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ORIGINAL ARTICLE

Relationship of Parental Genetic Distance with Heterosis and Specific Combining Ability in Sesame (*Sesamum indicum* L.) Based on Phenotypic and Molecular Marker Analysis

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Abstract The genetic distance analysis for selection of suitable parents has been established and effectively used in many crops; however, there is dearth of conclusive report of relationship of genetic distance analysis with heterosis in sesame. In the present study, an attempt was made to estimate the associations of genetic distances using SSR (GDSSR), seed-storage protein profiling (GDSDS) and agro-morphological traits (GDMOR) with hybrid performance. Seven parents were selected from 60 exotic and Indian genotypes based on genetic distance from clustering pattern based on SSR, seed-storage protein, morphological traits and per se performance. For combining ability analysis, 7 parents and 21 crosses generated from 7 × 7 half diallel evaluated at two environments in a replicated field trial during pre-kharif season of 2013. Compared with the average parents yield (12.57 g plant^{-1}), eight hybrids had a significant ($P < 0.01$) yield advantage across environments, with averages of 26.94 and 29.99% for better-parent heterosis (BPH) and mid-parent heterosis (MPH), respectively, across environments. Highly significant positive correlation was observed between specific combining ability (SCA) and per se performance (0.97), while positive non-significant correlation of BPH with GDSSR (0.048), and non-significant negative correlations with GDMOR (− 0.01) and GDSDS (− 0.256) were observed. The linear regressions of SCA on MPH, BPH and per se performance of F_1s were significant with R^2 value of 0.88, 0.84 and 0.95 respectively. The present findings revealed a weak association of

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GDSSR with F_1's performance; however, SCA has appeared as an important factor in the determination of heterosis and per se performance of the hybrids. The present findings also indicated that parental divergence in the intermediate group would likely produce high heterotic crosses in sesame.

Keywords GCA · Heterosis · Genetic distances · SCA · Sesame · SSR

Introduction

Sesame (*Sesamum indicum* L.) is an ancient oil-yielding crop in tropical and subtropical regions of Asia, Africa and South America producing the highest - quality of oil among the major oilseed crops including peanut, soybean and rapeseed (Bhat et al. 1999). Sesame seeds contain about 50–60% edible oil, which is consumed as a traditional health food for its specific antihypertensive effect and anti-oxidative activity (Jan et al. 2011). The consumption of vegetable oil is expected to touch almost 200 billion kilograms by 2030 resulting in huge demand of oil seed crops (Wang et al. 2014). To fill the gap between demand and supply of oil seed, it is necessary to further increase both yield level and total production by exploiting heterosis. Indian sesame collection represents wide diversity for morphological and agronomic characteristics over diverse eco-geographical regions (Bisht et al. 2004). In the present era, molecular techniques and biometrical methods have unlocked the several ways to evaluate germplasm regarding their suitability as parents. To achieve higher yield, it is required to identify elite parents that can produce exceptionally high yielding hybrids. The use of molecular markers for assessing the diversity amongst parental lines has been suggested for overcoming bottlenecks in hybrid development and selection (Ndhlela et al. 2015). The identification of best hybrid combinations basically relies on the combining ability of the parental genotypes and the gene effects that are associated to the expression of the traits of interest. For any hybrid breeding programme, the information on the effects of general combining ability (GCA) and specific combining ability (SCA) is crucial for the selection of parental genotypes. Best parental combinations are likely to produce heterotic F_1 progeny. The successful breeding and utilization of elite lines in diverse heterotic groups have not only assisted in increasing the maize productivity by a big difference but also encouraged breeders to adopt this technique in other crops (Hallauer 1999). Very few studies have used genetic distance to predict hybrid performance in sesame. Some researchers reported association between marker-based genetic distance and heterosis (Banerjee and Kole 2010), whilst others have reported no association with heterosis (Dikshit and Swain 2000). The potential application of markers in determining the degree of heterosis in sesame is, therefore, inconclusive. In this context, the present study is an attempt to classify the accessions according to their relationships by means of the genetic distance based on SSR (GD_{SSR}), Seed-storage protein profiling (GD_{SDS}) and 37 agro-morphological traits (GD_{MOR}) for their future use in hybrid breeding. The objectives of this study were as follows: (i) to classify sesame genotypes based on GD_{SSR}, GD_{SDS} and GD_{MOR}, (ii) to estimate GCA, SCA and heterosis effects, and

(iii) to correlate the estimated parental genetic diversity based on GD_{SSR}, GD_{SDS} and GD_{MOR} with SCA and heterosis effects.

Materials and Methods

Experimental Material

In an earlier study reported by Pandey et al. (2015), a collection of 60 sesame genotypes including exotic collections, indigenous collections and landraces were classified based on morphological and marker analysis which served as a base population for selection of seven parents. Based on three clustering pattern and yield performance records, the seven parents namely, Gujarat Til-2 (Western India), TKG-22 (Central India), OSC-593 (South Eastern India), RT-348 (North Western India), TKG-352 (Central India), UMA (South Eastern India) and one indigenous collection, NIC-8316 (Eastern India) (Table 1) from five major sesame-growing states of India were selected for a 7 × 7 half-diallel mating design. Twenty-one F_1s along with seven parents were again clustered based on GD_{SSR}, GD_{SDS} and GD_{MOR} according to the methods described below.

Field Experiment

All the possible crosses were made except the reciprocal ones. All F_1 hybrids with their parents were planted during *pre-kharif* season of 2013 using random complete block design with three replications in two environments: the first field site was in Nonaghata (latitude 23°42′ and longitude 88°44′) and the second was in Baruipur South 24-Paraganas (latitude 22°37′ and longitude 88°43′) of West Bengal, India. The soil characteristic was silty clay with pH 6.65 at Nonaghata and sandy loam type with pH 7.20 at Baruipur.

Agronomic Characteristics

The observations of following nine agronomic characters namely plant height (PH), days to 50% flowering (DTF) (days), days to maturity (DTM) (days), number of primary branches/plant (BP), number of capsules/plant (CP), capsule length (CL) (cm), number of seeds/capsule (SC), 1000 seed weight (SW) (g) and seed yield/plant (SY) (g) were recorded for combining ability analysis. Additional 28 traits namely seed coat colour, stem shape, stem pubescence, leaf arrangement, leaf shape, leaf angle, petal colour, petal hairiness, flowers/axil, capsule shape, capsule hairiness, branching habit, shape of stem hair, stem branching, leaf hairiness, basal leaf profile, basal leaf margin, lobe incision of basal leaf, petiole colour, petiole hairiness, extra floral nectaries, extra floral nectaries colour, calyx hairs, interior corolla colour, interior corolla pigment, lower lip colour, capsule arrangement and capsule beak shape were also recorded along with nine agronomic traits for diversity analysis based on 37 morphological traits.

