0.82**	68.35**	29.04**	0.01*	0.78**	0.42**	0.60**	2.23**	3.76**
Additive variance		15.17	2.29	1.86	77.07	39.46	0.00	0.24	0.14	0.65	1.47	2.88
Dominance variance		76.09	0.69	0.82	68.35	29.04	0.01	0.78	0.42	0.60	2.23	3.76
gca variance/sca variance		0.10	1.66	1.13	0.56	0.68	0.03	0.15	0.17	0.54	0.33	0.38

*Significant at $p < 0.05$; **Significant at $p < 0.01$

Table 2 - Estimates of general combining ability effects of inbred lines of maize.

Lines/Testers	Grain yield plant ⁻¹	Days to 50% pollen shed	Days to 50% silking	Plant height	Ear height	Number of ears plant ⁻¹	Ear length	Ear girth	Kernel rows	Number of kernels row ⁻¹	100 grain weight
KMLD-3	6.65**	1.48**	0.59	9.06**	9.45**	0.01	-0.13	0.33*	0.47	-0.76	0.10
KMLD-5	0.83	0.98	0.64	18.67**	18.06**	0.02	-0.12	0.64**	1.14**	-0.81	0.49
KMLD-6	3.13	1.15**	1.37**	3.84	3.12*	0.03	-0.24	0.61**	1.20**	0.58	0.38
KMLD-11	4.54*	0.20	0.64	-6.44**	-6.11**	-0.04	0.37	0.03	0.03	-0.31	1.05*
KMLD-18	-2.97	0.20	0.31	-5.72**	-3.11*	-0.10**	-0.49*	-0.00	1.25**	-1.53*	-1.29**
KMLD-19	8.75**	-0.46	-1.02**	8.84**	6.62**	0.06**	0.37	0.78**	-0.19	1.3	3.33**
KMLD-21	-0.36	0.32	0.76*	-2.72	-4.50**	0.04	0.01	-0.81**	-1.14**	1.58*	-0.51
KMLD-61	1.77	1.15**	1.14**	8.23**	2.62	0.05*	0.35	-0.11	-0.42	-0.37	-0.29
KMLD-65	-3.77*	-2.19**	-1.80**	-10.60**	-8.22**	-0.05*	-0.49*	-0.20	-1.19**	0.80	0.49
KMLD-66	-0.48	-0.52	-0.52	1.84	-2.50	-0.02	0.01	-0.00	-0.19	0.24	0.38
KMLD-68	-1.61	-1.46**	-1.13**	-2.66	-5.61**	-0.01	-0.27	-0.25	-0.64*	0.41	-0.51
KMLD-70	-7.38**	-0.30	0.26	-11.77**	-7.22**	0.04*	-0.93**	-0.59**	-0.08	-1.70*	-1.73**
KMLD-71	-5.56**	-0.74*	-1.19**	-11.66**	-6.05**	0.02	0.96**	-0.42**	-0.25	0.30	-1.45**
KMLD-73	-0.06	-0.52	-0.41	-0.83	2.50	0.03	0.40*	-0.14	0.36	1.30	0.29
KMLD-82	-3.48	0.70*	0.37	1.90	0.95	-0.09**	0.07	0.14	-0.36	-1.03	-0.17
SE (Lines) ±	1.85	0.33	0.37	2.11	1.38	0.02	0.20	0.15	0.26	0.67	0.46
BML-7	0.30	1.85**	1.69**	9.11**	2.24*	0.01	-0.48**	0.42**	-0.29	-1.00	2.10**
KML-9	3.18*	1.05**	0.89**	-3.99*	-1.83	-0.03*	0.21	0.33**	-0.09	1.27*	-0.13
KML-29	1.36	-0.15	0.06	-5.29**	-0.63	0.05**	-0.46**	0.03	1.07**	1.13*	-1.60**
KML-36	2.12	-0.32	-0.38	-3.83*	-0.93	-0.04*	0.02	0.07	0.57**	0.97	1.04**
KML-55	1.42	-1.09**	-0.84**	-5.99**	-0.66	-0.02	-0.04	0.02	0.17	0.10	-0.53
KML-99	-9.43**	0.28	0.66*	3.44*	5.60**	-0.01	-0.23	-0.36**	-0.03	-1.47**	-1.93**
KML-224	2.25	1.22**	0.79**	7.04**	-1.50	0.00	1.09**	0.08	-0.49*	-1.87**	2.10**
KML-801	-1.64	-1.49**	-1.18**	-1.16	-1.60	-0.01	-0.04	-0.25*	-0.06	0.67	-1.00**
KML-802	0.44	-1.35**	-1.68**	0.67	-0.70	0.04*	-0.08	-0.34**	-0.86**	0.20	-0.06
SE (Testers) ±	1.43	0.26	0.29	1.64	1.07	0.02	0.15	0.11	0.20	0.52	0.36

