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Research Article

Inheritance studies through generation mean analysis for quantitative traits in soybean (*Glycine max* (L.) Merrill.)

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Abstract
Most of the economically important traits in soybean are quantitatively inherited. The generation mean analysis involving a five-parameter model was carried out in four crosses, *viz.*, Pratap Soya- 2 × LP 5-2, Co 3 × LP 5-2, Co 3 × LP 5-1 and Co 3 × LP 13-1 to investigate additive, dominance and epistatic variance. Therefore, F_1, F_2 and F_3 generations of the above four crosses were evaluated along with their respective parents to estimate the gene action for eleven quantitative traits through generation mean analysis, which provides information about all the gene interactions. The crosses Co 3 × LP 5-1 and Co 3 × LP 13-1 for plant height, Pratap Soya-2 × LP 5-2 for protein content and Co 3 × LP 5-2 for both oil content and seed yield per plant exhibited the adequacy of the additive dominance model. The remaining crosses exhibited epistatic interactions with all other traits. Hence simple recurrent selection can be followed to increase the frequency of desirable genes in the population and the resulted improved population can be used to develop superior lines with desirable genes by pedigree breeding. The crosses Co 3 × LP 5-1 and Pratap Soya - 2 × LP 5-2 were best for further selection programmes with regard to seed yield and quality improvement.

Keywords: Additive gene effects, Gene action, Inheritance, Quantitative trait, Scaling test, Selection, Soybean

INTRODUCTION

Soybean (*Glycine max* (L.) Merrill.) is a versatile crop with numerous possibilities to improve agriculture and to support various industries. Soybean is a chief cause of raw material for many industries; it plays a substantial role in the development of various industrial sectors. The world needs more capital in food and agricultural sectors, not less, and soy will be an essential part of the 21st century human diet (Noleppa, 2012). Although soybean is a vital source of protein, it is not fully utilized by humans and monogastric consumers due to its inability to hydrolyze certain - naturally occurring organic compounds, such as phytate. Phytate hinders the uptake of essential dietary minerals *viz*., copper, calcium, magnesium, zinc and iron (Lydia Pramitha *et al.*, 2021). Hence, the development of high-yielding varieties with low phytate content is essential.

To maximize soybean yield through genetic improvement of the crop, soybean breeders need basic information regarding the nature of gene action involved in expressing different quantitative traits. Line x Tester analysis is usually performed to measure the combining ability of the parents but fails to detect epistasis, which remains the most complex problem. In addition to additive and dominance variation, many quantitative characteristics in soybean may be governed by epistatic gene interactions. However, nonallelic interactions are limited in soybean, and information on epistatic interactions would also be valuable to improve yield attributing traits in soybean (Abou Sen, 2020). The dominant variation and their interactions could not be exploited effectively in soybean, while the additive type of epistasis is potentially exploited, as it can be fixable. Therefore, the presence or absence of epistasis can be studied by generation mean analysis, which accurately measures epistasis at the digenic level. The duplicate epistasis which includes additive x dominance and dominance x dominance types of interaction and complimentary epistasis which includes additive x additive types of interaction. However, estimates of dominance (h) and dominance × dominance (l) can be considered together to determine the type of epistasis because both h and l are independent degrees of gene distribution (Mather and Jinks, 1982). The objective of this study was to derive information about the nature of gene action governing the quantitative traits in soybean, which would pave the way for adopting different selection methods to improve the soybean population.

MATERIALS AND METHODS

The present investigation was conducted using two commercial cultivars Pratap Soya -2 and Co 3, along with three low phytate genotypes LP 5-1, LP 5-2 and LP 13-1, at the Department of Pulses, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India. The experimental material for this study comprised five basic generations *viz*., P_1, P_2, F_1, F_2 and F_3 of four combinations Pratap Soya- 2 × LP 5-2, Co 3 × LP 5-2, Co 3 × LP 5-1 and Co 3 × LP 13-1. These five generations were generated during three seasons and all five generations were raised together during the fourth season for evaluation. Since the experimental population represents both homogeneous and heterogeneous populations, the sample size varied as follows: P_1, P_2 and F_1 generations had 30 plants; F_2 generations had 400 plants; and F_3 generations had 200 plants. Observations were recorded on 11 characters, *viz*., plant height (cm), number of branches, number of clusters, number of pods, number of seeds, hundred seed weight (g), seed yield (g), harvest index, phytate content (mg/g), protein content (%) and oil content (%).

