

Research Article

Combining ability studies for drought tolerance attributes in *kabuli* chickpea (*Cicer arietinum* L.)

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Abstract

An investigation was taken up with six *kabuli* chickpea genotypes and their 15 F_1 hybrids (excluding reciprocals) during *rabi* 2012 at Regional Agricultural Research Station, Nandyal, Andhra Prasesh, India to elucidate information on nature of gene action and to identify promising chickpea genotypes for drought tolerance attributes and seed yield. The results of analysis of variance for combining ability revealed predominance of non-additive gene effects for drought tolerant attributes like SPAD chlorophyll meter reading (SCMR), specific leaf area (cm² g-¹), relative water content (%), root length (cm) and root weight (g/plant). Superior parental genotypes with significant and desirable combing ability were KAK 2 for specific leaf area, and root length; Vihar for relative water content and seed yield per plant; MNK 1 for SCMR, specific leaf area, root length and root weight; Phule G 05107 for SCMR and root weight; ICCV 95333 for specific leaf area ; NBeG 72 for specific leaf area and seed yield per plant which can be utilized in breeding programmes for improving drought tolerance in chickpea. Promising F₁s with desirable *sca* effects (Vihar x KAK 2 for yield and rooting traits; MNK 1 x Phule G 05107 and KAK 2 x NBeG 72 for SCMR) were identified which can be exploited through suitable breeding methodology for recovering superior segregants with enhanced drought tolerance coupled with high yield.

Keywords

Chickpea, combining ability, gene action, drought tolerance attribute

Introduction:

Chickpea is the third most important grain legume in the world after dry beans and dry pea. Its cultivation is mainly confined to Asia with 90% of global area and production. Annually 11.6 m t chickpeas are produced in the globe from a cultivated area of over 13.2 m ha (FAO STAT, 2011). In India, chickpea occupies an area of 9.21 m ha with the production of 8.88 m t. There has been a significant change in the scenario of chickpea cultivation in India during the past three decades. The expansion of irrigated agriculture in northen India has led to displacement of chickpea with wheat in large area. With respect to Andhra Pradesh, there has been a dramatic increase in chickpea area, production and productivity levels since 1995-96 (110,000 ha, 75000 tonnes and 225 kg/ha to 6,47,000 ha, 8,47,000 tonnes and 1309 kg/ha respectively in 2009-10). The increase is mainly observed in Kurnool, Prakasam, Anantapur and Kadapa districts. Expansion of this crop in Telangana districts like Nizamabad, Medak, Mahaboobnagar and Adilabad is also drastic since 2005. In Andhra Pradesh chickpea is grown during rabi on receding soil moisture levels and crop frequently suffers due to drought. Breeding approach for improving drought tolerance in chickpea would be to improve drought resistance in high-yielding genotypes through incorporation of morphological and physiological mechanisms of drought resistance. Several physiological, morphological and phenological traits have been listed to play a significant role in crop adaptation to drought stress (Ludlow and Muchow 1990; Saxena and Johansen 1990). Rapid progress in drought resistance breeding has been achieved based on characters such as Harvest Index (HI), Water Use Efficiency (WUE), Specific Leaf Area (SLA) and SPAD (soil plant analysis development) Chlorophyll Meter Reading (SCMR) (Nigam et al. 2005). The SLA and SCMR have been found highly correlated with WUE (Sheshshayee et al. 2006) and have been identified as surrogate traits for WUE (Nigam et al. 2005; Sheshshayee et al. 2006 and Arunyanark et al. 2009). Early studies have indicated differential responses for relative water content (RWC) in chickpea (Bahavar et al. 2009) and it was positively correlated with chlorophyll content and grain yield in rice under drought conditions (Pirdashti et al. 2009). Root systems play a crucial role in determining shoot water status and therefore effective water uptake is an important determinant of drought resistance (Kashiwagi et al. 2006). Many root characteristics have been shown to be under genetic control and quantitatively inherited (O'Toole and Bland 1987). Genetic variation for root characters has been found among chickpea genotypes (Kashiwagi et al. 2006). The information on the combining ability and gene action governing these important physiological traits will be useful for planning suitable breeding strategies to improve drought tolerance in chickpea.