Table 1 Characteristic features of seven selected parents for 7 × 7 half diallel analyses

Parent ids	Parent	Origin	Salient feature	GCA for SY	SY (mean)	Groups based on GD_{SSR}	Groups based on GD_{MOR}	Groups based on GD_{SDS}
G1	GUJARAT TIL-2	Gujarat-Western India	Tolerant to bacterial blight and wilt	− 0.791**	14.26	IIB	IIB	IIA
G2	TKG-22	MP-Central India	High oil and iron, zinc content	− 0.232**	13.22	IA	IIA	IIC
G3	OSC-593	Orissa-South Eastern India	Less branching; high yielding	0.337**	12.15	IIIB	IC	IIB
G4	RT-348	Rajasthan-North Western India	High seed weight and high cobalt content	− 0.293**	11.44	IIB	IC	IIB
G5	UMA	Orissa-South Eastern India	Tolerant to Root Rot and Phyllody	0.498**	11.49	IIIB	IA	IIB
G6	NIC-8316	Indigenous collection—Eastern India	High adaptability with high iron content	0.247**	12.83	IIIA	IIC	IIB
G7	TKG-352	MP-Central India	High oil content and seed yield	0.234	12.62	IA	IC	IIA

Molecular Marker Analyses

DNA Extraction

DNA extraction was done from apical young leaves of 10–12 days old. After grinding them in liquid nitrogen, the leaves were treated with CTAB buffer following the method of Saghai-maroof et al. (1984), and then the DNA was purified with RNaseA followed by phenol: chloroform. Purified DNA was quantified in Nanodrop Lite (Thermo Scientific, USA).

SSR Primers

Initially, 36 SSR and EST-SSR markers were used, but final genetic divergence was measured based on 11 highly polymorphic SSR markers (Bhattacharya et al. 2014). The details of 11 polymorphic markers are given in Supplementary Table 1.

PCR Amplification

DNA amplification was done in 25 μL reaction mixture that consists of 0.2 μmol L^{-1} SSR primers, 0.2 mM of each dNTPs, 2 mmol L^{-1} $MgCl_2$, 1X PCR buffer and 0.5 unit Taq polymerase, and 50 ng sample DNA. The procedures for SSR and Est-SSR were performed on a DNA thermocycler kit (Eppendorf AG 6321, Germany) as described by Pandey et al. (2015). 3% agarose gel (Sigma USA) was used for separating the amplified PCR products. A 50 base-pair ladder marker (GeneRuler 50 bp DNA Ladder, Thermo Scientific, USA) was used to estimate PCR fragment size.

Seed-Storage Protein Extraction and Profiling

Seed-storage protein extraction and protein profiling were performed according to Lowry et al. (1953) and Laemmli (1970). Standard marker protein (Fermentes, PageRuler™ Pre-stained Protein Ladder—SM0671) was used for estimation of molecular weights of sample protein bands using Gel Documentation Unit (UVP, USA). Molecular weights (MWs) and relative mobility (Rm values) of each band were obtained using the Life Sciences Software loaded in gel documentation unit (UVP GelDoc) by characterizing the molecular weights of each band of the known marker protein. Genetic similarity (GS) coefficients were computed using SIMQUAL program. Dendrogram was constructed using Unweighted Pair Group Method with Arithmetic average to assess relationship among genotypes.

Genetic Distance Analysis Using SSR, Protein and Morphological Data

The clear and reproducible bands from both protein and DNA fragments were selected for data analysis. The presence or absence of bands was scored as '1' or '0', respectively, for all genotypes. Effective allele/locus was calculated following Weir (1990). To eliminate the effect of different measurements, the data were first

standardized using the program STAND. The distance coefficient through DICE similarity index was then calculated, and dissimilarity coefficients between genotypes were worked out following Jaccard's coefficient method. Genetic distances were calculated as 1—genetic similarity (GS). The morphological dissimilarity matrix was calculated using program SIMINT, whereas SIMQUAL was used for molecular dissimilarity matrix through NTSYS-pc (Rohlf 2005). Dendrogram was constructed using the NJ method based on dissimilarity matrix using DARwin 6.0.13 software program.

Statistical Analyses

Griffing's Method 2 (no reciprocals) (Griffing 1956) was used to determine the estimates of general combining ability and specific combining ability of F_1s, which are developed to study the yield of sesame. Combined and environment-wise analyses of variance of hybrid trial were performed using MIXED procedure of SAS 9.4 (SAS 2015; Zhang and Kang 1997) considering environment, hybrid and replication as fixed effects. Individual environment variances were modelled into combined analysis. *F*-test was used for testing the significance of fixed effect factor. The linear model for combined analysis of hybrids across environments for yield is

$$\begin{aligned} Y_{ijk} = {} & \mu + \mathrm{env}_i + \mathrm{rep(env)}_{ki} + \mathrm{GCA}_j + \ \mathrm{SCA}_{jj'} \\ & + \ (\mathrm{GCA}\times\mathrm{env})_{ij} + (\mathrm{SCA}\times\mathrm{env})_{ijj'} + \epsilon_{ijk}, \end{aligned}$$

where μ is the overall mean; env_i is *i*th environment, $i = 1,2$, $\mathrm{rep(env)}_{ki}$ is the effect of k replication within *i*th environment; GCA_j is *j*th parent general combining ability, $j = 1$ to $p - 1$; $\mathrm{SCA}_{jj'}$ is *jj*′th F_1 hybrid specific combining ability, $j' = j + 1$ to p; $(\mathrm{GCA} \times \mathrm{env})_{ij}$ is the interaction of GCA and environment; $(\mathrm{SCA} \times \mathrm{env})_{ijj'}$ is the interaction of SCA and environment; and ϵ_{ijk} is the random error NID(0, $\sigma^2 e$). The relative importance of GCA and SCA effects on yield was assessed using the formula $(2\sigma^2_{\mathrm{GCA}}/(2\sigma^2_{\mathrm{GCA}} + \sigma^2_{\mathrm{SCA}}))$ (Baker 1978; Lu and Myers 2011)—the closer the ratio to unity, greater is the predictability of a specific hybrid's performance based on the GCA alone (Hung and Holland 2012).

Mid-parent heterosis (MPH) and best-parent heterosis (BPH) were calculated for yield. The MPH was calculated as follows: $[(F_1 - \mathrm{MP})/\mathrm{MP}] \times 100$; where, F_1 is the mean performance of the hybrid; MP is the mid-parent value given by $(\mathrm{P1} + \mathrm{P2})/2$; P1 and P2 are the means of parent 1 and parent 2, respectively. The BPH was calculated as $[(F_1 - \mathrm{BP})/\mathrm{BP}] \times 100$: where BP = the mean of the best parent. Simple linear regression was computed to determine the relationships between SW, SY, SCA, BPH and MPH. The binary data from SSR scoring were used to compute pairwise similarity coefficients (Jaccard1908). The similarity matrix thus obtained was subjected to cluster analysis using the UPGMA algorithm using NTSYS-pc software (Rohlf 2000). Relationships among F_1s and parents were visualized in dendrograms. Means per environment and across environments were used to calculate Pearson's correlation coefficients (*r*) between genetic distances, F1SY, MPH, BPH and SCA using SAS (SASV9.4).