Five genetic parameters viz., mid-parental effect (m), additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) were determined using a five parameter model of generation mean analysis to assess the type of gene action involved in the inheritance of various traits. Means of five generations viz., P1, P2, F1, F2 and F3 were used to estimate genetic parameters as given by Cavalli (1952). Scaling tests C and D were employed to detect the adequacy of the simple additive-dominance model suggested by Mather and Jinks (1971). When any one of the two scales, *viz*., C and D was found to deviate significantly from zero, the additive-dominance model was considered inadequate. The type of epistasis was decided by the significance of dominance (*h*) and dominance x dominance (*l*) effects. When the signs of *h* and *l* were the same, the epistasis was complementary whereas different signs showed duplicate epistasis (Kearsey and Pooni, 1996).

RESULTS AND DISCUSSION

The mean and standard error of the five generations for four crosses with eleven traits are presented in Table 1. Scales C and D calculated by using mean measurements of five generations and the genetic parameters (m), (d), (h), (i) and (l) providing information about the gene action and are presented in Table 2 for four crosses.

The testing of epistasis is essential before estimating the components of genetic variation, which helps todecide the method of analysis. Estimates of the scaling test suggested the inadequacy of a simple additive dominance model to explain all the characteristics in most of the crosses except protein content in Pratap Soya - 2 × LP 5-2, seed yield per plant and oil content in Co 3 × LP 5-2 and plant height in Co 3 × LP 5-1 and Co 3 × LP 13-1. Hence, the model was further analysed with an assumption of the role of interallelic interaction for the remaining traits.

Plant height

The crosses *viz*., Pratap Soya - 2 × LP 5-2 and Co 3 × LP 5-2 recorded nonsignificant additive (*d)* and significant additive × additive (*i)* values, which inferred that alleles were dispersed in the parents. The gene effects (h), (i) and (l) were significant in the Pratap Soya - 2 × LP 5-2 cross indicating the influence of nonadditive interactions on the expression of plant height and the parameters (h) and (l) had different signs, suggesting that the duplicate epistasis was involved in the inheritance of this trait. Rahangdale and Raut (2002) and Thakare *et al.* (2017) reported similar results for this character in soybean. The gene effects (h) and (i) were significant in the Co 3 × LP 5-2 cross, indicating the presence of dominance and additive × additive types of epistasis. Similar findings of dominance and nonadditive gene action for plant height were also supplemented by Maloo and Nair (2005), Nassar (2013) and Abou Se, (2020) in soybean.

Number of branches per plant

The gene effects (h) and (i) were significant in the Co 3 × LP 5-2 cross, indicating the presence of dominance and additive × additive types of epistasis. The gene effects (h), (i) and (l) were significant in the Co 3 × LP 5-1 cross, indicating the influence of dominance and other epistatic interactions. However, the dominance effect (h) and dominant × dominant (l) interaction were significant in the Co 3 × LP 13-1 cross. Components (h) and (l) exhibited opposite signs in both the crosses Co 3 × LP 5-1 and Co 3 × LP 13 -1, indicating the duplicate gene interaction controlling this trait. These results are in accordance with Thangavel *et al.* (2004), Amrita *et al.* (2014) and Thakare *et al.* (2017) in

Table 1. Mean and standard errors of various generations involved in generation mean analysis

