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Inheritance studies for morphological characters and sex expression in pistillate lines of castor (*Ricinus communis* L.)

C. Lavanya and V. Gopinath[1]

Senior Scientist, Directorate of Oilseeds Research, Rajendranagar, Hyderabad 500 030

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Abstract

Inheritance of morphological characters in four crosses of pistillate x pistillate lines indicated that stem colour was controlled by single gene while red stem colour was dominant over green stem colour. However, green stem colour in the cross DPC 13 x M 574 and green colour of petiole, capsules and spines in cross M 574 x DPC 11 showed digenic epistatic ratio to red stem colour, red colour of petiole, capsules and spines. The characters plant type and bloom were monogenically controlled while normal plant type and presence of bloom were dominant over dwarf plant type and absence of bloom respectively. Joint segregation analysis indicated that stem colour, plant type and bloom were segregating independently in all the four crosses. Pistillate character was dominant over pistillate with interspersed staminate flowers [ISF] and controlled by one [P_1] or two [P_1P_2] to four genes [$P_1P_2P_3P_4$]. Joint segregation analysis indicated linkage between stem colour and dwarf plant type in the cross DPC 13 x DPC 11 and pistillate character [P_1] and plant type [PtN] in cross M 574 x DPC 11. The distance between stem colour [Rst/gst] to plant type [PtDw] and single gene for pistillate character and plant type was estimated as 40.2 centimorgans and 47.6 centimorgans based on square root of frequency of double recessive phenotypes in F_2 data.

Key words: Castor [*Ricinus communis* L.,], sex expression, morphological characters, independent segregation and linkage

Introduction

Morphological characters like colour of stem, petiole, capsule, spines, rachis, midrib, bloom, plant type, spike type, number of nodes to primary spike are important markers used for distinctness, uniformity and stability (DUS) tests in castor (*Ricinus communis* L.) under different environments. Stem colour in castor is classified as red, green and mahogany based on the pigmentation of sap colour in epidermal palisade cells and parenchymatous areas of the stem [1]. Majority of the pistillate lines which are derivatives of the VP-1 back ground have dwarf plant type with condensed internodes and cup shaped leaf and serve as distinct morphological markers and facilitate rouging in seed production plots. However, information on inheritance of morphological markers *viz*., stem colour, plant type, and arrangement of nodes on the stem, leaf shape etc., and their linkage has not been worked out and the available information is either scanty or very old. Castor, a sexually polymorphic species produces pistillate spikes with interspersed staminate flowers (ISF), monoecious or revertants [2]. Pistillate lines are maintained by interspersed staminate flowers (ISF) called refined or modified method of seed production of pistillate lines. The production of these interspersed staminate flowers is highly environmentally sensitive [3]. Information on inheritance of genes for ISF and interaction with other morphological characters in pistillate lines is less worked out. The present study is an attempt to study the inheritance of morphological characters and sex expression in four crosses of pistillate x pistillate lines of castor.

Materials and methods

Three pistillate lines *viz*., DPC 9, DPC 11, DPC 13 developed by conventional breeding methods and two pistillate lines *viz*., M 571, M 574 developed by gamma ray (55 Kr) treatment of VP-1 seeds [4] differing in morphological characters like stem colour, bloom, plant type, spike nature, duration to maturity were chosen for the present study [Table 1]. Four crosses *viz*., DPC 9 x M571, DPC 13 x DPC 11, DPC 13 x M 574, M 574 x DPC 11 were made in *Rabi* 1999. The F_1s were raised in *Rabi* 2000, selfed and back crossed to both of their parents. All the three generations *viz*., P_1, P_2, F_1, F_2, B_1 and B_2 were planted in *Rabi* 2001 and observations on both morphological characters and sex expression were recorded on individual plants in each generation. Observations on stem colour were recorded in all

populations of four crosses while colour on other external parts like petiole, capsules, spines, rachis, midrib were recorded in progeny of the cross IV-M 574 x DPC 11 only. Observations on ≥20 plants were recorded on parents, F_1s, B_1, B_2 while sample size in F_2 varied in different crosses. The chi-square test was applied for the goodness of fit for different expected genetic ratios. Joint segregation analysis and linkage analysis was done based on the formulae for the estimation of linkage from F_2 data [4].

