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INHERITANCE AND LINKAGE STUDIES IN SOYBEAN

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ABSTRACT

Inheritance of nine morphological characters in six crosses of soybean revealed hypocotyl colour (Hphp), petal colour (W_1w_1), leaflet shape (Ln_2ln_2), growth habit (Dt_1dt_1), pubescent pods (P_2p_2) and pod shattering (Sh_1sh_1) each to be governed by a single gene whereas, seed coat colour ($G_1G_2g_1g_2$) and defective seed coat ($De_1De_2de_1de_2$) were under digenic control. Pod colour ($L_1L_2l_1l_2$) gave monogenic and digenic segregation in different crosses. Out of 122 joint segregations, significant linkages was observed in 35 cases with the crossing over values for different gene pairs in the range of 1.08–46.60%. Based on the pool data of straight and reciprocal crosses three gene maps are constructed. Linkage association for the characters, viz., hypocotyl colour, leaflet shape, growth habit, pod shattering, etc. could not be established.

Key words: Inheritance, morphological characters, *Glycine max*, linkage.

Morphological characters being less influenced by environmental variations are used as markers in identification of species or varieties. Naturally, genetic constitutions of such marker characters have obvious importance. Limited work has been carried out on inheritance and linkage in soybean [1, 2]. Earlier workers have reported 14 linkage groups involving characters, viz., pubescence colour, seed coat colour, cotyledon colour, growth habit, pod colour etc. The present study is an attempt to supplement information on inheritance and linkage of soybean.

MATERIALS AND METHODS

The study was carried out using the soybean strains Monetta, E.C. 36960 and PLSO-91 with several contrasting morphological characters. They were crossed in all possible combinations including reciprocals. There was no difference in the behaviour of F_1 plants or segregation in F_2 and F_3 generation of the direct and reciprocal crosses. Therefore, the data for both were pooled for analysis. Details of the characters studied are given in Table 1. The data were analysed by the standard procedures [3, 4]. The χ^2 test was applied to confirm segregation ratios in F_2 and F_3 generations. First 50 F_2 plants of each cross were considered for F3 confirmation. Details are given in Table 3. The Fisher's score method [5] was adopted where one of the expected recombinant classes was not represented to estimate linkage intensities. Gene maps have been constructed by applying the Kosambi's formula [6].

RESULTS AND DISCUSSION

The results on the morphological characters collected in parents, F_1, F_2 and F_3 generations (Tables 1, 2, 3) show that characters are controlled by one or two genes, i.e., their inheritance is under monogenic and digenic control.

Table 1. Characters of parents and F_1 plants in soybean

Character	Phenotype of parents			F_1 phenotype		
	Monetta	E.C. 36960	PLSO-91	Monetta x E.C. 36960	Monetta x PLSO-91	E.C. 36960 x PLSO-91
Hypocotyl colour	Purple	Green	Purple	Purple	Purple	Purple
Petal colour	Purple	White	Purple	Purple	Purple	Purple
Leaflet shape	Ovoid	Ovoid	Lanceolate	Ovoid	Lanceolate	Lanceolate
Growth habit	Determinate	Determinate	Indeterminate	Determinate	Indeterminate	Indeterminate
Pod colour	Brown	Tan	Black	Brown	Black	Black
Pubescence on pod	Pubescent	Glabrous	Pubescent	Pubescent	Pubescent	Pubescent
Pod shattering	Shattering	Shattering	Nonshattering	Shattering	Nonshattering	Nonshattering
Seed coat colour	Yellow	Yellow	Black	Yellow Normal	Green Normal	Green Normal
Seed coat texture	Normal	Defective	Normal			

Note. Phenotype of F_1 plants were the same in direct as well as reciprocal crosses of each combinations.

Hypocotyl and petal colour. The hypocotyl may be either purple or green and petals either purple or white. Purple colour was dominant over green and white for these characters with monogenic control in F_2 generation. Similar results were reported by Raut et al. [7]. However, digenic control with complementary gene action was observed by Choudhari et al. [8]. Peter [9] also observed monogenic control for hypocotyl colour, but also suggested presence of several minor genes based on a wide range of pigment intensity in hypocotyl. In the present study, plants with purple hypocotyl of varying densities were classified as purple and those with absence of purple pigmentation as green. The gene proposed for hypocotyl colour is Hphp and for petal colour is W_1w_1.

