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Gene effects for oil content and other quantitative traits in soybean [*Glycine max* (L.) Merrill]

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Abstract

Six parental lines i.e., four cultivars and two promising lines of soybean [*Glycine max* (L.) Merrill] were crossed in four combinations to develop F_1, F_2 and F_3 hybrid progenies. Five generations viz., P_1, P_2, F_1, F_2 and F_3 were grown in an experiment under compact family block design to estimate the gene effects for oil content and other quantitative traits. Additive and dominance gene effects were important in determining inheritance of seed oil content in all the four crosses. Complementary epistasis was important for oil content in 'MACS 684' × 'RSC 1' and in 'PK 472' × 'RSC 2'. Additive gene effects also determined inheritance of, days to 50 % flowering, days to maturity, plant height, clusters/plant, biomass and harvest index. Dominance gene action was critical in determining the yield and oil content. Duplicate epistasis were significantly important in inheritance of plant height, no. of branches per plant, clusters per plant, pods/plant, no. of seeds per plant, plant biomass, 100 seed weight and yield per plant.

Key words : Soybean, gene effect, epistasis, inheritance

Introduction

Soybean [*Glycine max* (L.) Merrill] is a major oilseed crop in the world. In India, now it ranks second in oilseeds after groundnut surpassing the rapeseed mustard [1]. Demand for soybean is increasing for its seed oil, proteins and various soy-products. To increase oil content and yield, recurrent selection method is mostly suggested [2,3]. Most of the reports for gene action in soybean are based on the diallel or half diallel set and *gca/sca* analysis [4-7]. Taledo *et al.* [8] suggested that the five parameter model was as good as the back cross studies for estimation of gene effects and gives satisfactory results. Lal and Rana [9] suggested that soybean cultivars should be developed based on '*plant ideotype concept*' for different agro-climatic zones to improve yield potential. In the development of new elite varieties the released varieties have been extensively used [9]. Basic requirement in adopting a suitable breeding method is a sound understanding of the genetic behaviour. Therefore, success in development of genotypes with desired characters depend on the knowledge of genetic make up of the characters and their behaviour in different genetic backgrounds. Hence, a study was conducted to determine the gene effects for oil content, yield and other quantitative characters in four crosses of soybean.

Materials and methods

Six soybean cultivars, *viz.*, 'MACS 124' (high yielding, low oil content), 'RSC 1' (high yield, better oil content), 'RSC 2' (high yield, better oil content), 'PK 472' (short, better harvest index), 'MACS 629' (high yield, high oil content), and 'MACS 684' (high oil content) were selected on the basis of agronomic performance. Four combinations, *viz.*, 'MACS 684' × 'MACS 124', 'MACS 684' × 'RSC 1', 'PK 472' × 'MACS 629', and 'PK 472' × 'RSC 2' were made in rainy season of 1999. Five generations *viz.*, P_1, P_2, F_1, F_2, and F_3 were developed in subsequent *kharif* as well as summer seasons.

A trial with five generations, *viz.*, P_1, P_2, F_1, F_2, and F_3 was raised during 2001 rainy season at Agharkar Research Institute's Experimental Farm at Hol, Dist., Pune, Maharashtra State. Experiment was laid down in compact family block design with three replications. Seeds were sown in 3 m long rows at 0.05 m depth and spacing between and within rows was 0.45 m × 0.05 m. Parents were represented by two rows, F_1s by one row, F_2s by 4 rows and the F_3s by 20 rows. Standard cultivation practices were followed as per recommendation. Observations were recorded on 5 randomly selected plants per row for 15 quantitative characters.

ANOVA was performed as per Panse and Sukhatme [10] for each generation in each cross. The scale tests 'C' and 'D' [11] were applied to test the presence or absence of non-allelic interaction. Joint scaling test was applied to confirm the presence of interactions and estimate the m, d and h parameters. The gene effects were estimated by five parameter model of Hayman [12] in only those crosses, where joint scaling test showed presence of epistatic interactions.