Result and Discussion

Genetic Distance and Groups of Parents

Grouping of original 60 genotypes were done based on GD_{SDS} (range 1.98–12.44), GD_{MOR} (range 3.29–13.65) and GD_{SSR} (range 3.31–11.91). The original 60 genotypes were clearly clustered into three groups based on genetic distance (GD_{SSR}) through SSR markers. GD_{SSR} of the seven parents ranged from 0.05 to 0.55, with an average of 0.301, which was lower than that of the original parent population. To select seven diallel parents, two parents each from groups—GI and GII, and three parents from GIII were selected based on GD_{SSR}. Based on GD_{SDS}, the 60 genotypes clustered into two main groups GI and GII; Group GI was further subclustered into IA and IB, and GII subclustered into IIA, IIB and IIC. According to the grouping based on GD_{SDS}, all the selected seven genotypes fall in the subgroups of GII—IIA, IIB and IIC. Following the same pattern of GD_{SDS}, GD_{MOR} also grouped the 60 genotypes into two main groups (GI and GII), both with three subclusters IA, IB and IC; and IIA, IIB and IIC respectively. As evident from the results, similar fashion of grouping was observed based on GD_{SDS} and GD_{MOR}, and both these grouping patterns were remarkably different from the clustering based on GD_{SSR}.

These selected seven parents were further clustered into different subgroups based on genetic distances revealed by agro-morphological traits (GD_{MOR}; range 0.002–0.041) (Fig. 1), seed-storage protein banding pattern (GD_{SDS}; range 0.055–0.250) (Fig. 2); and SSR (GD_{SSR}; range 0.05–0.55) (Fig. 3), and they maintained clustering pattern similar to their respective original cluster structure for 60 genotypes. Similar clustering pattern has been observed in a different study by Huang et al. (2015). Clusters originating from GD_{MOR}, GD_{SSR} and GD_{SDS} grouped the seven parents in a different manner. In case of clustering based on GD_{SDS} and GD_{MOR} for parents, the grouping of genotypes was not in accordance with their

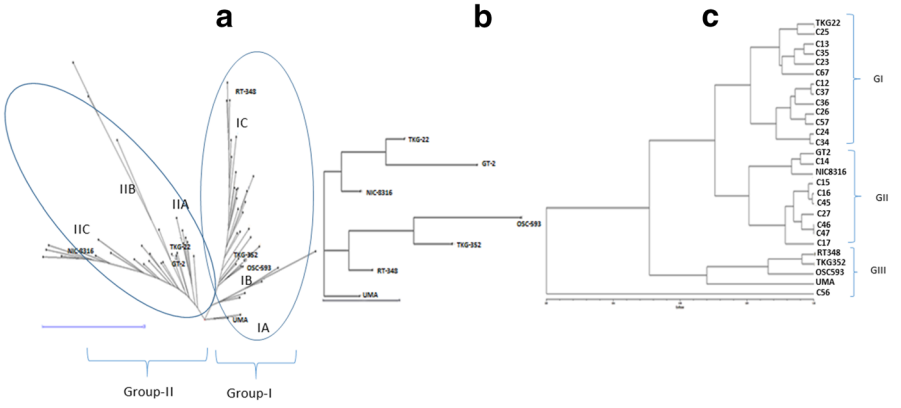

Fig. 1 Unweighted neighbour-joining tree of **a** the 60 sesame lines and **b** the 7 selected parents for diallel crosses. **c** 21 F_1s and 7 parents, based on *Jaccard's coefficient* derived from morphological traits

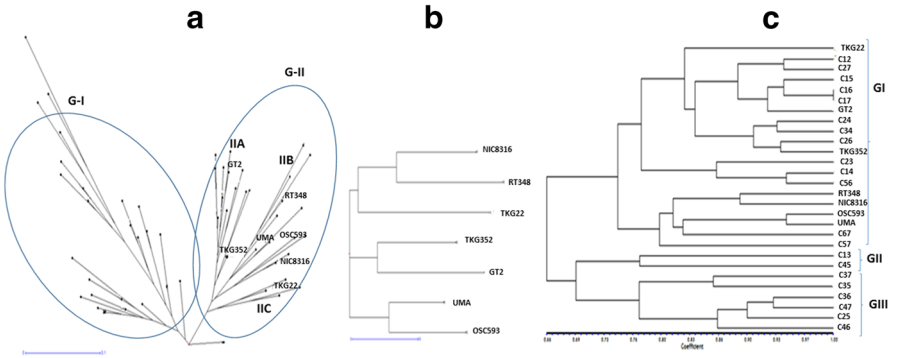

Fig. 2 Unweighted neighbour-joining tree of **a** the 60 sesame lines and **b** the 7 selected parents for diallel crosses. **c** 21 F_1s and 7 parents, based on *Jaccard's coefficient* derived from seed-storage protein profiling

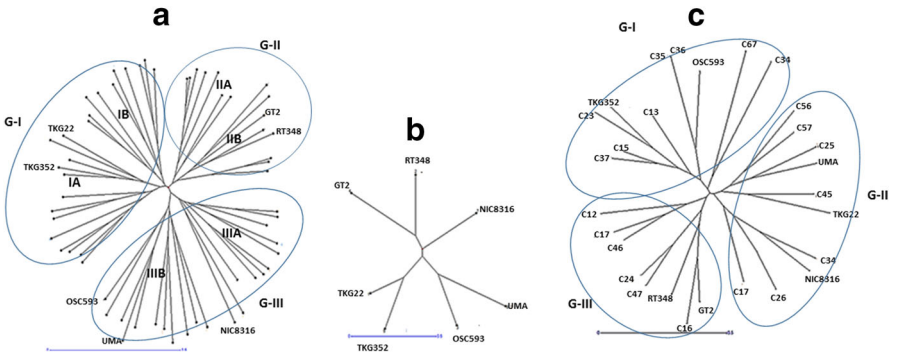

Fig. 3 Unweighted neighbour-joining tree of **a** the 60 sesame lines and **b** the 7 selected parents for diallel crosses. **c** 21 F_1s and 7 parents, based on *Jaccard's coefficient* derived from SSR marker

geographic origin, as P2 (TKG-22) and P7 (TKG-352) were from same geographical region, occupying different clusters. On the contrary, cluster analysis-based SSR grouped P2 and P7 in same cluster during the clustering of parents.