Leaflet shape. This character is controlled by a single gene with lanceolate leaf shape being dominant over ovoid. The gene symbol Ln_2ln_2 is proposed for leaflet shape.

Growth habit. Soybean varieties are classified as having determinate and semideterminate/indeteminate growth habit based on the nature of termination of apical bud. This character is also governed by a single gene, the indeterminate growth habit being dominant over determinate. These results agree with the findings of Ting [10]. However, Bernard [11] reported two pairs of alleles (genes) controlling this character. The gene symbol proposed is Dt_1dt_1.

Table 2. Segregation for different characters in F_2 generation of soybean tested against expected ratios (pooled over reciprocals)

Character	F_2 class	Cross combinations		
		Monetta x EC 36960	Monetta x PLSO-91	EC 36960 x PLSO-91
Hypocotyl colour	Purple	978	1173	877
	Green	320	0	276
		(3:1)		(3:1)
Petal colour	Purple	977	1173	883
	White	321	0	270
		(3:1)		(3:1)
Leaflet shape	Lanceolate	0	866	869
	Ovoid	1298	307	284
			(3:1)	(3:1)
Growth habit	Indeterminate	0	880	847
	Determinate	1298	293	306
			(3:1)	(3:1)
Pod colour	Black	0	868	830
	Brown	987	305	241
	Tan	311	0	82
		(3:1)	(3:1)	(12:3:1)
Pubescence on pod	Pubescent	986	1173	893
	Glabrous	312	0	260
		(3:1)		(3:1)
Pod shattering	Nonshattering	0	857	859
	Shattering	1298	316	294
			(3:1)	(3:1)
Seed coat colour	Green	0	651	650
	Yellow	1298	236	244
	Black	0	286	259
			(9:3:4)	(9:3:4)
Seed coat texture	Normal	1204	1173	1065
	Defective	94	0	88
		(15:1)		(15:1)

Note. Figures in parentheses indicate the F_2 generation ratio confirmed by χ^2 test, and further supported by observations in F_3 generation.

Pod colour. Soybean pods are always green when immature and at maturity, change to characteristic pod colour of the variety: black, brown and tan. In crosses between parents with brown and tan pods, brown pod colour was monogenic dominant over tan. Whereas, black pod colour was monogenic dominant over brown in crosses between parents with black and brown pod colour. However, in crosses between parents with black and tan pods, black pod was dominant over tan and in F_2 generation, segregations for pod colour were

Table 3. F_3 behaviour of different crosses in soybean

Character	Cross No.	No. of homozygous families		No. of heterozygous families			
		dominant	recessive	3:1	15:1	12:3:1	9:3:4
Hypocotyle colour	1	29	23	48	0	0	0
	2	100	0	0	0	0	0
	3	30	25	45	0	0	0
Petal colour	1	29	23	48	0	0	0
	2	100	0	0	0	0	0
	3	30	25	45	0	0	0
Leaflet shape	1	0	100	0	0	0	0
	2	25	23	52	0	0	0
	3	31	20	49	0	0	0
Growth habit	1	0	100	0	0	0	0
	2	19	22	59	0	0	0
	3	31	50	19	0	0	0
Pod colour	1	28	21	51	0	0	0
	2	24	23	53	0	0	0
	3	33*	11	35	0	21	0
Pubescence on pod	1	33	23	44	0	0	0
	2	100	0	0	0	0	0
	3	28	28	44	0	0	0
Pod shattering	1	0	100	0	0	0	0
	2	22	22	56	0	0	0
	3	22	33	45	0	0	0
Seed coat colour	1	0	100	0	0	0	0
	2	8	32	38	0	0	22
	3	9	33	36	0	0	22
Seed coat texture	1	42	8	25	25	0	0
	2	100	0	0	0	0	0
	3	38	10	26	26	0	0

Note. Cross No. 1. Monetta x EC 36960 & reciprocal. Cross. No. 2. Monetta x PLSO 91 & reciprocal. Cross No. 3. EC 36960 x PLSO 91 & reciprocal.
*25 families homozygous for black pod colour and 8 families homozygous for brown pod colour.

observed in the proportion of 12 black : 3 brown : 1 tan suggesting the epistatic gene action where black pod colour was epistatic over brown and tan. Bernard [12] and Choudhari et al. [8] also reported similar results. The gene symbol for black pod (L_1L_2), brown (l_1L_2) and tan (l_1l_2) are suggested.