Material and Methods

The present investigation was taken with six *kabuli* chickpea genotypes and their 15 F_1 hybrids (excluding reciprocals) during *rabi* 2012 at



Regional Agricultural Research Station, Nandyal. The six parental genotypes chosen for the study were Vihar, ICCV 95333, KAK 2, MNK 1, Phule G 05107 and NBeG 72. Each genotype was sown in a row length of 4m with a spacing of 45 cm between the rows and 10 cm within the row. For raising a normal crop recommended package of practices were followed. In each genotype, five plants were randomly selected and used for collecting data on physiological characters like SPAD chlorophyll meter reading (SCMR), specific leaf area $(cm^2 g^{-1})$, relative water content (%), root length (cm), root weight (g/plant) apart from seed yield per plant (g). Data collected was subjected to statistic analysis using Windostat statistical package according to Griffing's (1956) model I and method II of combining ability analysis.

Results and Discussion

The analysis of variance (Table 1) revealed significant differences among the six parents and their 15 F₁s genotypes for six characters viz., seed yield and also drought tolerance attributes studied indicating appreciable variability among the genotypes studied. The results of analysis of variance for combining ability for these traits were presented in Table 2. It is observed from the analysis, that both sca and gca variances were significant for six characters. The significance of gca and sca variances indicates that both additive and non-additive gene action were important in the inheritance or expression of these attributes. In order to improve these traits breeding methodologies that exploit both additive and nonadditive gene effects i.e. recurrent selection, biparental mating and modified pedigree method (selection in later generations) have to be followed. Further perusal of components due to gca and sca revealed that there is preponderance of additive gene action for seed yield per plant. The predominance of additive gene action was also supported by higher values of heritability estimate recorded. Additive gene action for seed yield per plant was reported by Branvand et al. (2008), Bhardwaj et al. (2009) and Jayalakshmi and Trivikrama Reddy (2013). SCMR, SLA, RWC, root length and root weight exhibited higher values of component due to sca thus indicating the preponderance of non-additive gene effects i.e., dominance and epistasis in the expression of these characters.. Non additive gene action for SCMR (Vasanthi et al. 2004 in groundnut and Reddy Yamini 2012 in chickpea; Specific leaf area (Jayalakshmi et al. 1999, Nigam et al. 2001 in groundnut); root length (Kashiwagi et al. 2006 and Reddy Yamini 2012) and root weight (Ekanayake et al. 1995 in rice) were reported in previous studies.

Evaluation and characterization of the varieties for drought related parameters helps in identifying suitable donors for such a traits. These donors can be utilized for genetic enhancement of drought tolerance. The per se performance of parents and hybrids, general combining ability effects of six parents and specific combining ability effects of 15 F₁s for drought tolerant attributes and yield were presented on tables 3 and 4. Leaf chlorophyll content is a key indicator of the physiological status of a plant. The ability to maintain high chlorophyll density under water deficit conditions has been suggested as a drought tolerance index in potato (Van der Mescht et al. 1999) and peanut (Arunyanark et al. 2009). SCMR, an indicator of leaf chlorophyll content ranged from 54.4 (Vihar) to 62.0 (Phule G 05107) in parents with a mean value of 58.3. In case of F_{1s} , it ranged from 55.8 (Vihar x Phule G 05107) to 60.7 (KAK 2 x Phule G 05107) with the mean value of 57.3. For this trait, two parents (MNK 1 and Phule G 05107) and two F₁s (KAK 2 x Phule G 05107 and KAK 2 x NBeG 72) recorded significantly higher values than the respective mean values.

General combining ability effects for SCMR ranged from -1.65 (Vihar) to 1.35 (Phule G 05107). Two genotypes Vihar (-1.650) and ICCV 95333 (-0.661) recorded significant negative gca effects where as Phule G 05107 (1.353) and MNK 1 (0.530) recorded significant positive gca effects. The sca effects for SCMR ranged from -2.04 (KAK 2 x MNK 1) to 2.61 (KAK 2 x NBeG 72). Three crosses [MNK 1 x NBeG 72 (-1.97), Phule G 05107 x NBeG 72 (-1.51), Vihar x Phule G 05107 (-1.46)] and two crosses [KAK 2 x NBeG 72 (2.61) and KAK 2 x Phule G 05107 (1.59)] respectively registered significant negative and positive sca effects. KAK 2 x Phule G 05107 (poor x good) and KAK 2 x NBeG 72 (poor x poor) displayed highly significant positive sca effects due to non additive gene action (dominance x additive and dominance x dominance). Hence, these crosses could be exploited by internating amongst the desirable segregants in biparental fashion in segregating generations which is expected to break undesirable linkages and may result in rare desirable recombinations.