Cross	P_1	P_2	F_1	F_2	F_3
Plant height (cm)					
Pratap Soya - 2 × LP 5-2	36.90±3.09	36.22±1.74	33.24±0.99	34.98±0.55	39.28±0.55
Co 3 × LP 5-2	33.02±2.68	36.22±1.74	27.86±1.76	35.14±0.46	39.48±0.48
Co 3 × LP 5-1	33.02±2.68	35.74±1.99	29.31±2.60	33.79±0.52	33.32±0.47
Co 3 × LP 13-1	33.02±2.68	37.30±2.86	29.26±2.42	32.82±0.58	35.19±0.48
Number of branches/plant					
Pratap Soya - 2 × LP 5-2	4.60±0.81	4.40±0.60	4.00±0.33	3.93±0.11	3.63±0.12
Co 3 × LP 5-2	3.20±0.37	4.40±0.60	3.60±0.40	4.65±0.12	4.93±0.13
Co 3 × LP 5-1	3.20±0.37	3.80±0.58	3.10±0.28	4.78±0.11	3.58±0.11
Co 3 × LP 13-1	3.20±0.37	3.80±0.37	4.70±0.30	4.85±0.12	3.85±0.11
Number of clusters/plant					
Pratap Soya - 2 × LP 5-2	31.80±2.96	27.20±4.09	28.00±2.02	22.61±0.63	23.96±0.70
Co 3 × LP 5-2	22.60±1.81	27.20±4.09	23.40±0.92	26.82±0.59	25.83±0.61
Co 3 × LP 5-1	22.60±1.81	29.20±1.77	27.30±0.76	23.91±0.56	22.73±0.54
Co 3 × LP 13-1	22.60±1.81	24.20±1.98	24.60±2.84	28.74±0.73	21.94±0.59
Number of pods/plant					
Pratap Soya - 2 × LP 5-2	119.40±14.17	84.40±11.40	103.90±6.39	66.42±2.38	71.60±2.70
Co 3 × LP 5-2	64.40±2.98	84.40±11.40	75.50±2.49	84.18±2.48	73.94±2.13
Co 3 × LP 5-1	64.40±2.98	79.40±4.17	79.40±2.61	65.04±1.79	61.99±2.15
Co 3 × LP 13-1	64.40±2.98	77.60±9.34	93.10±4.61	78.70±2.16	65.28±1.97
Number of seeds/pod					
Pratap Soya - 2 × LP 5-2	2.00±0.00	2.00±0.00	2.10±0.10	2.19±0.03	2.25±0.04
Co 3 × LP 5-2	2.00±0.00	2.00±0.00	2.00±0.00	2.16±0.03	2.32±0.04
Co 3 × LP 5-1	2.00±0.00	2.00±0.00	2.00±0.00	2.17±0.03	2.19±0.03
Co 3 × LP 13-1	2.00±0.00	2.00±0.00	2.00±0.00	2.19±0.03	2.17±0.03
Hundred seed weight (g)					
Pratap Soya - 2 × LP 5-2	11.23±0.36	10.21±0.40	10.74±0.28	9.44±0.11	9.57±0.13
Co 3 × LP 5-2	11.33±0.39	10.21±0.40	11.49±0.28	9.64±0.11	9.58±0.15
Co 3 × LP 5-1	11.33±0.39	11.52±0.48	11.28±0.28	10.06±0.10	9.69±0.14
Co 3 × LP 13-1	11.48±0.44	10.78±0.16	11.56±0.28	9.90±0.11	9.50±0.15
Seed yield/plant (g)					
Pratap Soya - 2 × LP 5-2	23.76±2.37	14.61±1.86	21.00±1.53	11.15±0.54	11.89±0.58
Co 3 × LP 5-2	12.54±0.87	14.61±1.86	14.72±0.53	14.77±0.58	13.27±0.60
Co 3 × LP 5-1	12.54±0.87	14.36±0.92	15.30±0.64	11.33±0.32	11.08±0.50
Co 3 × LP 13-1	12.56±0.68	14.21±1.39	18.59±1.31	14.29±0.44	11.28±0.44
Harvest index					
Pratap Soya - 2 × LP 5-2	0.45±0.68	0.43±1.18	0.47±0.96	0.33±0.63	0.40±0.65
Co 3 × LP 5-2	0.43±1.18	0.43±1.18	0.44±0.76	0.39±0.64	0.38±0.74
Co 3 × LP 5-1	0.43±1.18	0.44±1.07	0.45±3.13	0.31±0.61	0.38±0.63
Co 3 × LP 13-1	0.46±0.76	0.47±1.85	0.50±1.35	0.42±0.72	0.40±0.62
Phytate content (mg/g)					
Pratap Soya - 2 × LP 5-2	5.91±0.16	2.01±0.07	2.99±0.30	4.90±0.11	3.72±0.16
Co 3 × LP 5-2	5.94±0.19	2.01±0.07	3.09±0.26	5.00±0.12	3.73±0.16
Co 3 × LP 5-1	5.94±0.19	2.05±0.14	2.91±0.31	4.80±0.12	3.76±0.15
Co 3 × LP 13-1	5.94±0.19	2.71±0.12	3.29±0.27	5.03±0.11	3.89±0.16
Protein content (%)					
Pratap Soya - 2 × LP 5-2	34.11±0.38	37.63±0.69	38.31±0.39	36.82±0.13	36.26±0.23
Co 3 × LP 5-2	35.86±0.55	37.63±0.69	38.59±0.59	36.59±0.15	36.34±0.21
Co 3 × LP 5-1	35.86±0.55	36.19±0.51	36.99±0.38	35.98±0.15	37.18±0.16
Co 3 × LP 13-1	35.86±0.55	37.22±0.21	38.46±0.40	35.25±0.20	36.68±0.21
Oil content (%)					
Pratap Soya - 2 × LP 5-2	18.09±0.63	17.01±0.39	18.53±0.43	15.37±0.21	15.60±0.21
Co 3 × LP 5-2	18.49±0.24	17.01±0.39	18.49±0.47	20.02±4.59	16.04±0.23
Co 3 × LP 5-1	18.49±0.24	18.30±0.32	18.88±0.43	16.01±0.19	15.97±0.20
Co 3 × LP 13-1	18.49±0.24	16.98±0.36	18.73±0.39	16.63±0.24	15.75±0.22