Results and discussion

The mean squares from trial's ANOVA presented in Table 1, showed that, there were significant differences among generations. The estimates of 'C' and 'D' scaling tests and gene effects from five parameter model are presented in the Table 3. The joint scaling test revealed that, additive dominance model was sufficient to explain inheritance of oil content in 'MACS 684' × 'MACS 124' and 'PK 472' × 'MACS 629', for yield in 'MACS 684' × 'MACS 124' and for 100 seed weight in 'MACS 684' × 'RSC 1' and 'PK 472' × 'RSC 2'.

Generation means (Table 2) for oil content differ significantly within crosses in all combinations. For oil content, additive and dominance gene effects and additive × additive epistatic interaction were important. Additive and dominance gene effects were significant in all the crosses for oil content. In 'MACS 684' × 'MACS 124' and 'PK 472' × 'MACS 629' additive-dominance model was adequate to explain inheritance of oil content. Among non-allelic interactions, both, additive × additive and dominance × dominance epistatic interactions were significant in 'PK 472' × 'RSC 2', while only additive × additive genic interaction was significant in 'MACS 684' × 'RSC 1'. As the estimates of 'h' and 'l' were significant and in the same direction, there was complementary epistasis for oil content in 'MACS 684' × 'RSC 1' and 'PK 472' × 'RSC 2'. Zhu *et al.* [13] reported additive gene effects responsible for inheritance of oil content. Duplicate epistasis was reported to be important as well as type of interaction was also present for oil content [14]. Sharma et al., [6] showed that, dominance gene effects were more important than additive gene effects for oil content. Additive gene action has been reported as the main component for genetic variance for seed oil content in soybean [15]. Additive × additive epistatic interaction was reported important in the genetics of oil content [14, 16-17]. Chauhan and Singh [4] observed significant partial dominance for oil content. Complementary epistasis present in 'MACS 684' × 'RSC 1' and 'PK 472' × 'RSC 2' may be useful for further exploitation of gene effects for improvement in oil content.

Dominance gene effects were important in inheritance of yield in 'MACS 684' × 'RSC 1', 'PK 472' × 'MACS 629' and 'PK 472' × 'RSC 2', while the additive gene effects were significant in 'PK 472' × 'MACS 629' and 'PK 472' × 'RSC 2'. Additive × additive epistatic interaction was significant in all the crosses except in 'MACS 684' × 'MACS 124', where the non-allelic interactions were absent. In 'PK 472' × 'MACS 629' all the genetic estimates were highly significant for yield. Since, the estimates of 'h' and 'l'were significant and in opposite direction there was duplicate epistasis in 'MACS 684' × 'RSC 1' and 'PK 472' × 'MACS 629' for yield. The overall governance of yield per plant in soybean was by both, dominance and additive × additive gene effects. For seed yield, dominance gene effects were reported to be important [7, 18-19]. Raut *et al.* [14] observed the complementary epistasis for grain yield in soybean.

Additive gene effects were significantly important in, inheritance of days to 50 % flowering, days to maturity, plant height, clusters/plant and 100 seed weight with strong dominance genetic interactions. Additive gene effects were also reported important for these characters [5-6, 16, 19-21]. Dominance gene effects were significant for days to 50 % flowering, plant height, branches/plant, clusters/plant, pods/plant, seeds/plant, above ground biomass, harvest index and 100 seed weight in nearly all the crosses with few exceptions. Dominance gene effects were also reported for pods/plant, seeds/plant and grain yield [7, 18-19]. Complementary epistasis was reported for pods/plant [14].

Dominance × dominance interaction significantly contributed for days to 50 % flowering, days to maturity and nodes on main stem in 'PK 472' × 'MACS 629' and for plant height, branches/plant, clusters/plant, pods/plant, seeds/plant, biomass and harvest index in 'MACS 684' × 'RSC 1' and 'PK 472' × 'MACS 629'. In 'MACS 684' × 'MACS 124', '*l*' interaction was significant for days to maturity, main stem nodes, branches/plant, clusters/plant and 100 seed weight. For most of the above mentioned characters and crosses, there was duplicate epistasis contributing strongly to the particular characters. Kaw and Menon [22] reported that there was significant association of pods/plant, seeds/plant, plant height and maturity with the seed yield/plant and number of pods and maturity contribute the most to yield/plant.

