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Inheritance of resistance to two isolates of sterility mosaic pathogen in pigeonpea (*Cajanus cajan* (L.) Millsp.) *

Inheritance to isolates of sterility mosaic

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Summary

Studies were conducted to determine the inheritance of resistance to two isolates of the sterility mosaic pathogen, in three crosses of pigeonpea, involving resistant (ICP 7035, ICP 7349 and ICP 8850) and susceptible (ICP 8863) lines. Observations of F_1 and F_2 plants were explained on the basis of two independent non-allelic recessive genes for the less virulent, old Patancheru isolate (isolate 1). The backcrosses corroborated the segregation pattern observed in the F_2 generation. For the more virulent, new Patancheru isolate (isolate 2), differential behavior of the F_1's was observed. Resistance was dominant in two crosses (ICP 7035 X ICP 8863 and ICP 7349 X ICP 8863), and susceptibility in the other cross (ICP 8850 X ICP 8863). The disease reaction for isolate 2, appeared to be governed by a single gene with three alleles, with one resistance allele exhibiting dominance and the other being recessive, over the allele for susceptibility. Monogenic inheritance of resistance to both isolates was noticed in the cross ICP 8850 X ICP 8863.

Introduction

Sterility mosaic disease is considered to be one of the major constraints for low productivity of pigeonpea in India. The disease is known to occur in major pigeonpea growing areas of India (Kannaiyan et al., 1984) and at times can cause yield losses upto 95 per cent (Reddy & Nene, 1981). The disease is characterized by proliferation, mosaic symptoms, cessation of reproductive growth and a reduction in the size of the leaflets (Kandaswamy & Ramakrishnan, 1960). The pathogen causing the disease was reported to be a virus (Capoor, 1952), transmitted by the eriophyid mite, *Aceria cajani* Channabasavanna (Seth, 1962).

Several lines resistant or tolerant to the disease have been identified (Nene & Reddy, 1976a; Nene et al., 1981; Nene et al., 1989; Amin et al., 1993). However, resistance breakdown was noticed in the recent years. The possible role of pathogenic strains of the etiologic agent in the breakdown of resistance was first suggested by Nene et al., (1989). Later, Reddy et al., (1991) reported the occurrence of a new virulent form of the Patancheru strain of the sterility mosaic pathogen and recorded the breakdown of resistance in few pigeonpea cultivars. A comprehensive study of variability in the sterility mosaic pathogen of pigeonpea by Reddy et al., (1993), revealed the occurrence of five different variants of the pathogen in India. The results were based on the differential reaction of seven genotypes, at nine different locations in India. This has necessitated the identification and use of strain-specific resistance sources in the crop improvement programs. Further, information on genetics and mode of inheritance of strain-specific resistance are also lacking for the disease.

The present investigation was hence, undertaken to identify strain-specific resistance sources and elucidate

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Figure 1. Leaf-stapling technique using large diseased leaflet (folded leaf method of inoculation

the strain-specific inheritance pattern of resistance, for two isolates of the sterility mosaic pathogen in pigeonpea.