Thicker leaves (low SLA) indicate potential for greater assimilate under drought stress. Low SLA, as a selection criterion for enhancing TE, could be an economically surrogate trait for drought tolerance (Nigam *et al.* 2005). The mean SLA ranged from 107.8 cm² g⁻¹ (ICCV 95333) to 156.8 cm² g⁻¹ (Vihar) in parents with a mean value of 129.3 cm² g⁻¹. In F₁s, it ranged from 120.6 cm² g⁻¹ (MNK 1 x NBeG 72) to 171.4 cm² g⁻¹ (Vihar x ICCV 95333) with the mean value of 143.9 cm² g⁻¹. Parental genotypes ICCV 95333 (107.8 cm² g⁻¹) and NBeG 72 (119.1 cm² g⁻¹) and five F₁s *viz.*, ICCV 95333 x KAK 2 (129.8 cm² g⁻¹), KAK 2 x NBeG 72 (135.54 cm² g⁻¹), MNK 1 x Phule G 05107 (123.89 cm² g⁻¹) and Phule G 05107 x NBeG 72



 $(107.8 \text{ cm}^2 \text{ g}^{-1})$ recorded significantly lower SLA than the mean values.

General combining ability effects for SLA varied from -5.35 (ICCV 95333) to 18.20 (Vihar). Significant negative gca effects were recorded by ICCV 95333 (-5.357), KAK 2 (-5.141), MNK 1(-3.834) and NBeG 72 (-2.281) and significant positive gca effects were exhibited by Vihar (18.208). Sca effects in F₁s ranged from -12.97 (MNK 1 x NBeG 72) to 27.42 (Vihar x NBeG 72). MNK 1 x NBeG 72 (-12.97) and MNK 1 x Phule G 05107 (-10.4) exhibited significant negative sca effects. Significant positive sca effects were observed in as many as six crosses viz., Vihar x NBeG 72 (27.4), Vihar x ICCV 95333 (18.8), ICCV 95333 x MNK 1 (12.6), KAK 2 x MNK 1 (10.1), ICCV 95333 x NBeG 72 (7.3) and Phule G 05107 x NBeG 72 (7.13).

Relative water content represents a useful indicator of the state of water balance of a plant, essentially because it expresses the absolute amount of water, which the plant requires to reach artificial full saturation. The tissues, which are able to maintain higher RWC with decreasing water potential, are more resistant to drought conditions and desiccation resulting from this stress (Ferrat and Lovatt 1999). The mean value of RWC ranged from 68.7 (NBeG 72) to 75.8 (Vihar) in parents with a mean value of 71.2. In case of F_1 s, it ranged from 61.1 (KAK 2 x NBeG 72) to 75.0 (Vihar x Phule G 05107) with the mean value of 68.6. Vihar x Phule G 05107 (75.0) and Vihar x NBeG 72 (74.59) were the two hybrids which significantly exceeded the mean value.

A range of -2.18 (KAK 2) to 3.34 (Vihar) *gca* effects were noticed for RWC. Among parents, Vihar (3.346) and KAK 2 (-2.183) respectively recorded significant positive and negative *gca* effects. *Sca* estimate of RWC in F₁s ranged from - 5.19 (KAK 2 x NBeG 72) to 2.75 (Vihar x NBeG 72). Among fifteen crosses, three crosses *viz.*, KAK 2 x NBeG 72 (-5.19), ICCV 95333 x Phule G 05107 (-3.9) and Vihar x KAK 2 (-4.0) recorded significant negative *sca* effects while none of the crosses registered significant positive *sca* effects. The only one genotype Vihar was the best general combiner for RWC indicating the possibility of utilizing this parent in breeding for enhanced drought tolerance in *kabuli* chickpea.

