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Nature of gene action and combining ability analysis of yield and yield-related traits in chickpea (*Cicer arietinum*) under heat stress

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ABSTRACT

Increasing incidence of heat stress (HS) is appearing as an important abiotic stress, limiting chickpea (*Cicer arietinum* L.) yield globally. Therefore, understanding of the nature of gene action of yield- related traits could help in breeding heat tolerant chickpea genotype for its sustainable production under HS. In the present investigation a total of six chickpea genotypes, viz. ICC 4958, ICC 92944, ICC 1205, DCP 92-3, ICC 96030 and KWR 108 were used as parents for 6 × 6 diallel analysis (excluding reciprocal crosses) to estimate gene action for various phenological and yield-related traits by growing them under normal sown (NS) and late sown (LS) conditions. Genetic analysis revealed the presence of both additive and non-additive genetic variances. However, higher magnitude of general combining ability (GCA) variance than specific combining ability (SCA) variance, with predictability ratio > 0.5 for most of the traits studied under both NS and LS conditions indicated preponderance of additive gene action. The estimates of GCA effects revealed that the parents ICC 92944 and KWR 108 were better general combiners for yield and yield- related traits, under both NS and LS conditions. Likewise, ICC 4958 × ICC 92944 (under both conditions) and DCP 92-3× KWR 108 (under LS) F_1 crosses were the most suitable cross combinations for yield and yield-related traits. High estimates of broad sense heritability for most of the traits, and low to medium estimates of narrow sense heritability for the studied traits were noted under both conditions. Therefore, inclusion of parent with high GCA effect in cross-breeding programme could be a potential strategy for improving HS tolerance in chickpea.

Key words: Combining ability, Diallel crosses, Genetic variability, Gene action, Heat stress

Chickpea (*Cicer arietinum* L.) ranks as the second most important grain legume crop grown across the world (FAO 2016). Being a grain legume, chickpea serves as an affordable source of plant-based dietary protein and vital mineral nutrients to the malnourished human population in the developing countries, thus it helps in combating protein based global food insecurity (Bohra *et al.* 2014). Annually, a total of 13.73 million tonnes of chickpea is harvested from 13.98 Mha area worldwide (FAO, 2016). Predominantly, it is grown in semi-arid and arid region of sub-Sahara and Asian countries under rainfed and poor resource conditions (Gaur *et al.* 2012). Chickpea yield is seriously challenged by various biotic and abiotic stresses (Jha *et al.* 2014a). Simultaneously, increasing episodes of heat stress (HS) events under the uncertainties of global climate have imposed serious challenge on plant growth and yield in various crops including chickpea worldwide (Hasanuzzaman *et al.* 2013, Jha *et al.* 2014b, Jha *et al.* 2017). Significant alteration in reproductive phenology in chickpea has been witnessed in tropical and sub-tropical countries including northern part of India due to increasing events of HS, resulting in serious concern for chickpea yield (Krishnamurthy *et al.* 2011). Consequences of HS received during reproductive phase inhibit vital processes such as pollen formation, pollen tube germination and fertilization, resulting in poor pod and seed setting, and ultimately causing significant yield loss in chickpea (Devasirvatham *et al.* 2012, Devasirvatham *et al.* 2013, Jha *et al.* 2017, 2018). Notably, increase in 1°C temperature beyond the optimum temperature during chickpea growing season may cause yield loss up to 15% (Upadhyaya *et al.* 2011). In this context, several efforts is terms physiology based studies have been made to improve the current understanding of physiological basis of HS tolerance in chickpea (Devasirvatham *et al.* 2012, Kumar *et al.* 2012, Devasirvatham *et al.* 2013, Kaushal *et al.* 2013, Jumrani and Bhatia 2014). However, limited genetic inheritance studies on yield-related and phenological traits under HS have constrained the progress of development of heat-tolerant chickpea. Therefore, breeding of improved chickpea genotypes with high genetic yield potential under HS has become one of the prime breeding objectives. HS tolerance is a complex trait, and mostly governed by

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polygenes (Upadhyaya *et al.* 2011), and is highly influenced by genotype × environment (G × E) interaction. Thus, genetics of HS tolerance remains poorly understood in chickpea. Therefore, to gain insights into the genetics of HS tolerance, a preliminary study was conducted to understand the gene action for various traits of phenological and yield importance in chickpea grown under both NS and LS conditions through diallel cross analysis. Thus, deciphering the genetic inheritance of various phenological and yield related traits could provide excellent opportunity to incorporate the yield-related traits and the promising cross-combinations into the chickpea breeding programme. This could help in developing chickpea cultivars to tackle the growing challenges of HS and providing sustainable yield.