Additive × additive interaction played significant role in the inheritance of days to maturity, plant height and clusters/plant in all the crosses. This interaction was also important for seeds/plant and biomass in 'MACS 684' × 'RSC 1', 'PK 472' × 'MACS 629' and 'PK 472' × 'RSC 2'. Li *et al.* [19] reported the same results. They also suggested that additive gene effects were important to determine nodes/plant, branches/plant and 100 seed weight.

Highly significant additive gene effects, additive × additive epistatic interaction and complementary epistasis for oil content can be exploited to develop the soybean cultivars with desired oil content and other

Table 1. Analysis of variance (Mean squares) for 15 characters in four crosses and five generations as per compact family block design

Between crosses			Between generations within crosses					
					Mean squares within crosses			
Source	D. F.	M. S.	Source	D. F.	Cross I	Cross II	Cross III	Cross IV
			Days to 50 % flowering					
Replications	2	0.577	Replications	2	9.786**	5.205*	0.813	1.605
Crosses	3	1.297	Generations	4	1.755	3.640*	27.389**	4.373**
Error	6	0.968	Error	8	0.877	0.841	1.076	0.483
			Days to maturity					
Replications	2	1.956*	Replications	2	0.476	3.520	3.773	6.947
Crosses	3	10.046**	Generation	4	16.728*	13.581	23.394*	16.745
Error	6	0.329	Error	8	2.391	3.897	4.239	4.569
			Plant height					
Replications	2	4.658	Replications	2	76.305	34.085	2.549	7.896
Crosses	3	188.439**	Generations	4	44.909	429.417*	185.509**	180.690**
Error	6	6.996	Error	8	133.681	99.361	23.903	19.134
			Nodes on main stem					
Replications	2	0.104	Replications	2	1.009	0.533	0.357	0.921
Crosses	3	3.683**	Generations	4	1.387	0.211	3.180**	4.400**
Error	6	0.153	Error	8	3.037	0.323	0.270	0.459
			Branches per plant					
Replications	2	0.240	Replications	2	1.461	0.358	0.338	0.373
Crosses	3	0.254	Generations	4	0.592	1.415	2.083**	2.500*
Error	6	0.089	Error	8	0.501	0.573	0.269	0.498
			Clusters per plant					
Replications	2	0.200	Replications	2	2.872	1.069	0.715	5.317
Crosses	3	6.495**	Generations	4	9.139	16.266	60.429**	26.311'
Error	6	0.598	Error	8	10.351	6.417	6.334	8.136
			Pods per cluster					
Replications	2	0.019	Replications	2	0.037	0.245**	0.395**	0.039
Crosses	3	0.027	Generations	4	0.027	0.090*	0.086	0.054
Error	6	0.042	Error	8	0.020	0.023	0.033	0.016
			Pods per plant					
Replications	2	17.576	Replications	2	49.622	31.643	89.728	67.352
Crosses	3	78.579*	Generations	4	57.982	233.310	717.684**	244.269
Error	6	10.761	Error	8	106.951	69.349	77.720	84.043
			Seeds per pod					
Replications	2	0.001	Replications	2	0.015	0.009	0.001	0.015
Crosses	3	0.012	Generations	4	0.004	0.008	0.041**	0.021
Error	6	0.003	Error	8	0.019	0.011	0.004	0.013
			Seeds per plant					
Replications	2	72.444	Replications	2	435.196	168.991	381.422	474.127
Crosses	3	322.867	Generations	4	120.955	933.631*	2805.436**	801.320
Error	6	73.177	Error	8	499.178	211.752	211.839	337.678
			Biomass					
Replications	2	5.957	Replications	2	47.016	7.080	29.558	25.797
Crosses	3	13.761	Generations	4	10.101	45.994*	210.593*	63.004
Error	6	5.312	Error	8	29.867	11.265	30.292	24.545
			Harvest index					
Replications	2	11.316**	Replications	2	27.381*	1.566	28.080	3.892
Crosses	3	9.354**	Generations	4	10.552	16.449**	18.214	16.409*
Error	6	0.772	Error	8	3.541	2.164	7.364	3.342
			Oil content					
Replications	2	0.269**	Replications	2	0.108	0.847**	0.453**	0.326*
Crosses	3	0.672**	Generations	4	4.706**	0.531	1.809**	4.207**
Error	6	0.020	Error	8	0.090	0.073	0.051	0.046
			100 seed weight					
Replications	2	0.235**	Replications	2	0.155	0.385	0.382	0.446
Crosses	3	4.580**	Generations	4	3.501**	2.124	1.655	0.141
Error	6	0.013	Error	8	0.335	0.947	0.692	0.386
			Yield per plant					
Replications	2	0.848	Replications	2	7.798	2.472	5.837	10.786
Crosses	3	5.606	Generations	4	1.334	11.140	60.250**	15.475
Error	6	1.510	Error	8	9.291	3.975	6.142	7.332