Root traits such as depth, length, density, and biomass have been proposed as the main drought avoidance traits to contribute to seed yield under terminal drought environments (Ludlow and Muchow 1990; Turner *et al.* 2001). Among parental lines it ranged from 27.1 cm (Phule G 05107) to 38.6 cm (KAK 2) with an average of 32.3 cm, which was significantly exceeded by KAK 2 (38.6 cm) and MNK 1 (36.0 cm). In case of

F₁s, it varied from 26.7 cm (Phule G 05107 x NBeG 72) to 46.7 cm (MNK 1 x Phule G 05107) with an average of 38.2 cm, which was significantly exceeded by five F₁s *viz.*, ICCV 95333 x Phule G 05107 (44.0 cm), ICCV 95333 x NBeG 72 (43.0 cm), KAK 2 x MNK 1 (47.75 cm), MNK 1 x Phule G 05107 (46.75 cm) and MNK 1 x NBeG 72 (43.0 cm).

Excessive and deep root system have been recognized as most important traits for improving crop productivity under progressively receding soil moisture condition. *Gca* effects for this trait ranged from -1.90 (Vihar) to 2.93 (MNK 1). Parental genotypes Vihar (-1.9) and Phule G 05107 (-1.6) and NBeG 72 (-1.6) exhibited highly significant negative *gca* effect and MNK 1 (2.9) and KAK 2 (1.9) exhibited highly significant positive *gca* effects for root length.

Sca effects for root length ranged from -8.31 (KAK 2 x NBeG 72) to 8.96 (MNK 1 x Phule G 05107). Significant positive sca effects were registered by seven crosses viz., MNK 1 x Phule G 05107 (8.96), ICCV 95333 x Phule G 05107 (8.77), Vihar x NBeG 72 (7.99), ICCV 95333 x NBeG 72 (7.71). KAK 2 x MNK 1 (6.37). MNK 1 x NBeG 72 (5.15) and Vihar x KAK 2 (3.46). Vihar x KAK 2 (poor x good), MNK 1 x Phule G 05107 (good x poor) and MNK 1 x NBeG 72 (good x poor) displayed significant positive sca effect and involved at least one good general combiner indicating the predominant role of additive x dominance epistasis . Three crosses ICCV 95333 x Phule G 05107 (poor x poor) and ICCV 95333 x NBeG 72 (poor x poor) exhibited significant positive sca effect due to dominant x dominant type of epistasis. These crosses exhibited superior sca effects due to complementary type of gene action or involvement of non allelic interaction of fixable and non fixable genetic variance. KAK 2 x MNK 1 exhibited significant sca effects apart from high gca effects thereby indicating the fixable additive x additive type of epistasis. Such good x good cross combinations can be used to isolate superior segregants in segregating generation by single plant selection.

Root weight in parental genotypes ranged from 0.35 g (NBeG 72) to 0.69 g (MNK 1) with an average of 0.48 g, which was significantly exceeded by MNK 1 (0.69 g). In case of F_1 s, it varied from 0.27 g (ICCV 95333 x MNK 1) to 0.81 g (ICCV 95333 x Phule G 05107) with an average of 0.50 g, which was significantly exceeded by Vihar x NBeG 72 (0.73 g), ICCV 95333 x Phule G 05107 (0.81 g), KAK 2 x MNK 1 (0.58 g) and MNK 1 x Phule G 05107 (0.63 g).

General combining ability effects for root weight ranged from -2.76 (NBeG 72) to 5.98 (MNK 1). Vihar (-1.55), ICCV 95333 (-1.88), KAK 2 (-2.43)



and NBeG 72 (-2.76) exhibited negative gca effect and MNK 1 (5.98) and Phule G 05107 (2.65) exhibited highly significant positive gca effects. In F_1 sca effects for root weight ranged from -26.20 (ICCV 95333 x MNK 1) to 31.12 (ICCV 95333 x Phule G 05107). ICCV 95333 x Phule G 05107 (31.12), Vihar x NBeG 72 (27.54), ICCV 95333 x NBeG 72 (10.87), Vihar x KAK 2 (6.87), KAK 2 x MNK 1 (5.33) and MNK 1 x Phule G 05107 (5.25) are the six crosses which registered significant positive sca effects. MNK 1 x Phule G 05107 (good x good) exhibited significant positive sca owing additive x additive epistasis gene action and could be exploited to produce progeny superior for rooting traits through single plant selection. Other crosses viz., Vihar x KAK 2 (poor x poor) and ICCV 95333 x NBeG 72 (poor x poor) exhibited significant positive sca effect, due to dominant x dominant type of epistasis. ICCV 95333 x Phule G 05107 (poor x good) and KAK 2 x MNK 1 (poor x good) were superior owing additive x dominant type of gene action.

