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Inheritance of genes imparting resistance to pod fly (*Melanagromyza obtusa*) in pigeonpea (*Cajanus cajan*)

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ABSTRACT

A study was conducted during 2002–05 to examine the mode of inheritance of field resistance in 8 crosses involving 4 resistant parents, viz. 'PDA 88-2E', 'PDA 89-2E', 'PDA 92-2E' and 'PDA 93-2E' and 4 susceptible parents, viz. 'DA11', 'NDA1', 'ICP 5174' and 'ICP12386' and their allelic relationship among genes imparting resistance to pod fly (*Melanagromyza obtusa* L. Malloch.) in resistant parents. The parental lines, their F_1s, F_2s and back crosses were evaluated for the pest reaction. In the F_1 of all crosses between resistant and susceptible parents, a susceptible reaction was observed that indicates dominance of susceptibility over the resistance. The segregation pattern in F_2 of these crosses revealed that resistance was controlled by 2 genes (*mor1mor1Mor2Mor2*) with interaction between recessive and dominant alleles in resistant donors, 'PDA 88-2E' and 'PDA 89-2E' and 2 homozygous recessive genes (*mor1 mor1 mor2 mor2*) were responsible for resistance in the parents, 'PDA 92-2E' and 'PDA 93-2E'. From the reaction of individuals in F_2 and backcross generations of crosses between resistant parents, the same genes were present in resistant lines, 'PDA 88-2E' and 'PDA 89-2E' which were allelic but differed for a single gene with the genes present in 'PDA 92-2E' and 'PDA 93-2E'.

Key words: Allelic relationship, *Cajanus cajan*, Inheritance, *Melanagromyza obtusa*, Pigeonpea, Pod fly, Resistance

Pod fly (*Melanagromyza obtusa* L. Malloch.) is one of the most important insect pests of pigeonpea and causes heavy loss to the pigeonpea production in north, central and south India. But, interest in adopting insecticide application technology by farmers is minimum. Therefore, the only way to reduce pod fly damage effectively is to utilize the resistant varieties. However, in the past due to non-availability of resistant donors, no success could be achieved in developing resistant varieties. Now the resistant donors with desirable levels of resistance have been identified by Lal (1998) and their combining ability for resistance to pod fly has been reported by Lal *et al.* (1999). But, prior to starting a sound resistance breeding programme for development of pod fly resistant varieties, it is imperative to study the mode of inheritance of resistance and allelic relationship among genes imparting resistance.

The present investigation was hence undertaken to elucidate the inheritance of resistance and allelic relationship among genes responsible for resistance to *M. obtusa* in resistant donors of pigeonpea.

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MATERIALS AND METHOD

Plant materials of pigeonpea [*Cajanus cajan* (L.) Millsp.] were grown at the research farm of the Institute during the crop season (July–April) of 2002–03 to 2004–05. They comprised 8 parents, of which 4 parents, viz. 'PDA 88-2E', 'PDA 89-2E', 'PDA 92-2E' and 'PDA 93-2E' were resistant and the remaining 4 parents, viz 'DA-11', 'NDA-1', 'ICP 5174' and 'ICP12386' were susceptible to pod fly (*Melanagromyza obtusa* L. Malloch.). In 2002–03, parents were grown and all possible crosses were made (except reciprocals) between resistant, resistant and susceptible and susceptible parents. Parents and their 16 F_1 hybrids (Table 1) were grown in 2003–04 and observations were recorded on the reaction of individual plants of both parents and hybrids to pod fly. True F_1s which were unlike the female parent and possessed intermediate morphological traits of both the parents were identified and backcrossed to both the parents as well as advanced to F_2 in 2003–04. The F_2s, BC_1s and BC_2s of all crosses were grown along with the parents in 2004–05 and observations on the reaction of individual plants to pod fly were recorded. The materials were planted in 5 m long rows with spacing of 75 and 25 cm, between rows and plants, respectively. A highly susceptible variety 'Bahar' was used as susceptible check.

For screening against pod fly all the pods of individual plants were examined for the presence of typical pin head exit hole (identification mark of infected/damaged pods), which is a marker of susceptibility to pod fly and the percentage of infected/damaged pods was recorded at maturity. The test entries were then graded on a susceptibility rating scale of 1–9, where 1, highly resistant (<10% infected/damaged pods) 3, resistant (>10–20% infected/damaged pods) 5, moderately resistant (>20–30% infected/damaged pods) 7, susceptible (>30–75% infected/damaged pods) and 9, highly susceptible (>75% infected/damaged pods). A rating scale from 1 to 5 was considered as resistant and from 7 to 9 as susceptible.