Materials and methods

Screening for resistance

A set of 153 lines, earlier reported as resistant or tolerant (Nene et al., 1981), were screened at International Crops Research Institute for Semi-Arid Tropics (ICRISAT) Asia Center (IAC), Patancheru during 1993-1995, against two isolates of the sterility mosaic pathogen, representing the variants 2 and 3 identified by Reddy et al. (1993). The identity of these isolates was established by their reaction on the pigeonpea differentials viz., ICP 2376 and ICP 10976. These lines exhibited ring spot reaction (localized necrotic lesions) to isolate 1 while, for isolate 2, the line ICP 2376, exhibited susceptible reaction (severe mosaic). Further, resistant reaction (no apparent symptoms) was noticed for the line, ICP 10976, when infected with isolate 2 of the pigeonpea sterility mosaic pathogen. These isolates were obtained from sterility mosaic infected pigeonpea fields of local cultivars, located at different places within the state of Andhra Pradesh, India. Isolate 1 was collected from the infected pigeonpea fields of Bibinagar Mandal of Nalgonda district, Andhra Pradesh, India, during January 1993 while, isolate 2 was obtained from the sterility mosaic infected fields of Narsapur Mandal, Medak district, Andhra Pradesh, India, during November 1994. The inoculum carrying sufficient number of mites (7–10 per leaf, on average) was brought in moistened muslin cloth bags and used for inoculation of seedlings of pigeonpea differentials at primary leaf stage, including the susceptible, ICP 8863, by leaf-stapling technique (Nene & Reddy, 1976a). The diseased leaflets were stapled to the primary leaves of test seedlings. One diseased leaflet per primary leaf was generally used. The diseased leaflet was folded on the primary leaf in such a way that its lower surface came into contact with the primary leaf of the test seedlings. It was then stapled with a small paper stapler (Figure 1). Alternatively, two diseased leaflets were used, if they were too small. The leaflets were placed in such a way that the lower surface of one of the leaves came in contact with the lower surface of the primary leaf while, the lower surface of the other was in contact with the upper surface of the primary leaf. The primary leaf and the two diseased leaflets were then stapled together (Figure 2).

Multiplication of the isolates was taken up after confirmation, in isolation on the susceptible cultivar, grown in pots at different locations to avoid cross-contamination. Isolate 1 was multiplied in the residential areas of Hyderabad, Andhra Pradesh, India, devoid of any pigeonpea, within a radius of 5 kms while, isolate 2 was multiplied in the sterility mosaic and wilt screening nurseries of ICRISAT Asia Center, Patancheru, Andhra Pradesh, India. The inoculum, thus multiplied was used for subsequent screening.

The 153 lines were first screened for their reaction to the less virulent old Patancheru isolate (isolate 1) of sterility mosaic pathogen during May 1993 and for the more virulent, new Patancheru isolate (isolate 2) during May 1994. The screening was taken up in pots using the infector-hedge technique (Nene & Reddy, 1976b). An infector-hedge consisting of a few widely spaced rows of the susceptible cultivar, ICP 8863 was grown, well in advance of regular screening (at least four months), on the upwind border of the field. Ten day old seedlings of the hedge were inoculated by leaf-stapling and spreading of diseased twigs infested with mites among the seedlings. The pathogen and mites that multiplied on the hedge plants served as source of inoculum and disease spread occurred through wind onto the test materials during the screening period. The pots sown with test material were placed beside the infector-hedge (Figure 3). Plastic pots, 15 cm in diameter filled with alfisols (60% sand, 33% clay, 7% silt), and sown with 10 seeds in each pot were used for the screening experiment.

