GENETICS OF RESISTANCE TO STERILITY MOSAIC DISEASE OF PIGEONPEA (*Cajanus cajan* (L.) Millsp.)

By
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CERTIFICATE

Mr. T. Srinivas has satisfactorily prosecuted the course of research and that the thesis entitled "GENETICS OF RESISTANCE TO STERILITY MOSAIC DISEASE IN PIGEONPEA (*Cajanus cajan* (L.) Millsp.)" submitted is the result of original research work and is of sufficiently high standard to warrant its presentation to the examination. I also certify that the thesis or part thereof has not been previously submitted by him for a degree of any University.

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This is to certify that the thesis entitled "GENETICS OF RESISTANCE TO STERILITY MOSAIC DISEASE IN PIGEONPEA (*Cajanus cajan* (L.) Millsp.)" submitted in partial fulfillment of the requirements for the degree of 'Doctor of Philosophy in Agriculture' of Andhra Pradesh Agricultural University, Hyderabad is a record of bonafide research work carried out by Mr. T. Srinivas under my guidance and supervision. The subject of the thesis has been approved by the Student's Advisory Committee.

No part of the thesis has been submitted for any other degree or diploma. The published part has been fully acknowledged. All assistance and help received during the course of the investigations has been duly acknowledged by the author of the thesis.

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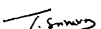
(T. SRINIVAS)

DECLARATION

I, T. Srinivas, hereby declare that the thesis entitled "GENETICS OF RESISTANCE TO STERILITY MOSAIC DISEASE IN PIGEONPEA (*Cajanus cajan* (L.) Millsp.)" is a result of the original research work done by me. It is further declared that the thesis or any part thereof has not been published earlier in any manner.



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ABSTRACT

Investigations on genetics of resistance to sterility mosaic (SM) disease in pigeonpea were carried out (1993-96) at ICRISAT Asia Center, Patancheru, India, to determine the inheritance of resistance for three different isolates of pigeonpea sterility mosaic pathogen and to study the combining ability of few resistant and tolerant lines

In this direction, available lines (resistant/tolerant) were screened against two isolates of the SM pathogen Breakdown of resistance was noticed in several lines, against isolate 2 of the pathogen However, few lines resistant and tolerant to both the isolates were identified

Inheritance of resistance and tolerance, in few of these lines was investigated Screening was carried out in pots, using leaf-stapling technique for isolates 1 and 3 and infector-hedge, for isolate 2 Observations in F_1 and segregating generations indicated the recessive nature of resistance and role of two independent non-allelic genes for isolates 1 and 3 Resistance against these isolates appeared to be dependent on the presence of recessive alleles, at least at one of the loci However, against isolate 2 resistance was observed recessive in some crosses and dominant in other crosses Further disease reaction for isolate 2, appeared to be governed by two independent non-allelic genes with at least three multiple alleles, at one of the loci

Combining ability studies of the resistant, tolerant and susceptible lines included in the inheritance studies, were carried out with line x tester mating design, involving two male steriles and eleven pollen parents The analysis of variance revealed significant differences for parents, hybrids, parents vs hybrids and males, for all characters studied Pre-ponderance of non-additive gene action was recorded for yield and all yield component characters studied

ICP MS288 female was found to be a good combiner for early maturity, dwarf and compact growth habit while ICP MS3783 tolerant to isolate 1 of pigeonpea sterility mosaic pathogen and wilt disease was better combiner for seed yield, pods per plant, test weight, primary and secondary branches Among the males, LRG 30 recorded high general combining ability, for seed yield and majority of yield components The sterility mosaic resistant parents were however, poor combiners for yield and majority of the component characters

The expression of heterosis was most evident for yield per plant, pods per plant and number of secondary branches It was maximum in mid-late x medium crosses, followed by early x medium crosses Significant and desirable *sca* effects were also recorded in several hybrids, for various traits studied Crosses with high *sca* effects for yield, were further found associated with high and desirable *sca* effects for most component characters The studies on variability, heritability, genetic advance, character associations and path analysis had also indicated the need for selection based on component characters such as pods per plant and plant height

Four promising hybrids (ICP MS288 X ICP 7349, ICP MS3783 X BDN 1 ICP MS3783 X LRG 30 ICP MS3783 X ICP 8863) were identified, in the present study, based on their *per se* performance heterosis and *sca* effects Of these, ICP MS3783 X BDN 1, ICP MS3783 X LRG 30 and ICP MS3783 X ICP 8863 crosses, involved parents with high *gca* effects, indicating the role of fixable additive x additive gene interactions These may hence be advanced through conventional breeding procedures coupled with screening and selection for resistance, pods per plant and plant height towards development of high yielding disease resistant cultivars

LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
CD	Critical difference
cm	Centimeter
DAS	Days after sowing
g	Grams
gca	General combining ability
GCV	Genotypic coefficient of variation
ha	Hectare
Kg	Kilogram
PCV	Phenotypic coefficient of variation
SE	Standard error
sca	Specific combining ability
SM	Sterility mosaic

INTRODUCTION

CHAPTER I

INTRODUCTION

Pigeonpea (*Cajanus cajan* (L.) Millspaugh) is one of the major pulse crops of the tropics and subtropics. It is widely grown in the Indian subcontinent, which accounts for almost 90 per cent of the world's crop (Nene and Shiela, 1990). In India, it is grown in almost all states, but the major concentration is in the state of Uttar Pradesh in northern India, eastern parts of Gujarat and Maharashtra and north-eastern parts of Karnataka in Western India, and western parts of Madhya Pradesh in central India (Fig.1). It is widely used as a pulse, green vegetable, fodder, and for a variety of other purposes (Nene and Shiela, 1990). The seed protein content of pigeonpea (21%) compares well with that of other important grain legumes. The average yields of the crop are however, very low (750 Kg ha^{-1}). High sensitivity of the crop to the attack of insect-pests and diseases appears to be the main reason for such disappointingly low yields.

The crop is attacked by more than 100 pathogens (Nene *et al.*, 1996) including fungi, bacteria, viruses, mycoplasma like organisms and nematodes. However, only a few of them cause economic losses (Kannaiyan *et al.*, 1984). The diseases of considerable economic importance at present are sterility mosaic (SM), Fusarium wilt, Phytophthora blight (PB), Macrophomina root rot and stem canker, and Alternaria blight in the Indian subcontinent.

Sterility mosaic is the most important disease of pigeonpea in India and at times can cause yield losses upto 95 per cent (Reddy and Nene, 1981). An annual loss of 205,000 tonnes of grains, valued at Rs. 676.5 millions is estimated due to the disease (Kannaiyan *et al.*, 1984). The disease was first reported from Pusa in Bihar in India (Mitra, 1931). However, of late, it has posed a serious threat to the successful cultivation of pigeonpea in several parts of India (Lal *et al.*, 1981). It is present in all major pigeonpea producing states and is a serious problem in north eastern (Bihar and Uttar Pradesh), and southern (Tamil Nadu) states (Kannaiyan *et al.*, 1984). Prevalence of the disease in various states of India is presented in Fig. 2. No satisfactory cultural control has been found so far, to protect the crop from this disease (Singh

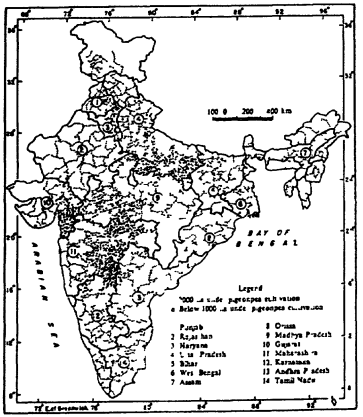


Fig 1 Distribution of pigeonpea in Ind a (1979 80)
Source : Data from Governme t of India (Ministry of Agriculture) 1981

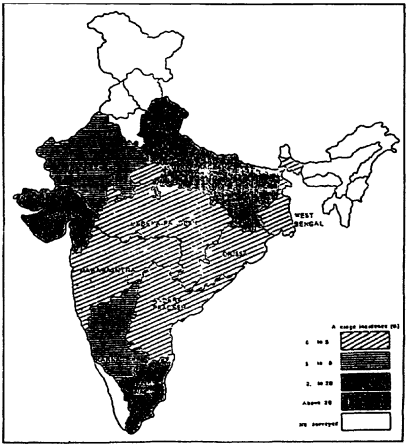


Fig 2 Prevalence of pigeonpea sterility mosaic disease in different states of India (1975 80)
Source : Kannaiyan et al (1984)

et al, 1983) Further, chemical methods of control, while effective are not considered economical (Nene *et al*, 1989) Therefore, breeding of resistant varieties, recognized as the most effective and economic method of reducing crop losses (Stakman and Harrar, 1957) has received high priority for the disease

Development of resistant pigeonpea cultivars against the disease was first initiated by Alam (1931) Systematic resistance breeding was later initiated at ICRISAT, Patancheru, India in 1975, and several resistant and tolerant source(s) for the disease were identified (Nene *et al*, 1981) The genetics of resistance for the disease was also worked out (Singh *et al*, 1983 , Sharma *et al*, 1984) However, the task of developing resistant varieties has been complicated in view of the reported genetic plasticity of the pathogen The presence of strains of SM pathogen of varying virulence was reported by Nene *et al* (1989), based on the results of multi-location pigeonpea trials Lines resistant at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru broke down, when grown at other locations within India A comprehensive study of the phenomena, by Reddy *et al* (1993) over a period of four consecutive years, using a set of seven differentials at nine different locations in India, revealed the occurrence of five different variants of the sterility mosaic pathogen of pigeonpea in India

The foregoing knowledge, on the dynamic nature of sterility mosaic pathogen has warranted the identification and use of strain-specific sources of resistance in crop improvement programs Further, it has also necessitated studies on genetics of strain-specific resistance to aid resistance breeding programs

Pigeonpea improvement programs aimed at evolving high yielding disease resistant varieties may be carried out effectively if information is available on combining ability of the recipient and donor parents This is more so, in the case of sterility mosaic disease, since most of the donors are poor yielders Application of line x tester mating design (Kempthorne 1957) was suggested for pigeonpea (Green *et al*, 1979) to obtain information on the combining ability of the lines involved, for traits of economic importance towards identification of potential parents and cross combinations Further, owing to the existence of male sterility (Reddy *et al*, 1979 , Wallis *et al*, 1981) and a considerable degree of natural out-crossing (Green *et al*, 1979 , Onim, 1981), evaluation of a large number of lines, for their combining ability has become possible, adopting the line x tester mating design

An understanding of the nature and magnitude of existing variability for important yield contributing characters is also necessary for a successful breeding program (Singh *et al*, 1995) Selection for yield *per se* generally remains unsuccessful in achieving desirable results, because yield is dependent on its various component characters Therefore, knowledge of association and cause and effect relationship of yield component traits with yield would help in formulating effective selection schemes (Talwar and Joshi, 1983)

The present investigation was hence undertaken with the following objectives

1 To determine the genetics of strain-specific resistance for sterility mosaic pathogen of pigeonpea
2 To study the combining ability of few resistant and tolerant cultivars
3 To study the nature and extent of genetic variation and character associations for yield and other economic traits
4 To suggest a suitable breeding strategy for exploitation of the material towards development of high yielding resistant varieties

REVIEW OF LITERATURE

CHAPTER II

REVIEW OF LITERATURE

A brief review of the relevant literature for the present investigation is presented hereunder.