MATERIALS AND METHODS

A total of six parents (Table 1) were selected and crossed in a diallel model (Griffing 1956a) during the year 2016-17. The resultant 15 cross combinations excluding reciprocals along with the parents were grown under normal sown (NS) [third week of November] and late sown (LS) [first week of January] conditions at the experimental farm of Indian Institute of Pulses Research (26º29' N, 80º16'E and 130 m) Kanpur during the next growing season of year 2017-18. In order to know the response of studied traits under HS, the parental and F_1 were planted under LS to face HS. All the parents and F_1's were grown in randomized complete block design (RCBD) with three replications. Each plot consisted of one ridge of 3 m length and 30 cm width. Plant to plant spacing was 10 cm. Same agronomic packages and practices were followed and two irrigations were given for each set of trial. Five competitive plants were randomly sampled from each plot during harvest. The following traits: days to first flowering (FF), plant height (PH), days to pod initiation (DPI), days to pod filling (DPF), days to maturity (DM), total pods/plant (TPOD/P), empty pods/plant (EP/P), biological yield/plant (BYPP), yield/plant (YPP), 100 seed weight (100 SW) were studied for the given experiment.

Statistical computations and estimations were performed by using INDOSTAT software. Half diallel analysis relying on Griffing's method I of model II was performed by using the same software. Significant genetic variance of each trait was further partitioned to GCA, SCA, and experimental error. Progeny performance could be predicted by estimating the predictability ratio = $2\delta^2$GCA/ (δ^2SCA+2 δ^2GCA) [Baker 1978], where, δ^2GCA =Mean square due to GCA, δ^2SCA = Mean square due to SCA.

Broad sense heritability, h^2_{bs} = additive variance + dominance variance/phenotypic variance, and narrow sense heritability, h^2_{ns} = additive variance/phenotypic variance, was calculated by the method suggested by Wray and Visscher (2008).

RESULTS AND DISCUSSION

Genetic variability of traits in chickpea diallel crosses under NS and LS conditions

The statistical analysis suggested significant difference among parents and their 15 F_1 crosses for all the traits studied under NS and LS conditions (Table 2). The results revealed presence of significant amount of genetic variability in the given parents and their F_1 hybrids, that provides a great opportunity for selecting and utilizing these traits for yield improvement in chickpea under HS. ANOVA for combining ability suggested variances due to GCA and SCA of all the ten traits studied were significant under NS and LS conditions (Table 2). The results of significant GCA and SCA variance for the given traits under both conditions indicated presence of both additive and non-additive gene action controlling the traits. The results were consistent with the result observed by Malemba *et al*. (2017) in rice and Mia *et al*. (2017) in wheat under drought stress. Moreover, high predictability factor also supported that most of the traits were under the control of preponderant additive gene action under both conditions. In the context, Bicer and Sakar (2008) recorded higher magnitude of additive gene effects for the various phenological and yield-related traits investigated in chickpea. Likewise, significant additive genetic effects were noted for two important traits, viz. flower bud formation and pod filling traits under HS in common bean (Shonnard and Gepts 1994). Likewise, Naveed *et al*. (2016) also recorded higher additive variance for yield-related traits under HS in maize. However, Rainey and Griffiths (2005a) explained that pods/plant was under the control of dominant gene action in common bean under HS. Reduction in PH, TPOD/P, BYPP, and YPP grown under LS confirmed serious loss in yield attributes due to incidences of HS during reproductive phase. Reduction in YPP in chickpea was previously suggested (Kalra *et al*. 2015, Jha *et al*. 2018).