*,** Significant at 5 % and 1 % levels respectively. Cross I = 'MACS 684' × 'MACS 124' Cross II = 'MACS 684' × 'RSC 1', Cross III = 'PK 472' × 'MACS 629' and Cross IV = 'PK 472' × 'RSC 2'

Table 2. Means for five generations for quantitative characters in four crosses of soybean

Cross	Generations				
	P_1	P_2	F_1	F_2	F_3
		Days to 50 % flowering			
'MACS 684' × 'MACS 124'	43.03	44.20	44.47	43.47	42.88
'MACS 684' × 'RSC 1'	42.83	45.30	43.47	42.95	42.55
'PK 472' × 'MACS 629'	39.83	46.83	41.47	46.25	43.33
'PK 472' × 'RSC 2'	40.80	44.13	42.33	41.88	42.05
		Days to maturity			
'MACS 684' × 'MACS 124'	87.83	93.73	91.27	88.87	89.05
'MACS 684' × 'RSC 1'	90.97	95.53	91.93	90.43	90.53
'PK 472' × 'MACS 629'	90.73	98.27	94.13	95.98	93.81
'PK 472' × 'RSC 2'	92.60	94.60	95.07	90.72	89.65
		Plant height (cm)			
'MACS 684' × 'MACS 124'	62.33	66.20	60.47	67.13	70.15
'MACS 684' × 'RSC 1'	61.83	60.23	54.53	55.68	63.94
'PK 472' × 'MACS 629'	36.40	57.63	52.20	46.45	48.40
'PK 472' × 'RSC 2'	39.30	59.53	55.60	49.40	47.90
		Nodes on main stem			
'MACS 684' × 'MACS 124'	13.13	12.57	12.67	14.12	13.78
'MACS 684' × 'RSC I'	13.20	12.80	12.73	13.28	12.75
'PK 472' × 'MACS 629'	9.80	11.93	12.27	11.80	10.66
'PK 472' × 'RSC 2'	9.37	12.77	11.27	11.23	10.90
		Branches per plant			
'MACS 684' × 'MACS 124'	4.03	3.70	2.93	3.95	3.44
'MACS 684' × 'RSC 1'	4.10	3.03	4.47	4.47	3.22
'PK 472' × 'MACS 629'	3.40	3.80	3.87	5.57	4.07
'PK 472' × 'RSC 2'	2.53	2.93	3.07	4.17	4.70
		Clusters per plant			
'MACS 684' × 'MACS 124'	16.60	14.00	14.67	18.37	16.68
'MACS 684' × 'RSC I'	17.27	15.53	18.87	20.95	15.48
'PK 472' × 'MACS 629'	11.57	16.10	16.13	23.87	15.18
'PK 472' × 'RSC 2'	9.93	16.23	12.13	15.38	16.87
		Pods per cluster			
'MACS 684' × 'MACS 124'	2.71	2.94	2.72	2.76	2.74
'MACS 684' × 'RSC 1'	2.90	2.95	2.67	3.15	2.98
'PK 472' × 'MACS 629'	3.10	2.79	3.26	3.12	3.07
'PK 472' × 'RSC 2'	3.02	2.86	2.73	2.98	3.05
		Pods per plant			