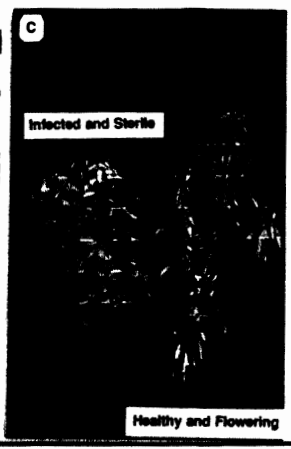
2.1 GEOGRAPHICAL DISTRIBUTION, SYMPTOMS AND ECONOMIC IMPORTANCE

The disease was first reported from Pusa in Bihar, India (Mitra, 1931). Subsequently, it was reported from Tamil Nadu, Maharashtra, Gujarat, Punjab and Uttar Pradesh states (Capoor, 1952). Now, the disease is known to occur in all major pigeonpea producing states of India and is a serious problem in north-eastern (Bihar and Uttar Pradesh) and southern (Tamil Nadu) states (Kannaiyan *et al.*, 1984). Its incidence in farmer's field is reported to vary between 0 and 100 per cent. The disease has also been reported from Bangladesh, Nepal and Thailand (Nene *et al.*, 1989), Myanmar (Su, 1931) and Sri Lanka (Newton and Peiris, 1953).

The disease, characterized by proliferation, mosaic symptoms, stunting, cessation of reproductive growth and a reduction in the size of the leaflets (Plate 1A), is transmitted by an eriophyid mite vector, *Aceria cajani* Channabasavanna (Plate 1B). It results in sterility of the plant (Plate 1C), which directly affects the yield. Alam (1933) reported a negative correlation between the degree of sterility and yield.

Reddy and Nene (1980) made a systematic study on the estimation of yield loss in pigeonpea due to sterility mosaic. They found 95 per cent yield loss when the plants got infected at seedling stage. The susceptibility of plants decreased with age. However, infection upto 45 days after planting mostly resulted in complete sterility. The number of secondary and tertiary branches increased along with prolonged duration of crop when the plants were infected at early stages. The yield loss also varied with the genotype. Some genotypes, such as ICP 2376, that exhibited ring spot symptoms did not show any sterility and suffered no obvious yield loss while, genotypes such as NP(WR) 15, that developed mild mosaic symptoms, were partially sterile and their yield loss was less (19-64%). The disease incidence was usually

Plate 1 Sterility mosaic disease of pigeonpea



higher in ratooned and perennial pigeonpea Losses from sterility mosaic in India are about double those from wilt (*Fusarium udum*) the second most important disease amounting to 205 000 tons annually valued at Rs 676 5 millions (Kannaiyan *et al* 1984)

2.2 PATHOGENIC VARIABILITY

The pathogen causing the disease may be a virus (Capoor 1952) but its exact identity is yet to be established (Reddy *et al* 1990) Possibility of more than one strain of pigeonpea sterility mosaic pathogen has long been suspected on the basis of differential disease reactions observed on some host genotypes in the multi location trials (Nene *et al* 1989) Lines resistant at ICRISAT Patancheru India had broken down when grown at other locations within India Virulence of SM isolates from Bangalore Dholi Vamban and Varanasi was higher compared to those at Badnapur Hyderabad Pantnagar Kanpur Ludhiana and Faizabad

A virulent form of the Patancheru strain of SM pathogen was noticed in the wilt and sterility mosaic screening nursery at ICRISAT Center Patancheru India during 1990/1991 rainy season (Reddy *et al* 1991) It was identified based on the altered reaction of ICP 2376 Ring spot symptoms that had been consistently observed on the line in the screening nurseries between 1975 and 1990 turned to severe mosaic in 1991 Resistance also broke down in few other pigeonpea cultivars against the new isolate

A comprehensive study of variability in the SM pathogen of pigeonpea was taken up between 1987 and 1990 to clarify the differential reactions and breakdown of resistance noticed in multi location trials (Reddy *et al* 1993) The study involved sixteen pigeonpea genotypes tested for their reaction to isolates of the sterility mosaic pathogen from nine disease endemic locations in India Differential reaction of seven genotypes (Table 1) noticed in 51 field and pot tests was used to categorize the nine isolates into five distinct groups The isolate from Gwalior was designated as variant 1 Badnapur and Patancheru isolates as variant 2 Coimbatore Kumargunj and Pudukottai isolates as variant 3 Bangalore and Dholi isolates as variant 4 and Kanpur isolate as variant 5 Thus five different variants of the sterility mosaic pathogen were reported to occur in India Further a comparison of the strains of sterility mosaic pathogen of

pigeonpea, in Nepal and India (Chaurasia, 1993), using a set of five differentials (Table 2), revealed differences in the strains of SM, prevalent at ICRISAT Center, India and Nepalganj, Nepal.

Table 1 Reaction of pigeonpea differential genotypes to variants of sterility mosaic pathogen in India (1987-1990)

Pigeonpea genotypes	Sterility mosaic reaction				
	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5
ICP 2376	R	RS	S	S	S
ICP 7035	R	R	R	R	S
ICP 8862	R	R	R	R	S
ICP 8863	S	S	S	S	S
ICP 10976	R	RS	R	R	S
ICP 10984	R	R	R	S	R
ICP 11146	R	R	R	S	S
Isolates	**Gwalior**	**Badnapur, Patancheru**	**Coimbatore, Kumargunj, Pudukottai**	**Bangalore, Dholi**	**Kanpur**

R = Resistant (No symptoms) S = Susceptible (Mosaic symptoms), RS = Ring spot symptoms

Table 2 Sterility mosaic reaction of five pigeonpea lines at Nepalganj, Nepal and ICRISAT Center, India

Differential line	ICRISAT isolate	Nepalganj isolate
ICP 2376	RS	M
ICP 7035	R	R
ICP 8862	R	M
ICP 8863	M	M
ICP 10976	RS	M

RS = Ring spot, R = Resistant, M = Mosaic

2.3 IDENTIFICATION OF SOURCES OF RESISTANCE

Alam (1933), was the first to make observations on resistance to sterility mosaic. He reported

Sabour 2E (Arhar) and some other Sabour types of pigeonpea to be resistant Kandaswamy and Ramakrishnan (1960) reported all 176 pigeonpea varieties grown at Coimbatore as susceptible to the disease Seth (1965) suggested *Atylosia* I W 1431 as a promising material for incorporation of resistance into pigeonpea cultivars

Ramakrishnan and Kandaswamy (1972) identified NP(WR) 15 P 1100 P 1289 P 1778 P 2621 A and P 4834 lines as tolerant However they were unable to identify good sources of resistance out of 4514 collections tested Further Janarthan *et al* (1972) tested 18 varieties and found them susceptible to the disease Similarly Subramanian *et al* (1973) found all 549 pigeonpea lines tested as susceptible to sterility mosaic Further as many as 234 germplasm lines were evaluated for their reaction to sterility mosaic during 1973 74 at Ludhiana (Singh *et al* 1975) Out of these L 3 and P 47895 were found resistant while 16 others were tolerant Rathi (1977) reported lines P 4785 and L 26 as resistant but L 3 as susceptible

Systematic efforts were initiated at ICRISAT Center in 1975 (Nene and Reddy 1976b) About three thousand accessions were screened for resistance to sterility mosaic (Nene and Reddy 1976a b) Five pigeonpea lines ICP 2376 3783 6497 7035 7119 were identified as immune Rathi (1977) found ICRISAT lines ICP 3783 5444 6497 7035 7119 and Pantnagar lines Pant B 76 Pant B 77 and E 41 free from disease Rathi (1980) screened germplasm lines in sterility mosaic sick plot and identified 25 resistant lines

Nene *et al* (1980) reviewed the work on resistance of pigeonpea to sterility mosaic carried out at ICRISAT A total of 7555 germplasm lines and 10 *Atylosia* species were screened for resistance to sterility mosaic at ICRISAT Center during 1975 80 Of these 66 resistant lines were identified directly from germplasm 433 resistant lines were developed through single plant selections and 54 lines were identified tolerant One *Atylosia* species (*A volubilis*) was found to be resistant Thirty five lines were found to be resistant at more than one location Venkateswarlu *et al* (1980) identified 28 pigeonpea lines free from sterility mosaic out of 90 lines tested Gupta *et al* (1981) identified 15 sterility mosaic resistant early maturing lines (upto 140 days) with higher yield Zote and Dandanaik (1986) identified six resistant and two tolerant (ring spot) lines among 22 lines screened against sterility mosaic during 1981 84 at Badnapur

India

In field screening trials (Kusum Dwivedi and Shukla 1986) with 20 cultivars exposed to natural infection of sterility mosaic three lines were observed tolerant with localized ring spots on the leaves Four lines were found moderately susceptible while the rest were susceptible Field screening with infector rows, for resistance to pigeonpea sterility mosaic was taken up with 591 lines (Gurdip Singh *et al* 1987) Seven early, six medium and thirty late maturing lines were observed resistant and free from infection While, another 16, early and 10 late lines had 10 per cent or less disease incidence

In field trials with 150 lines showing 0 100 per cent infection (Gupta *et al* 1988) 24 were reported resistant, 34 moderately resistant and 32 tolerant while the remainder were highly susceptible Gupta *et al* (1988) also screened 162 lines of pigeonpea for resistance to sterility mosaic during the rainy season of 1984-87, under artificial epiphytotic conditions Nine lines were immune while three were moderately resistant

Among 172 local and exotic accessions screened for resistance to pigeonpea sterility mosaic (Onkar Singh *et al* 1989) only one of local origin was completely free from infection while another, showed symptoms in only 5 per cent of the plants in Nepal Seven promising lines showed disease incidence ranging from 16 2 to 50 per cent Further of 43 advanced germplasm lines screened with artificial inoculation for resistance to pigeonpea sterility mosaic (Mishra and Prasad 1989) six belonging to the late maturity group were found free from infection while five lines showed less than 5 per cent infection Three lines, ICP 786 10976 and 10977 were resistant across 10 different locations tested within India (Nene *et al* 1989) Screening of 240 advanced breeding/ germplasm lines by hedge and leaf stapling inoculation was taken up by Chauhan *et al* (1991) and lines 124B and 125B were found tolerant while lines 134B and $124B_2$ were found resistant along with other 19 lines that were free from disease

A total of 141 germplasm accessions and 725 breeding lines of pigeonpea were evaluated for resistance to sterility mosaic (Amin *et al* 1993) at 13 different locations in India from 1983-84 to 1989-90 The trials were artificially inoculated by either leaf-stapling or infector-hedge method The line ICP 7035 was found resistant at 12 locations while 18 other lines were observed resistant at 10 locations