Mean performance of parents and their hybrids for yield and yield-related traits

The mean value of the parents and the respective crosses (Table 3) revealed that the P5 and P2 parents

Table 1 Chickpea genotypes used for diallel analysis

Code	Genotype	Source	Status	Pedigree
P1	ICC4958	ICRISAT, Patancheru, India	Accession	
P2	ICC92944	ICRISAT, Patancheru, India	Released variety	(GW 517 × P 326) × ICCL 83149
P3	DCP92-3	IIPR, Kanpur, India	Released variety	Selection
P4	ICC1205	ICRISAT, Patancheru, India	Accession	
P5	ICC96030	ICRISAT, Patancheru, India	Accession	
P6	KWR108	CSAUA&T, Kanpur, India	Released variety	Selection from genetic stock P108

Table 2 Analysis of variance for various traits of parents and their 6× 6 half diallel crosses under NS and LS

Traits	E	Treatment	Parents (P)	Hybrids (H)	P vs H	Error	Total	δ^2GCA	δ^2SCA	Error	δ^2GCA/ δ^2SCA	h^2_{ns}	$h^2_{by}{}^s$	Predictability ratio
Df		20	5	14	1	40	62	5	15	40				
FF	NS	170.0**	60.933 ***	220.356 **	12.292	3.285	57.311	53.043 **	57.918 **	1.095	0.92	0.183	0.985	0.64
	LS	92.210 ***	125.967 ***	86.714 ***	0.357	2.281	31.304	40.344 ***	27.534 ***	0.76	1.47	0.264	0.98	0.74
PH	NS	66.22**	59.414 ***	70.372 **	42.328 **	3.679	23.743	41.684 **	15.541 **	1.226	2.68	0.394	0.952	0.84
	LS	29.248 ***	44.034 ***	24.870 ***	16.612 **	2.088	11.062	5.164 ***	11.278 ***	0.69	0.46	0.09	0.944	0.47
DPI	NS	100.27**	42.089 ***	126.000 **	31.111 **	0.721	33.498	44.998 **	29.569 **	0.24	1.52	0.275	0.994	0.75
	LS	44.463 ***	39.022 ***	48.581 ***	14.025	6.385	21.096	23.037 ***	12.083 ***	2.12	1.91	0.302	0.877	0.95
DPF	NS	68.24**	28.500 ***	87.175 **	1.944	1.468	23.455	28.504 **	20.830 **	0.489	1.37	0.252	0.982	0.73
	LS	43.743 ***	58.267 ***	41.676 ***	0.057	2.019	15.562	25.928 ***	10.799 ***	0.67	2.40	0.369	0.961	0.85
DM	NS	119.94**	17.522 ***	151.279 **	193.335 **	2.026	40.24	41.939 **	39.328 **	0.675	1.07	0.208	0.986	0.68
	LS	44.276 ***	53.789 ***	43.222 ***	11.468	5.398	19.853	26.783 ***	10.751 ***	1.799	2.49	0.367	0.894	0.83
TPOD/P	NS	572.852 **	72.989 **	766.279 **	364.192 **	18.836	197.866	384.544 **	126.420 **	0.675	3.04	0.428	0.972	0.85
	LS	42.876 ***	20.322 **	48.946 ***	70.668 ***	4.998	17.111	30.556 ***	8.871 ***	1.666	3.44	0.449	0.896	0.87
EP/P	NS	1.254*	3.522 ***	0.508	0.357	0.461	0.716	1.109 **	0.188	0.154	5.90	0.56	0.64	0.92
	LS	2.254 **	2.400 *	2.308 *	0.768	0.928	1.34	0.598	0.802 **	0.309	0.75	0.083	0.646	0.59
BYPP	NS	48.55**	40.157 ***	54.999 **	0.307	6.48	20.061	25.050 **	13.229 **	2.16	1.89	0.302	0.88	0.79
	LS	11.576 **	3.498	12.700 **	36.216 **	4.57	6.928	4.512 *	3.641 *	1.523	1.24	0.17	0.653	0.71
YPP	NS	86.5**	201.182 ***	72.392 **	20.376 **	1.156	28.451	31.832 **	27.499 **	0.385	1.16	0.222	0.91	0.69
	LS	3.333 ***	1.2	4.071 ***	3.656 *	0.72	1.561	1.163 **	1.093 ***	0.24	1.06	0.174	0.819	0.68
100SW	NS	101.98**	46.828 ***	96.208 **	133.861 **	1.973	34.307	30.552 **	35.144 **	0.658	0.87	0.175	0.985	0.63
	LS	49.428 ***	38.389 ***	54.546 ***	32.965 ***	0.861	16.513	15.380 ***	16.841 ***	0.287	0.91	0.183	0.986	0.64

*P < 0.05; **P < 0.01; ***P < 0.001. E=environment

Table 3 Mean performance of various traits of parents and F1 crosses under NS and LS