Results and discussion

The inheritance of stem colour was studied in all the four crosses (Table 2). In three crosses involving either green x red (DPC 9 x M 571) or red x green (DPC 13 x DPC 11) or green x green (M 574 x DPC 11) red stem colour is dominant over green in F_1. The F_2 segregation ratios in three crosses indicated that stem colour is monogenic and segregated in to 3:1 ratio in all the three crosses mentioned above. A single gene *Rst/rst* is responsible for stem colour in three crosses of castor. Monogenic inheritance for stem colour and dominance of coloured stem over green stem was reported in earlier studies [5-7]. However, in cross DPC 13 x M 574, green stem colour is dominant over red stem colour in F_1 and F_2 population indicated a good fit to the digenic epistatic ratio of 9 green: 6 red: 1 mahogany where green stem colour is epistatic to red stem colour. The presence of either of two genes *Rst* or *Gst* individually produces red stem colour while presence of both the two genes *RstGst* polymerizes the effect to turn to green colour. The presence of two recessive genes *rstgst* produces mahogany stem colour in cross DPC 13 x M 574. Mahogany colour has both green and red colours with predominance of red colour. Epistatic ratios for stem colour were also reported [7, 8]. Epistatic interaction of two factors M and G resulted in three colours where factor G converts tinged green to green and mahogany to rose and M is the factor for mahogany [6].

The inheritance of colour on petiole, capsules, rachis, spines and midrib was studied in the cross M 574 x DPC 11 (Table 2). Petiole colour is governed by digenic supplementary epistatic gene action and F_2 population fits in 9 red: 4 green:3 mahogany ratio. A gene *gpt* has no effect of its own but modifies the action of *Rpt* which produces mahogany petiole colour. Presence of both the dominant genes *Rpt-Gpt-* produces red petiole colour while *rptrpt Gpt-* produces green petiole colour and *Rpt-gptgpt* mahogany stem colour.

Capsule colour is predominantly green in the cross M 574 x DPC 11 and F_2 population segregated to 15

Table 1. Pigmentation and morphological character states in 5 parents and the F_1s in 5 crosses of castor

Parents /crosses	Stem color	Bloom	Plant type	Leaf shape	Spike type*	Duration	No. of nodes to primary
Cross-1							
DPC 9	Green	Zero	Normal	Flat	SC	Early	9
M 571	Red	Triple	Dwarf	Cup	L	Medium	10
DPC 9 x M 571 (F_1)	Red	Double	Normal	Flat	L	Early	8
Cross II							
DPC 13	Red	Zero	Dwarf	Cup	C	Medium	11
DPC 11	Green	Double	Normal	Flat	L	Medium	14
DPC 13 x DPC 11 (F_1)	Red	Double	Normal	Flat	SC	Early	9
Cross III							
DPC 13	Red	Zero	Dwarf	Cup	C	Medium	15
M 574	Green	Triple	Dwarf	Cup	SC	Late	17
DPC 13 x M 574 (F_1)	Red	Triple	Dwarf	Cup	SC	Late	16
Cross IV							
M 574	Red	Triple	Dwarf	Cup	SC	Late	17
DPC 11	Green	Double	Normal	Flat	L	Medium	14
M 574 x DPC 11 (F_1)	Red	Triple	Normal	Flat	SC	Medium	13

*C = compact, SC = Semi compact, L = Loose

green:1 red capsule colour indicating the role of either of the duplicate genes *Rcp or Gcp* and both the genes producing green capsules while recessive duplicate genes rcp/gcp result in red colour. Similar ratios have been reported earlier [1]. However, monogenic inheritance of capsule colour and dominance of green colour was reported in other studies [9, 10].