Again, the 21 F_1s along with seven parents were together classified into different clusters based on agro-morphological traits (GD_{MOR} ranging from 0.0004 to 0.079), SDS-PAGE (GD_{SDS} ranging from 0.056 to 0.769) and SSR (GD_{SSR} ranging from 0.103 to 0.414). As shown in Fig. 1 and 2, the dendrograms constructed using GD_{MOR} and GD_{SDS} divided the seven parents and F_1s into three major groups. Although the number of lines clustered in each major group was different for both the clustering systems, i.e. SDS-PAGE and SSR, there is a similarity in both grouping patterns based on GD_{SDS} and GD_{MOR}; four out of the seven parents were present in a separate group along with one or two F_1 lines. The parental lines did not form distinct groups based on their origin, but the grouping followed the pedigree record. On the contrary, Cluster analysis based on SSR provided a fairly good resolution of the F_1 lines from the parents. The F_1 lines clustered into three groups, indicating existing pedigree records. The parents were distinctly separated among

each other in the dendrograms, as expected, based on their genetic backgrounds (Fig. 3). Cluster analysis using the GD_{SSR} matrix classified the 28 lines into three main groups (Fig. 3). Viewing these associations from the top of the dendrograms, the first group consists of two parents namely parent-3 (OSC-593) and parent-7 (TKG352) and 8 F_1s and most of which having either one of the parents in their parentage. The second group has a mixture of seven F_1s along with parent 2 (TKG22), parent 5 (UMA) and Parent 6 (NIC-8316). The third group consists of six F_1s along with two parents, P1 (GT-2) and P4 (RT-348). Within each group, mostly the F_1s bred with a common parentage cluster together (Figs. 1, 2, 3).

Combining Ability Analysis and Genetic Parameters

Results of ANOVA for two environments and pooled are given in Table 2. All main effects (environments and hybrids) were highly significant ($P < 0.01$), as were all possible two-way interactions between the main effects, but replication was insignificant for most of the traits except BP and DTF at $P < 0.05$ in pooled analysis. The significant genotype × environments interactions strongly suggested that SY and other traits of genotype depended on the environments in which they were grown. The GCA × environment interaction was significant at $P < 0.05$, and SCA × environment interaction was significant at $P < 0.01$ for SY; however, for few other traits like PH, DTF, CP and SC, both GCA × environment and SCA × environment were significant at $P < 0.01$. These results suggested that the GCA and SCA effects were environment specific and that a single-environment testing would be inadequate. Involvement of both additive and non-additive types of gene action was revealed by components of GCA and SCA mean sums of squares which were highly significant for all the traits (Table 2). Variance due to SCA ($\sigma^2 s$) was higher than the variance due to GCA ($\sigma^2 g$) (Table 3) for all the traits indicating the predominance of non-additive type of gene action in controlling the expression of these traits. This was further confirmed by low magnitude of GCA/SCA ratios, indicating the non-additive type of gene action controlling the expression of most of the traits and suggests exploitation of these non-additive genetic variation through hybrid breeding (Ramalingam et al. 1997). Predictability ratio calculated from GCA and SCA variances exhibits the extent to which character is transmitted to the progeny (Banerjee and Kole, 2009). The predictability ratio (Baker 1978) was high in case of the character plant height (0.52) which is higher than 0.50 indicating the importance of additive gene action (Table 3) (Saravanan and Nadarajan 2003). On the contrary, the ratios were lower than 0.50 for all other characters, indicating that both additive and non-additive gene actions influenced the performance of the hybrids (Table 3) (Banerjee and Kole 2009; Solanki et al. 2006).

General Combining Ability Effects of the Parents

Usually, GCA effects of individual lines are considered to be controlled by genes with additive effects, and these effects can be passed on to the next generation (Hallauer and Miranda Filho 1988; Kang 1994). Thus, GCA effects are a major criterion for evaluating lines for their potential application in hybrid development

Table 2 Analysis of variance (ANOVA) for yield, yield components' traits based on a half diallel of 7 parents for each environment and combined analysis over two environments

SOV	DF	PH	BP	DTF	DTM	CP	CL	SC	SW	SY
Environment 1										
Replication	2	3.52	0.35	8.65	7.43	1.88	0.04	3.15	0.75	0.08**
Genotype	27	3207.3**	860.97**	37.55**	79.74**	1677.48**	215.68**	559.75**	1346.6**	253.5**
GCA	6	8423.9**	866.73**	13.28**	33.09**	2067.54**	199.02**	141.05**	2065.4**	70.27**
SCA	21	1716.8**	859.33**	44.49**	93.06**	1566.03**	220.44**	679.38**	1141.3**	305.85
Error	54	0.14	0.00176	0.224	0.2226	0.18505	0.0005	0.2243	0.0004	0.06463
Environment 2										
Replication	2	0.34	1.11	2.75	0.29	0.10	3.95	0.87	0.64	0.11
Genotype	27	231.28**	19.16**	43.31**	14.18**	49.77**	51.99**	338.11**	155.51**	44.19**
GCA	6	687.54**	24.74**	18.63**	6.82**	56.96**	25.52**	49.15**	207.10**	19.33**
SCA	21	100.91**	17.57**	50.37**	16.29**	47.72**	59.55**	420.66**	140.77**	51.29**
Error	54	2.01090	0.0702	0.7059	1.4656	7.3307	0.0043	0.409	0.004	0.410
Pooled										
Environment	1	2034.60**	1228.4**	90.29**	1067.0**	18277.5**	28.50**	468.41**	320.1**	5311.3**
Replication	4	1.91	0.72	5.63	3.81	0.98	1.97	1.99	0.69	0.09
Genotypes	27	838.77**	77.50**	70.71**	42.88**	175.52**	131.44**	825.16**	513.93**	135.61**
GCA	6	2387.97**	87.95**	23.87**	18.27**	207.02**	86.24**	157.50**	733.9**	47.15**
SCA	21	396.14**	74.51**	84.10**	49.90**	166.53**	144.36**	1015.92**	451.08**	160.89**
G × E	27	17.01**	2.07	13.14**	2.78	4.17**	10.11**	7.83**	4.37**	9.71**
GCA × E	6	9.34**	2.77	10.82**	2.30	5.91**	4.62	5.81**	3.67	5.36*
SCA × E	21	19.21**	1.87	13.80**	2.92	3.68**	11.68**	8.41**	4.57**	10.95**
Error		1.07	0.46	0.46	0.84	3.75	0.0024	0.317	0.0024	0.237

E1 Environment 1 (Nonaghata, WB), *E2* Enviornment 2 (Baruipur, WB), *PH* plant height, *BP* branches/plant, *DTF* days to flowering, *DTM* days to maturity, *CP* number of capsules/plant, *CL* capsule length, *SC* number of seeds/capsule, *SW* 1000 seed weight, *SY* seed yield/plant, * $P < 0.05$, ** $P < 0.01$

Table 3 Estimates of various genetic parameters for yield and yield contributing traits of sesame across environments and pooled over environments