Trait	FF		PH		DPI		DPF		DM		TPOD/P		EP/P		BYPP		YPP		100SW	
	NS	LS	NS	LS	NS	LS	NS	LS	NS	LS	NS	LS	NS	LS	NS	LS	NS	LS	NS	LS
P1	53.7	41.7	45	33.13	74.7	59.7	89.7	70.7	129	95.7	60	30.7	4	6.7	26.7	9.5	14.9	4.00	29.1	25.40
P2	47	42.0	54.4	33.20	67.7	53.7	86	66.0	121	87.3	55	29.7	5	6.0	25.8	13.6	17.9	6.52	27	25.04
P3	62.3	47.0	45.5	24.63	77.3	62.7	94.3	75.0	132	98.3	38	27.7	5	8.0	24.7	11.4	18.7	2.97	16.1	14.28
P4	63.3	49.7	51.5	29.77	78.3	65.7	94.3	79.0	131	95.7	33	26.0	5	7.0	26.2	10.0	13.9	3.44	17.6	18.61
P5	37.3	33.0	45.4	30.73	57.3	64.0	77	73.3	108	88.3	31	23.7	5	8.7	23.9	11.5	15.3	4.63	28.2	25.08
P6	62.7	48.3	56.1	31.00	77	66.0	94.3	81.0	128	95.7	39	27.7	5	7.0	18.8	10.0	10.8	4.32	27.4	25.60
P1× P2	53.3	50.3	40	25.63	72.3	63.3	89.3	76.7	128	92.0	78	31.7	5	5.7	24.2	10.0	13.2	4.09	23.8	21.29
P1× P3	51	50.3	53.3	30.70	74	66.0	88.3	77.0	132	95.0	71	32.0	6	7.7	30.2	17.0	17.1	5.98	23.2	26.47
P1× P4	44	44.3	48.3	31.67	69	57.7	85.7	74.3	131	96.7	76	31.3	5	7.3	29	14.5	12.5	6.02	38.5	26.79
P1 × P5	60.7	48.7	45.7	29.33	79.7	61.0	92.7	77.3	134	99.7	63	32.7	5	6.7	20.4	15.8	10.3	3.99	18	20.91
P1× P6	54.3	45.3	46.4	32.67	77.3	60.7	92.3	74.3	136	96.0	69	30.7	5	7.7	27.5	12.8	18.6	6.28	30.9	20.57
P2 ×P3	64.7	47.3	53.1	29.20	82.3	60.7	97	72.3	129	102.7	61	33.3	6	8.3	30.4	11.7	15.3	4.75	23.6	17.40
P2× P4	65.3	53.7	52.3	27.20	81.7	63.7	97.7	74.3	127	101.3	74	31.7	5	8.7	35.5	9.8	16.9	4.22	20.6	19.90
P2 × P5	64	54.3	48.1	37.63	78.3	67.7	92.3	76.0	128	98.3	59	31.7	5	6.7	27.9	12.9	22.5	5.10	24.3	23.80
P2 × P6	54.7	45.7	53.4	29.27	70.3	62.3	88.3	76.3	132	94.0	72	30.7	4	5.7	29.2	13.0	31.6	6.55	25.4	24.20
P3 × P4	57.7	48.0	48.7	32.37	77.3	63.7	92.3	77.0	132	95.7	63	31.7	6	7.3	25.3	11.5	16.6	4.25	27.9	23.84
P3× P5	62.3	44.7	48	31.23	80.3	63.7	96.3	79.0	132	99.0	62	30.0	6	7.0	23.5	13.5	25.7	6.33	20	18.64
P3 × P6	52.3	41.7	50.5	32.17	70.3	58.0	86.3	76.3	133	96.3	65	30.0	6	6.7	25.2	12.4	16.3	5.42	31.3	24.71
P4 × P5	59.7	55.0	55.3	25.50	76.3	69.7	91.7	83.3	127	101.0	61	31.0	6	6.7	25	11.1	13	4.64	22.6	18.44
P4 × P6	61.7	51.3	39.7	29.93	77.7	68.3	94	81.7	128	95.0	75	33.7	5	8.0	22.3	12.0	24.4	4.82	27.4	26.43
P5 × P6	50.3	36.7	44.7	34.90	71	65.7	88.7	76.0	117	93.3	73	35.0	5	7.3	18.4	12.3	29.7	5.71	30.5	25.84
Mean	56.3	46.6	48.8	30.6	74.8	63.0	90.9	76.0	128.3	96.0	60.9	30.6	5.2	7.2	25.7	12.2	17.9	5.0	25.4	22.54