In the same cross M 574 x DPC 11, colour of spines on the capsule was recorded as red, green and mahogany and F_2 population fit to the epistatic gene ratio of 12 red : 3 green: 1 mahogany. Two genes *Rsp* and *Gsp* control two colours- red and green spine colours while the presence of dominant *Rsp* masks the effect of *Gsp* and *gsp* resulting in *Rsp- Gsp-* as red colour while *rsp rsp Gsp-* produces green spine colour and absence of both the dominant genes (*rspgsp*) resulted in mahogany spine colour.

Unlike the other parts, midrib of castor leaves is of two colours red and white and the F_2 population indicated the role of trigenes and fit into the ratio of 15 red: 49 white while red is dominant over white midrib colour.

Bloom or waxy coating in castor is an important morphological marker and serves as a natural protection against drought, cold, jassids etc., Castor plants are mainly classified as bloom or no bloom based on the presence or absence of bloom on external parts of the plant. However, based on the presence of bloom on combination of plant parts, genotypes in castor were usually classified as single bloom (stem + petiole + capsule stalks), double bloom [stem, petiole, capsule + lower side of the leaf] and triple bloom (all the above parts + upper side of the leaf) [1]. Though the data on different bloom types were recorded in segregating generations of all the four crosses, none of the data could fit into any genetic ratios. Differences in bloom distribution on different plant parts may be due to variation in the penetrance and expressivity of the genes controlling the bloom character or due to multiple alleles. In the present study, inheritance of bloom character indicated that presence of bloom is dominant over no bloom in F_1 and F_2 population has a good fit to 3:1 ratio (Table 3). In cross, M 574 x DPC 11, as both the parents M 574 [triple bloom] and DPC 11 (double bloom) are bloom types, F_2 population is classified as triple vs either single or double and fit to the 3: 1 ratio indicating the role of single gene [PtBl] for bloom character. Similar monogenic inheritance for bloom character was reported by earlier authors [6, 7, 8, 11]. Epistatic interaction was reported in a cross between double bloom and no bloom

Table 2. Inheritance of stem color in four crosses of castor and color of petiole, rachis, spine and midrib in cross 4

Cross/generation	No. of plants observed				Expected ratio	χ^2 value
	Total	Red	Green	Mahogany		
Stem color						
Cross-I (DPC 9 x M 571)						
F_2	66	52	16	0	3:1	0.15
F_1 x DPC 9	22	12	10		1:1	
F_1 X M 571	20	20				
Cross II (DPC 13 x DPC 11)						
F_2	190	142	48	0	3:1	0.007
F_1 x DPC 13	26	14	12		1:1	
F_1 x DPC 11	24		24			
Cross III (DPC 13 x M 574)						
F_2	170	61	99	10	6:9:1	0.209
F_1 x DPC 13	22	7	8	6	1:1:1	
F_1 x DPC 11	21			21		
Cross IV (M 574 x DPC 11)						
F_2	197	146	51		3:1	0.11
F_1 x M 574	20	20				
F_1 x DPC 11	20	11	10		1:1	
Petiole color						
F_1	20	20				
F_2	92	99	55	38	9 : 4: 3	1.88
F_1 x M 574	20	20				
F_1 x DPC 11	20	7	7	6	1:1:1	
Capsule color						
F_1	20	20				
F_2	192	16	176		15:1	1.419
F_1 x M 574	20	20				
F_1 x DPC 11	20	11	10		1:1	
Spine color						
F_1	21		21			
F_2	153	10	114	29	12:3:1	0.119
F_1 x M 574	20	7	8	5		
F_1 x DPC 11	20		20			
Midrib color						
		Red	White			
F_1	20	20				
F_2	124	32	92		15:49	0.405
F_1 x M 574	20	20				
F_1 x DPC 11	20	11	10		1:1	

and F_2 ratio of 9 double boom: 3 single bloom: 4 no bloom was due to epistatic effect of factor B over factor C and factor C has no role on its own and it merely intensifies the action of factor B [12].