The above screening for resistance to sterility mosaic were not against any specific strain of the disease However in view of the reported genetic plasticity of the sterility mosaic pathogen in India (Nene *et al* 1989 Reddy *et al* 1991 Reddy *et al* 1993) the need for screening against specific strains of the SM disease became apparent In this direction 153 lines reported resistant/tolerant (Nene *et al* 1981) were screened against two different strains of the disease identified by Reddy *et al* (1991) at ICRISAT The results indicated resistance for SM disease to be strain specific Only 37 lines were found resistant to variant 2 while 17 lines were resistant to variant 3 Fifteen lines were found resistant to both variants (Srinivas and Reddy 1995)

2 4 GENETICS OF RESISTANCE

Resistance or susceptibility of a crop to a particular pathogen is the manifestation of host parasite interaction controlled by the co evolving genetic systems of both the host and parasite In centers of origin and crop diversity host population contains a wide spectrum of protective mechanisms that ensure survival against a high diversity of pathogenicity in the parasite This results in a host/parasite equilibrium and most of the host genotypes have some degree of resistance against the parasite However in new areas of crop adaptation and intensive cultivation of a particular genotype genes for virulence to overcome the narrow genetic base of the host are favored causing susceptibility in the new cultivar In the past pigeonpea cultivation in India and areas of Africa and Latin America had been confined to subsistence agriculture based on adapted landraces The development of improved varieties by hybridization and selection under experimental conditions and cultivation in intensive production systems under irrigated conditions is a relatively recent phenomenon which has upset the delicate host/parasite equilibrium favoring the outbreak of diseases such as sterility mosaic For planned disease management it is essential that genetic systems operating in a given host/pathogen environment are well understood At present studies on genetics of disease resistance in pigeonpea are limited and preliminary

Studies on inheritance of resistance to sterility mosaic disease of pigeonpea are also few and limited Singh *et al* (1983) studied the inheritance of resistance to sterility mosaic in 15 crosses involving

five resistant and three susceptible genotypes F_1 F_2 BC_1 and BC_2 generations were studied Resistance was under the control of four independent non allelic genes The symbols Sv_1 Sv_2 sv_3 and sv_4 were assigned to the four resistance genes Sv_1 and Sv_2 were reported to exhibit duplicate dominant epistasis while, sv_3 and sv_4 exhibited duplicate recessive epistasis It was further concluded that presence of at least one dominant allele at locus 1 or 2 and homozygous recessive genes at locus 3 or 4 were essential for resistance reaction

The influence of extra nuclear factors in the control of sterility mosaic resistance was reported by Sivasubramanian *et al* (1983) based on observations of reciprocal differences in the study of F_1 and F_2 of CO-3 X ICP 4782 cross

Inheritance of resistance and allelic relationships for the disease were also studied by Sharma *et al* (1984) in pigeonpea crosses involving susceptible tolerant (ring spot) and resistant genotypes F_1 and F_2 generations were studied Dominance of susceptibility over resistance and tolerance was noticed in all crosses Resistant lines were however reported to differ in the expression of their resistance in crosses with tolerant genotypes Tolerance was found dominant over resistance of certain lines in few crosses, while it was recessive to resistance in other lines In crosses between resistant and susceptible lines 9 7 and 3 1 segregation ratios were observed The disease reaction in F_1 and segregation in F_2 was explained on the basis of two genes and more than two alleles per locus Inheritance of resistance to sterility mosaic was reported to be complicated and determined by multiple allelic series

The control of resistance trait by non allelic interaction of two factors was reported by Amala Balu and Rathnaswamy (*Personal Communication*) They studied F_1 and F_2 generations of four cross combinations involving two susceptible male steriles viz MS Prabhat (DT) and MS CO 5 and two resistant parents, ICPL 83024 and ICPL 83027 F_1 s were all susceptible indicating dominance of susceptibility over resistance while, F_2 s segregated in 13 susceptible 3 resistant ratio

The above inheritance studies have little significance in the wake of reports of variability in the sterility mosaic pathogen Studies on genetics of strain-specific resistance for the disease are necessary However, such studies are lacking for pigeonpea sterility mosaic

2.5 HETEROSIS AND COMBINING ABILITY

The selection of suitable parents is important in a breeding program particularly if the aim is to improve a quantitative character such as yield The *per se* performance of a parent need not necessarily be a good indicator Therefore gathering information on the nature of gene effects and their expression in terms of combining ability is necessary Further heterosis has been extensively used to realize substantial yield gains in crops like maize sorghum bajra cotton and castor Considerable extent of heterosis for yield and other traits has been reported in many legumes (Singh 1974) including pigeonpea (Saxena *et al*, 1986 Saxena *et al* 1989 Zaveri *et al* 1989) A brief review of the relevant literature is presented hereunder

2.5.1 Heterosis

The term "Heterosis was coined by Shull (1914) to refer to the phenomenon in which the F_1 obtained by crossing two genotically dissimilar individuals showed an increase or decrease in vigor over the mid-parent value The term heterobeltiosis was proposed later (Bitzer *et al* 1968 Fonesca and Patterson 1968) to denote the expression of heterosis over better parent

The potency of heterosis breeding is enormous in terms of increasing the productivity of crop plants It has already become popular in the breeding of cross pollinated crops like maize millet, onion sugarbeet and sunflower and is increasingly being utilized for enhancing the productivity of self-pollinated crops (Rai, 1979)

The discovery of heterosis in chickpea (Pal 1945) opened the way for heterosis breeding in pulses Varying degrees of heterosis with respect to yield and yield components have been observed in several pulse crops

Solomon *et al* (1957) were the first to report hybrid vigor in pigeonpea for grain yield A wide range of heterosis is also present for almost all characters in pigeonpea The range in percentage of mid and better parent and standard hetero is for different characters is presented in Table 3 The expression of heterosis is most evident for plant height branch number pod number plant spread and cluster number (Veeraswamy *et al* 1973) A mean heterosis of 80 per cent for number of pods per plant was reported

Table 3 Range of mid-parent better parent and standard heterosis for yield and yield component characters in pigeonpea

Character	Mid-parent heterosis	Reference	Better parent heterosis	Reference	Standard heterosis	Reference
Days to flowering	9 4 to 18 1	Singh *et al* (1983)	0 00 to 65 90	Reddy *et al* (1979)		
	10 7 to 6 9	Cheralu *et al* (1989)	26 40 to 0 00	Cheralu *et al* (1989)	28 5 to 5 9	Cheralu *et al* (1989)
	20 2 to 21 4	Mehetre *et al* (1992)	18 4 to 60 0	Mehetre *et al* (1992)	3 63 to 10 75	Bajpai *et al* (1994)
Days to maturity	19 0 to 8 0	Singh *et al* (1983)	0 3 to 30 7	Reddy *et al* (1979)		
	8 50 to 22 30	Mehetre *et al* (1992)	17 0 to 26 2	Patel *et al* (1991)	23 9 to 23 7	Patel *et al* (1991)
			4 70 to 56 90	Mehetre *et al* (1992)	3 50 to 13 28	Bajpai *et al* (1994)
Plant height (cm)	6 2 to 30 1	Singh *et al* (1983)	61 1 to 16 3	Shrivastava *et al* (1976)		
	8 5 to 34 2	Cheralu *et al* (1989)	19 6 to 8 5	Cheralu *et al* (1989)	13 7 to 27 0	Cheralu *et al* (1989)
			9 7 to 76 1	Patel *et al* (1991)	13 7 to 50 3	Patel *et al* (1991)
	47 7 to 50 6	Mehetre *et al* (1992)	52 4 to 99 59	Mehetre *et al* (1992)	12 34 to 37 7	Bajpai *et al* (1994)
Number of primary branches	6 5 to 45 6	Singh *et al* (1983)				
Number of secondary branches			116 7 to 750 0	Shrivastava *et al* (1976)		
Pods per plant	58 4 to 185 1	Singh *et al* (1983)	55 6 to 315 5	Shrivastava *et al* (1976)		
			22 7 to 188 7	Reddy *et al* (1979)		
	0 5 to 46 5	Cheralu *et al* (1989)	6 8 to 17 1	Cheralu *et al* (1989)	4 8 to 37 0	Cheralu *et al* (1989)
			74 9 to 116 1	Patel *et al* (1991)	3 8 to 161 5	Patel *et al* (1991)
			57 04 to 169 31	Patel and Patel (1992)	68 3 to 73 25	Patel and Patel (1992)
	5 8 to 183 6	Mehetre *et al* (1992)	13 9 to 183 90	Mehetre *et al* (1992)	9 41 to 90 33	Bajpai *et al* (1994)
Seeds per pod	13 6 to 17 8	Singh *et al* (1983)	14 25 to 15 58	Patel and Patel (1992)	26 36 to 8 70	Patel and Patel (1992)
	17 2 to 66 0	Mehetre *et al* (1992)	26 8 to 26 7	Mehetre *et al* (1992)		
Yield per plant	95 0 to 221 0	Singh *et al* (1983)	48 0 to 301 4	Shrivastava *et al* (1976)		
			3 6 to 118 4	Reddy *et al* (1979)		
	4 0 to 51 00	Cheralu *et al* (1989)	13 4 to 21 0	Cheralu *et al* (1989)	17 0 to 54 0	Cheralu *et al* (1989)
			48 08 to 136 49	Patel and Patel (1992)	64 93 to 41 54	Patel and Patel (1992)
	26 0 to 193 5	Mehetre *et al* (1992)	41 6 to 168 4	Mehetre *et al* (1992)	42 4 to 185 42	Bajpai *et al* (1994)
100 seed weight	4 3 to 23 5	Singh *et al* (1983)	9 8 to 31 9	Shrivastava *et al* (1976)		
			50 8 to 1 4	Reddy *et al* (1979)		
			30 0 to 25 32	Patel and Patel (1992)	31 18 to 8 78	Patel and Patel (1992)
					1 2 to 17 63	Bajpai *et al* (1994)

(Shrivastava *et al.*, 1976) over the better parental values. Medium x medium and low x medium crosses were generally observed to result in high heterotic performance over the better parent.

The magnitude of heterosis for yield and related characters between crosses involving different maturity groups was investigated by Reddy *et al.* (1979). The study revealed negative heterosis over better parent for plant height, days to flower, days to maturity and seed weight while, heterosis for pod number and seed yield over better parent were generally positive. Yield as well as heterosis were found maximum in early x late and medium x late crosses involving diverse plant types. Hybrids based on mid-late parents were also reported to give higher hybrid vigor as compared to those with early parents (Patel,1988).

A considerable degree of heterosis was observed among a set of 63 hybrids derived through line x tester mating between three genetic male sterile lines and 21 short duration pollen parents, in respect of seed yield and component characters (Rao, 1989). The hybrids based on mid-late females recorded greater hybrid vigor compared to those based on early females. Significant standard heterosis with regards to yield, over C 11 parent for all hybrids studied, in a 5 x 5 diallel was reported by Cheralu *et al.* (1989).

Favorable heterosis for developmental traits such as plant height and number of days to 50 per cent flowering to complete maturity was also noticed for six early *Cajanus cajan* hybrids studied at Varnasi, India during 1987-88 (Singh *et al.*, 1989). Most of these hybrids were also heterotic for number of pods per plant. Positive heterosis for plant height, seeds per pod and seed yield was also recorded in 15 medium-duration hybrids, obtained from crosses between male-sterile ICP 3783 and 15 advanced breeding lines.