Environment	PH	BP	DTF	DTM	CP	CL	SC	SW	SY
$\sigma^2 g$									
E1	106.0	0.0015	− 0.778	− 1.48	10.312	− 0.001	− 13.416	0.044	− 1.69
E2	131.07	0.056	− 2.489	− 1.54	7.527	− 0.016	− 16.92	0.033	− 1.458
Combined	− 1.501	0.039	− 15.12	− 0.008	8.45	− 1.483	1.556	0.027	119.13
$\sigma^2 s$									
E1	244.08	1.517	9.76	20.49	289.6	0.123	152.16	0.486	19.702
E2	200.91	1.165	34.84	22.40	342.46	0.253	172.03	0.625	20.64
Combined	18.99	0.552	160.92	0.175	311.01	20.641	19.327	1.324	212.69
Predictability ratio									
E1	0.465	0.002	− 0.189	− 0.169	0.07	− 0.022	− 0.214	0.152	− 0.207
E2	0.566	0.088	− 0.167	− 0.159	0.042	− 0.148	− 0.245	0.095	− 0.165
Combined	0.528	0.039	− 0.19	− 0.168	0.052	− 0.1	− 0.231	0.122	− 0.188

E1 Environment 1 (Nonaghata, WB), *E2* Enviornment 2 (Baruipur, WB), *PH* plant height, *BP* branches/plant, *DTF* days to flowering, *DTM* days to maturity, *CP* number of capsules/plant, *CL* capsule length, *SC* number of seeds/capsule, *SW* 1000 seed weight, *SY* seed yield/plant

programmes (Fan et al. 2014; Yao et al. 2013). After comparing the nature of GCA effects of different groups, it was evident that relative magnitudes of the GCA effects of lines within each group were quite similar, with very few exceptions; similar results in pigeon pea have been reported by Saxena and Sawargaonkar (2014). Estimates of the GCA effects of the parents in F_1 generation are shown in Table 4. Although significant GCA was observed in all the traits, no parent was found having significant GCA for all the traits studied. OSC-593 and UMA were indicated as the best general combiners because they showed highly positive significant GCA effects for CP, SC and SY, and negative GCA effects for DTM indicating early maturity. These genotypes can be exploited to transfer gene in crossing programme because of favourable expression for SY and SC. Crossing between these parents would likely produce wide genetic variability of fixable nature in segregating generation and thus would offer good scope to select desirable segregating lines with higher yield.

Specific Combining Ability (SCA) Effects

SCA effects of the crosses in F_1 generation are given in Table 5. Maximum positive SCA effect for SY was observed in cross-combination of UMA × NIC-8316. Considering the SCA effects and per se performance, crosses RT-348 × TKG-352 and UMA × NIC-8316 were the top combinations. It was observed that on a pooled basis, the data of different cross-combinations for SY revealed that the crosses involved five types of parental combinations, viz. positive, significant gca effects × positive significant gca effects (H × H), positive significant gca effects × positive but insignificant gca effects (H × M or M × H), positive significant gca effects × negative gca effects (H × L or L × H), positive but insignificant gca effects × negative gca effects (M × L or L × M) and negative gca effects × negative gca effects (L × L). The H × H, type of combinations are desirable in self-pollinated crops like sesame as they involve additive and additive × additive type of interaction which is fixable in early generations and this kind of combination for SY was observed in cross-combinations UMA × NIC-8316 and UMA × OSC-593. Solanki and Gupta (2003) reported that crosses expressing high sca effects for SY and its components had parental combinations of H × L, M × L, L × M and L × L gca effects. No cross-combinations exhibited significantly positive sca effects for all the characters. It was observed that on a pooled basis, all the nine cross-combinations showing MPH showed significant and positive SCA effects for SY. Out of nine, two exhibited H × H combinations (UMA × NIC-8316 and UMA × OSC-593); four showed H × L or L × H type of combinations (TKG22 × OSC-593; GT-2 × OSC-593; OSC-593 × RT-348; RT-348 × NIC-8316); two showed H × M type of combinations (UMA × TKG-357; NIC-8316 × TKG-357); and one cross RT-348 × TKG-352 showed L × M type of combinations. Majority of the cross-combinations came under L × H, H × L type that represents at least one parent with high gca effect and thus additive effect was preponderant in the genetic control of these cross-combinations, and this would obviously lead to useful outcome of these combinations as desirable segregants;

Table 4 Estimates of general combining ability effects of yield and yield attributing traits of parents (7 × 7 diallel) across environments and pooled over environments

Traits	Environment	G1	G2	G3	G4	G5	G6	G7
PH	E1	− 4.67**	4.36**	8.778**	− 8.31**	1.25**	5.48**	− 6.88**
	E2	− 6.00**	5.15**	8.49**	− 8.23**	1.89**	6.42**	− 7.72**
	Combined	− 5.34**	4.75**	8.63**	− 8.27**	1.57**	5.95**	− 7.30**
BP	E1	− 0.19**	− 0.29**	− 0.004	− 0.05**	0.419**	0.18**	− 0.05**
	E2	− 0.171	− 0.198*	0.039	− 0.113	0.494**	0.145	− 0.196*
	Combined	− 0.18**	− 0.248**	0.017	− 0.082	0.456**	0.162**	− 0.123**
DTF	E1	0.0052	− 0.513**	0.338*	− 0.105	0.079	0.449**	− 0.253*
	E2	0.190	− 0.365	0.894**	0.450	0.339	− 0.254	− 1.254**
	Combined	0.097	− 0.439**	0.616**	0.172	0.209	0.097	− 0.754**
DTM	E1	0.058	0.280	− 0.608**	− 0.719**	0.021	0.798**	0.169
	E2	0.534	0.238	− 1.169**	− 0.206	− 0.058	0.683	− 0.021
	Combined	0.296	0.259	− 0.889**	− 0.463*	− 0.018	0.74**	0.074
CP	E1	− 2.251**	− 0.449**	− 0.165	− 5.794**	2.539**	6.298**	− 0.177
	E2	− 1.050	0.938	0.666	− 7.704**	1.513	5.352**	0.284
	Combined	− 1.65	0.244	0.250	− 6.749	2.026	5.825	0.053
CL	E1	0.041**	− 0.023**	0.091**	− 0.045**	0.057**	− 0.089**	− 0.032**
	E2	− 0.013	0.005	0.105**	− 0.064**	0.053**	− 0.079**	− 0.007
	Combined	0.014**	− 0.009	0.098	− 0.054**	0.055**	− 0.084**	− 0.019
SC	E1	− 0.455**	1.652**	1.257**	− 0.570**	0.169	− 1.190**	− 0.863**
	E2	0.161	1.046**	1.022**	− 0.559**	0.260	− 1.153**	− 0.777**
	Combined	− 0.147	1.348	1.139**	− 0.5646**	0.214**	− 1.171**	− 0.82
SW	E1	− 0.111**	− 0.063**	0.038**	0.373**	− 0.119**	− 0.153**	0.034**
	E2	− 0.087**	− 0.051**	0.059**	0.381**	− 0.108**	− 0.189**	− 0.005
	Combined	− 0.099	− 0.056**	0.048**	0.377**	− 0.113	− 0.171**	0.0143**