Majority of the pistillate lines derived from VP-1 back ground have dwarf stem, condensed nodes, cup shaped leaves and convergent branching which are highly linked characters [13]. In two crosses, DPC 9 (N) x M 571 (Dw) and M 574 (Dw) x DPC 11(N) involving normal (N) and dwarf (DW) plant types, normal plant type is dominant over dwarf in F_1 and F_2 segregated in to 3 normal : 1 dwarf indicating the role of single gene – *PtN* as reported earlier [14, 15 and 11] (Table 3). The F_1 population of the cross -DPC 13 (Dw) x DPC 11 (N), indicated that normal plant type is dominant over dwarf plant type. The F_2 segregation fits in to 45:19 ratio indicating the role of three genes for plant type. However, in the cross III involving both dwarf type parents – DPC 13 and M 574, dwarf plant type is dominant over normal plant type and F_2 population indicated the role of duplicate dominant genes – either PtDw or PtN producing the same plant type – dwarf while duplicate recessive genotype – ptdw / ptn results in normal plant type.

In castor, spikes are classified based on the arrangement or density of capsules on the spike as Loose, Compact and Semi compact [1]. Compact and Semi compact spikes are highly susceptible to fungal diseases like *Botrytis* under conditions of high humidity, rainfall, cloudy weather due poor aeration and ventilation. Earlier studies on inheritance pattern [5] indicated incomplete dominance and F_2 populations had all the patterns of spike nature. In the present study also, the distinction between semi compact and compact types is not clear as majority of the pistillate lines had medium long or long compact/semi compact spikes except the genotype M 571, which has a loose spike. In a cross between compact (DPC 13) x semi compact (M 574), single gene *SpSc* controlled the compactness of spike and F_2 population segregated in to 3 semi compact : 1 loose spike indicating the dominance of semi compact spike over loose spike. In cross II, DPC 13 x DPC 11, two epistatic inhibitory genes controlled the spike type while F_2 population fit into the ratio of 13 semi compact: 3 compact spike types. The presence of dominant gene at one locus (*SpSc*) and recessive gene at other locus (Spll) produced the same phenotype – semi compact spike while presence of dominant gene at other locus (spL) resulted in loose spike types. The F_2 population in cross IV indicated test cross ratio of 1 loose: 1 semi compact spike types (Table 4).

Number of nodes to primary spike in castor indicates the duration of the flower initiation of the primary spike and on an average every node takes 4

Table 3. Inheritance of bloom and plant type in four crosses of castor

Cross/generation	No. of plants observed					No. of plants observed				
	Total	With bloom (BI)	No bloom (Nbl)	Expected ratio	χ^2 value	Total	Normal	Dwarf	Expected ratio	χ^2 value
Cross I										
F_2	66	48	18	3:1	0.181	66	55	11	3 : 1	2.44
F_1 x DPC 9(B_1)	22	11	10	1:1		22	22	0		
F_1 x M 571(B_2)	20	20				20	11	9		
Cross II										
F_2	188	149	41	3:1	1.12	190	127	63	45 : 19	1.15
F_1 x DPC 13(B_1)	26	14	13	1:1		26	12	14	1 : 1	
F_1 x DPC 11(B_2)	24	24				24	24	0		
Cross III										
F_2	170	133	37	3:1	0.879	170	8	162	15 : 1	0.875
F_1 x DPC 13(B_1)	22	11	11	1:1		22		22	1 : 1	
F_1 x M 574(B_2)	21	21				21	10	11		
Cross IV		Triple	Double							
F_2	197	144	53	3:1	0.39	197	145	52	3 : 1	0.24
F_1 x DPC 11(B_1)	20	11	9	1:1		20	20			
F_1 x M 574(B_2)	20	20				20	11	9	1 : 1	

Table 4. Inheritance of Spike type in cross II, III, IV and node number in cross II and IV