A high expression of heterosis for seed yield was recorded for a set of 45 hybrids (Rana, 1990) derived through line x tester mating between three genetic male sterile lines and 15 short duration pollen parents. The heterosis for seed yield was found associated with greater amount of heterosis for component characters like number of pods per plant, branches per plant and per day production.

The study of Patel (1990) involving 45 hybrids obtained from three male sterile lines and 15 medium duration pollinators, crossed in a line x tester fashion also revealed a profound degree of useful and significant heterosis for days to flowering, days to maturity, branches per plant, seeds per pod, seed yield per plant and per day production.

High heterosis for seed yield per plant due to high heterosis for pods per plant, plant height and branches per plant was noticed for 60 hybrids grown during 1985-86 (Patel *et al.*, 1991). Hybrids with two early parents were superior for early maturity but not for yield, while high heterotic hybrids had at least one medium maturing parent.

Patel and Patel (1992) indicated highest heterotic response for number of pods per plant, for 30 hybrids obtained from six diverse pigeonpea lines, crossed with five testers. It was followed by seed yield per plant. Mehetre *et al.* (1992) noticed significant and positive heterosis to an extent of 60 per cent for days to 50 per cent flowering and 56.9 per cent for days to maturity in their study of 9 x 9 diallel crosses of pigeonpea.

Significant heterosis of few determinate and indeterminate hybrids over checks (ICPH 8, UPAS 120 and Manak), for seed yield and yield component characters was recorded by Bajpai *et al.* (1994). Desirable relative heterosis for seed yield in 38 hybrids out of a total of 60 cross combinations was also reported by Sinha *et al.* (1994). Heterosis was also noticed for pods/cluster, pods per plant and 100-seed weight while, poor or negative heterosis was recorded for seeds per pod. Malik *et al.* (1995) reported low heterosis in cross combinations of pigeonpea involving less divergent parents. Crosses involving divergent parents also exhibited low or no heterosis when majority of the dominant alleles were present in one parent and majority of the recessive alleles in the other parent, coupled with the absence of overdominance.

2.5.2 Combining ability and gene action

The concepts of general and specific combining abilities were coined by Sprague and Tatum (1942). General combining ability (GCA) was defined as the average performance of a line in hybrid combinations, while specific combining ability (SCA) referred to those crosses, wherein certain hybrid combinations did relatively better or worse than was expected, on the basis of average performance of the lines involved.

Griffing (1956) pointed out the usefulness of information on the relative magnitude of additive and non-additive gene effects in designing an efficient breeding program. The information could be obtained through the study of combining ability, as variance due to GCA involved mostly additive gene action while

that, due to SCA involved dominance and epistatic components of genetic variances. The need to study combining ability in self-pollinated crops was stressed by Allard (1960).

Sidhu and Sandhu (1981) and Reddy *et al.* (1981) had summarized the results of studies on combining ability and gene action in pigeonpea. Yield in general appeared to be additively inherited (Green *et al.*, 1979). Pre-ponderance of additive gene action was also observed for majority of the traits (Sharma *et al.*, 1973b; Venkateswarlu and Singh, 1982; Lakhan *et al.*, 1986). The nature of gene action for various traits in pigeonpea as reported by different workers is summarized in Table 4. The estimates of *gca* effects of individual parental lines recorded a close agreement with ranking of the lines for such effects and ranking based on parental performance *per se* (Sharma *et al.*, 1973b; Venkateswarlu and Singh, 1982). The best cross between two parents was reported to be the one, chosen on the basis of low *gca* for flowering time and high *gca* for other traits (Dahiya and Brar, 1977). The *gca* effects for most characters were generally negative, for early and medium parents and positive for late groups (Reddy *et al.*, 1979). Specific medium x late and early x late cross combinations were reported more likely to yield recombinants of economic worth.

2.6 GENETIC VARIABILITY

The phenotypic expression of quantitative characters is a combination of the genotype, environment and their interaction. Further, progress of selection in a population is conditioned by the nature and magnitude of variation. A wide range of genetic variability is reported for virtually all important agronomic characters (Sharma and Green, 1977) in pigeonpea.

Bashiruddin and Sreeramulu (1981) reported high genotypic coefficient of variation (GCV) for 100-seed weight, cluster number and pod number, and low GCV for seed number. Highest estimates of GCV were also reported for pods per plant and seed yield per plant (Jag Shoran, 1985; Natarajan *et al.*, 1990; Holker *et al.*, 1991; Patel and Patel, 1992). High variability for pods per plant and low variability for seeds per pod was also reported by Sidhu *et al.* (1985). Moderate to high GCV values were reported for number of primary branches and secondary branches by Balyan and Sudhakar (1985). High GCV for number of

Table 4 Gene action for yield and yield component characters in pigeonpea

Character	Gene action(s)	Reference
Days to flowering	Additive	Pandey, 1972; Sharma *et al.* (1973a); Laxman Singh and Pandey (1974); Chaudhari *et al.* (1980); Venkateswarlu and Singh (1981); Reddy *et al.* (1981); Omanga *et al.* (1992)
	Non-additive	Dahiya and Brar (1977)
	Additive and non-additive	Sharma *et al.* (1973b)
Days to maturity	Additive	Sharma *et al.* (1972); Patel *et al.* (1992)
	Additive and non-additive	Sharma *et al.* (1973b); Lakhan *et al.* (1986); Ghodke *et al.* (1993)
Plant height	Additive	Laxman Singh and Pandey (1974); Ghodke *et al.* (1993)
	Non-additive	Pandey (1972)
	Additive and non-additive	Sharma *et al.* (1973b); Reddy *et al.* (1981); Lakhan *et al.* (1986)
Number of primary and secondary branches	Additive	Ghodke *et al.* (1993)
	Additive and non-additive	Reddy *et al.* (1981)
Pods per plant	Additive	Singh *et al.* (1983); Omanga *et al.* (1992); Ghodke *et al.* (1993)
	Non-additive	Reddy *et al.* (1979)
	Additive and non-additive	Venkateswarlu and Singh (1982); Lakhan *et al.* (1986)
Seeds per pod	Additive	Omanga *et al.* (1992)
	Additive and non-additive	Venkateswarlu and Singh (1982)
Yield per plant	Additive	Pandey (1972); Chaudhari *et al.* (1980); Omanga *et al.* (1992)
	Non-additive	Laxman Singh and Pandey (1974); Reddy *et al.* (1979); Singh *et al.* (1983); Patel *et al.* (1992)
	Additive and non-additive	Sharma *et al.* (1973b); Dahiya and Satija (1978); Reddy *et al.* (1981); Venkateswarlu and Singh (1982)
100-seed weight	Additive	Sharma *et al.* (1972); Patel *et al.* (1992)
	Non-additive	Singh *et al.* (1983); Reddy *et al.* (1979)
	Additive and non-additive	Venkateswarlu and Singh (1982); Ghodke *et al.* (1993)

branches per plant was also reported by Patil *et al.* (1989). Further, high GCV for days to maturity and plant height was reported by Saxena and Kataria (1993).

The traits, days to 50 per cent flowering and days to maturity were found to be less influenced by environment, in comparison to seed yield, seed size, seeds per pod, pods per plant and plant height (Sidhu *et al.*, 1985). Natarajan *et al.* (1990) reported minimum difference between phenotypic and genotypic coefficient of variations for 100-seed weight while, branch number and seed number exhibited wider gap between PCV and GCV.

2.7 HERITABILITY AND GENETIC ADVANCE

Observed variability is a combined measure of genetic and environmental causes. Genetic variability alone is heritable. However, heritability has to be considered in conjunction with genetic advance (Natarajan *et al.*, 1990) to have an idea about the expected genetic gain in the next generation.

The maximum and minimum values of broad sense heritability for different traits of pigeonpea are presented in Table 5. High heritability estimates were reported for pod number, and cluster number (Suresh Kumar and Reddy, 1982; Premsagar and Jatarsa, 1983; Natarajan *et al.*, 1990); seed yield (Premsagar and Jatarsa, 1983; Natarajan *et al.*, 1990); days to flowering (Singh *et al.*, 1979; Gupta *et al.*, 1980; Konwar and Hazarika, 1988; Holker *et al.*, 1991); days to maturity (Konwar and Hazariaka, 1988; Holkar *et al.*, 1991); 100-seed weight, plant height and number of secondary branches (Konwar and Hazarika, 1988). Low heritability estimates were recorded for pods per cluster, primary branches, pods per plant, seed per pod (Konwar and Hazarika, 1988) and 100-seed weight (Gupta *et al.*, 1980). High genetic advance was reported for cluster number and seed yield (Bashiruddin and Sreeramulu, 1981; Premsagar and Jatarsa, 1983; Natarajan *et al.*, 1990).

Number of leaves per plant and seeds per plant had exhibited high heritability in broad sense and high genetic advance as per cent of mean (Kumar and Haque, 1973). Days to flowering and days to maturity (Konwar and Hazarika, 1988; Holker *et al.*, 1991); plant height (Konwar and Hazarika, 1988) and pods per plant (Holker *et al.*, 1991) were also reported to exhibit high heritability and genetic advance in pigeonpea.

Table 5 Broad sense heritability (%) for yield and yield component characters in pigeonpea

Character	Maximum	Reference	Minimum	Reference
Days to flowering	98.70	Konwar and Hazarika (1988)	31.00	Kumar and Haque (1973)
Days to maturity	98.97	Konwar and Hazarika (1988)	61.30	Kumar and Haque (1973)
Plant Height	85.00	Khan and Rachie (1972)	36.00	Munoz and Abrams (1971)
Branches per plant	89.89	Patil *et al.* (1989)	30.76	Natarajan *et al.* (1990)
Pods per plant	82.99	Natarajan *et al.* (1990)	40.20	Kumar and Haque (1973)
Seeds per pod	45.45	Patil *et al.* (1989)	16.29	Natarajan *et al.* (1990)
100-Seed weight	99.59	Natarajan *et al.* (1990)	30.70	Sidhu *et al.* (1985)
Yield per plant	87.00	Khan and Rachie (1972)	34.06	Patil *et al.* (1989)

2.8 CORRELATIONS AND PATH-COEFFICIENTS

Yield is a complex character governed by several contributing traits. Hence, study of associations of component characters with yield, would aid in planning of efficient breeding programs. A brief review of the relevant literature is presented hereunder.

Grain yield in pigeonpea was reported to be positively correlated with days to flowering (Veeraswamy *et al.*, 1973; Patil *et al.*, 1989); plant height (Sidhu *et al.*, 1985; Patil *et al.*, 1989; Natarajan *et al.*, 1990; Patel and Patel, 1992); total number of branches (Beohar and Nigam, 1972; Joshi, 1973; Veeraswamy *et al.*, 1973); primary branches (Wakankar and Yadav, 1975); secondary branches (Sharma *et al.*, 1971; Singh and Malhotra, 1973; Wakankar and Yadav, 1975), pod bearing length (Sharma *et al.*, 1971); pods per plant (Sidhu *et al.*, 1985; Patil *et al.*, 1989; Natarajan *et al.*, 1990; Patel and Patel, 1992); seeds per pod (Sidhu *et al.*, 1985; Patil *et al.*, 1989) and with 100-seed weight (Patil *et al.*, 1989). However, non-significant association between days to flowering and days to maturity with seed yield was also reported by several workers (Pankaj Reddy *et al.*, 1975; Dahiya *et al.*, 1978; Sidhu *et al.*, 1985) while, Patil *et al.* (1989) reported significantly negative association of seed yield with days to maturity. The negative association of plant height with seed yield (Dahiya *et al.*, 1978) and pods per plant with seed yield (Beohar and Nigam, 1972) were also reported.