Basic generations : P_1, P_2, F_1, F_2 and F_3

Table 2. Scaling test and estimates of genetic parameters for the quantitative traits in soybean

Cross	Scales		Parameters				
	C	D	m	d	h	i	L
Plant height (cm)							
Pratap Soya - 2 × LP 5-2	0.32±4.63	14.06**±4.32	34.98**±0.55	0.34±1.77	-12.64**±1.95	-8.64*±4.02	18.33**±5.94
Co 3 × LP 5-2	15.59**±5.10	18.42**±3.84	35.14**±0.46	-1.60±1.60	-16.44**±1.97	-12.88**±3.68	3.77±6.49
Co 3 × LP 5-1	7.80±6.51	-3.08±3.97	33.79**±0.52	-1.36±1.67	-1.72±2.38	-	-
Co 3 × LP 13-1	2.44±6.65	4.80±4.52	32.82**±0.58	-2.14±1.96	-8.69**±2.37	-	-
Number of branches/plant							
Pratap Soya - 2 × LP 5-2	-1.29±1.29	-2.36*±1.14	3.93**±0.11	0.10±0.51	0.86±0.45	1.56±1.05	-1.42±1.43
Co 3 × LP 5-2	3.82**±1.17	2.80**±0.91	4.65**±0.12	-0.60±0.35	-1.43**±0.50	-2.43**±0.71	-1.35±1.59
Co 3 × LP 5-1	5.91**±0.99	-2.24**±0.84	4.78**±0.11	-0.30±0.35	2.08**±0.41	1.88**±0.65	-10.86**±1.29
Co 3 × LP 13-1	3.00**±0.93	-1.29±0.73	4.85**±0.12	-0.30±0.26	2.56**±0.43	0.76±0.62	-5.71**±1.38
Number of clusters/plant							
Pratap Soya - 2 × LP 5-2	-24.57**±6.94	-8.39±5.91	22.61**±0.63	2.30±2.52	0.00±2.62	6.10±4.64	21.57**±8.27
Co 3 × LP 5-2	10.66*±5.39	-0.09±5.23	26.82**±0.59	-2.30±2.24	0.34±2.10	-2.76±3.49	-14.35*±6.26
Co 3 × LP 5-1	-10.75**±3.71	-8.70*±3.50	23.91**±0.56	-3.30**±1.26	5.41**±1.89	-2.59±2.85	2.74±5.70
Co 3 × LP 13-1	18.98**±6.92	-16.51**±3.86	28.74**±0.73	-0.80±1.34	15.37**±2.86	12.57**±3.74	-47.32**±10.05
Number of pods/plant							
Pratap Soya - 2 × LP 5-2	-145.92**±24.18	-50.23*±21.68	66.42**±2.38	17.50±9.10	11.16±9.62	44.16*±19.13	127.60**±29.31
Co 3 × LP 5-2	36.92*±16.19	-21.39±15.36	84.18**±2.48	-10.00±5.89	21.51**±7.71	0.41±10.00	-77.74**±23.80
Co 3 × LP 5-1	-42.43**±10.24	-25.94*±10.62	65.04**±1.79	-7.50**±2.56	17.72*±6.98	-4.78±7.41	21.99±19.62