appeared to be the earliest for FF trait that ranged from 37.3 to 47 days under NS and 33 to 42 days under LS. In this context P1 × P4 and P5 × P6 cross-combinations under NS, and P3 × P6 and P1 × P4 cross-combinations under LS were the earliest for FF with 44-50.3 days and 36.7-41.7 days, respectively. For PH, P2 and P6 parents possessed highest values ranging from 54.4 cm to 56.1 cm under NS, whereas P1 and P2 showed highest PH value (33.1-33.2 cm) under LS. The cross-combination P5 × P6 showed highest value for PH (34.9cm) under LS. The parent P5 displayed earliest for DPI with 57.3 days under NS and P2 exhibited earliest for this trait with 53.7 days under LS condition. For DPF and DM traits P5 parent remained promising with the earliest values of 77 days and 108 days, respectively under NS. Under LS condition the P2 parent appeared earliest for DPF (66 days) and DM (87.3 days) traits. Thus, this parent could be used in chickpea breeding for developing early chickpea genotype for escaping HS. In terms of yield related traits the parent P1 (ICC4958) had the highest number of pods per plant (60) under NS. Several F_1 crosses (P1 × P2, P1 × P3, P1 × P4, P1 × P5, P1 × P6, P2 × P3, P2 × P4, P2 × P6, P3 × P4, P3 × P5, P3 × P6, P4 × P5, P4 × P6 and P5 × P6) showed the high values for this trait under NS. Likewise P1 (ICC4958) provided highest TPOD/P under LS. The following crosses (P1 × P2, P1 × P3, P1 × P4, P1 × P5, P2 × P3, P2 × P4, P4 × P6 and P5 × P6) depicted high values for TPOD/P. Thus, these F_1s could be effectively exploited for developing superior HS tolerant chickpea genotypes. Under NS considering BYPP trait, P1 parent showed highest value (26.7g), and P2 parent depicted highest value under LS. The F_1 (P1 × P6, P2 × P3, P2 × P4, P2 × P5, P2 × P6, P1 × P3, and P1 × P4) possessed highest value for this trait under NS, whereas, P1 × P3, P1 × P4, and P1 × P5 cross-combinations showed highest value for the same trait under LS. Importantly, the parent P3 revealed highest yield per plant, YPP (18.7g) under NS and P2 showed highest value (6.52 g) for this trait under LS. The following F_1s (P4 × P6, P5 × P6, P3 × P5, P2 × P6 and P2 × P5) showed highest value for this trait under NS and P2 × P6 cross showed highest value for this trait under LS condition. Notably for 100-seed weight trait (100 SW), P1 (ICC 4958) and P6 (KWR 108) showed highest values under NS and LS conditions, respectively. A total of four F_1s (P1 × P6, P1 × P4, P3 × P6 and P5 × P6) possessed highest value for this trait under NS and three cross-combinations P1 × P3, P1 × P4 and P4 × P6 exhibited the highest values under LS. Thus, the parents and F1 cross-combinations exhibiting superior performance for the traits under heat stress condition could be utilized in crop breeding programme for improving heat stress tolerance in chickpea. These results are in close agreement with the results obtained in cotton (Rahman 2006), in wheat (Yildirim *et al.* 2009), and in maize (Naveed *et al.* 2016) under HS.