Significant at $p < 0.05$; **Significant at $p < 0.01$

Hybrids with good specific combining ability and per se performance could be selected to recover transgressive segregants. The superiority of high \times low or average \times low combiners as parents could be explained on the basis of interaction between positive alleles from good/average combiners and negative alleles for the poor combiners as parents. The high yield of such crosses or hybrids would be non fixable and thus could be exploited for heterosis breeding. The superior cross combinations involving low \times low general combiners could result from over dominance or epistasis (Hallauer and Miranda, 1988).

The results on standard heterosis indicated that, line KMLD-5 with tester KML-801 exhibited highest heterotic effect in number of kernels row⁻¹ and with tester BML-7 had the highest heterotic effect in plant height. On the other hand, the best desirable heterotic effect in days to 50% pollen shed was exhibited by the lines KMLD-65 and KMLD-68 with tester KML-55 whereas for 50% silking, the highest heterotic effect was exhibited by KMLD-68 \times KML-802. Negative heterosis is actually desirable for days to 50% pollen shed and silking, implying that these hybrids would mature earlier and could escape drought. The hybrid KMLD-6 \times KML-36 had the highest heterotic effect in grain yield plant⁻¹ and ear girth. High heterosis values are desirable for grain yield in maize. Similar findings were reported by Joshi et al (2002). Premlatha and Kalamani (2010) reported that in maize, tall plants are preferred over short types, and therefore positive heterosis is considered desirable for plant height. But, in the present study, none of the hybrids was found significant and positive economic heterotic effect in plant height.

Four parents viz. KMLD-3, KMLD-11, KMLD-19,

and KML-9 were identified as the best general combiners for grain yield and its attributing characters. These parents could therefore be utilized for the development of an elite breeding population by allowing random mating to achieve novel genetic recombination and the resultant populations could then be subjected to recurrent selection. These populations could invariably serve as a source of new desirable inbred lines. For the exploitation of hybrid vigour, per se performance, sca effects and the extent of heterosis among hybrids could be important. Selection based on one of the aforementioned criteria alone may not be effective. The hybrid with high per se performance need not always reveal high sca effect and vice versa. So selection must be based on significant sca and high heterotic effects coupled with high mean performance.

The present study identified hybrids KMLD-3 \times KML-99, KMLD-5 \times BML-7, KMLD-5 \times KML-801, KMLD-6 \times KML-36, and KMLD-11 \times KML-29 with significant positive sca, standard heterosis and high mean values for grain yield plant⁻¹ and two or more yield components. These hybrids were found to be early in flowering with significant negative heterosis suitable to drought prone situations. Further testing of the new inbred lines viz. KMLD-3, KMLD-5, KMLD-6, KMLD-11, KML-29, KML-36, and KML-99 for use in a crossing program is recommended to combine major yield components with high yield under moisture stress conditions.

Implications

Dry matter yield and composition of maize whole-plant for silage can be controlled by multiple management factors. Despite this, uncontrollable environmental factors, such as drought stress and heat

Table 3 - Estimates of sca effects, standard heterosis and per se performance of best performing crosses.