Positive associations of plant height with branch number (Natarajan *et al.*, 1990); seeds per pod (Sidhu *et al.*, 1985); days to flowering (Sidhu *et al.*, 1985; Patel and Patel, 1992); pods per plant (Sidhu *et al.*, 1985; Patel and Patel, 1992); 100-seed weight (Natarajan *et al.*, 1990); and primary branches per plant (Patel and Patel, 1992) has been reported. Branch number was also reported to be positively and significantly associated with seed number and 100-seed weight (Natarajan *et al.*, 1990). Further, primary branches per plant was reported to exhibit significant positive association with days to flowering and days to maturity (Patel and Patel, 1992) while, days to flowering was positively and significantly associated with days to maturity (Patel and Patel, 1992). Seeds per pod was found positively associated with 100-seed weight (Patel and Patel, 1992). Negative association was observed for days to flowering and days to maturity with seeds per pod (Sidhu *et al.*, 1985).

The technique of path analysis was outlined by Wright (1921) for partitioning the observed

correlation into direct and indirect effects. It was applied in plant breeding for the first time by Dewey and Lu (1959).

Path analysis in pigeonpea revealed the highest direct effect of pods per plant on seed yield (Dumbre and Deshmukh, 1985; Sidhu *et al.*, 1985; Natarajan *et al.*, 1990). However, seeds per pod (Jag Shoran,1982; Singh *et al.*, 1982; Patil *et al.*, 1989) and days to maturity (Patel and Patel,1992) were reported to exert high direct effect on seed yield in other studies. On contrary, Baniwal and Jastra (1985) reported high negative direct effect of seeds per pod on seed yield. Days to flowering was reported to exert indirect effect on seed yield via plant height; pods per plant (Sidhu *et al.*, 1985; Patel and Patel, 1992) and also via seeds per pod and 100-seed weight (Patel and Patel, 1992). Plant height and pods per plant were found to be the most important contributors to yield in pigeonpea (Sidhu *et al.*, 1985; Natarajan *et al.*, 1990) while, number of seeds per pod, days to flower, 100-seed weight and number of branches per plant were also reported important (Patil *et al.*, 1989) in pigeonpea improvement programs.

MATERIALS AND METHODS

CHAPTER III

MATERIALS AND METHODS

The present investigations were carried out at ICRISAT Asia Center (IAC), Patancheru, India during 1993-1996.

3.1 EXPERIMENTAL MATERIAL

3.1.1 Pathogen

Three different isolates of pigeonpea sterility mosaic pathogen viz., isolate 1, 2 and 3, representing the variants 2, 3 and 1, respectively, of those, identified by Reddy *et al.* (1993), were involved in the present investigations. The identity of these isolates was established by their reaction on few pigeonpea differentials presented below.

Pigeonpea differentials	Sterility mosaic reaction		
	Isolate 1	Isolate 2	Isolate 3
ICP 2376	RS	S	R
ICP 7035	R	R	R
ICP 8862	R	R	NT
ICP 8863	S	S	S
ICP 10976	RS	R	NT
ICP 10984	R	R	NT
ICP 11146	R	R	NT

R-Resistant (No apparent symptoms); S-Susceptible (Mosaic symptoms); RS-Ring Spot; NT-Not tested

The isolates involved in the study, were obtained from SM infected pigeonpea fields of local cultivars, located at different places within Andhra Pradesh. Isolate 1 was collected from the infected pigeonpea fields of Bibinagar Mandal of Nalgonda district, during January 1993 while, isolates 2 and 3 were obtained from the SM infected fields of Narsapur Mandal, Medak district, during November 1994 and Ghanpur village of Ramachandrapuram Mandal, Medak district, during September 1995, respectively. 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 and Reddy, 1976a). Observations were recorded on both disease incidence and symptom type (no apparent symptoms, ring spot and mosaic symptoms), two months after inoculation.

Multiplication of the isolates was taken up after confirmation, in isolation, on the susceptible cultivar, ICP 8863, grown in pots, at different locations to avoid cross-contamination. Isolate 1 was multiplied in the residential areas of Hyderabad, devoid of any pigeonpea, within a radius of 5Kms while, isolate 2 was multiplied in the SM and wilt screening nurseries of ICRISAT Asia Center, Patancheru, Andhra Pradesh. The inoculum of isolate 3 was however, multiplied in a mite-proof nethouse at ICRISAT Asia Center, Patancheru, Andhra Pradesh. The inoculum of the three different isolates, thus multiplied was used for subsequent screening experiments.

3.1.2 Host

Parents for the investigation on inheritance of resistance to sterility mosaic disease of pigeonpea were selected from a preliminary screening experiment. Lines, earlier reported resistant/ tolerant (Nene *et al.*, 1981) were evaluated for their reaction against different isolates of the sterility mosaic pathogen. The selected parents are presented in Table 6. Details regarding their origin and other salient features are presented in Table 7. Crosses were made with the susceptible parents and part of the F_1 was advanced to F_2 generation. Backcrosses were also made simultaneously. The parents, F_1 and segregating generations were then screened against the isolates to determine the mode of inheritance of resistance. The resistant and susceptible parents selected for isolate 2 were also intercrossed among themselves to obtain information on their allelic relationships.

The selected pigeonpea lines were further crossed in a line x tester fashion. The lines, ICP 2376, ICP 7035, ICP 7349, ICP 7994, ICP 8006, ICP 8136, ICP 8850, ICP 8863, ICP 11251, BDN 1 and LRG 30 were crossed with the male steriles, ICP MS288 and ICP MS3783 and the resulting 22 F_1 hybrids along with the parents, including standard checks constituted the material for study on heterosis, combining ability and nature of gene action.

Table 6 Parent's selected for studies on inheritance of resistance to different isolates of the sterility mosaic pathogen

	Isolate 1
Resistant	ICP 7035, ICP 7349, ICP 8006, ICP 8136, ICP 8850
Tolerant	ICP MS 3783
Susceptible	ICP 8863
	Isolate 2
Resistant	ICP 7035, ICP 7349, ICP 8850
Susceptible	ICP 2376, ICP 7994, ICP 11251, BDN1, LRG 30, ICP 8863
	Isolate 3
Resistant	ICP 7035, ICP 2376
Susceptible	ICP 8863

Table 7 **Salient features of the selected pigeonpea lines**

Line	Origin	Pedigree	Plant characters
ICP MS 288	India (Andhra Pradesh)	(MS Prabhat x ICP 288) x $^{a}BC_{4}$	Early, indeterminate with compact growth habit. Yellow flowers with sparse red streaks. Green colored pods. Creamy white, bold, oval shaped seeds.
ICP MS 3783	India (Madhya pradesh)	(MS 3A x ICP 3783) x $^{b}BC_{4}$	Mid-late, indeterminate with semi-spreading growth habit. Yellow flowers with medium red streaks. Mixed green and purple colored pods. Creamy brown, oval seeds.
ICP 2376	India (Andhra Pradesh)	P - 3888 germplasm line	Medium maturing, indeterminate with semi-spreading growth habit. Yellow flowers with dense purple streaks. Green pods. Creamy white, oval seeds.
ICP 7035	India (Madhya Pradesh)	DSLR - 55 germplasm line	Mid-late, indeterminate with semi-spreading growth habit. Red flowers with dense purple streaks. Purple colored pods. Mottled reddish brown, bold, pea shaped seeds.
ICP 7349	India (Madhya Pradesh)	ANM - 28 germplasm line	Medium maturing, indeterminate with semi-spreading growth habit. Yellow flowers with sparse red streaks. Green colored pods. Brown, bold and square shaped seeds.
ICP 7994	India (Orissa)	ANM - 359 germplasm line	Late, indeterminate with semi-spreading growth habit. Yellow flowers. Purple colored pods. Creamy white and pea shaped seeds.
ICP 8006	India (Orissa)	ANM - 367 germplasm line	Late, indeterminate with compact growth habit. Yellow flowers. Mixed green and purple colored pods. Mottled creamy white, bold and pea shaped seeds.
ICP 8136	India (Bihar)	ANM - 489 germplasm line	Late, indeterminate with compact growth habit. Yellow flowers. Mixed green and purple colored pods. Creamy white and oval seeds.
ICP 8850	India (Andhra Pradesh)	IC - SMR - Sel. - 6986	Medium maturing, indeterminate with semi-spreading growth habit. Yellow flowers. Green colored pods. Orange colored, bold, oval seeds.
ICP 8863	India (Andhra Pradesh)	ICWR - 6	Medium maturing, indeterminate with semi-spreading growth habit, Yellow flowers with sparse red streaks. Green pods with purple streaks. Orange to dark brown oval seeds.
ICP 11251	India (Andhra Pradesh)	IC - SMR - Sel. - 3678	Medium maturing, indeterminate with semi-spreading growth habit. Yellow flowers with dense purple streaks. Green colored pods. Creamy white, oval seeds.
BDN 1	India (Maharashtra)	ICP 7182	Medium maturing, indeterminate with semi-spreading growth habit. Yellow flowers with sparse red streaks. Green colored pods with purple streaks. Orange brown color, oval seeds.
LRG 30	India (Andhra Pradesh)	ICP 8518	Medium maturing, indeterminate with semi-spreading growth habit. Yellow flowers. Green colored pods with purple streaks. Orange colored, oval seeds.

a - Four generations of backcross to ICP 288; b - Four generations of backcross to ICP 3783

3.2 METHODS

3.2.1 Screening for resistance to isolates of sterility mosaic pathogen

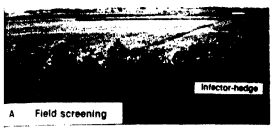
A set of 152 lines, earlier reported resistant/tolerant (Nene *et al.*, 1981) were screened against isolate 1 of the sterility mosaic pathogen. The lines were screened for their reaction, during May-July 1993. Screening was carried out using the infector-hedge technique (Nene and Reddy, 1976b). The infector-hedge was established by growing the susceptible cultivar, ICP 8863 on the upwind border of the field (Plate 2 a)A). Ten days old seedlings of the hedge were inoculated with the isolate 1 of the SM pathogen, by leaf-stapling (Nene and Reddy, 1976a) 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. Disease spread occurred through wind onto the test materials during the screening period. For screening, the pots sown with the test material were placed beside the infector-hedge (Plate 2 a)B).