Co 3 × LP 13-1	-13.41±15.98	-38.28**±13.30	78.70**±2.16	-6.60±4.90	45.38**±7.46	10.08±9.29	-33.16±23.64
Number of seeds/pod							
Pratap Soya - 2 × LP 5-2	0.57*±0.23	0.61**±0.16	2.19**±0.03	0.00±0.00	-0.21±0.13	-0.31**±0.12	0.05±0.39
Co 3 × LP 5-2	0.63**±0.10	0.95**±0.17	2.16**±0.03	0.00±0.00	-0.53**±0.12	-0.53**±0.10	0.43±0.29
Co 3 × LP 5-1	0.67**±0.10	0.41**±0.14	2.17**±0.03	0.00±0.00	-0.16±0.10	-0.16±0.09	-0.35±0.27
Co 3 × LP 13-1	0.77**±0.11	0.32*±0.14	2.19**±0.03	0.00±0.00	-0.08±0.10	-0.08±0.09	-0.60*±0.27
Hundred seed weight (g)							
Pratap Soya - 2 × LP 5-2	-5.18**±0.88	-2.02**±0.77	9.44**±0.11	0.51±0.27	0.50±0.44	1.50*±0.61	4.21**±1.31
Co 3 × LP 5-2	-5.98**±0.90	-2.51**±0.86	9.64**±0.11	0.56*±0.28	1.40**±0.50	1.79**±0.65	4.62**±1.40
Co 3 × LP 5-1	-5.17**±0.92	-4.19**±0.85	10.06**±0.10	-0.10±0.31	1.79**±0.45	1.74**±0.64	1.31±1.29
Co 3 × LP 13-1	-5.78**±0.84	-4.07**±0.79	9.90**±0.11	0.35±0.23	2.17**±0.49	2.45**±0.66	2.28±1.39
Seed yield/plant (g)							
Pratap Soya - 2 × LP 5-2	-35.78**±4.81	-13.09**±3.95	11.15**±0.54	4.57**±1.51	4.58*±2.15	11.90**±3.48	30.25**±6.70
Co 3 × LP 5-2	2.47±3.27	-3.63±3.35	14.77**±0.58	-1.04±1.03	3.97**±2.00	-	-
Co 3 × LP 5-1	-12.18**±2.22	-5.23*±2.45	11.33**±0.32	-0.91±0.63	3.31**±1.54	-0.36±1.70	9.26**±4.08
Co 3 × LP 13-1	-6.80±3.51	-10.24**±2.50	14.29±0.44	-0.83±0.78	10.90**±1.71	4.03**±1.97	-4.58±5.49
Harvest index							
Pratap Soya - 2 × LP 5-2	-47.32**±3.44	7.11*±3.18	0.33**±0.63	0.67±0.68	-10.22**±2.23	-11.30**±2.30	72.57**±6.61
Co 3 × LP 5-2	-17.07**±3.42	-13.57**±3.65	0.39**±0.64	-0.21±0.83	7.22**±2.42	5.78*±2.62	4.67±6.80
Co 3 × LP 5-1	-50.85**±6.91	1.29±3.21	0.31**±0.61	-0.81±0.80	-8.42**±2.94	-10.96**±3.33	69.51**±10.24
Co 3 × LP 13-1	-25.24**±4.42	-16.28**±3.50	0.42**±0.72	-0.49±1.00	10.47**±2.37	5.66*±2.66	11.95±7.55

Contd…..

Table.2 Contd…..