Combining ability

Combining ability introduced by Sprague and Tatum (1942) explains the ability of a parent to transfer its superior performance to the F_1 cross progenies. GCA remains an important parameter for representing the performance of parent involved in crossing with another parent, and it is related to additive gene action of parental genes. Thus, GCA remains instrumental in selecting superior parent plants in crop breeding programme. Estimates of GCA effects recorded for the studied traits in all the parental genotypes are given in Table 4. For phenology related traits such as FF trait, the parent P1 showed desirable, highly significant and negative GCA effect under both NS and LS, and P3 and P5 exhibited high and significant positive effect under LS. Concerning PH trait, P2, P5 and P6 parents exhibited high and significant GCA effect under NS, and P6 displayed high and significant GCA effect under LS. While for DPI trait, P1, P2, and P5 parents showed high and significant desirable negative GCA effects under NS, whereas only P1, P2 parent showed high and negatively significant GCA effect under LS. Importantly, P1 and P2 parents (under both conditions) and P5 parent (under NS) showed negative and significant GCA effects for DPF trait. Moreover, for DM trait P1 and P5 parents revealed negative and significant GCA effects under (NS) and P1, P2 and P6 showed negative and significant GCA effects under LS conditions (see Table 4). Thus, ICC 4958, ICC 92944 and ICC 96030 parents can be employed as donor for transferring early phenological traits for improving HS tolerance in chickpea. Similarly, Murtadha *et al.* (2018) identified important donor for early days to tasselling in maize under water stress. Notably, for yield-related traits such as TPOD/P, P6 parent showed positive and highly significant GCA effects under NS (4.83) and LS (1.50) conditions. The desirable highly negative significant GCA effect for EP/P was recorded for P1 (under NS) and for P2 (under LS). For BYPP and 100 SW traits, the following parents P2 and P6 (under NS) and P2 (under LS) showed high and significant positive GCA effects. While for YPP, ICC 92944 (3.23) and ICC 1205 (0.97) parents (under NS) and KWR 108 (0.51) parent (under LS) revealed high and positive significant GCA effects. Taking note of 100SW trait, ICC 92944, ICC 96030 and KWR 108 parents (under NS) and KWR 108 parent (under LS) exhibited high and positive significant GCA effects. Therefore, P2 (ICC 92944) and P6 (KWR 108) parents could be potentially utilized as good general combiners for improving the above mentioned yield-related traits under both conditions in chickpea.

The SCA effect enables us to estimate the non-additive gene effects. The values of SCA effects are given in Table 5. A set of eight crosses (P1 × P2, P1 × P4, P1× P5, P1×P6, P2 × P3, P2 × P6, P3 × P5, and P4 × P5) showed positive and high significant SCA effect for FF trait under NS. The cross combinations (P1 × P2, P1 × P5, P2 × P4, P4 × P5 and P4 × P6) displayed desirable negative and significant SCA effects under LS. For PH trait, (P1 × P2, P3 × P6, P4 × P5 and P5 × P6) parental combinations revealed high and positive significant SCA effect under NS and P1 × P2 and P3 × P5 cross-combinations showed high and positive significant SCA effects under LS. Three F_1's (P1 × P2, P1

Table 4 Estimate of general combining ability effects of parents for different traits

Trait	E	P1	P2	P3	P4	P5	P6
FF	NS	-1.764 **	-2.889 **	1.153 **	4.194 **	-1.472 **	0.778 *
	LS	-2.875 ***	0.625 *	2.417 ***	0.458	1.958 ***	-2.583 ***
PH	NS	0.143	1.593 **	-4.278 **	-0.549	1.301 **	1.789 **
	LS	0.335	-0.511	-0.636 *	-0.294	-0.382	1.489 ***
DPI	NS	-2.056 **	-2.514 **	1.444 **	3.236 **	-1.639 **	1.528 *
	LS	-1.236 *	-1.944 ***	0.306	-0.653	2.847 ***	0.681
DPF	NS	-1.361 **	-2.111 **	0.972 **	2.722 **	-1.361 **	1.139 **
	LS	-2.083 ***	-1.250 ***	-1.125 ***	0.583 *	2.708 ***	1.167 ***
DM	NS	-2.500 **	1.792 **	1.333 **	1.667 **	-3.333 **	1.042 **
	LS	-1.958 ***	-1.708 ***	2.500 ***	1.000 *	1.250 **	-1.083 *
TPOD/P	NS	-13.292 *	4.875 **	4.042 **	-0.458	0	4.833 **
	LS	-3.917 ***	0.792	0.542	0.542	0.542	1.500 ***
EP/P	NS	-0.278 *	-0.528 **	-0.153	0.264 *	0.389 **	0.306 *
	LS	-0.028	-0.444 *	0.389 *	0.139	0.014	-0.069
BYPP	NS	-0.919	1.714 **	-2.761 **	0.126	-0.207	2.047 **
	LS	-1.238 **	1.021 *	0.272	-0.27	0.302	-0.087
YPP	NS	-2.350 **	3.238 **	0.021	0.979 **	-0.525	-1.363 **
	LS	-0.602 ***	0.286	-0.043	-0.092	-0.067	0.518 **
100 SW	NS	-0.403	3.085 **	-1.640 **	-2.532 **	0.693 **	0.797 **
	LS	0.269	0.014	-1.287 ***	-0.16	-1.313 ***	2.477 ***

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. E = environment

× P6, and P2 × P4) depicted negative and high significant SCA effects under NS for DPI. The P1 × P2, P2 × P4, P2× P5 and P4 × P6 crosses displayed desirable negative and significant SCA effects for this trait under LS.