'MACS 684' × 'MACS 124'	45.57	41.60	41.00	52.02	45.55
'MACS 684' × 'RSC 1'	49.33	45.13	53.00	66.85	46.06
'PK 472' × 'MACS 629'	35.27	44.97	51.67	76.52	46.33
'PK 472' × 'RSC 2'	29.80	46.10	34.07	45.47	51.34
		Seeds per pod			
'MACS 684' × 'MACS 124'	1.99	1.99	2.05	1.95	1.97
'MACS 684' × 'RSC 1'	1.96	2.02	2.08	2.07	2.08
'PK 472' × 'MACS 629'	1.73	1.87	2.05	1.85	1.94
'PK 472' × 'RSC 2'	1.88	1.93	2.09	1.99	1.90
		Seeds per plant			
'MACS 684' × 'MACS 124'	88.87	81.97	86.40	99.25	88.95
'MACS 684' × 'RSC 1'	97.50	91.00	108.40	134.52	94.51
'PK 472' × 'MACS 629'	60.23	83.53	104.13	142.83	89.43
'PK 472' × 'RSC 2'	56.00	88.53	72.80	89.93	96.49
		Biomass (kg × 10^{-3})			
'MACS 684' × 'MACS 124'	20.30	23.97	20.37	23.79	23.17
'MACS 684' × 'RSC 1'	20.62	22.17	22.68	30.45	21.93
'PK 472' × 'MACS 629'	14.86	23.51	28.96	37.85	24.84
'PK 472' × 'RSC 2'	13.92	22.99	19.21	22.99	25.78
		Harvest index (%)			
'MACS 684' × 'MACS 124'	54.60	52.49	56.90	53.11	52.30
'MACS 684' × 'RSC 1'	55.73	57.32	60.06	53.99	55.18
'PK 472' × 'MACS 629'	61.26	55.43	59.39	55.74	57.82
'PK 472' × 'RSC 2'	60.43	55.99	57.02	57.78	54.90
		Oil content (%)			
'MACS 684' × 'MACS 124'	21.24	17.82	20.32	19.87	19.69
'MACS 684' × 'RSC 1'	20.97	20.34	20.67	20.07	19.96
'PK 472' × 'MACS 629'	18.49	20.56	20.12	19.76	19.52
'PK 472' × 'RSC 2'	18.61	20.61	20.46	18.40	18.17
		100 seed weight (kg × 10^{-3})			
'MACS 684' × 'MACS 124'	12.50	15.29	13.23	12.90	13.69
'MACS 684' × 'RSC 1'	12.01	14.20	12.61	12.33	12.88
'PK 472' × 'MACS 629'	14.90	15.55	16.46	14.68	16.01
'PK 472' × 'RSC 2'	14.99	14.55	15.11	14.90	14.76
		Yield per plant (kg ×10^{-3})			
'MACS 684' × 'MACS 124'	11.01	12.46	11.49	12.59	12.06
'MACS 684' × 'RSC 1'	11.38	12.82	13.63	16.33	12.01
'PK 472' × 'MACS 629'	8.88	12.98	16.97	20.88	14.26
'PK 472' × 'RSC 2'	8.39	12.84	11.04	13.22	14.12

Table 3. Estimates of scaling test and gene effects for 15 characters in four crosses of soybean.