Seed yield per plant in parental genotypes studied ranged from 7.8 g (MNK 1) to 13.6 g (NBeG72). In F₁s, the range was from 8.5 g (KAK 2 x Phule G 05107) to 14.8 g (Vihar x KAK 2). Only one F₁ (Vihar x KAK 2) and one parent (NBeG 72) respectively had significantly higher seed yield than the mean value of F₁s (11.1 g) and the parents (10.9 g).

General combining ability effects for seed yield per plant ranged from -1.267 (MNK 1) to 1.193 (Vihar). Among them MNK 1 (-1.26) and Phule G 05107 (-0.93) showed significant negative *gca* effects, whereas Vihar (1.19) and NBeG 72 (0.71) exhibited significant positive *gca* effects. The magnitude of *sca* effects ranged from -1.66 (KAK 2 x Phule G 05107) to 2.46 (Vihar x KAK 2). Vihar x KAK 2 (2.463) and KAK 2 x Phule G 05107 (-1.66) respectively registered significant positive and negative *sca* effects, for seed yield per plant.

From the foregoing, it is clear that KAK 2 was the best general combiners specific leaf area and root length; Vihar for relative water content and seed yield per plant; MNK 1 for SCMR, specific leaf area, root length and root weight; Phule G 05107 for SCMR and root weight; ICCV 95333 for specific leaf area ; NBeG 72 for specific leaf area and seed yield per plant. Since physiological attributes like, SCMR, root length and chlorophyll content have good correlation with water use efficiency; the parental genotypes identified in this study with good combining abilities for these attributes can be utilized for improving drought tolerance in chickpea. In chickpea, though sca effects cannot be exploited readily in breeding programmes, high sca effects of a particular cross combination will be useful if it is accompanied by high *gca* effects of the respective parents. The progeny from the crosses of parents having the high *gca* will tend to produce progeny superior to those of other combinations (Baker, 1978). Promising crosses in this study *viz.*, Vihar x KAK 2 for yield and rooting traits; MNK 1 x Phule G 05107 and MNK 1 x NBeG 72 for SLA; KAK 2 x Phule G 05107 and KAK 2 x NBeG 72 for SCMR can be exploited through suitable breeding methodology for recovering superior segregants.

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Source	D.F	Mea	n Squares				
		SPAD chlorophyll meter reading	Specific Leaf Area (cm ² gm ⁻¹)	Relative Water Content (%)	Root length (cm)	Root weight (g)	Seed yield (g/plant)
Replications	2	4.10	2.34	35.53	58.33	356.77	0.18
Treatments	20	11.79**	932.22**	39.75**	123.48**	618.61**	8.06**
Error	40	1.75	24.19	8.38	3.32	16.82	2.06

Table 1. Analysis of variance for drought tolerance attributes and seed yield in chickpea

* Significant at 5 % level

** Significant at 1% level

Table 2. Analysis of variance for combining ability for drought tolerance attributes and seed yield in chickpea

	Source	D.F	Me	an Square				
			SPAD chlorophyll meter reading	Specific Leaf Area $(cm^2$ $gm^{-1})$	Relative Water Content (%)	Root length (cm)	Root weight (g)	Seed yield (g/plant)
gca		5	8.57*	654.57*	26.97*	34.44*	99.84*	163.86*
sca		15	2.38*	196.13*	8.67*	43.40*	241.65*	15.37*
	Error	40	0.58	8.06	2.79	1.10	5.60	0.68
	$\sigma^2 gca$		0.99	80.81	3.02	4.16	0.00	0.80
	$\sigma^2 sca$		1.79	188.06	5.88	42.29	0.02	0.51
6	Significant at 5.04 laval		** 6:	mificant at	10/ loval			

Significant at 5 % level

Table 3. Per se performance and of general combining ability effects of parent genotypes for drought
tolerance attributes and seed yield in chickpea