Two F_1s (P1 × P6, P2 × P4) exhibited highly significant and negative SCA effects, and P1 × P2 and P1 × P5 crosses exhibited high and negative significant SCA effects for DPF trait under NS. Likewise, P1 × P2, P1 × P5, P2 × P6 and P3 × P5 crosses displayed negative significant SCA effects for the same trait under LS. Negative and highly significant SCA effects were recorded for DM in four F_1s (P1 × P4, P2 × P5, P3 × P6 and P4 × P6). P1 × P2, P1 × P5 and P3 × P6 cross-combinations depicted negative and significant SCA effects for DM under LS. A total of 10 F_1s exhibited positive and significant values for TPOD/P trait under NS. Concerning BYPP, only four F_1s (P1×P2, P4 × P5, P4×P6 and P5 × P6) showed positive and highly significant SCA effect under NS. While, only P2 × P3 cross displayed positive and highly significant SCA effect under LS. Taking note of YPP trait three F_1s (P1 × P2, P1 × P4, P2 × P5 and P3 × P5) revealed positive and high significant effects under NS. Importantly, ICC 4958 × ICC 92944, ICC 1205× ICC 96030 and DCP 92-3 × KWR 108 crosses displayed positive and significant SCA effect under LS. For 100SW, a total of seven F_1s (P1 × P3, P1 × P6, P2 × P4, P3 × P4, P3 × P5, and P3 × P6) showed high and positive SCA effects. Likewise, for this trait a total of nine F_1s (P1 × P2, P1 × P5, P1 × P6, P2 × P3, P2 × P4, P3 × P4, P3 × P5, P3 × P6 and P5 × P6) exhibited positive and highly significant SCA effect under NS.

In order to maximize desirable plant traits, it requires at least one parent in crossing programme having high GCA effect and additive effect that can complement the *epistatic effects* of other parent in the same direction (Singh and Chaudhary 1995, Murtadha *et al.* 2018). Considering this, ICC 92944 displayed positive and significant GCA effect under NS and KWR 108 showed positive and significant GCA effect under LS. These two parents produced some important crosses such as P1 × P2, P2 × P5, P4 × P6, P5 × P6 (under NS) and P3 × P6, P1 × P2 (under LS) which exhibited high and significantly positive SCA effects for these traits. Thus, KWR 108 and ICC 92944 parents and DCP 92-3 × KWR 108 and ICC 92944 × ICC 4958 crosses could be utilized for development of HS tolerance in chickpea breeding programme. These results were in agreement with the results suggested by Rainey and Griffiths (2005b) in common bean under HS, Zeinab and Hilal (2014) in faba bean, Rodrigues *et al.* (2018) in cowpea under drought stress**.**

Heritability of traits

Estimates of broad sense heritability, for all the traits studied, showed high values that ranged from 64% (for EP/P) to 99.4% (DPI) under NS and from 64.6% (EP/P)