Cross/generation	No. of plants observed			Expected ratio	χ^2 value	No. of plants observed				Expected ratio	χ^2 value
	Total	Loose	SC/ compact			Total	Early	Medium	Late		
Cross II							(<12N)	(13-16N)	>17N		
F_2	154	26	128	3:13	0.382	143	75	60	8	9 : 6 : 1	1.35
F_1 x DPC 13	26		26			26	10	8	8	1 : 1 : 1	
F_1 x DPC 11	24	12	12	1:1		24	24				
Cross IV											
F_2	196	89	107	1:1	1.652	196	128	68		45 : 19	2.45
F_1 x DPC 11	20	9	11	1:1		20	11	9			
F_1 x M 574	20		20			20	20				
Cross III											
F_2	162	43	119	1:3	0.258						
F_1 x DPC 13	22		22	1:1							
F_1 x M 574	21	11	10								

days to develop [14]. However, node number varies within and among genotypes based on the season of planting and location and within a location; node number of a genotype is constant for each planting season and hereditary [15]. Based on the previous records at Directorate of Oilseeds Research, Hyderabad, genotypes were classified as early (<12 nodes), medium (13-16 nodes) and late (>17 nodes) based on the node number. Inheritance of node number indicated that in a cross between medium x medium (DPC 13 x DPC 11), F_1 was early and F_2 population segregated in to 9 early: 6 medium: 1 late ratio. The presence of two dominant genes (N_1-N_2-) results in low node number (<12) while the presence of dominant gene at the second locus (n_1-N_2-) results in medium node number (13-16N) while the double recessive genotype $n_1n_1n_2n_2$ produces higher node number (>17N). In cross III, inheritance of node number indicated that three genes- $n_1n_2n_3$ control the character and F_2 population segregates to inhibitory epistatic ratio of 45 early : 19 medium types (Table 4).

Sex expression in castor is polymorphic and varies from monoecious, pistillate, ISF and revertants. A pistillate spike with staminate flowers interspersed in between the female flowers from the base to the top is termed as Interspersed staminate flower (ISF). In the present study, pistillate lines are crossed with interspersed staminate flowers of other pistillate lines. The F_1s in all the four crosses were pistillate with production of occasional ISF in higher temperatures indicating the dominance of pistillate over pistillate lines with ISF. Sex expression in F_2 population was recorded in both primary and secondary spikes in all the four crosses (Table 5). The number of genes controlling pistillate expression varied from one (P_1) to two genes (P_1P_2) in cross I and cross IV to three genes ($P_1P_2P_3$) and four genes ($P_1P_2P_3P_4$) in cross II and III. In all the cases pistillate expression is dominant over pistillate with ISF as reported by earlier authors [13, 3]. The F_2 population segregated to simple monogenic ratios like 3 pistillate:1 pistillate with ISF (in cross I) or 1 pistillate: 1 ISF (cross IV) or digenic epistatic ratios like 13 pistillate:3 ISF in secondary of cross IV. In cross II, F_2 population was a good fit to tetragenic epistatic ratios in primary (162:94) and secondary (229: 27). The change in the segregation pattern of secondary spikes denotes the interaction of genotype with environment *viz*., daily maximum temperatures, day length etc. The interaction of sex expression with environmental conditions is well documented earlier [2, 3]. More number of genes was activated along with the production of spikes to cope up with the changing environmental conditions. The role of modifying genes was indicated in the earlier study of the author [3]. However, earlier report [3], indicated that gene F_1 for monoecious controls a genetically stable series of sex variants ranging from female 'f' to strong male inbreds and sex expression of such strains is controlled by non genetic variations which occur intermittently during the development of individual plants.

Table 5. Pattern of segregation for Pistillate vs ISF in segregating material of four crosses of castor