For recording the data on parents and F_1s, percentage of infected/damaged pods of each plant of all parents and F_1s was recorded and mean percentage of infected/damaged pods was worked out for each of the parents / F_1s. On the basis of mean percentage of infected/damaged pods parents / F_1s were classified as resistant / susceptible, following the above mentioned rating scale. In each of F_2s, BC_1s and BC_2s percentage of infected/damaged pods of each plant was worked out and classified as resistant (30 or <30% infected/damaged pods) and susceptible (>30% infected/damaged pods). Chi-square method formulated by Snedecor and Cochran (1967) was used to test the goodness-of-fit of the segregating F_2 and backcross populations (BC_1 and BC_2) with the observed phenotypic ratios.

RESULTS AND DISCUSSION

The resistant and susceptible parents showed consistent reaction to pod fly in both years (Table 1). The F_1s of crosses, between resistant and susceptible parents were susceptible,

Table 1 Reaction of parents and hybrids (F_1s) to *Melanagromyza obtusa*

Parent /F_1 hybrid	Year	Number of plants observed	Mean pod damage (%)	Rating score (1–9)	Pest reaction
'PDA 88-2E'	2002	76	12.9	3	Resistant
	2003	65	13.4	3	Resistant
'PDA 89-2E'	2002	88	10.0	3	Resistant
	2003	79	14.2	3	Resistant
'PDA 92-2E'	2002	75	12.0	3	Resistant
	2003	56	13.5	3	Resistant
'PDA 93-2E'	2002	82	14.9	3	Resistant
	2003	88	11.9	3	Resistant
'DA11'	2002	41	79.5	9	Susceptible
	2003	74	81.0	9	Susceptible
'NDA1'	2002	59	77.7	9	Susceptible
	2003	95	85.3	9	Susceptible
'ICP 5174'	2002	90	73.8	7	Susceptible
	2003	78	88.2	9	Susceptible
'ICP 12386'	2002	85	79.0	9	Susceptible
	2003	90	76.3	9	Susceptible
'DA11' × 'PDA 88-2E'	2003	90	76.3	9	Susceptible
	2003	58	74.9	9	Susceptible
'NDA1' × 'PDA 88-2E'	2003	72	65.6	7	Susceptible
'DA11' × 'PDA 89-2E'	2003	74	63.7	7	Susceptible
'NDA1' × 'PDA 89-2E'	2003	86	82.5	9	Susceptible
'ICP 5174' × 'PDA 92-2E'	2003	77	64.9	7	Susceptible
'ICP 12386' × 'PDA 92-2E'	2003	91	79.3	9	Susceptible
'ICP 5174' × 'PDA 93-2E'	2003	98	84.5	9	Susceptible
'ICP 12386' × 'PDA 93-2E'	2003	69	78.4	9	Susceptible
'PDA 88-2E' × 'PDA 92-2E'	2003	71	12.6	3	Resistant
'PDA 89-2E' × 'PDA 92-2E'	2003	70	8.9	3	Resistant
'PDA 88-2E' × 'PDA 93-2E'	2003	70	8.9	3	Resistant
'PDA 89-2E' × 'PDA 93-2E'	2003	98	12.0	3	Resistant
'PDA 92-2E' × 'PDA 93-2E'	2003	69	11.6	3	Resistant
'PDA 88-2E' × 'PDA 89-2E'	2003	52	13.5	3	Resistant
'DA11' × 'NDA1'	2003	61	99.3	9	Susceptible
'ICP 5174' × 'ICP 12386'	2003	82	95.5	9	Susceptible

Year '2002' denotes the crop season 2002–03
Year '2003' denotes the crop season 2003–04

Table 2 Segregation for resistance to *Melanagromyza obtusa* in F_2, BC_1 and BC_2 generations of crosses between susceptible and resistant parents