Table 4 continued

Traits	Environment	G1	G2	G3	G4	G5	G6	G7
SY	E1	− 0.67**	− 0.209**	0.473**	− 0.164*	0.513**	0.047	0.010
	E2	− 0.913**	− 0.256	0.201	− 0.422*	0.483**	0.448*	0.460*
	Combined	− 0.791**	− 0.232**	0.337**	− 0.293**	0.498**	0.247**	0.234

E1 Environment 1 (Nonaghata, WB), *E2* Environment 2 (Baruipur, WB), *PH* plant height, *BP* branches/plant, *DTF* days to flowering, *DTM* days to maturity, *CP* number of capsules/plant, *CL* capsule length, *SC* number of seeds/capsule, *SW* 1000 seed weight, *SY* seed yield/plant, * $P < 0.05$, ** $P < 0.01$

Table 5 Estimates of specific combining ability effects of yield and yield attributing traits of F_1 crosses (7 × 7 half diallel) of sesame across environments

Traits	Environment	G1/G2	G1/G3	G1/G4	G1/G5	G1/G6	G1/G7	G2/G3	G2/G4	G2/G5	G2/G6	G2/G7
PH	E1	1.688**	2.886**	2.112**	− 12.196**	− 13.852**	− 8.633**	− 4.210**	6.795**	5.308**	− 8.04**	− 6.46**
	E2	− 2.384	− 3.057	0.812	− 10.52**	− 12.47**	− 6.03**	− 2.295	8.35**	6.972**	− 6.34**	− 3.96**
	Combined	− 0.348	− 0.085	1.462	− 11.36**	− 13.16**	− 3.25**	7.573**	6.139**	− 7.197**	5.41**	2.06**
BP	E1	− 1.299**	− 0.619**	0.468**	− 0.016	− 0.777**	0.457**	− 0.491**	− 0.811**	0.118**	0.29**	0.558**
	E2	− 0.822**	− 0.796**	0.513	− 0.094	− 0.711**	0.596**	− 0.655**	− 0.847**	0.139	0.329	0.640**
	Combined	− 1.0605	− 0.707**	0.490**	− 0.055	− 0.744**	− 0.573**	− 0.829**	0.128**	0.3113	− 0.68**	− 0.36**
DTF	E1	1.139**	− 0.713	− 0.269*	− 1.120**	− 0.824	− 0.120	− 2.194**	0.250	− 0.602	− 0.639	− 0.602
	E2	− 0.528	− 2.454**	− 2.009**	− 2.898**	− 0.972	− 0.306**	− 3.898**	− 1.787	− 2.009	− 0.75**	− 0.417
	Combined	0.305	− 1.583	− 1.139**	− 2.00	− 0.898	− 0.21	− 3.04	− 0.768	− 1.30**	− 0.69	− 0.509
DTM	E1	− 0.731	− 0.843	0.269	− 1.139**	− 1.250**	− 0.620	− 2.065**	− 0.954	− 0.694	− 1.47**	− 0.843
	E2	− 3.463**	− 2.056	0.981	− 1.167	1.093	1.463	− 2.093	− 0.389	− 0.204	− 1.278	− 0.241
	Combined	− 2.09**	− 1.44**	0.62	− 1.15	− 0.078	0.42	− 2.07	− 0.67	− 0.44	− 1.37	− 0.54
CP	E1	− 4.133**	9.706**	− 5.141**	− 3.915**	− 12.79**	− 1.072**	16.25**	0.544**	4.643**	− 6.32**	2.24**
	E2	− 4.828	9.567**	− 3.873	− 3.863	− 15.15**	− 2.841	12.60**	− 2.040	3.843	− 3.543	4.285
	Combined	− 4.480**	9.6364**	− 4.507**	− 3.889**	− 13.97**	− 1.9562	14.4286	− 0.748	4.243**	− 4.93**	3.262**
CL	E1	− 0.017	0.252**	− 0.235**	0.276**	0.213**	0.046	0.203**	0.039	0.068**	0.08**	0.05**
	E2	− 0.060	0.206**	− 0.244**	0.275**	0.360**	0.169**	0.252**	0.118	0.154**	0.19**	0.261
	Combined	− 0.0385	0.229**	− 0.2396	0.275**	0.286**	0.107**	0.227**	0.0787	0.110**	0.14**	0.155**
SC	E1	1.898**	6.293**	− 9.00**	3.618**	4.66**	− 3.62**	4.306**	10.23**	− 6.573**	2.70**	− 1.45**
	E2	0.629	8.022**	− 7.51**	5.02**	6.117**	− 3.98**	5.487**	11.17**	− 6.276**	1.93**	− 2.27**
	Combined	1.263**	7.15**	− 8.2579	4.319**	5.38**	− 3.80**	4.896**	10.70**	− 6.424**	2.32**	− 1.86**
SW	E1	− 0.004**	− 0.511**	− 0.856**	0.046**	0.054**	− 0.317**	− 0.230**	− 0.204	− 0.049**	− 0.001	− 0.44**
	E2	− 0.066	− 0.566**	− 0.91**	− 0.005	0.072	− 0.308**	− 0.252**	− 0.257	− 0.041	− 0.064	− 0.49**
	Combined	− 0.0346	− 0.538**	− 0.883**	0.02037	0.0629	− 0.31**	− 0.240**	− 0.2307	− 0.0453	− 0.032	− 0.46**

Table 5 continued

Traits	Environment	G1/G2	G1/G3	G1/G4	G1/G5	G1/G6	G1/G7	G2/G3	G2/G4	G2/G5	G2/G6	G2/G7
SY	E1	− 0.938**	1.889**	− 3.17**	− 1.061**	− 1.631**	− 2.654**	2.918**	− 1.861**	− 1.101**	− 0.56**	− 1.79**
	E2	0.091	2.644**	− 2.263**	− 0.049	− 1.383	− 2.122**	4.07**	− 0.517	− 0.376	− 0.623	− 1.339
	Combined	− 0.4238	2.266**	− 2.716**	− 0.5546	− 1.507**	− 2.387**	3.497**	− 1.188**	− 0.738**	− 0.5927	− 1.56**