Generation	Obs/exp	No. of plants Primary		No. of plants Secondary		χ^2 value
		Pistillate	ISF	Pistillate	ISF	
Cross I	DPC 9 x M 571					
F_2	(O)	52	14	-	-	0.51
	(E)	49	17	-	-	
	Ratio	3 :	1			
B_1	(O)	12	10			
	(E)	11	11			
Genetic ratio used		1 :	1			
B_2	(O)	20				
	(E)	20				
Cross II	DPC 13 x DPC 11					
	(O)	102	62	131	16	0.105
	(E)	104	60	131	16	0.0
	Ratio	162 :	94 :	229	27	
B_1	(O)	26				
	(E)	26				
B_2	(O)	24		24		
	(E)	13	11	14	10	
Genetic ratio used		1 :	1 :	1	1	
Cross III	DPC 13 x M 574					
	(O)	157	4	112	0	0.339
	(E)	158	3			
	Ratio	63 :	1			
B_1	(O)	22				
	(E)	22				
B_2	(O)	14	10			
	(E)	12	12			
Genetic ratio used		1	1			
Cross IV	M 574 x DPC 11					
	(O)	90	99	154	37	0.338
	(E)	94	95	155	36	0.033
	Ratio	1 :	1	13 :	3	
B_1	(O)	20				
	(E)	20				
B_2	(O)	12	8			
	(E)	10	10			
Genetic ratio used		1 :	1			

Joint segregation analysis for stem colour and bloom and stem colour vs plant type in three crosses – I, II, IV (Table 6 and Table 7) indicated independent segregation of stem colour and bloom which are controlled by single genes – *Rst* / *gst* and *Bl* / *bl*. In case of stem colour vs plant type also, independent segregation of characters was observed in cross I, II

Table 6. Pattern of joint segregation for stem color vs bloom in crosses I, II and IV

Generation	Genetic ratio used	No. of plants				χ^2 value
		Stem colour vs. bloom				
Cross I	DPC 9 x M 571	RBl	GBl	RNbl	GNbl	
F_2	9:3:3:1 (O)	37	14	11	4	0.38
	(E)	37	12	12	4	
B_1	1:1:1:1 (O)	5	4	6	5	
	(E)	5	5	5	5	
B_2	(O)	20				
	(E)	20				
Cross II	DPC 13 x DPC 11					
F_2	9:3:3:1 (O)	108	34	41	7	
	(E)	106	36	36	12	2.95
B_1	1:1 (O)	26	24			
	(E)	25	25			
B_2	1:1 (O)	12		8		
	(E)	10		10		
Cross IV	M 574 x DPC 11					
F_2	9:3:3:1 (O)	110	36	34	11	
	(E)	107	36	36	12	0.274
B_1	(O)	22				
	(E)	22				
B_2	1:1:1:1 (O)	8	9	7	7	
	(E)	8	8	8	8	

RBl = Red bloom, GBL = Green no bloom, RNbl = Red no bloom, GNbl = green no bloom

Table 7. Pattern of joint segregation for stem color vs plant type in crosses I, II and IV

Gene-ration	Genetic ratio used	No. of plants					χ^2 value
		O/E	RN	Rdw	GN	Gdw	
Cross I	DPC 9 x M 571						
F_2	9:3:3:1	(O)	44	7	11	4	3.48
		(E)	37	12	12	4	
B_1		(O)	11			9	
		(E)	10			10	
B_2		(O)	12	8			
		(E)	10	10			
Cross II	DPC 13 x DPC 11						
F_2	135:57: 45:19	(O)	92	50	31	17	11.69**
		(E)	100	34	42	14	
B_1	1:1	(O)	11	9			
		(E)	10	10			
B_2	1:1	(O)	11		13		
		(E)	12		12		
Cross IV	M 574 x DPC 11						
F_2	9:3:3:1	(O)	105	36	38	17	2.37
		(E)	110	37	37	12	
B_1	1:1	(O)	12	8	11	9	
		(E)	10	10	10	10	
B_2		(O)			20		
		(E)			20		

RN = Red normal, Rdw = Red dwarf, GN = Green normal, Gdw = green dwarf

and IV where the characters were controlled by single genes *Rst*/*gst* and *Dw*/*dw* and no linkages were obtained. However, in cross II, DPC 13 x DPC 11, stem colour red is linked to dwarf plant type based on the deviation of χ^2 from the estimated 9:3:3:1 ratio. Linkage is estimated based on the square root method of frequency of double recessive non cross over gametes in the case of coupling phase type of linkage [16]. The distance between the locus for stem colour (*Rst*/*gst*) to that for plant type (PtDw) is estimated as 40.2 centimorgans. Joint segregation of stem colour and plant