Cross	Generation	Plants	Observed	Expected	Chi-square value	P-value
		Resistant	Susceptible	Genetic ratio		
'DA11' × 'PDA 88-2E'	F_2	49	255	3 : 13	1.382	0.2398 (0.25–0.10)
	BC_1		173			
	BC_2	86	75	1 : 1	0.375	0.5403 (0.75–0.50)
'NDA1' × 'PDA 88-2E'	F_2	53	219	3 : 13	0.096	0.7567 (0.90–0.75)
	BC_1		171			
	BC_2	79	91	1 : 1	0.423	0.5154 (0.75–0.50)
'DA11' × 'PDA 89-2E'	F_2	47	213	3 : 13	0.077	0.7814 (0.90–0.75)
	BC_1		163			
	BC_2	95	81	1 : 1	0.557	0.4555 (0.50–0.25)
'NDA1' × 'PDA 89-2E'	F_2	29	155	3 : 13	1.079	0.2989 (0.50–0.25)
	BC_1		181			
	BC_2	86	70	1 : 1	0.820	0.3652 (0.50–0.25)
'ICP 5174' × 'PDA 92-2E'	F_2	23	281	1 : 15	0.898	0.3433 (0.50–0.25)
	BC_1		181			
	BC_2	45	125	1 : 3	0.196	0.6580 (0.75–0.50)
'ICP 12386' × 'PDA 92-2E'	F_2	28	329	1 : 15	1.546	0.2137 (0.25–0.10)
	BC_1		133			
	BC_2	39	110	1 : 3	0.109	0.7413 (0.75–0.50)
'ICP 5174' × 'PDA 93-2E'	F_2	18	207	1 : 15	1.176	0.2782 (0.50–0.25)
	BC_1		95			
	BC_2	17	69	1 : 3	1.253	0.2630 (0.50–0.25)
'ICP 12386' × 'PDA 93-2E'	F_2	25	325	1 : 15	0.476	0.4902 (0.50–0.25)
	BC_1		129			
	BC_2	22	86	1 : 3	1.235	0.2664 (0.50–0.25)

BC_1 (backcross with parent 1): cross between F1 (female) and susceptible parent (male)
BC_2 (backcross with parent 2): cross between F1 (female) and resistant parent (male)
In parentheses significance thresholds of chi-square statistics are given

between resistant parents were resistant and between susceptible parents were susceptible to the pest (Table 1). Individuals of F_2 resulted from the crosses between resistant ('PDA 88-2E' and 'PDA 89-2E') and susceptible ('DA11' and 'NDA1') parents, segregated in the ratio of 3 (resistant): 13 (susceptible) which was confirmed by the segregation pattern observed in backcrosses (BC_1 and BC_2). This segregation behaviour indicated that digenic dominant epistatic gene interaction is responsible for the inheritance of resistance. On the other hand, individuals resulted from the crosses between resistant ('PDA 92-2E' and 'PDA 93-2E') and susceptible ('ICP 5174' and 'ICP12386') parents, segregated in the ratio of 1 (resistant): 15 (susceptible) in the F_2 which was confirmed by the segregation pattern observed in backcross generations (BC_1 and BC_2). Such segregation pattern indicated that 2 recessive genes were responsible for inheritance of resistance (Table 2). The individuals resulted from the crosses between resistant parents were resistant and between susceptible parents were susceptible in F_2, BC_1 and BC_2 (Table 3).

The susceptible reaction of F_1's resulted from the crosses between susceptible and resistant parents indicated that resistance to pod fly is recessive. Singh and Lal (2002) have also reported that resistance to *M. obtusa* is recessive. However, Singh and Singh (2003) have reported that resistance to pod fly is dominant over susceptibility and resistance is under the control of single dominant gene.

Cubero (1999) reported that the epistatic action of one dominant gene to another and the suppressive effect of the recessive alleles of the second gene is a known case of interaction which occurs generally in the regulation of the resistance of plant species to diseases. But this study has indicated that such type of interaction of genes may also occur in the control of the resistance of plant species to insect pests. The proposed hypothesis establishes the existence of *mor1mor1Mor2Mor2* which corresponds to resistant genotypes, viz. 'PDA 88-2E' and 'PDA 89-2E'. According to this hypothesis, the reaction of F_1 progenies would have been of susceptibility independently of the homozygosity (*Mor2Mor2* or *mor2mor2*) or heterozygosity of the gene (*Mor2 mor2*) since the susceptible line would always contribute allele *'Mor1'* to the progeny. The hypothesis of genetic regulation of resistance to *M. obtusa* in 'PDA 88-2E' and 'PDA 89-2E' is in full agreement with those of Singh