The screening for isolate 1 was done in two replications. Plastic pots, 15 cm in diameter, were filled with alfisol (60% sand, 33% clay, 7% silt) and ten seeds were sown in each pot. These pots were then placed beside the infector-hedge. Susceptible checks, BDN 1, LRG 30 and ICP 8863 were planted at frequent intervals for indication on disease spread. Observations on symptom type and severity, were recorded at 75 days after sowing (DAS), when the susceptible controls had exhibited 100 per cent severe mosaic symptoms on each individual plant, in each entry and replication. Individuals with no apparent symptoms were classified as resistant (Plate 2 b)A) while, those with ring spot (green islands surrounded by a chlorotic halo) and mild mosaic (few mosaic patches) symptoms were classified as tolerant (Plates 2 b)B and C). Those exhibiting severe mosaic symptoms were classified as susceptible (Plate 2 b)D). Lines with less than 10 per cent disease, over replications, were classified as resistant. While, lines with either ring spot or mild mosaic symptoms and less than 10 per cent severe mosaic symptoms were classified as tolerant (ring spot) or tolerant (mild mosaic), respectively. Lines exhibiting more than 10 per cent severe mosaic symptoms were classified as susceptible.

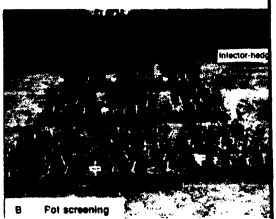
Pot-screening of the lines using infector-hedge technique was also adopted for isolate 2. A set of 410 lines, earlier reported resistant/tolerant for the disease (Nene *et al.*, 1981) including the 152 lines

Plate 2

Screening against sterility mosaic disease of pigeonpea using infector-hedge technique

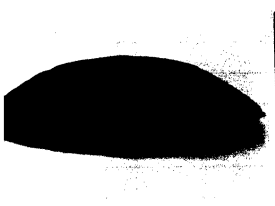


A Field screening

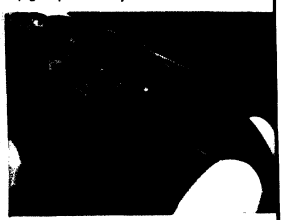


B Pot screening

Types of symptoms noticed against pigeonpea sterility mosaic disease



A Resistant



B Ring spot

C Mild mosaic

D Severe mosaic

screened against isolate 1 were sown in a single replication besides the infector-hedge. Susceptible checks, BDN 1, LRG 30 and ICP 8863 were placed at frequent intervals for indication on disease spread. Plastic pots, 15 cm in diameter, filled with alfisols group (60% sand, 33% clay, 7% silt) were used. Ten seeds were sown in each pot. Observations on the symptom type and severity were recorded for each plant of each entry, in each replication, at 75 DAS. The lines were classified as resistant, tolerant (ring spot), tolerant (mild mosaic) and susceptible, similar to that of isolate 1.

3.2.2 Selection of parents for inheritance studies

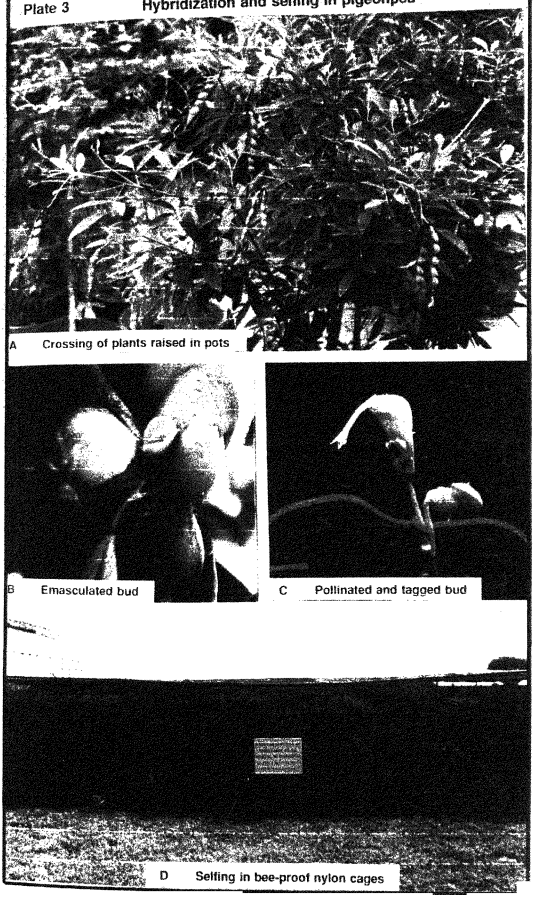
Resistant and tolerant parents were selected from the preliminary screening experiment, for study on inheritance of resistance. Lines of medium to late maturity duration exhibiting uniform reaction or symptom type across the replications were selected as parents.

3.2.3 Hybridization

Crosses were made between the selected parents during Kharif 1993. Reciprocal crosses were avoided. The parents were sown in four sets at intervals of 15 days in 30 cm pots and placed beside the infector-hedge. The susceptible parents were however, raised under disease-free conditions, as the disease would have prevented their flowering, essential for crossing. The confirmed resistant and tolerant plants, alone, were used for crossing with susceptible parent. Further, hybridization was carried out on true-to type, vigorous and healthy plants raised in 30 cm pots (Plate 3A).The hybridization was restricted to early phase of flowering, because of higher success rates (Ramanatha Rao, 1988). All flowers on the female parents were removed, at the onset of flowering, for one-two days to stimulate profuse flowering.

For crossing, upto ten tightly closed buds, approximately two-thirds the size of mature buds were selected on each branch of the female plant. Smaller, mature, open buds and flowers were removed to prevent competition for photosynthates within the inflorescence. These buds were emasculated (Plate 3B) to avoid selfing. Standard hybridization technique detailed by Pathak (1970) and Sharma and Green (1980) was adopted. Large, mature, unopened buds with abundant pollen were collected from the male plants and bulked for each male parent. The staminal column of the pollen bud was extracted and used for pollinating the stigma of female (Plate 3C). Each female plant was pollinated by several male parents. Different

Plate 3 **Hybridization and selfing in pigeonpea**



A Crossing of plants raised in pots

B Emasculated bud

C Pollinated and tagged bud

D Selfing in bee-proof nylon cages

colored threads were tied to each flower (Plate 3C) to facilitate identification of crosses at the time of harvest. The pollinated buds were not bagged as pod setting was greatly reduced under bagging (Sharma and Green, 1980). However, hybridization was carried out under bee-proof nylon cages (Plate 3D) to prevent any chance of contamination by natural out-crossing.

3.2.4 Generation advancement

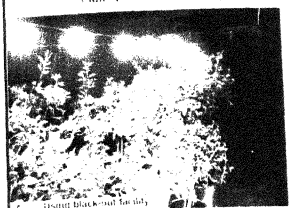
Off-season advancement of the F_1's was taken up during December 1993, under greenhouse conditions to facilitate the rapid advancement of generations. Flower initiation, flower color, seed size and other contrasting characters among the parents (Table 7) were used as markers to check the trueness of F_1 plants. Only true F_1's were used for backcrossing and advancement to F_2 generation. The growth of F_1 plants was hastened by providing extra light (14 hr) while, flowering was induced by providing short days of 8 hrs light and 16 hrs dark in a black out facility (Plate 4 a)A) at IAC's Greenhouse and Controlled Environment Facility. Backcrossing of the F_1's with their respective parents, maintained as ratoon (Plate 4 a)B) was initiated under greenhouse conditions with the commencement of flowering in the F_1's, raised in the black-out facility. The F_1's were also advanced to F_2 generation, during Kharif 1994, by selfing in bee-proof nylon cages.

3.2.5 Screening of parents, F_1 and segregating generations

The parents, F_1 and segregating generations were screened for their reaction to sterility mosaic disease during 1995-1996. Seedlings were raised in 15 cm pots with ten seedlings per pot.

Screening against isolate 1 of the sterility mosaic pathogen was taken up in a mite-proof net-house (Plate 4 b) during May-July 1995 using the leaf-stapling technique (Nene and Reddy, 1976a). Diseased leaflets carrying sufficient numbers of the vector, *Aceria cajani* 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 seedling (Plate 4 c)A). It was then stapled with a small paper stapler. Alternatively, two diseased leaflets

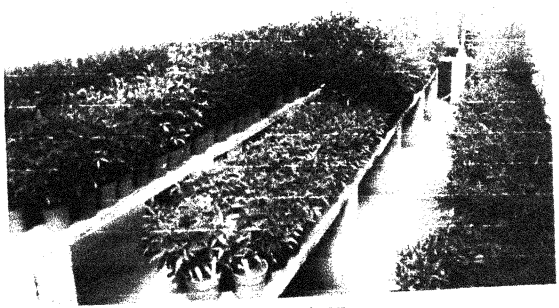
Plate 4 Off-season Advancement of Generations



A Using blackout facility

B Backcrossing with parents maintained at Tukuyu

Screening in mite-proof nethouse



Leaf-stapling technique

A Using single dissected leaflet

B Using two small leaflets

were used, if they were too small (Plate 4 c)B). 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 (Plate 4 c)B). The primary leaf and the two diseased leaflets were then stapled together.

For isolate 2, the parents, F_1 and segregating generations were screened using the infector-hedge technique (Nene and Reddy, 1976b) in an isolated field during May-July 1995 while, for isolate 3, screening was taken up in a mite-proof net-house using the leaf-stapling technique, during Dec. 1995-Feb. 1996.

The susceptible check, ICP 8863 was included in all sets, at frequent intervals for an indication of disease spread. Observations on disease reaction were recorded at 75 DAS. The plants were classified as resistant (no apparent symptoms), tolerant (ring spot symptoms) or susceptible (severe mosaic symptoms) for isolate 1 and as resistant (no apparent symptoms) and susceptible (severe mosaic symptoms) for isolate 2 and isolate 3.

3.2.6 Evaluation for heterosis and combining ability

The investigation consisted of a line x tester trial with eleven pollen parents (ICP 2376, ICP 7035, ICP 7349, ICP 7994, ICP 8006, ICP 8136, ICP 8850, ICP 8863, ICP 11251, BDN 1, and LRG 30) and two male steriles (ICP MS288 and ICP MS3783). The resultant 22 hybrids were evaluated along with the parents (including checks) in randomized block design of three replications. Each plot consisted of a single row of four meters length. A spacing of 75 x 20 cm was adopted. The experiments were planted on a medium deep vertisol at ICRISAT Asia center, Patancheru on 24th of June 1994 and all recommended package of practices were adopted to raise a successful crop.

Observations

Apart from days to 50 per cent flowering and days to maturity, observations for all other traits were recorded on ten randomly selected plants, from the center of each plot. For days to flowering and maturity, observations were however, recorded from the entire plot. The hybrid plants were identified at flowering and pod formation stages, by comparing various plant characteristics, such as flower, pod and stem

pigmentation with that of parents. Any off-type noticed was promptly rouged out.

Days to 50 per cent flowering :

Number of days from sowing to the day when 50 per cent of the plants in the plot had flowered.

Days to maturity :

Number of days taken from sowing to the day when 75 per cent of the pods in the plot had turned brown and matured.

Plant height (cm) :

Height of stretched plant from ground level to its tip at harvest.

Number of primary branches :

Number of branches arising form the main-stem recorded at harvest.

Number of secondary branches :

Total number of branches arising from primary branches recorded at harvest.

Number of pods per plant :

Total number of mature pods per plant observed at harvest.