Phytate content (mg/g)							
Pratap Soya - 2 × LP 5-2	5.69**±0.78	-2.84**±0.69	4.90**±0.11	1.95**±0.09	1.87**±0.52	6.74**±0.50	-11.37**±1.47
Co 3 × LP 5-2	5.85**±0.73	-3.03**±0.69	5.00**±0.12	1.97**±0.10	2.11**±0.51	6.93**±0.50	-11.84**±1.42
Co 3 × LP 5-1	5.40**±0.82	-2.56**±0.68	4.80**±0.12	1.95**±0.12	1.52**±0.51	6.50**±0.52	-10.61**±1.50
Co 3 × LP 13-1	4.89**±0.74	-3.16**±0.71	5.03**±0.11	1.62**±0.11	1.89**±0.51	6.16**±0.51	-10.73**±1.44
Protein content (%)							
Pratap Soya - 2 × LP 5-2	-1.10±1.23	-0.34±1.24	36.82**±0.13	-1.76**±0.40	2.49**±0.72	-	-
Co 3 × LP 5-2	-4.32**±1.59	-1.29±1.26	36.59**±0.15	-0.89*±0.44	1.98**±0.75	-1.64±0.99	4.04±2.27
Co 3 × LP 5-1	-2.11±1.22	4.71**±1.03	35.98**±0.15	-0.17±0.37	-2.53**±0.58	-3.83**±0.86	9.09**±1.78
Co 3 × LP 13-1	-9.00**±1.28	3.16**±1.10	35.25**±0.20	-0.68*±0.29	-1.68**±0.74	-4.96**±0.93	16.21**±2.23
Oil content (%)							
Pratap Soya - 2 × LP 5-2	-10.69**±1.41	-3.43**±1.18	15.37**±0.21	0.54±0.37	1.48±0.75	1.58±1.02	9.68**±2.30
Co 3 × LP 5-2	7.59±18.38	-11.36±9.23	20.02**±4.59	0.74**±0.23	9.58±9.20	-	-
Co 3 × LP 5-1	-10.51**±1.22	-4.91**±0.96	16.01**±0.19	0.10±0.20	2.01**±0.71	1.72*±0.75	7.46**±2.19
Co 3 × LP 13-1	-6.41**±1.31	-5.72**±1.08	16.63**±0.24	0.76**±0.21	3.74**±0.79	4.26**±0.83	0.91±2.46

C - Scale for dominance × dominance epistasis, D - Scale for additive × additive epistasis, m - Mean effects, d - Additive effects, h - Dominance effects, i- additive × additive gene interaction, l - dominance × dominance gene interaction

soybean.

Number of clusters per plant

Thakare et al. (2017) reported the duplicate type of gene interaction for this trait. In present study, the number of clusters per plant was governed by dominance × dominance gene effects in Pratap Soya - 2 × LP 5-2, Co 3 × LP 5-2; additive and dominance gene effects in Co 3 × LP 5-1 and duplicate types of epistasis in Co 3 × LP 13-1. The magnitude of dominance was greater than the additive gene effect in the Co 3 × LP 5-1 cross, indicating a preponderance of dominance for the number of clusters per plant. The similar result was previously reported by Annadurai and Subbalakshmi (2010), Mahesh *et al.* (2014) and Thakare *et al.* (2017) in soybean.

Number of pods per plant

The estimates of (i) and (l) were significant in the Pratap Soya - 2 × LP 5-2 cross, which indicated the predominant role of interacting gene effects. Dominance (h) and dominant × dominant (l) interactions were significant in Co 3 × LP 5-2 and the signs of these two components (h) and (l) were opposite representing duplicate gene interactions. Similar results were reported by Rahangdale and Raut (2002) and Thakare *et al.* (2017). Additive and dominance effects were significant in Co 3 × LP 5-1. However, the degree of dominance was higher than the additive gene effect, indicating the preponderance of the dominant gene effect on the number of pods per plant in Co 3 × LP 5-1. It was observed that dominance effects alone was significant in Co 3 × LP 13-1. The results are akin with Abirami (2014), Thakare *et al.* (2017) and Abou Sen (2020) in soybean.