Table 3 Segregation for resistance to *Melanagromyza obtusa* in F_2, BC_1 and BC_2 generations of crosses between resistant parents

Cross	Generation	Plants	Observed
		Resistant	Susceptible
'PDA 88-2E' × 'PDA 92-2E'	F_2	220	
	BC_1	111	
	BC_2	114	
'PDA 89-2E' × 'PDA 92-2E'	F_2	244	
	BC_1	131	
	BC_2	118	
'PDA 88-2E' × 'PDA 93-2E'	F_2	271	
	BC_1	98	
	BC_2	133	
'PDA 89-2E' × 'PDA 93-2E'	F_2	228	
	BC_1	119	
	BC_2	110	
'PDA 92-2E' × 'PDA 93-2E'	F_2	288	
	BC_1	129	
	BC_2	101	
'PDA 88-2E' × 'PDA 89-2E'	F_2	266	
	BC_1	102	
	BC_2	114	
'DA11' × 'NDA1'	F_2		213
	BC_1		82
	BC_2		122
'ICP 5174' × 'ICP 12386'	F_2		310
	BC_1		92
	BC_2		89

BC_1 (backcross with parent 1): cross between F1 (female) and resistant/susceptible parent 1 (male)
BC_2(backcross with parent 2): cross between F1 (female) and resistant/susceptible parent 2 (male)

and Lal (2002). Therefore, on the basis of this hypothesis genes can be designated as *Mor1 / mor1* at locus 1 and *Mor2 / mor2* at locus 2, where, *Mor1 / Mor2* are dominant alleles and *mor1 / mor2* are recessive alleles to *M. obtusa* resistance and genotypes of resistant parents 'PDA 88-2E' and 'PDA 89-2E' can be symbolized as *mor1mor1Mor2Mor2* and susceptible parents 'DA11' and 'NDA1' can be symbolized as *Mor1Mor1mor2mor2*. Therefore, it may be concluded that resistant parents 'PDA 88-2E' and 'PDA 89-2E' differ for 2 genes with those of susceptible parents 'DA11' and 'NDA1'.

The segregation of individuals in a ratio of 1 (resistant): 15 (susceptible) in the F_2 and confirmation of this segregation pattern by the segregation of individuals in BC_1's and BC_2's indicated that two recessive genes which may be designated as mor_1 mor_1 mor_2mor_2 are responsible for the resistance in 'PDA 92-2E' and 'PDA 93-2E'. Here it is evident that whenever either of the dominant genes was present in homozygous/heterozygous dominant condition (*Mor1Mor1mor2mor2 / Mor1mor1mor2 mor2* or *mor1mor1Mor2Mor2 / mor1mor1Mor mor2*) susceptibility of individuals resulted. Therefore, it may be concluded that resistant parents 'PDA 92-2E' and 'PDA 93-2E' differ for 2 genes with those of susceptible parents 'ICP 5174' and 'ICP 12386'.

Uniform resistant reaction of all individuals in the F_2, BC_1 and BC_2 of 'PDA 92-2E'×'PDA 93-2E' and 'PDA 88-2E'×'PDA 89-2E' confirmed that the same genes (*mor1 mor1 mor2 mor2)* are present in the resistant parents 'PDA 92-2E' and 'PDA 93-2E' and the resistant parents 'PDA 88-2E' and 'PDA 89-2E' also carry the same genes (*mor1mor1Mor2Mor2)*. In F_2 , BC_1 and BC_2 of all crosses (except 'PDA 92-2E'×'PDA 93-2E' and 'PDA 88-2E'×'PDA 89-2E') between resistant parents only resistant individuals were observed which suggested that the genes present in resistant parents 'PDA 88-2E' and 'PDA 89-2E' (*mor1mor1Mor2Mor2*) are allelic to the genes present in resistant parents 'PDA 92-2E' and 'PDA 93-2E' *(mor1 mor1 mor2 mor2)*. Thus, the genes present in resistant donors, 'PDA 92-2E' and 'PDA 93-2E' are allelic but different in respect of single gene to the genes present in resistant donors, 'PDA 88-2E' and 'PDA 89-2E'.

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