Character		Cross combinations										SE (m) ±
		KMLD-3 × KML-9	KMLD-5 × BML-7	KMLD-5 × KML-801	KMLD-6 × KML-29	KMLD-6 × KML-36	KMLD-11 × KML-29	KMLD-11 × KML-224	KMLD-19 × KML-802	KMLD-61 × KML-55	KMLD-65 × KML-9	
Grain yield plant ⁻¹ (g)	sca	11.69*	20.90*	27.84**	19.03**	27.77**	24.62**	16.24**	22.33**	16.78**	22.62**	5.54
	het.	77.22**	78.59**	92.33**	82.71**	108.81**	101.94**	81.34**	104.69**	72.96**	78.59**	7.84
	per se	64.5	65.0	70.0	66.5	76.0	73.5	66.0	74.5	63.0	65.0	-
Days to 50% pollen shed	sca	-1.05	-0.85	-0.02	-0.02	-0.35	-1.57	-0.94	-0.20	-1.08	0.62	0.99
	het.	-4.63**	-3.70**	-8.33**	-5.56**	-6.48**	-10.19**	-6.48**	-11.11**	-9.26**	-8.33**	1.40
	per se	51.5	52.0	49.5	51.0	50.5	48.5	50.5	48.0	49.0	49.5	-
Days to 50% silking	sca	-0.72	-1.08	-0.71	-0.67	-0.73	-0.94	-1.68	-1.04	-1.04	-0.83	1.11
	het.	-8.47**	-7.63**	-11.86**	-8.47**	-9.32**	-10.17**	-10.17**	-16.10**	-11.02**	-12.71**	1.18
	per se	54.0	54.5	52.0	54.0	53.5	53.0	53.0	49.5	52.5	51.5	-
Plant height (cm)	sca	5.27	20.06**	10.33	-0.71	-5.67	5.07	-2.26	-0.17	7.10	13.94*	6.34
	het.	-15.92	3.98	-6.63	-22.55*	-24.40**	-24.93**	-22.28*	-16.45	-16.45	-21.75	8.97
	per se	158.5	196.0	176.0	146.0	142.5	141.5	146.5	157.5	157.5	147.5	-
Ear height (cm)	sca	3.55	13.87**	13.71**	6.69	2.49	11.91**	2.27	-5.75	-7.28	1.72	4.14
	het.	0.68	31.97**	26.53**	-2.04	-8.16	-7.48	-21.77**	-14.29**	-21.77**	-25.85**	5.86
	per se	74.0	97.0	93.0	72.0	67.5	68.0	57.5	63.0	57.5	54.5	-
Number of ears plant ⁻¹	sca	0.04	0.10	0.07	0.04	0.13*	0.10	0.10	0.02	-0.06	0.10	0.06
	het.	50.00**	66.67**	58.33**	66.67**	66.67**	66.67**	58.33**	66.67**	41.67**	50.00**	0.09
	per se	0.90	1.00	0.95	1.00	1.00	1.00	0.95	1.00	0.85	0.90	-
Ear length (cm)	sca	-0.21	1.37*	2.18**	-0.68	-0.66	0.96	0.66	0.58	-0.43	0.90	0.59
	het.	7.27**	14.55**	23.64**	-1.82	1.82	14.55**	23.64**	14.55**	7.27**	12.73**	0.83
	per se	14.8	15.8	17.0	13.5	14.0	15.8	17.0	15.8	14.8	15.5	-
Ear girth (cm)	sca	-0.367	0.756	0.343	0.109	1.033*	1.221**	-0.084	-0.935*	0.155	0.388	0.44
	het.	-10.17**	3.39**	-5.08**	-1.69**	3.39**	0.00	-8.47**	-5.08**	-10.17**	-3.39**	0.63
	per se	13.3	15.3	14.0	14.5	15.3	14.8	13.5	14.0	13.3	14.3	-
Kernel rows	sca	0.09	1.13	0.89	0.826	-0.80	2.70**	1.37	-0.06	0.53	0.22	0.77
	het.	3.57**	14.29**	14.29**	10.71**	32.14**	17.86**	-3.57**	-3.57**	0.00	-14.29**	1.09
	per se	14.5	16.0	16.0	15.5	18.5	16.5	13.5	13.5	14.0	12.0	-
Number of kernels row ⁻¹	sca	3.46	1.28	7.11**	2.76	1.42	4.14*	2.64	1.47	0.73	3.40	2.01
	het.	49.30**	23.94**	66.20**	52.11**	43.66**	54.93**	29.58**	43.66**	29.58**	57.75**	2.84
	per se	26.5	22.0	29.5	27.0	25.5	27.5	23.0	25.5	23.0	28.0	-
100 grain weight (g)	sca	-1.20	-0.33	2.77*	1.49	0.85	1.32	3.12*	-0.49	3.09*	1.91	1.39
	het.	-26.19**	-9.52	-9.52**	-19.05**	-9.52**	-16.67**	9.52**	-7.14**	-9.52**	-9.52**	1.97
	per se	15.5	19.0	19.0	17.0	19.0	17.5	23.0	19.5	19.0	19.0	-

Significant at p<0.05; **Significant at p<0.01

stress, can have major effects on DM yield and composition of maize whole-plant for silage. Results from this study show that low DM yields and poor quality of maize whole-plant for silage are beyond drought stress. Daily maximum temperatures should be considered when planning strategies to insure good quality forage supply and reduce risk in dairy farming systems.

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