Parent	SPAD			Specific Leaf		Relative Water		Root length		Root weight		ield
	chlorophyll		Area ($cm^2 gm^{-1}$)		Content (%)		(cm)		(g/plant)		(g/plant)	
	meter re	ading										
	Per se	gca	Per	gca	Per se	gca	Per	gca	Per	gca	Per	gca
			se				se		se		se	
Vihar	54.5	-1.65**	156.8	18.20**	75.8	3.34**	29.0	-1.90**	0.4	-1.55*	12.1	1.19**
ICCV 95333	56.9	-0.66*	107.8	-5.35**	71.1	-0.33	33.3	0.37	0.4	-1.88*	11.9	0.23
KAK 2	57.3	0.218	123.3	-5.14**	70.2	-2.18**	38.6	1.90**	0.5	-2.43*	10.6	0.06
MNK 1	61.3	0.53*	131.9	-3.83**	72.3	0	36.0	2.93**	0.7	5.98**	7.9	-1.26**
Phule G 05107	62.0	1.35**	137.3	-1.59	69.5	0.04	27.1	-1.68**	0.5	2.65*	9.8	-0.93*
NBeG 72	58.3	0.21	119.1	-2.28*	68.7	-0.88	30.3	-1.62**	0.4	-2.76**	13.7	0.71*
SE (gi)		0.24		0.91		0.53		0.33		0.76		0.26
SE (gi-gi)		0.38		1.41		0.83		0.52		1.18		0.41
* Significa	nt at 5 0/	loval		** Signif	joont at 1	0/10001						

* Significant at 5 % level

** Significant at 1% level

^{**} Significant at 1% level



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Table 4. Per se performance and specific combining ability effects of F₁s for drought tolerance attributes and seed yield in chickpea

F_1	SPAD chlorophyll meter reading		Specific Leaf Area (cm ² gm- ¹)		Relative Water Content (%)		Root length (cm)		Root weight (g/plant)		Seed yield (g/plant)	
	Per se	sca	Per se	sca	Per se	sca	Per se	sca	Per se	sca	Per se	sca
Vihar x ICCV 95333	55.9	0.569	171.4	18.812**	72.7	0.304	31.5	-3.504**	0.4	-2.667	11.7	-0.864
Vihar x KAK 2	56.0	-0.183	148.5	-4.383	66.5	-4.006*	40.0	3.464**	0.5	6.875**	14.8	2.463**
Vihar x MNK 1	56.6	0.101	155.1	0.99	72.0	-0.702	36.5	-1.067	0.5	-2.542	11.8	0.761
Vihar x Phule G 05107	55.9	-1.467*	152.3	-4.08	75.0	2.231	33.5	0.558	0.4	-15.875**	11.4	-0.013
Vihar x NBeG 72	56.9	0.729	183.1	27.42**	74.6	2.755	41.0	7.996**	0.7	27.542**	13.5	0.447
ICCV 95333 x KAK 2	56.8	-0.419	129.8	0.528	66.4	-0.466	40.5	1.683	0.4	-3.792	11.7	0.306
ICCV 95333 x MNK 1	57.3	-0.208	143.3	12.691**	67.8	-1.264	33.3	-6.598**	0.3	-26.208**	10.3	0.267
ICCV95333x Phule G 05107	57.5	-0.806	135.8	3.015	65.1	-3.987*	44.0	8.776**	0.8	31.125**	11.1	0.706
ICCV 95333 x NBeG 72	56.9	-0.264	139.5	7.388**	68.8	0.67	43.0	7.714**	0.6	10.875**	11.0	-1.071
KAK 2 x MNK 1	56.3	-2.04**	140.9	10.146**	66.6	-0.632	47.8	6.37**	0.6	5.333*	10.4	0.451
KAK 2 x Phule G 05107	60.8	1.594*	136.0	2.986	67.1	-0.112	37.0	0.245	0.4	-10.333**	8.6	-1.666*
KAK 2 x NBeG 72	60.7	2.617**	135.5	3.199	61.1	-5.195**	28.5	-8.317**	0.3	-15.583**	11.5	-0.373
MNK 1 x Phule G 05107	58.4	-1.144	123.9	-10.451**	69.0	-0.46	46.8	8.964**	0.6	5.250*	9.4	0.484
MNK 1 x NBeG 72	56.4	-1.978**	120.7	-12.974**	65.8	-2.722	43.0	5.152**	0.6	3.667	10.0	-0.552
Phule G 05107 x NBeG 72	57.7	-1.51*	143.0	7.136**	70.9	2.334	26.8	-6.474**	0.4	-8.000**	10.2	-0.666
S.E of Sii-Sjj		0.765		2.840		1.672		1.053		2.368		0.829
S.E of Sij-Sik		1.012		3.757		2.212		1.393		3.133		1.097
S.E of Sij-Skl		0.937		3.478		2.048		1.289		2.901		1.016

* Significant at 5 % level

** Significant at 1% level