Table 8. Joint segregation in cross III for stem color Vs plant type

Generation	Observed/expected	No. of plants						χ^2 value
		GDw	RDw	MDw	GN	RN	MN	
F_2	(O)	99	56	8	1	5	2	7.02
	(E)	90	60	10	5	4	1	
	Ratio	135	90	15	9	6	1	
B_1	(O)	12	11	13				
	(E)	12	12	12				
	Ratio	1	1	1				
B_2	(O)	25						
	(E)	25						

G = Green, R = Red, M = Mahogany, Dw = Dwarf, N = Normal

Table 9. Joint segregation in cross III for stem color Vs bloom

Generation	Observed/expected	No. of plants						χ^2 value
		GBl	RBl	MBl	GNbl	RNbl	MNbl	
F_2	(O)	73	44	15	25	12	1	2.76
	(E)	72	48	8	24	16	2	
	Ratio	27	18	3	9	6	1	
BC_1	(O)	7	6	4	5	5	3	
	(E)	5	5	5	5	5	5	
Ratio		1	1	1	1	1	1	
BC_2	(O)	11	9	10				
	(E)	10	10	10				
	Ratio	1	1	1				

G = Green, R = Red, M = Mahogany; Bl = Bloom, NBl = No bloom

Table 10. Joint segregation for plant type and sex expression in segregating material of four crosses of castor

Character	Ratio observed	Generation	No. of plants				χ^2 value
			O/E	DwP	dwP	DWp	dwp	
Cross II	DPC 13 x DPC 11							
Plant type	45:19 (DW:dw)	F_2	(O)	65	37	51	11	6.69
Sex expression	162:94 (P:p)		(E)	73	31	42	18	
		Ratio		7290	3078	4230	1786	
Secondary								
Plant type	45:19 (DW:dw)	F_2	(O)	102	29	9	7	5.68
Sex expression	229:27 (P:p)		(E)	109	22	12	4	
		Ratio		10305	2061	1215	243	
Cross III	DPC 13 x M 574							
Plant type	15:1 (DW:dw)	F_2	(O)	7	150	0	4	2.91
Sex expression	63:1 (P:p)		(E)	10	149	0	2	
		Ratio		945	63	15	1	
Cross IV	M 574 x DPC11							
Plant type	3:1 (DW:dw)	F_2	(O)	57	33	86	13	14.84**
Sex expression	1:1 (P:p) 0000000		(E)	71	24	70	24	
		Ratio		3	1	3	1	
Secondary								
Plant type	3:1 (DW:dw)	F_2	(O)	109	45	33	4	5.44
Sex expression	13:3 (P:p)		(E)	116	39	27	9	
		Ratio		39	13	9	3	

type and stem colour and bloom (Tables 8 and 9) in cross III with its six phenotypic classes unlike the other three crosses also indicated independent segregation of the two genes controlling each of the character-stem colour (Rst_1Rst_2/gst_1gst_2) and bloom (Bl_1Bl_2/bl_1bl_2).

Pistillate character has been introduced along with TSP 10 R, an exotic pistillate line with dwarf, condensed internodes and cup shaped leaves [3]. Thus joint segregation analysis for plant type and pistillate expression was studied in both primary and secondary spikes of three crosses (Table 10). In two crosses, II and III, plant type and pistillate expression had independent segregation between double (Dw_1Dw_2)/ triple genes ($Dw_1Dw_2Dw_3$) of plant type and three ($P_1P_2P_3$) and four ($P_1P_2P_3P_4$) genes for pistillate expression. However, in cross IV, monogenic genes for plant type and sex expression were linked as indicated by the frequency of double recessive non cross over gametes as the characters were linked in coupling phase. Linkage between genes for plant type and sex expression was estimated as 47.6 centimorgans based on square root of frequency of double recessive phenotypes of F_2 data [16]. Presence of linkage between morphological characters like stem colour and plant type and plant type and sex expression has not yet been reported.

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