Number of seeds per pod

None of the crosses showed a significant additive component effect (d). The estimates of genetic parameters revealed that the additive × additive type of epistasis in Pratap Soya - 2 × LP 5-2 and the dominance and additive × additive type of epistasis in Co 3 × LP 5-2 were mainly responsible for the inheritance of the number of seeds. Co 3 × LP 5-2 registered a negatively significant dominance effect (h). Similar findings were reported by Mahesh *et al.* (2014) and Thakare *et al.* (2017) in soybean.

Hundred seed weight

In the Pratap Soya - 2 × LP 5-2 cross, the gene effects (i) and (l) had significant values indicating epistatic gene effects. Additive dominance and interaction effects were important in Co 3 × LP 5-2 and the signs of these two components (h) and (l) were the same representing the preponderance of complementary gene interactions. The gene effects (h) and (i) were significant in the crosses Co 3 × LP 5-1 and Co 3 × LP 13-1, indicating the presence of dominance and additive × additive types of epistasis. These findings are in line with Maloo and Nair (2005) and

Thangavel *et al.* (2004) Thakare *et al.* (2017) and Abou Sen, (2020) in soybean.

Seed yield per plant

The high significance of scales C and D except Co 3 × LP 5-2 showed a dominant gene effect on seed yield per plant. Dominance (h) and dominant × dominant (l) interactions were significant and the signs of these two parameters (h) and (l) were the same in both crosses *viz*., Pratap Soya - 2 × LP 5-2 and Co 3 × LP 5-1 which revealed the preponderance of complementary epistasis. The effects (h) and (i) had significant values, which indicated the involvement of dominance and additive × additive types of epistatic interactions in Co 3 × LP 13-1. The results are in concordance with Gadag *et al.* (1999), Maloo and Nair (2005) and Mahesh *et al.* (2014) and Abou Sen, (2020) in soybean.

Harvest index

Regarding the harvest index, dominance and epistatic gene effects were significant in Pratap Soya - 2 × LP 5-2 and Co 3 × LP 5-1 and the signs of these two parameters (h) and (l) were opposite, clearly specifying the duplicate type of epistasis involved in the inheritance of the harvest index. However, this trait was mainly governed by dominance and additive × additive type of gene action in the crosses Co 3 × LP 5-2 and Co 3 × LP 13-1. The same results were reported by Maloo and Nair (2005).

Phytate content

The significance of the C and D scales showed that all four crosses had inadequate with additive-dominance models which indicated the presence of epistasis. All the crosses showed significant additive (d), dominance (h) and nonalleleic interactions *viz*.,additive × additive (i) and dominance × dominance (l) . In the case of interaction components, component (i) was more than component (l), which implied the importance of additivity in all four crosses. The parameters *h* and *l* were significant and opposite in all four crosses indicating that the expression of this trait was governed by a duplicate type of nonallelic interaction. Ahmad *et al.* (2013) in wheat, Abirami (2014) in soybean, Chiangmai *et al.* (2013) and Lydia Pramitha *et al.* (2021) in maize and noticed that nonadditive gene effects operated for the trait phytate content.

Protein content

The Co 3 × LP 13-1 cross recorded significant values for additive (d) and dominance (h) effects and the interactions (i and l) and the Co 3 × LP 5-1 cross showed significant values for dominance (h) and interactions both i and l. The opposite signs of the parameters (h) and (l) indicated duplicate epistasis in the two crosses *viz*., Co 3 × LP 13-1 and Co 3 × LP 5-1. The other two crosses exhibited additive (d) and dominance (h) effects. The magnitude of dominance was greater than that of additive gene effects in these crosses indicating the preponderance of dominant effects for protein content. The results are akin with Sharma and Phul (1994), Gadag *et al.* (1999), Ganesamurthy