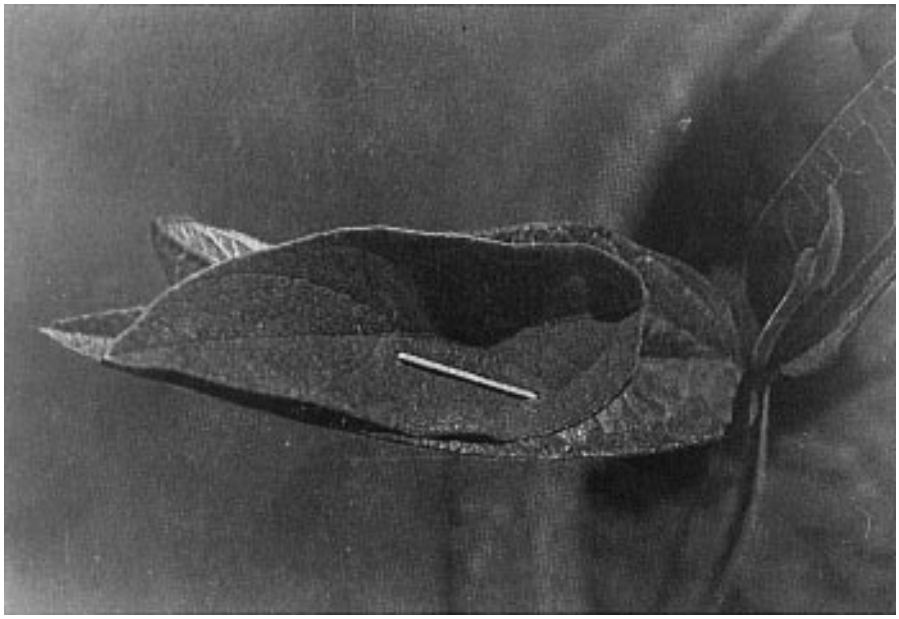

Figure 2. Leaf-stapling technique using two small diseased leaflets.

Figure 3. Pot-screening using infector-hedge technique.

Two replications were taken up for each of the 153 entries for screening against isolate 1 while, for isolate 2, the lines were screened in three replications. BDN1, LRG30 and ICP 8863 were used as susceptible controls in the screening. Observations on disease reaction were recorded 75 days after sowing (DAS). Lines were classified as resistant when the disease incidence recorded was less than 10 per cent while, they were classified as susceptible when the disease incidence was more than 10 per cent (Nene et al., 1981).

Table 1. Characteristic of pigeonpea lines used in the study of inheritance of resistance to sterility mosaic disease

Parent	Characteristic
ICP 7035	Mid-late maturing, indeterminate with semi-spreading growth habit.
	Red flowers with dense purple streaks.
	Purple pods.
	Mottled reddish brown, bold, pea-shaped seeds.
ICP 7349	Medium maturing, indeterminate with semi-spreading growth habit.
	Yellow flowers with few red streaks.
	Green pods.
	Brown, bold and square-shaped seeds.
ICP 8850	Late maturing, indeterminate with semi-spreading growth habit.
	Yellow flowers.
	Green pods.
	Orange, oval shaped, bold seeds.
ICP 8863	Medium maturing, indeterminate with semi-spreading growth habit.
	Yellow flowers with few red streaks.
	Green pods with purple streaks.
	Orange to dark brown oval shaped seeds.

Selection, crossing and advancement of generations

Three lines (ICP 7035, ICP 7349 and ICP 8850) of medium to late maturity duration having resistance (with no apparent symptoms) to both the isolates, were selected as parents for the inheritance study. These were crossed with the susceptible (severe mosaic symptoms) line, ICP 8863.

The resistant parents were sown in four sets at intervals of 15 days in 30 cm pots and placed beside the infector-hedge, while the susceptible parent was raised under disease-free conditions. The confirmed resistant plants were used for crossing with the susceptible parent and sufficient F_1 seed was obtained in each cross combination. Part of the F_1 seed was advanced to the F_2 generation during 1994. The F_1 plants were selfed by covering them with bee-proof nylon cages. Flower initiation, flower color, pod color, seed color, seed size and other contrasting characters among the parents (Table 1) were used as markers to check the trueness of F_1 plants. Only true F_1's were advanced to F_2. Sufficient F_2 seed was obtained. Backcrossing with the respective parents was also taken up simultaneously and sufficient backcross seed was also obtained in each backcross combination.

Screening of Parents, F_1, F_2 and backcross generations

Parents, F_1, F_2 and backcrosses of the resistant x susceptible cross combinations were screened during May - December 1995 for their reaction to isolate 1 in a mite-proof net-house. Seedlings were raised in 15 cm pots with 10 seedlings per pot and were inoculated using the leaf-stapling technique (Nene & Reddy, 1976a). For isolate 2 of the pathogen, parents, F_1 and F_2 were screened during May - December 1995, in an isolated field, using the infector-hedge technique (Nene & Reddy, 1976b). The susceptible control ICP 8863, was included in both sets, at frequent intervals, to monitor the disease spread. Observations on disease reaction were recorded at 75 DAS. The plants were classified as resistant (no apparent symptoms) and susceptible (severe mosaic symptoms) and the Chi-square method (Snedecor & Cochran, 1967) was used to test the goodness of fit of the segregating F_2 populations with the expected phenotypic ratios.