Cross	Scaling Test		Genetic parameter					Type of epistasis
	C	D	m	d	h	I	I	C/D
Days to 50% flowering								
'MACS 684' × 'MACS 124'	-2.30*	-2.65*	43.47	-0.58**	2.23**	-0.46	0.22	D
'MACS 684' × 'RSC 1'	-3.27*	-3.82*	42.95	-1.23**	1.40**	-0.74	-0.46	D
'PK 472' × 'MACS 629'	15.40*	-5.84*	46.25	-3.50**	4.60**	-28.32**	-5.13**	D
'PK 472' × 'RSC 2'	-2.07*	-0.50	41.88	-1.67**	-0.15	2.09	-3.35**	D
Days to maturity								
'MACS 684' × 'MACS 124'	-8.63*	-3.09*	88.87	72.95**	1.10	7.39*	-5.28**	C
'MACS 684' × 'RSC 1'	-8.63*	-5.26*	90.43	-2.28**	0.75	4.50	-2.50*	C
'PK 472' × 'MACS 629'	6.67*	-5.73*	95.98	-3.77**	4.56**	-16.53**	-7.17**	D
'PK 472' × 'RSC 2'	-14.47*	-10.05*	90.72	-1.00**	5.75**	5.89	2.29	C
Plant height (cm)								
'MACS 684' × 'MACS 124'	19.07*	17.81	67.13	-1.93**	-12.50**	-1.67	-12.57**	C
'MACS 684' × 'RSC 1'	-8.40	22.34*	55.68	0.80	-22.79**	40.99**	-14.69**	D
'PK 472' × 'MACS 629'	-12.63*	6.65*	46.45	-10.62**	-1.36	25.71**	-26.42**	D
'PK 472' × 'RSC 2'	-12.43*	-6.05*	49.40	-10.12**	5.14**	8.52	-18.28**	C
Nodes on main stem								
'MACS 684' × 'MACS 124'	5.43*	1.17	14.12	0.28	-0.06	-5.68*	0.69	C
'MACS 684' × 'RSC 1'	1.67	-1.55*	13.28	0.20	1.05	-4.29*	1.71*	D
'PK 472' × 'MACS 629'	0.93	-2.71	11.80	-1.07**	3.37**	-4.86**	-3.53**	D
'PK 472' × 'RSC 2'	0.26	-0.99	10.86	-1.56*	0.39	-	-	-
Branches per plant								
'MACS 684' × 'MACS 124'	2.20*	-1.87*	3.95	0.167	0.68	-5.43**	1.95**	D
'MACS 684' × 'RSC 1'	1.80	-3.19*	4.47	0.53**	3.33**	-6.65**	3.49**	D
'PK 472' × 'MACS 629'	7.33*	-2.06*	5.57	-0.20	2.86**	-12.53**	-0.67	D
'PK 472' × 'RSC 2'	5.07*	5.01*	4.17	-0.20	-2.16**	-0.08	-2.90**	C
Clusters per plant								
'MACS 684' × 'MACS 124'	13.53*	-0.60	18.37	1.30**	2.02	-18.85**	5.26*	D
'MACS 684' × 'RSC 1'	13.27*	-12.77*	20.95	0.87	13.19**	-34.71**	12.46**	D
'PK 472' × 'MACS 629'	35.54*	-14.68*	23.87	-2.27**	18.01**	-66.95**	-6.83*	D
'PK 472' × 'RSC 2'	11.10*	10.54*	15.38	-3.15**	-6.12**	-0.75	-11.47**	C
Pods per cluster								
'MACS 684' × 'MACS 124'	-0.06	-0.20	2.78	-0.12	-0.10	-	-	-
'MACS 684' × 'RSC 1'	1.41*	-0.22	3.15	-0.03	0.13	-2.18**	0.33	D
'PK 472' × 'MACS 629'	0.08	0.13	2.98	-0.17	0.29	-	-	-
'PK 472' × 'RSC 2'	0.57	0.38	2.98	0.08	-0.37*	-0.24	0.00	-
Pods per plant								
'MACS 684' × 'MACS 124'	38.90*	-9.00	45.01	-2.21	1.52	-	-	-
'MACS 684' × 'RSC 1'	66.93*	-43.94*	66.85	2.10	46.22**	-147.83**	44.65**	D
'PK 472' × 'MACS 629'	122.50*	-47.94*	76.52	-4.85**	63.93**	-227.26**	-21.25	D
'PK 472' × 'RSC 2'	37.83*	38.51*	45.47	-8.15**	-23.25**	0.91	-35.67**	D
Seeds per pod								
'MACS 684' × 'MACS 124'	-0.28	-0.02	1.96	-0.00	0.04	-	-	-
'MACS 684' × 'RSC 1'	0.13	0.20	2.04	-0.04	-0.08	-	-	-
'PK 472' × 'MACS 629'	-0.19	0.41*	1.88	-0.07*	-0.06	0.81**	-0.39**	D
'PK 472' × 'RSC 2'	-0.05	-0.20	1.86	-0.01	0.20	-	-	-
Seeds per plant								
'MACS 684' × 'MACS 124'	53.37	-13.53	86.72	-3.70	8.97	-	-	-