Table 5 Estimate of specific combining ability effects of F1 crosses

Trait	E	P1 × P2	P1 × P3	P1 × P4	P1 × P5	P1 × P6	P2 × P3	P2 × P4	P2 × P5	P2 × P6	P3 × P4	P3 × P5	P3 × P6	P4 × P5	P4 × P6	P5 × P6
FF	NS	2.976**	-3.565**	5.226***	4.268***	12.35***	3.018**	-5.19	2.518*	5.560***	-2.399*	3.643**	2.351*	4.768***	2.143*	-1.482
	LS	-2.369**	0.839	5.464***	-12.702***	7.173***	0.673	-3.369***	-0.536	0.673	4.173***	3.339***	-0.786	-4.369***	-2.827**	5.339***
PH	NS	6.428***	-0.639	-0.739	2.078	-2.026	-0.86	-8.260***	-3.176**	-10.080**	-0.326	0.824	3.253**	5.690***	0.686	2.170*
	LS	2.959**	-5.483***	-0.691	0.363	-1.241	1.43	2.055*	-0.191	1.271	-2.287**	8.234***	2.004*	1.492	0.555	-1.591*
DPI	NS	-1.208*	0.125	1.875***	1.625**	-6.583***	3.500***	-3.083***	3.333***	3.125***	-0.75	4.000***	2.125***	3.750***	2.208***	2.292***
	LS	-6.185***	0.565	4.524**	-0.643	3.524*	4.607**	-2.768*	-2.935*	-1.101	0.982	1.482	-1.685	-1.56	-5.060**	1.774
DPF	NS	0.333	0.042	0.458	1.292	-5.625***	0.292	-2.625***	3.542***	2.625***	0.083	2.917***	1.333*	2.667***	2.417**	-0.083
	LS	-6.714***	2.161**	4.452***	-3.339***	5.869***	3.327***	-1.048	-0.173	-1.631*	-1.173	-1.631*	0.244	-0.339	-1.464	1.744*
DM	NS	3.089***	1.923*	-3.286***	7.006***	-0.661	4.714***	0.839	-4.202***	1.131	-0.994	5.298***	-3.369***	3.423***	-2.244**	8.381***
	LS	-5.048***	1.744	0.577	-7.006***	2.661*	-1.839	1.327	4.077**	2.744*	1.786	-1.464	-3.464*	0.702	0.369	-1.214
TPOD/P	NS	1.024	8.149**	-4.685	3.607	10.190***	0.982	13.482***	11.107***	7.690**	7.274**	9.899***	3.482	6.399*	13.982***	12.940**
	LS	1.744	-6.673***	-0.339	-4.006**	-2.298	0.952	0.286	1.619	-1.339	0.869	0.869	-1.089	-0.798	-1.756	1.911
EP/P	NS	-0.339	0.036	-0.214	0.536	-0.256	-0.089	-0.339	0.077	0.286	0.702	-0.214	0.327	0.536	-0.256	0.494
	LS	-0.702	0.464	-0.286	1.506**	-0.077	0.548	0.464	-0.077	1.006	0.964	-0.911	-1.827**	-0.327	-0.577	0.881
BYPP	NS	3.676*	0.726	0.008	-1.016	1.126	-3.129*	-0.824	-4.570**	4.146	-2.262	-2.874*	1.08	4.488**	8.092***	4.913**
	LS	1.606	0.202	-0.653	0.185	-0.856	3.467**	1.569	2.28	-0.328	-2.415*	0.153	0.601	1.298	0.547	-0.462
YPP	NS	10.480**	0.138	4.588***	-2.124**	-4.008***	-9.945***	-6.362***	9.526***	-0.958	0.541	8.696***	-0.883	-0.233	1.917*	1.638*
	LS	1.879***	-1.342**	-0.823	0.345	-0.553	0.786	0.872	-1.184*	0.526	-0.598	0.256	1.125*	1.535**	0.044	-0.585
100SW	NS	-3.963***	4.908***	-0.996	-0.196	7.974***	-4.459***	2.137**	3.204***	1.411	6.242***	1.708**	4.008***	0.079	-2.192**	-5.159**
	LS	1.578**	-7.884***	-4.675***	2.945***	4.676***	4.561***	3.753***	-0.967	-5.096***	2.802***	3.222***	3.709***	-3.063***	-0.786	2.088***

*P < 0.05; **P < 0.01; ***P < 0.001. E=environment to 98.6% (100SW) under LS. Whereas estimates of narrow sense heritability was high for EP/P (56%) and low (8.3%) for 100SW trait under NS, and high narrow sense heritability (44.9%) for TPOD/P and low narrow sense heritability (8.3%) for EP/P were evident under LS. Considering broad sense heritability 100SW, FF traits showed high broad sense heritability under NS. Similar results have been reported by Bicer and Sakar (2008) in chickpea, Toker *et al.* (2004) in faba bean and Mia *et al.* (2017) in wheat for various physiological and yield-related traits under drought stress.

Conclusion

The present study was aimed at understanding the gene action of various yield-related traits under HS through combining ability analysis in chickpea. It helped selecting parental genotypes possessing high GCA and producing superior cross-combinations with high SCA under HS for improving chickpea yield. Combining ability analysis indicated presence of both additive and non-additive gene action, controlling the studied traits with preponderance of higher additive gene action. Therefore, selection of superior crosses with high SCA, through incorporating parents possessing high GCA could be one of the potential breeding strategies for developing heat tolerant chickpea variety.

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