Traits	Environment	G3/G4	G3/G5	G3/G6	G3/G7	G4/G5	G4/G6	G4/G7	G5/G6	G5/G7	G6/G7
PH	E1	4.597**	1.193**	− 12.40**	− 5.01**	− 10.8**	− 8.66**	− 0.06**	9.259**	2.641**	1.122**
	E2	6.224**	2.929	− 11.630	− 2.469	− 8.49**	− 7.25**	4.117**	10.22**	3.93**	4.45**
	Combined	− 12.01**	− 9.68**	− 7.95**	9.74**	− 7.33**	− 5.21**	− 3.73**	2.02**	3.28**	2.78**
BP	E1	− 0.725**	− 0.40**	0.023	0.261	− 0.09**	0.173**	0.318**	1.306**	− 0.19**	0.11**
	E2	− 0.647**	− 0.321	0.209	0.433	0.078	0.154	0.171	1.080	− 0.569	− 0.186
	Combined	− 0.68**	− 0.36**	0.11	0.34**	− 0.010	0.16	0.24	1.19**	− 0.38**	− 0.03
DTF	E1	− 1.602**	2.213**	− 1.157**	− 1.12**	− 1.34**	− 0.713	− 0.009	− 1.89**	− 2.19**	− 1.56**
	E2	− 2.04**	1.065	− 2.34**	− 2.00**	− 2.49**	− 0.898	− 0.898	− 2.78**	− 2.78**	− 0.528
	Combined	− 1.82	1.63	− 1.75	− 1.56	− 1.91	− 0.80	− 0.45	− 2.34	− 2.49	− 1.04
DTM	E1	− 1.398**	− 2.80**	− 2.583**	− 1.28**	− 1.69**	− 1.80**	− 1.84**	− 0.546	0.417	− 1.69**
	E2	− 1.315	− 2.463	− 3.870	− 2.167	− 2.759	− 1.500	− 1.130	1.019	0.722	− 2.019
	Combined	− 1.35	− 2.63	− 3.22	− 1.72	− 2.22	− 1.65	− 1.48	0.23	0.56	− 1.85
CP	E1	− 0.188	4.002**	− 11.06**	− 7.09**	− 5.11**	− 0.14**	5.455**	27.51**	0.034	5.292**
	E2	5.117	3.091	− 13.385	− 11.823	− 5.623	0.941	5.463	29.711	3.493	11.004
	Combined	2.4649	3.5464	− 12.2229	− 9.4573	− 5.370	0.4001	5.459	28.6116	1.7638	8.1479
CL	E1	0.252**	− 0.19**	− 0.014*	− 0.07**	0.006	0.189**	0.095**	0.070**	− 0.044	0.209**
	E2	0.431**	0.064	− 0.058	− 0.046	0.033	0.215	0.091	0.058	− 0.114	0.158
	Combined	0.341**	− 0.063	− 0.03574	− 0.06	0.0194	0.202	0.09278	0.06389	− 0.0787	0.1839

Table 5 continued

Traits	Environment	G3/G4	G3/G5	G3/G6	G3/G7	G4/G5	G4/G6	G4/G7	G5/G6	G5/G7	G6/G7
SC	E1	10.81**	2.226**	− 4.572**	− 0.682	1.176**	4.942**	4.168**	10.59**	4.026**	1.415**
	E2	9.699**	1.470	− 5.054	− 1.213	0.396	4.584	4.502	10.896	5.753	3.932
	Combined	10.25**	1.848	− 4.8131	− 0.9477	0.7858	4.763	4.335	10.7441	4.8895	2.6734
SW	E1	− 0.052**	− 0.13**	− 0.586**	0.331**	− 0.14**	0.173**	0.326**	0.061**	− 0.042	0.013
	E2	− 0.154	− 0.091	− 0.648	0.302	− 0.156	0.147	0.367	− 0.077	− 0.114	− 0.024
	Combined	− 0.103	− 0.110	− 0.6167	0.3163	− 0.150	0.1602	0.3465	− 0.007	− 0.078	− 0.0055
SY	E1	1.424**	0.266*	− 4.698**	− 0.77**	− 1.77**	2.12**	3.24**	4.97**	2.30**	1.242**
	E2	2.803	1.178	− 4.187	− 0.709	− 1.089	2.200	3.514	5.074	2.385	0.827
	Combined	2.1134	0.7219	− 4.4424	− 0.7431	− 1.432	2.1597	3.3773	5.0265	2.3458	1.0349

E1 Environment 1 (Nonaghata, WB), *E2* Enviornment 2 (Baruipur, WB), *PH* plant height, *BP* branches/plant, *DTF* days to flowering, *DTM* days to maturity, *CP* number of capsules/plant, *CL* capsule length, *SC* number of seeds/capsule, *SW* 1000 seed weight, *SY* seed yield/plant; * $P < 0.05$, ** $P < 0.01$

being additive in nature, they were early fixable and might lead to evolve high yielding varieties.

Analysis of Heterosis

The variation patterns of MPH and BPH over environments were very similar in nature. Environment was the major source of variation contributing to the total sum of squares followed by genotype, and G x E interaction factor. On comparing with the average parents yield (12.57 g plant^{-1}), eight hybrids (38.09%) had a significant ($P < 0.01$) yield advantage over their parents in both the environments, with an average of 26.94% and a range of − 28.26–47.7% for BPH; and an average of 29.99% and a range of − 27.00 to 55.84% for MPH in both the environments. Comparatively high MPH and BPH were observed in the environments 1 (Supplementary Table 3 and 4). The inter-group hybrids had significantly ($P < 0.001$) higher yield and yield heterosis than the intra-group hybrids. Among the nine hybrids that showed significant high MPH and BPH (> 10% of the average yield), seven were from inter-group and two from intra-group crossing based on GD_{SSR}. The hybrids in the G3 and G1 group had the highest SY plant^{-1}, heterosis for SY and combining ability amongst the hybrid groups, followed by the G2 hybrid group. The parents involved in those nine heterotic hybrids were mainly from the groups of G3 (56.25%), G1 (25.0%) and G2 (18.75%). The parent UMA had the highest GCA for SY followed by OSC-593 and NIC-8316, and they belong to the group G3 (Table 6). Among the individual hybrid groups, the highest yielding hybrid group was an intra-cluster cross of UMA × NIC-8316 (G-IIIB × G-IIIA) which produced 18.95 g plant^{-1}, significantly ($P < 0.01$) higher than the yields of other 20 hybrids. The G-IIB × G-IA hybrid group was the second highest yielding group which produced 16.50 g plant^{-1} (significant at $P < 0.01$).

Table 6 Description of eight cross-combinations showing better-parent heterosis for seed yield plant^{-1}

Cross-combination (♀/♂)	% BPH	% MPH	GD_{SSR}	Mean seed yield plant^{-1}	Group based on GD_{SSR} for ♀ parent	Group based on GD_{SSR} for ♂ parent
TKG22/OSC-593	26.93	32.28	0.24138	16.78	IA	IIIB
OSC-593/RT-348	26.26	30.06	0.34483	15.34	IIIB	IIB
OSC-593/UMA	21.32	24.70	0.17241	14.74	IIIB	IIIB
RT-348/NIC-8316	19.17	26.00	0.20690	15.29	IIB	IIIA
RT-348/TKG-352	30.74	37.17	0.27586	16.50	IIB	IA
UMA/NIC-8316	47.70	55.84	0.24138	18.95	IIIB	IIIA
UMA/TKG-352	28.84	34.88	0.24138	16.26	IIIB	IA
NIC-8316/TKG-352	14.58	15.52	0.27586	14.70	IIIA	IA