Number of seeds per pod :

The average of observations on ten fully developed, mature, undamaged pods taken at random from each selected plant.

Plant seed yield (g) :

The average seed weight of ten randomly selected plants measured to the nearest grams.

100-Seed weight (g) :

The weight of randomly collected one hundred, clean, whole, dry seeds.

3.3 STATISTICAL ANALYSIS

3.3.1 Inheritance studies

Observations on disease symptom type and severity were recorded on the parents, F_1 and segregating generations. The plants were classified as resistant, tolerant and susceptible. The Chi-square

method (Snedecor and Cochran, 1967) was adopted to test the goodness of fit for the phenotypic ratios.

3.3.2 Analysis of variance

The data for each trait was analyzed separately. Randomized complete block design method, suggested by Panse and Sukhatme (1978) was adopted. The treatment sum of squares in the ANOVA was further partitioned as per the procedure outlined by Singh and Chaudhary (1985).

3.3.3 Heterosis

The performance of F_1 hybrid over the mid-parent, best parent and checks was expressed as per cent for each cross. It was calculated using the formula suggested by Liang *et al.* (1972). The significance was tested using t-test suggested by Snedecor and Cochran (1967) and Paschal and Wilcox (1975).

3.3.4 Combining Ability

The analysis of combining ability was carried out based on the methods suggested by Comstock and Robinson (1952) and Kempthorne (1957). The estimates of heritability and genetic advance were also obtained adopting the procedures outlined by Burton and Devane (1953) and Johnson *et al* (1955), respectively. The genotypic and phenotypic coefficients of variation were computed, following the methodology outlined by Burton (1952).

3.3.5 Character associations and Path analysis

Correlations for various traits studied, were computed using the statistical procedures outlined by Singh and Chaudhary (1985). The direct and indirect effects for yield, were estimated with the various yield components as independent variables. The procedures suggested by Wright (1921) and Dewey and Lu (1959) were adopted.

RESULTS

CHAPTER IV

RESULTS

Results of the present investigations on "Genetics of resistance to sterility mosaic disease in pigeonpea" are presented hereunder.

4.1 SCREENING FOR RESISTANCE TO DIFFERENT ISOLATES

A set of 152 lines were screened for resistance to isolate 1 of the pigeonpea sterility mosaic pathogen. Disease incidence varied from 0-100 per cent in different lines. The susceptible checks (BDN 1, LRG 30 and ICP 8863), showed 90-100 per cent disease, indicating a good spread of the disease. Among the 152 lines screened, 37 lines were resistant (less than 10 per cent disease incidence), while 83 lines exhibited tolerance (29 ring spot and 54 mild mosaic) and the rest (32 lines) were susceptible. The list of resistant and tolerant lines is given in Table 8

Screening for resistance to isolate 2 of the pigeonpea sterility mosaic pathogen was carried out with a set of 410 lines including 152 lines screened against isolate 1. The susceptible controls (BDN 1, LRG 30 and ICP 8863) placed at frequent intervals exhibited 100 per cent disease indicating good disease spread. Among the lines tested, 161 were resistant while 53 were found tolerant against the isolate. These lines are presented in Table 9

Among 152 lines screened for resistance to both isolates, 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 exhibited resistance to both isolates. Similarly, the line ICP 11245 recorded ring spot form of tolerance to both isolates, while the lines ICP 999, ICP 7201, ICP 7873, ICP 8125, ICP 8266, ICP 8857, ICP 11249 and ICP 11283 showed mild mosaic form of tolerance to both isolates.

4.2 GENETICS OF RESISTANCE FOR ISOLATES OF PIGEONPEA STERILITY MOSAIC PATHOGEN

The results on inheritance of resistance to three different isolates of the pigeonpea sterility mosaic

Table 8 Pigeonpea lines resistant/tolerant to isolate 1 of sterility mosaic pathogen

Resistant	Tolerant		
	Ring spot	Mild mosaic	
ICP 2630	ICP 2376	ICP 410	ICP 11257
ICP 3782	ICP 4344	ICP 999	ICP 11259
ICP 3783	ICP 4777	ICP 1923	ICP 11261
ICP 4725	ICP 4782	ICP 2014	ICP 11262
ICP 7035	ICP 6630	ICP 3678	ICP 11264
ICP 7119	ICP 7367	ICP 5125	ICP 11266
ICP 7188	ICP 7906	ICP 5551	ICP 11267
ICP 7239	ICP 7994	ICP 7201	ICP 11268
ICP 7281	ICP 8105	ICP 7583	ICP 11269
ICP 7349	ICP 8129	ICP 7636	ICP 11271
ICP 7353	ICP 8135	ICP 7683	ICP 11274
ICP 7403	ICP 8317	ICP 7823	ICP 11276
ICP 7867	ICP 9140	ICP 7871	ICP 11281
ICP 7942	ICP 9150	ICP 7873	ICP 11282
ICP 7997	ICP 9166	ICP 7882	ICP 11283
ICP 8006	ICP 9187	ICP 7898	ICP 11285
ICP 8040	ICP 11245	ICP 8109	
ICP 8051	ICP 11250	ICP 8110	
ICP 8077	ICP 11251	ICP 8113	
ICP 8116	ICP 11254	ICP 8125	
ICP 8117	ICP 11255	ICP 8216	
ICP 8118	ICP 11260	ICP 8266	
ICP 8120	ICP 11263	ICP 8852	
ICP 8123	ICP 11265	ICP 8857	
ICP 8124	ICP 11270	ICP 9134	
ICP 8131	ICP 11272	ICP 9144	
ICP 8136	ICP 11273	ICP 9155	
ICP 8145	ICP 11280	ICP 9182	
ICP 8501	ICP 11284	ICP 9183	
ICP 8850		ICP 9752	
ICP 8853		ICP 10222	
ICP 8856		ICP 10231	
ICP 8861		ICP 11243	
ICP 9689		ICP 11244	
ICP 11256		ICP 11247	
ICP 11258		ICP 11248	
ICP 11278		ICP 11249	
		ICP 11252	

Table 9 Pigeonpea lines resistant/ tolerant to isolate 2 of sterility mosaic pathogen

Resistant						Tolerant	
						Ring spot	Mild mosaic
ICP 2630	ICP 10997	ICP 11053	ICP 11143	ICP 11192	ICP 11239	ICP 7188	ICP 999
ICP 3782	ICP 10998	ICP 11057	ICP 11144	ICP 11194	ICP 11240	ICP 8118	ICP 7119
ICP 3783	ICP 10999	ICP 11058	ICP 11147	ICP 11195	ICP 11241	ICP 10993	ICP 7201
ICP 4725	ICP 11001	ICP 11062	ICP 11149	ICP 11199	ICP 11242	ICP 11010	ICP 7354
ICP 7035	ICP 11002	ICP 11069	ICP 11151	ICP 11201	ICP 11276	ICP 11025	ICP 7873
ICP 7239	ICP 11004	ICP 11070	ICP 11153	ICP 11202	ICP 11278	ICP 11027	ICP 7904
ICP 7281	ICP 11005	ICP 11071	ICP 11155	ICP 11203		ICP 11030	ICP 7906
ICP 7349	ICP 11006	ICP 11076	ICP 11157	ICP 11204		ICP 11039	ICP 7997
ICP 7403	ICP 11007	ICP 11081	ICP 11158	ICP 11205		ICP 11056	ICP 8006
ICP 7867	ICP 11009	ICP 11082	ICP 11159	ICP 11206		ICP 11060	ICP 8040
ICP 8116	ICP 11011	ICP 11083	ICP 11160	ICP 11208		ICP 11065	ICP 8051
ICP 8117	ICP 11014	ICP 11089	ICP 11162	ICP 11209		ICP 11066	ICP 8077
ICP 8850	ICP 11015	ICP 11091	ICP 11163	ICP 11210		ICP 11080	ICP 8109
ICP 8852	ICP 11016	ICP 11094	ICP 11164	ICP 11211		ICP 11097	ICP 8120
ICP 8853	ICP 11017	ICP 11098	ICP 11165	ICP 11212		ICP 11102	ICP 8124
ICP 8860	ICP 11018	ICP 11099	ICP 11167	ICP 11213		ICP 11103	ICP 8125
ICP 8861	ICP 11019	ICP 11106	ICP 11168	ICP 11215		ICP 11124	ICP 8131
ICP 8869	ICP 11020	ICP 11110	ICP 11170	ICP 11216		ICP 11129	ICP 8135
ICP 10976	ICP 11021	ICP 11111	ICP 11171	ICP 11218		ICP 11135	ICP 8266
ICP 10977	ICP 11023	ICP 11113	ICP 11172	ICP 11219		ICP 11136	ICP 8856
ICP 10979	ICP 11026	ICP 11114	ICP 11174	ICP 11220		ICP 11137	ICP 8857
ICP 10980	ICP 11035	ICP 11115	ICP 11178	ICP 11221		ICP 11148	ICP 11193
ICP 10981	ICP 11036	ICP 11122	ICP 11179	ICP 11222		ICP 11166	ICP 11249
ICP 10985	ICP 11037	ICP 11123	ICP 11181	ICP 11223		ICP 11197	ICP 11275
ICP 10988	ICP 11038	ICP 11125	ICP 11182	ICP 11225		ICP 11214	ICP 11283
ICP 10989	ICP 11040	ICP 11126	ICP 11183	ICP 11227		ICP 11231	
ICP 10990	ICP 11042	ICP 11127	ICP 11184	ICP 11230		ICP 11245	
ICP 10992	ICP 11043	ICP 11132	ICP 11186	ICP 11233		ICP 11257	
ICP 10994	ICP 11044	ICP 11133	ICP 11187	ICP 11234			
ICP 10995	ICP 11048	ICP 11141	ICP 11188	ICP 11235			
ICP 10996	ICP 11050	ICP 11142	ICP 11191	ICP 11238			

pathogen are presented in Tables 10-17

4.2.1 Genetics of resistance for isolate 1

The F_1, F_2 and backcross generations of five resistant x susceptible and one tolerant x susceptible cross combinations were studied to determine the inheritance of resistance/tolerance for isolate 1. The susceptible control, planted along with test materials, exhibited 100 per cent infection, indicating good disease spread. The parents, ICP 7035, ICP 7349, ICP 8006, ICP 8136 and ICP 8850 showed 100 per cent resistance, with no apparent symptoms, while ICP MS3783 showed ring spot form of tolerance. ICP 8863 recorded severe mosaic symptoms (Table 10). The F_1's were susceptible for all resistant x susceptible and tolerant x susceptible cross combinations studied.

A segregation of 7 resistant : 9 susceptible was observed in the F_2 generation of crosses involving ICP 7035, ICP 7349 and ICP 8006 resistant parents with the susceptible, ICP 8863 (Table 11). However, crosses with resistant parents, ICP 8136 and ICP 8850 showed 1 resistant : 3 susceptible segregation ratio. The backcrosses corroborated the segregation pattern of F_2 generation (Table 11). The backcross of ICP 7035 X ICP 8863, ICP 7349 X ICP 8863 and ICP 8006 X ICP 8863 F_1's with the respective resistant parents, segregated in a ratio of 3 resistant : 1 susceptible. While, backcross with the susceptible parent, did not segregate and the entire progeny was susceptible. The backcross of ICP 8850 X ICP 8863 F_1 with the resistant parent segregated in a segregation ratio of 1 resistant : 1 susceptible while, backcross with the susceptible parent did not segregate and the entire progeny was susceptible. The backcross of ICP 8136 X ICP 8863 F_1 with the resistant parent, also segregated in a ratio of 1 resistant : 1 susceptible while, the entire backcross progeny of the F_1 with the susceptible parent was susceptible.