'MACS 684' × 'RSC 1'	132.77*	-79.48*	134.52	3.25	89.27**	-283.00**	81.62**	D
'PK 472' × 'MACS 629'	219.30*	-71.70*	142.83	-11.65**	116.60**	-388.00**	-55.55*	D
'PK 472' × 'RSC 2'	69.60*	61.56*	89.93	16.27**	-28.91**	-10.72	-61.97**	C
Biomass (kg × 10^{-3})								
'MACS 684' × 'MACS 124'	10.14	0.83	22.88	-1.95	0.25	-	-	-
'MACS 684' × 'RSC 1'	33.67*	-15.99*	30.45	-0.78	17.56**	-66.21**	14.72**	D
'PK 472' × 'MACS 629'	55.13*	-14.72*	37.86	-4.32**	28.77**	-93.12**	-18.42**	D
'PK 472' × 'RSC 2'	16.63*	20.21*	22.99	-4.53**	-9.95**	4.77	-19.77**	D
Harvest index (%)								
'MACS 684' × 'MACS 124'	-8.46*	-4.09	53.11	1.06	4.67**	5.83	3.43	C
'MACS 684' × 'RSC 1'	-17.18*	-0.33	53.99	-0.79	0.89	22.47**	-4.23	C
'PK 472' × 'MACS 629'	-12.51*	3.12	55.74	2.92**	-3.12	20.84**	4.78	D
'PK 472' × 'RSC 2'	0.65	-12.37*	57.78	2.22**	7.16**	-17.36*	12.80**	D
Oil content (%)								
'MACS 684' × 'MACS 124'	-0.21	-0.04	19.52	1.71**	0.72*	-	-	-
'MACS 684' × 'RSC 1'	-2.39*	-1.60*	20.07	0.32**	0.68*	1.05	1.30**	C
'PK 472' × 'MACS 629'	-0.26	-0.49	19.45	-1.01**	0.57*	-	-	-
'PK 472' × 'RSC 2'	-6.53*	-3.34*	18.40	-1.00**	1.99**	4.25**	-0.86**	C
100 seed weight (kg × 10^{-3})								
'MACS 684' × 'MACS 124'	-2.66*	1.16	12.90	-1.39**	-1.89**	5.10*	-4.00**	D
'MACS 684' × 'RSC 1'	-2.10	0.66	12.33	-1.09**	-1.28*	-	-	-
'PK 472' × 'MACS 629'	-4.63*	4.22*	14.68	-0.33*	-2.35**	11.80**	-1.89*	D
'PK 472' × 'RSC 2'	-0.14	-0.30	14.90	0.22	0.52	-	-	-
Yield per plant (kg × 10^{-3})								
'MACS 684' × 'MACS 124'	3.92	-0.40	12.59	-0.73	0.68	-	-	-
'MACS 684' × 'RSC 1'	13.86*	-8.82*	16.33	-0.72	9.72**	-30.24**	6.75**	D
'PK 472' × 'MACS 629'	27.75*	-6.59*	20.88	-2.05**	15.02**	-45.78**	-10.13**	D
'PK 472' × 'RSC 2'	9.59*	8.80*	13.22	-2.23**	-3.84*	-1.06	-8.72**	C

*,**significantat 0.5% and 0.1% level respectively; C = Complementary epistasis, D = duplicate epistasis.

traits. The duplicate epistasis for most of the characters showed their complex nature of inheritance. Therefore the breeding strategies should be designed accordingly to get desired results. In the present study, there were negative dominance gene effects for days to maturity, which showed that the crop duration could be decreased by exploiting these effects to develop early maturing soybean cultivars. For plant biomass and harvest index, duplicate epistasts and dominance × dominance interaction, respectively, were contributing significantly along with additive gene effects. Therefore the improvement in these traits may not be feasible with the simple breeding methods, so the recurrent selection method may be applied. Here, it is suggested that the hybridization followed by pedigree selection for exploitation of additive and non-additive variances for oil content and other important traits should be followed.

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