Results and discussion

Screening for resistance sources

Susceptible controls exhibited 100 per cent infection indicating a good spread of the disease in both sets.

The disease incidence varied from 0–100 per cent in different lines, for both the isolates. Among 153 lines evaluated, 37 lines showed resistance, against isolate 1, while only 17 lines exhibited resistance for isolate 2.

It is apparent from this screening that resistance observed against isolate 1 was not completely effective against isolate 2. Similar breakdown of resistance in ICP 2376 and ICPL 85073, was reported by Reddy et al. (1991) against a more virulent new isolate of the Patancheru strain of sterility mosaic pathogen. However, lines, ICP 2630, ICP 3782, ICP 3783, ICP 4725, ICP 7035, ICP 7239, ICP 7281, ICP 7349, ICP 7403, ICP 7867, ICP 8116, ICP 8117, ICP 8850, ICP 8853, ICP 8861 and ICP 11278 maintained resistance to both the isolates.

Genetics of resistance

The susceptible control planted along with test materials, exhibited 100 per cent infection. ICP 7035, ICP 7349 and ICP 8850 were 100 per cent resistant to both isolates with no apparent symptoms, while the susceptible parent ICP 8863, exhibited 100 per cent severe mosaic symptoms.

Genetics of resistance to isolate 1

The reactions of F_1 and F_2 generations of the three resistant x susceptible crosses for isolate 1 are presented in Table 2. The F_1's were all susceptible indicating the dominance of susceptibility over resistance. Similar observations on the dominance of susceptibility have also been reported (Singh et al., 1983; Sharma et al., 1984).

The F_2 segregation pattern of the resistant x susceptible crosses for isolate 1 revealed digenic ratios of 7 resistant: 9 susceptible for the crosses involving the resistant parents ICP 7035 and ICP 7349 with the susceptible parent ICP 8863. In contrast, for the cross ICP 8850 X ICP 8863, a monogenic segregation ratio of 1 resistant: 3 susceptible was obtained. The backcrosses corroborated the segregation pattern of F_2 generation. The resistant parents, ICP 7035 and ICP 7349, thus appeared to differ from the susceptible parent, ICP 8863 in respect of two gene pairs while, the resistant parent, ICP 8850 and the susceptible, ICP 8863 differed in respect of a single gene pair. Similar variation in the number of genes governing the resistance trait, depending on the cross involved, has also been reported earlier (Singh et al., 1983; Sharma et al., 1984) for the disease.

These F_2 segregation ratios of 3:1 in certain crosses and 9:7 in other resistant x susceptible crosses coupled with the dominance of susceptibility over resistance observed for isolate 1 might have resulted from two recessive genes governing resistance. However, either pair of alleles governing resistance would be enough to confer resistance to the isolate. When a cross involving a resistant parent segregates for one of the genes, a monogenic ratio of 3 susceptible: 1 resistant is obtained. However, when parents differ by two genes, a digenic ratio of 9 susceptible: 7 resistant is obtained because of the complementary nature of the genes involved. It is therefore postulated that resistance to isolate 1 is under the control of two independent loci exhibiting complementary gene action. If locus 1 or 2 or both occur in homozygous recessive state, resistance reaction occurs while, dominant condition at both loci invariably results in susceptibility. Accordingly, resistance is dependent on the presence of recessive alleles at least at one locus.

Genetics of resistance to isolate 2

The reactions of F_1 and F_2 generations of the three resistant x susceptible crosses for isolate 2 are presented in Table 3. Dominance of resistance over susceptibility was observed in the F_1 generation of resistant x susceptible crosses involving the resistant parents ICP 7035 and ICP 7349, while susceptibility was dominant in the F_1 generation of resistant x susceptible cross involving the resistant parent, ICP 8850. A similar variation among different crosses in the dominance relationships of sterility mosaic disease reactions has been reported by Sharma et al., (1984).