Table 3. Exploitation of desirable crosses through pedigree breeding in soybean

Character	Desirable crosses	Gene action involved
Plant height	-	-
Number of branches/plant	-	-
Number of clusters/plant	-	-
Number of pods/plant	-	-
Number of seeds/pod	Pratap Soya - 2 × LP 5-2	Additive × Additive gene effects
Hundred seed weight	Co 3 × LP 5-2	Complementary epistasis
Seed yield/plant	Pratap Soya - 2 × LP 5-2	Complementary epistasis
	Co 3 × LP 5-1	Complementary epistasis
Harvest index	-	-
Phytate content	Pratap Soya - 2 × LP 5-2	Additive and additive × additive gene effects
	Co 3 × LP 5-2	Additive and additive × additive gene effects
	Co 3 × LP 5-1	Additive and additive × additive gene effects
	Co 3 × LP 13-1	Additive and additive × additive gene effects
Protein content	-	-
Oil content	Co 3 × LP 5-2	Additive gene effects
	Co 3 × LP 5-1	Complementary epistasis
	Co 3 × LP 13-1	Additive and additive × additive gene effects

and Seshadri (2002) and Anne *et al.* (2011) in soybean.

Oil content

The additive (d), dominance (h) and additive × additive types of epistatic effects (i) were significant in Co 3 × LP 13-1, whereas dominance (h) and two epistatic effects (additive × additive and dominance ×dominance) were significant in Co 3 × LP 5-1 and the signs of these two components (h) and (l) were the same which revealed the preponderance of complementary epistasis. Dominance × dominance effects (l) governed the inheritance of oil content in Pratap Soya - 2 × LP 5-2 and dominance gene effects (h) alone were found in Co 3 × LP 5-2 for oil content. Similar results were obtained by Sharma and Phul (1994) and Anne *et al.* (2011) in soybean.

In present study, the dominant gene action was observed for a number of clusters per plant, hundred seed weight, protein and oil content in the cross Pratap Soya - 2 × LP 5-2, seed yield per plant, number of clusters per plant, plant height, harvest index, number of branches per plant and protein content in the cross Co 3 × LP 5-2, number of pods per plant, hundred seed weight and number of clusters per plant, in the cross Co 3 × LP 5-1, seed yield per plant, number of pods per plant, plant height, number of seeds per pod and harvest index in the cross Co 3 × LP 13-1, suggested that conventional method of selection may not be suitable for yield improvement through various yield-related traits. Therefore, selection may be made at later generations or the selected segregants are allowed to intermate in all possible combinations followed by selfing for one or two generations, which could be recommended to accumulate the favourable alleles and break the undesirable linkage for the improvement of these traits.

Duplicate epistasis was involved in the expression of plant height (Pratap Soya - 2 × LP 5-2), number of branches per plant (Co 3 × LP 5-1 and Co 3 × LP 13-1), number of clusters per plant (Co 3 × LP 13-1), number of pods per plant (Co 3 × LP 5-2), harvest index (Pratap Soya - 2 × LP 5-2 and Co 3 × LP 5-1), phytate content (all four crosses) and protein content (Co 3 × LP 5-1 and Co 3 × LP 13-1). Fixing genotypes is difficult with the presence of duplicate epistasis because the desirable effect of one trait would be nullified by the undesirable effect of another trait. However, intermating in early generations is a key way to obtain desirable recombinants in addition to segregating favourable genes from unfavourable combinations and upholding heterozygosity present in the population. Hence, these traits may be improved by adopting the biparental mating design or reciprocal recurrent selection.

In contrast , the hundred seed weight (Co 3 × LP 5-2), seed yield per plant (Pratap Soya - 2 × LP 5-2 and Co 3 × LP 5-1), and oil content (Co 3 × LP 5-1) were governed by complementary gene interactions. The characteristics controlled by additive (d) and additive × additive gene action (i) are fixable. The crosses governed by complementary epistasis are valuable since they can yield transgressive segregants. Hence, selection could be practiced from the F_3 generation onwards, which will be a productive way to be followed for the improvement of characters. Based on the abovementioned criteria, the possible exploitation of crosses through pedigree breeding is presented in Table 3.

Conclusion

From the above study, it may be concluded that yield and yield attributes in soybean were governed by additive, dominance and one or more epistatic interactions. Therefore one or two cycles of recurrent selection followed by pedigree breeding can be taken up for the development of superior lines with several desirable genes. Considering the seed yield per plant and quality improvement, the crosses Co 3 × LP 5-1 and Pratap Soya - 2 × LP 5-2 were judged as the best crosses for further selection programmes.

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Conflict of interest

The authors declare that they have no conflict of interest.

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