Correlation Between Heterosis and Genetic Divergence

Parental genetic diversity and combining ability along with per se performance have been effectively exploited to develop higher frequencies of heterotic hybrids in several crops (Betran et al. 2003). Further, advances in genome researches have raised the interest in predicting heterotic groups using molecular markers (Krystkowiak et al. 2009). Heterosis in relation to genetic divergence had been studied earlier in many crops, although in sesame, information is inadequate. Highly significant positive correlations were observed between SCA and per se performance of hybrids (0.97), while showing positive non-significant correlation with GD_{SSR} (0.048) but non-significant negative correlation with GD_{MOR} (− 0.01) and GD_{SDS} (− 0.256) (Supplementary Table 2). Results showed that positive non-significant correlation was found in GD_{SSR} with SCA (0.154) and hybrid performance for SY (0.108). Similar trends were found for MPH and other traits except for GD_{MOR} where positive non-significant correlation was observed (0.051). The linear regressions of GD_{SSR} on SCA, BPH and MPH were non-significant with R^2 value of 0.030, 0.0018 and 0.0031, respectively. Similar linear regression was observed for GD_{SDS} on BPH (0.038), MPH (0.032), SCA (0.085) and GD_{MOR} on BPH (0.049), MPH (0.057) and SCA (0.010). The mean performance of F_1s was little influenced by GD_{MOR} (0.089), GD_{SDS} (0.014) and GD_{SSR} (0.013) as evidenced from non-significant regression. The linear regressions of SCA on MPH, BPH and per se performance of F_1s were significant with R^2 value of 0.88, 0.84 and 0.95, respectively (Fig. 4a, d, e,). The MPH and BPH also established significant positive associations as well as linear regressions with per se performance of the hybrids along with R^2 value of 0.96 and 0.94, respectively (Fig. 4b, c). The present study strongly indicates that SCA is a main determinant of heterosis, as well as of F_1 performance and can be used consistently in the selection of parents (Hallauer and Miranda Filho 1988). Non-significant linear regression of heterosis for grain dry weight with mean performance of hybrids on GD has been reported by Shieh and Thseng (2002). The extents of correlation coefficients found between GD_{SSR} with BPH and MPH in the present study were not large enough for the prediction of hybrid performance in sesame as earlier reported by Banerjee and Kole (2010). Similar results with weak correlation have been reported in many crops (Oliveira et al. 2004). There can be many plausible reasons behind the weak correlation of GD_{SSR} with hybrid performance and heterosis; Some of the reasons could be lack of linkage between genes controlling the traits under study, inadequate genome coverage, and random marker distribution and diversified effect of dominance (Bernardo 1992). Bernardo (1992) suggested that prediction of hybrid through markers would be possible only if a significant number of markers were linked with QTL. In the present study, SSR grouping of the hybrids into different clusters are in agreement with their pedigree records signifying the efficiency of SSR marker for diversity analysis and clustering analysis. The cross-combinations from parents with intermediate genetic diversity group were more often heterotic than those obtained from parents with high levels of genetic divergence between them (Supplementary Table 2). The present investigation suggests that parental divergence in the intermediate group, i.e., being neither low nor high, would likely generate high

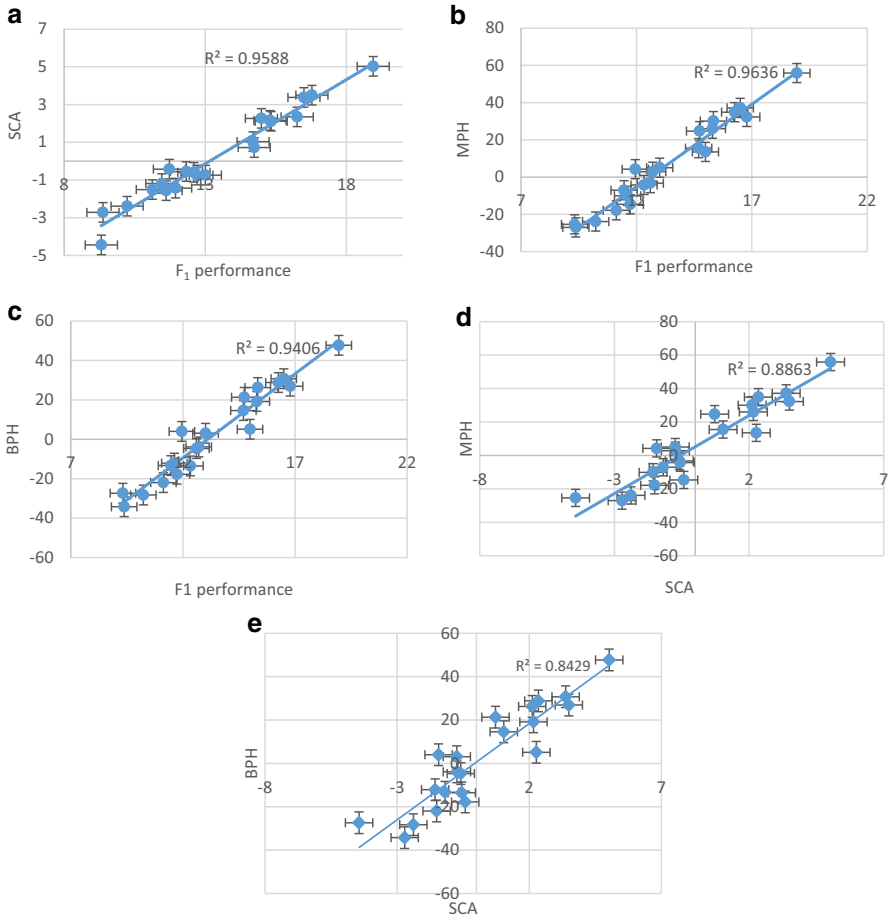

Fig. 4 Relationship between SCA and F_1 performance (**a**), per se performance of F_1 with MPH (**b**), per se performance of F_1 with BPH in sesame (**c**), SCA with BPH in sesame (**d**), and SCA with MPH in sesame (**e**)

heterotic crosses for SY in sesame irrespective of GD_{SSR}, GD_{MOR} and GD_{SDS}. The extent of parental divergence as predictive estimates of heterosis was studied earlier by many researchers in different crops like chilli (Geleta et al. 2004); maize (Ndhlela et al. 2015); wheat (Krystkowiak et al. 2009); and groundnut (Arunachalam et al. 1984).

Conclusion

Based on the present findings, we conclude that genetic distances, based on SSR marker, agro-morphological traits or seed-storage profile, were not efficient for the prediction of heterosis in sesame. Nevertheless, SSR-based clusters are in

accordance with their pedigree records signifying the efficacy of SSR marker for diversity analysis and clustering analysis. SCA, on the other hand, has appeared as the utmost important factor in the determination of heterosis and per se performance of the hybrids in sesame. In accordance with the earlier reports, weak correlation was observed in the present study which is not useful for predicting hybrid performance in sesame (Zhang et al. 1995; Ndhlela et al. 2015). However, this study also suggests that parental divergence in the intermediate group would like to generate high heterotic crosses for seed yield/plant in sesame as reported in other crops (Geleta et al. 2004).

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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