An F_2 segregation ratio of 3 resistant: 1 susceptible was recorded (Table 3) for crosses of ICP 7035 and ICP 7349 with ICP 8863, while the cross ICP 8850 X ICP 8863 recorded 1 resistant: 3 susceptible segregation ratio. The behavior of F_1's and F_2's suggested that ICP 7035, ICP 7349 and ICP 8850 differed from the susceptible parent ICP 8863 in respect of a single gene pair. The F_2 segregation ratios of 3 resistant: 1 susceptible in crosses involving the resistant parents ICP 7035 and ICP 7349 and 1 resistant: 3 susceptible with ICP 8850 as the resistant parent indicated the presence of multiple alleles. At least three allelic forms are present with the dominance relationship of $a_1 > a_2 > a_3$. The alleles a_1 and a_3 appear to be responsible for resistance, while the allele a_2 results in susceptibility. ICP 7035 and

Table 2. Reaction of parents, F_1, F_2 and backcross generations of resistant x susceptible crosses of pigeonpea for isolate 1 of the sterility mosaic pathogen at IAC, Patancheru, Andhra Pradesh, India

Generation	Total plants	Observed frequencies		Expected frequencies		Ratio R:S	X^2	Probability
		resistant plants (R)	susceptible plants (S)	resistant plants (R)	susceptible plants (S)			
ICP 7035 x ICP 8863								
ICP 7035	23	23	–	23	–	–	–	–
ICP 8863	42	–	42	–	42	–	–	–
F_1	10	–	10	–	10	–	–	–
F_2	265	112	153	115.94	149.06	7:9	0.2380	0.50-0
BC_1 *	94	67	27	70.5	23.5	3:1	0.6950	0.30
BC_2 **	85	–	85	–	85	–	–	–
ICP 7349 x ICP 8863								
ICP 7349	27	27	–	27	–	–	–	–
ICP 8863	42	–	42	–	42	–	–	–
F_1	7	–	7	–	7	–	–	–
F_2	281	117	164	122.94	158.06	7:9	0.5102	0.30-0
BC_1 *	115	84	31	86.25	28.75	3:1	0.2348	0.50
BC_2 **	108	1	107	–	108	–	–	–
ICP 8850 x ICP 8863								
ICP 8850	33	33	–	33	–	–	–	–
ICP 8863	42	–	42	–	42	–	–	–
F_1	12	–	12	–	12	–	–	–
F_2	252	57	195	63	189	1:3	1.0175	0.30-0
BC_1 *	124	68	56	62	62	1:1	1.1613	0.20
BC_2 **	92	2	90	–	92	–	–	–

* Backcross with the respective resistant parent.
** Backcross with the susceptible parent, ICP 8863.

ICP 7349 appear to possess the a_1 allele for resistance, while ICP 8850 possesses the a_3 allele for resistance. Further, the susceptible parent, ICP 8863, possessed the a_2 allele for susceptibility, thus explaining the differential reaction of the F_1's and F_2's. These observations were further confirmed in the study of resistant x resistant cross combinations (Table 4) wherein no segregation was observed, indicating the role of same locus for resistance in the parents.

Comparative study

Inheritance pattern of resistance to the two isolates revealed a variation in the F_1 reaction of the same cross. The F_1's of ICP 7035 X ICP 8863 and ICP 7349 X ICP 8863 were susceptible to isolate 1 but were resistant to isolate 2. A similar variation in the F_1 reaction of the same cross with the race involved has been reported (Luthra et al., 1967) in studies on inheritance of resistance to races of leaf rust in the wheat variety Bowie. F_1's of the cross Bowie X N.P.770 were resistant to Race 10 and Race 20 of leaf rust, but susceptible to Race 77. Similarly dominance of susceptibility was observed to biotype-1 of gall midge in rice as against the dominance of resistance to biotype-4 in crosses involving the same resistant donor Banglei (Prasad et al., 1992).