Pubescent pod. Soybean varieties mostly develop pubescence on pods, though glabrous, curly, dense, sparse and puberulent types may occur. Bernard and Singh [13] reported a single gene controlling this character with the dominance of glabrous pod over pubescent. However, pubescent type was reported to be dominant by Stewart and Wentz [14]. Our results confirmed the findings of [14]. It is generally expected that presence of a structure or substance is a consequence of normal gene function which is equivalent to dominant (functional) state of gene. The recessive allele is the malfunctioning or nonfunctioning condition (mutation) of the gene leading to total or partial loss of a structure or substance. In such a situation it is difficult to understand how absence of pubescence being dominant over its presence, as concluded by Bernard and Singh [13]. Thus, the two alleles for presence and absence of pubescence proposed are P_2p_2 and P_1p_1, respectively.

Pod shattering. Most of the soybean varieties have early pod shattering, though few varieties have less or delayed pod shattering. This situation is also sometimes described as "nonshattering". This attribute was governed by a single gene and late shattering (or nonshattering) habit was dominant over early shattering. The gene symbol proposed is Sh_1 for nonshattering and sh_1 for shattering.

Seed coat colour. A wide range variation occurs for seed coat colour and pattern in soybean : green, yellow, black, brown, buff or variegated. In four crosses F_1 plants produced green seeds although the parents were either yellow or black. The F_2 ratio suggested involvement of two genes with supplementary gene action where gene for black testa in combination with the gene for yellow testa produced green seed. Ting [10] has reported dominance of green over yellow, black and brown whereas, dominance of black over green and yellow has been noted by Choudhari et al. [10]. Similarly Raut et al. [7] has observed yellow to be dominant over black mottled. Based on our results, the gene symbols proposed for G_1G_2 for green, G_1g_2 for yellow and g_1G_2 for black testa colour.

Seed coat texture. This character is of special commercial significance as seed with defective seed coat gives poor germination. Normal seed coat has three distinct layers — epidermis, hypodermis and inner parenchyma layer. The first two layers are absent to varying degree in defective seed coat. Such defects facilitate easy entry of pathogens in seed. This character was found to be controlled by two genes with duplicate dominant gene action, normal seed coat being dominant over the defective one. However, Ting [10] observed monogenic control of this characters. Besides, Liu [15] reported digenic and trigenic control.

In linkage study, out of 122 joint segregations, significant linkages were observed in 35 cases while the remaining character combinations showed independent assortment. Among different gene pairs, recombination values range from 0.011 to 0.466 crossover units. The gene combinations with confirm linkages after pooling the frequencies of straight and reciprocal crosses are listed in Table 4.

Table 4. Crossing over percentages of character combinations with significant linkages in soybean (pooled data of straight and reciprocal crosses)

Character combination	Genes	Crossover %	Corrected values as per Kosambi [6]
Monetta x EC 36960:			
Hypocotyl colour/petal colour	Hp/W_1	1.95 ± 0.39	1.89
Hypocotyl colour/pubescence on pods	Hp/P_2	40.14 ± 1.84	38.92
Petal colour/pubescence on pods	W_1/P_2	40.48 ± 1.85	40.81
Monetta x PLSO-91:			
Leaflet shape/growth habit	Ln_2/Dt_1	30.63 ± 1.67	—
Leaflet shape/pod shattering	Ln_2/Sh_1	35.15 ± 1.80	—
Growth habit/pod colour	Dt_1/L_1L_2	40.04 ± 1.94	—
Growth habit/pod shattering	Dt_1/Sh_1	39.88 ± 1.93	—
Pod colour/seed coat colour	L_1L_2/G_1G_2	36.27 ± 2.09	—
E.C. 36960 x PLSO-91:			
Hypocotyl colour/petal colour	Hp/W_1	1.70 ± 0.38	1.68
Hypocotyl colour/pubescence on pods	Hp/P_2	16.52 ± 1.22	16.34
Petal colour/pubescence on pods	W_1/P_2	16.00 ± 1.20	18.02
Growth habit/pod colour	Dt_1/L_1L_2	37.30 ± 1.88	—
Growth habit/seed coat colour	Dt_1/G_1G_2	38.61 ± 2.09	—
Growth habit/pod shattering	Dt_1/Sh_1	34.46 ± 1.80	—
Growth habit/seed coat texture	Dt_1/De_1De_2	34.69 ± 1.80	—
Pod colour/seed coat colour	L_1L_2/G_1G_2	26.93 ± 1.70	21.26
Pod colour/defective seed coat	L_1L_2/De_1De_2	43.58 ± 2.40	40.80
Seed coat colour/seed coat texture	G_1G_2/De_1De_2	24.75 ± 1.50	19.54