The F_2 generation of the crosses involving the resistant parents ICP 7035 and ICP 7349 segregated in a digenic ratio of 7 resistant: 9 susceptible, indicating the presence of two independent non-allelic genes exhibiting complementary gene action for isolate 1 while, for isolate 2, they segregated in a monogenic ratio of 3 resistant: 1 susceptible, indicating the role of a single dominant gene in governing the resistance reaction. A similar variation in the number of genes governing disease reaction in the same cross with the strain involved has been reported in studies on 'Genetics of resistance

Table 3. Reaction of parents, F_1 and F_2 generations of resistant x susceptible crosses of pigeonpea for isolate 2 of the sterility mosaic pathogen at IAC, Patancheru, Andhra Pradesh, India

Generation	Total plants	Observed frequencies		Expected frequencies		Ratio R:S	X^2	Probability
		resistant plants (R)	susceptible plants (S)	resistant plants (R)	susceptible plants (S)			
ICP 7035 x ICP 8863								
ICP 7035	27	27	–	27	–	–	–	–
ICP 8863	34	–	34	–	34	–	–	–
F_1	11	11	–	11	–	–	–	–
F_2	284	211	73	213	71	3:1	0.0751	0.70-0.80
ICP 7349 x ICP 8863								
ICP 7349	24	24	–	24	–	–	–	–
ICP 8863	34	–	34	–	34	–	–	–
F_1	16	16	–	16	–	–	–	–
F_2	278	211	67	208.5	69.5	3:1	0.1199	0.70-0.80
ICP 8850 x ICP 8863								
ICP 8850	29	29	–	29	–	–	–	–
ICP 8863	34	–	34	–	34	–	–	–
F_1	11	–	11	–	11	–	–	–
F_2	367	97	270	91.75	275.25	1:3	0.4005	0.50-0.70

Table 4. Reaction of parents, F_1 and F_2 generations of resistant x resistant crosses of pigeonpea for isolate 2 of the sterility mosaic pathogen at IAC, Patancheru, Andhra Pradesh, India

Generation	Total plants	Observed frequencies		Expected frequencies		Ratio R:S	X^2	Probability
		resistant plants (R)	susceptible plants (S)	resistant plants (R)	susceptible plants (S)			
ICP 7035 x ICP 7349								
ICP 7035	27	27	–	27	–	–	–	–
ICP 7349	24	24	–	24	–	–	–	–
F_1	22	22	–	22	–	–	–	–
F_2	297	296	1	297	–	–	–	–
ICP 7035 x ICP 8850								
ICP 7035	27	27	–	27	–	–	–	–
ICP 8850	29	29	–	29	–	–	–	–
F_1	14	14	–	14	–	–	–	–
F_2	457	450	7	297	–	–	–	–
ICP 7349 x ICP 8850								
ICP 7035	24	24	–	24	–	–	–	–
ICP 8850	29	29	–	29	–	–	–	–
F_1	18	18	–	18	–	–	–	–
F_2	350	339	11	350	–	–	–	–

to five strains of turnip mosaic virus in chinese cabbage' (Suh et al., 1995). The cross between inbred chinese cabbage lines, 'SSD31' and 'O-2' resulted in digenic inheritance of resistance to strain C 1 and monogenic inheritance to strains C 3 and C 5.

The F_2 segregation pattern of the cross ICP 8850 X ICP 8863 (1 resistant: 3 susceptible) did not, however, vary with the isolate and monogenic inheritance of resistance was observed for both isolates. The inheritance of resistance to C 2, C 3 and C 5 strains of turnip mosaic virus also did not vary with the strain in the cross, Seoul X O-2 (Suh et al., 1995).

A detailed study involving all possible cross combinations is needed to classify the parents based on allelic relationship for the two isolates. Screening against both isolates and characterization of all available resistant sources for allelic relationship would be of immense value in breeding of diverse sterility mosaic resistant cultivars with broad genetic base.

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