Close linkage observed between hypocotyl and petal colour (1.95% and 1.70%) confirmed the earlier findings of Raut et al. [7]. However, Chaudhari et al. [16] concluded these characters to be a case of pleiotropic effect of a single gene. The gene for hypocotyl and petal colour are very closed linked. It is not a case of pleiotropy. Recombinants do occur if large F_2 population is screened. The recombination values observed for growth habit and pod colour are very close to those reported earlier [10, 17]. Similarly linkage observed for pod colour and seed colour is also of similar magnitude as reported by Choudhari et al. [16].

Based on the recombination values, a tentative gene map has been prepared (Fig. 1). The gene symbols used are according to Bernard and Weiss [1]. Most of the recombination

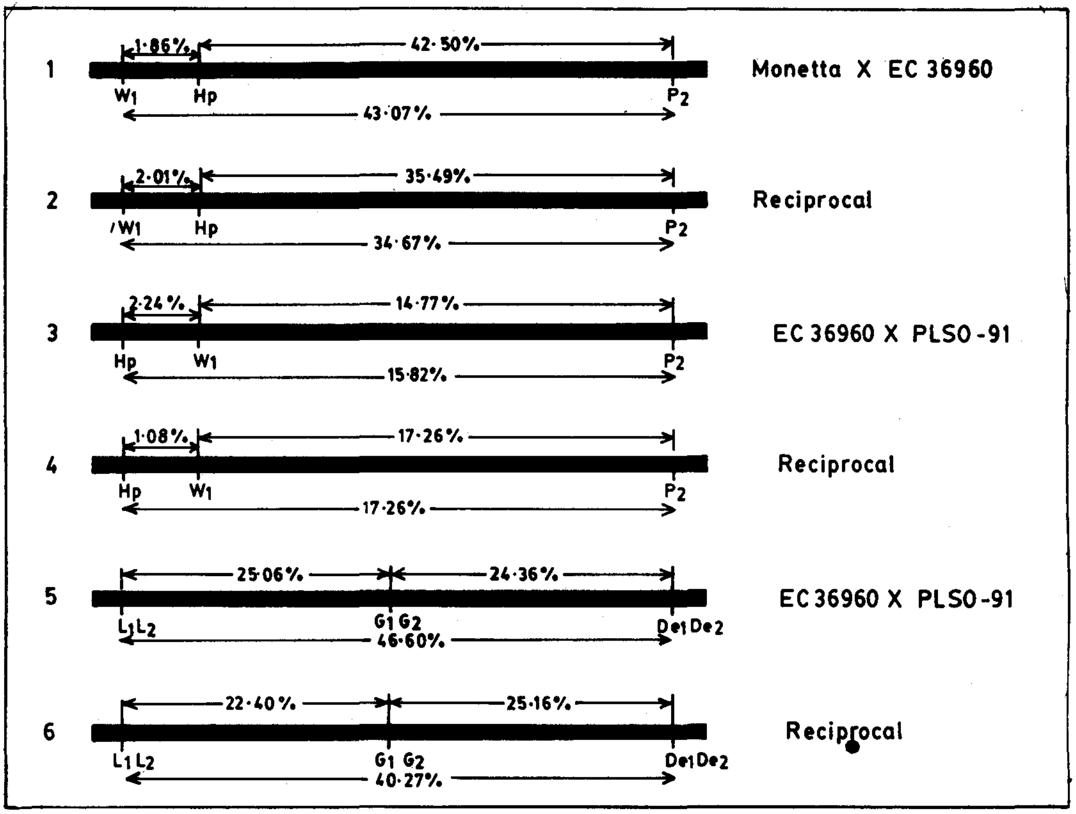

Fig. 1. Linkage intensity map.

values for linkages between two characters in straight as well as reciprocal combinations show little variation, which confirm absence of cytoplasmic effects on genic expression and their linkage relationships.

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