The F_1 of cross ICP MS3783 X ICP 8863 was susceptible (Table 10). Further, the F_2 plants exhibited a segregation ratio of 7 tolerant : 9 susceptible (Table 11). The segregation pattern of F_2 generation was supported by the segregation ratios observed in BC_1 and BC_2 generations. The backcross of F_1 with the tolerant parent segregated in the ratio 3 tolerant : 1 susceptible, while backcross of the F_1 with the susceptible parent resulted in susceptible backcross progeny.

4.2.2 Genetics of resistance for isolate 2

The cross combinations of three resistant parents, ICP 7035, ICP 7349 and ICP 8850 with six

Table 10 Reaction of parents and F_1 hybrids for isolate 1 of pigeonpea sterility mosaic pathogen

Material	Total plants	Resistant plants	Tolerant plants	Susceptible plants
Parents				
ICP 7035	23	23	-	-
ICP 7349	27	27	-	-
ICP 8006	41	41	-	-
ICP 8136	65	65	-	-
ICP 8850	33	33	-	-
ICP MS3783	68	-	68	-
ICP 8863	42	-	-	42
Resistant x Susceptible F_1 hybrids				
ICP 7035 X ICP 8863	10	-	-	10
ICP 7349 X ICP 8863	7	-	-	7
ICP 8006 X ICP 8863	11	-	-	11
ICP 8136 X ICP 8863	22	-	-	22
ICP 8850 X ICP 8863	12	-	-	12
Tolerant x susceptible F_1 hybrid				
ICP MS3783 X ICP 8863	24	-	-	24

Table 11 Reaction of segregating generations of resistant x susceptible and tolerant x susceptible crosses to isolate 1 of pigeonpea sterility mosaic pathogen

Generation	Observed frequencies			Expected frequencies		Ratio	Probability
	Total plants	Resistant /Tolerant plants (R/T)	Susceptible plants (S)	Resistant/Tolerant plants (R/T)	Susceptible plants (S)	R/T : S	
Resistant x susceptible crosses							
ICP 7035 X ICP 8863							
F_2	265	112	153	115.94	149.06	7 : 9	0.50-0.70
BC_1	94	67	27	70.5	23.5	3 : 1	0.30-0.50
BC_2	85	-	85	-	85	-	-
ICP 7349 X ICP 8863							
F_2	281	117	164	122.94	158.06	7 : 9	0.30-0.50
BC_1	115	84	31	86.25	28.75	3 : 1	0.50-0.70
BC_2	108	1	107	-	108	-	-
ICP 8006 X ICP 8863							
F_2	807	349	458	353.06	453.94	7 : 9	0.70-0.80
BC_1	121	93	28	90.75	30.25	3 : 1	0.50-0.70
BC_2	103	4	99	-	103	-	-
ICP 8136 X ICP 8863							
F_2	936	243	693	234	702	1 : 3	0.30-0.50
BC_1	87	49	38	43.5	43.5	1 : 1	0.20-0.30
BC_2	115	2	113	-	115	-	-
ICP 8850 X ICP 8863							
F_2	252	57	195	63	189	1 : 3	0.30-0.50
BC_1	124	68	56	62	62	1 : 1	0.20-0.30
BC_2	92	2	90	-	92	-	-
Tolerant x susceptible cross							
ICP MS3783 X ICP 8863							
F_2	845	371	474	369.69	475.31	7 : 9	0.90-0.95
BC_1	125	89	36	93.75	31.25	3 : 1	0.30-0.50
BC_2	147	-	147	-	-	-	-

susceptible parents, ICP 2376, ICP 7994, ICP 11251, BDN 1, LRG 30 and ICP 8863 were studied to determine the genetics of resistance for isolate 2 of pigeonpea sterility mosaic pathogen. The susceptible controls, planted at frequent intervals along with the test materials exhibited 100 per cent infection, indicating good disease spread. The parents, ICP 7035, ICP 7349 and ICP 8850 did not exhibit any apparent symptoms and were 100 per cent resistant, while ICP 2376, ICP 7994, ICP 11251, BDN 1, LRG 30 and ICP 8863 exhibited severe mosaic symptoms (Table 12).

The disease reaction of F_1 hybrids of resistant x susceptible cross combinations is presented in Table 13. F_1's of crosses involving ICP 7035 and ICP 7349 resistant parents were all resistant, while F_1 of crosses involving ICP 8850 were all susceptible. In the F_2 generation (Table 14), the crosses of resistant parents, ICP 7035 and ICP 7349 with ICP 2376, BDN 1 and ICP 8863 segregated in the ratio 3 resistant : 1 susceptible, while crosses with the susceptible parents ICP 7994, ICP 11251 and LRG 30 segregated in 9 resistant : 7 susceptible ratio. However, in the F_2 generation of the crosses involving the resistant parent, ICP 8850 and the susceptibles, ICP 2376, BDN 1 and ICP 8863, 1 resistant : 3 susceptible ratio was observed while, in combination with the susceptible parents, ICP 7994, ICP 11251 and LRG 30, 3 resistant : 13 susceptible ratio was noticed.

The F_1's of all resistant x resistant crosses were resistant, while F_1's of all susceptible x susceptible crosses were susceptible (Table 15). Further, no segregation was observed in the F_2 generation of either resistant x resistant or susceptible x susceptible crosses (Table 16).

4.2.3 Genetics of resistance for isolate 3

The cross combinations of two resistant parents, ICP 7035 and ICP 2376 with the susceptible, ICP 8863 was studied to elucidate the genetics of resistance for isolate 3 (Table 17). The parents, ICP 7035 and ICP 2376 did not exhibit any symptoms and were resistant. On the other hand, ICP 8863 recorded severe mosaic symptoms and was susceptible. The F_1's of the resistant x susceptible crosses were all susceptible. In the F_2 generation, a segregation ratio of 7 resistant : 9 susceptible was observed for the cross, ICP 7035 X ICP 8863. However, the cross, ICP 2376 X ICP 8863 segregated in 1 resistant : 3 susceptible ratio.

Table 12 Reaction of parents for isolate 2 of pigeonpea sterility mosaic pathogen

Parent	Total plants	Resistant plants	Tolerant plants	Susceptible plants
ICP 7035	27	27	-	-
ICP 7349	24	24	-	-
ICP 8850	29	29	-	-
ICP 2376	42	-	-	42
ICP 7994	23	-	-	23
ICP 11251	35	-	-	35
BDN 1	28	-	-	28
LRG 30	31	-	-	31
ICP 8863	34	-	-	34

Table 13 Reaction of F_1 hybrids of resistant x susceptible crosses to isolate 2 of pigeonpea sterility mosaic pathogen

Cross	Total plants	Resistant plants	Tolerant plants	Susceptible plants
ICP 7035 X ICP 2376	22	22	-	-
ICP 7035 X ICP 7994	19	19	-	-
ICP 7035 X ICP 11251	23	23	-	-
ICP 7035 X BDN 1	10	10	-	-
ICP 7035 X LRG 30	12	12	-	-
ICP 7035 X ICP 8863	11	11	-	-
ICP 7349 X ICP 2376	20	20	-	-
ICP 7349 X ICP 7994	25	25	-	-
ICP 7349 X ICP 11251	17	17	-	-
ICP 7349 X BDN 1	8	8	-	-
ICP 7349 X LRG 30	9	9	-	-
ICP 7349 X ICP 8863	16	16	-	-
ICP 8850 X ICP 2376	19	-	-	19
ICP 8850 X ICP 7994	23	-	-	23
ICP 8850 X ICP 11251	18	-	-	18
ICP 8850 X BDN 1	12	-	-	12
ICP 8850 X LRG 30	14	-	-	14
ICP 8850 X ICP 8863	11	-	-	11

Table 14 Reaction of F_2 generation of resistant x susceptible crosses to isolate 2 of pigeonpea sterility mosaic pathogen

Cross	Observed frequencies			Expected frequencies		Ratio	Probability
	Total Plants	Resistant plants (R)	Susceptible plants (S)	Resistant plants (R)	Susceptible plants (S)	R : S	
ICP 7035 X ICP 2376	332	241	91	249.00	83	3 : 1	0.30-0.50
ICP 7035 X ICP 7994	328	189	139	184.50	143.50	9 : 7	0.50-0.70
ICP 7035 X ICP 11251	290	161	129	163.13	126.88	9 : 7	0.80-0.90
ICP 7035 X BDN 1	248	199	49	186.00	62	3 : 1	0.30-0.50
ICP 7035 X LRG 30	360	209	151	202.50	157.5	9 : 7	0.30-0.50
ICP 7035 X ICP 8863	284	211	73	213.00	71.00	3 : 1	0.70-0.80
ICP 7349 X ICP 2376	381	280	101	285.75	95.25	3 : 1	0.30-0.50
ICP 7349 X ICP 7994	367	200	167	206.44	160.56	9 : 7	0.30-0.50
ICP 7349 X ICP 11251	329	188	141	185.06	143.94	9 : 7	0.70-0.80
ICP 7349 X BDN 1	450	329	121	337.50	112.50	3 : 1	0.30-0.50
ICP 7349 X LRG 30	327	195	132	183.94	143.06	9 : 7	0.20-0.30
ICP 7349 X ICP 8863	278	211	67	208.50	69.50	3 : 1	0.70-0.80
ICP 8850 X ICP 2376	309	85	224	77.25	231.75	1 : 3	0.30-0.50
ICP 8850 X ICP 7994	326	55	271	61.13	264.88	3 : 13	0.30-0.50
ICP 8850 X ICP 11251	388	78	310	72.75	315.25	3 : 13	0.30-0.50
ICP 8850 X BDN 1	398	87	311	99.50	298.50	1 : 3	0.10-0.20
ICP 8850 X LRG 30	220	49	171	41.25	178.75	3 : 13	0.10-0.20
ICP 8850 X ICP 8863	367	97	270	91.75	275.25	1 : 3	0.50-0.70

Table 15 Reaction of F_1 hybrids of resistant x resistant and susceptible x susceptible crosses to isolate 2 of pigeonpea sterility mosaic pathogen

Cross	Total plants	Resistant plants	Tolerant plants	Susceptible plants
Resistant x resistant F_1 hybrids				
ICP 7035 X ICP 7349	22	22	-	-
ICP 7035 X ICP 8850	14	14	-	-
ICP 7349 X ICP 8850	18	18	-	-
Susceptible x susceptible F_1 hybrids				
ICP 2376 X ICP 7994	23	-	-	23
ICP 2376 X ICP 11251	18	-	-	18
ICP 2376 X BDN 1	23	-	--	23
ICP 2376 X LRG 30	25	-		25
ICP 2376 X ICP 8863	27	-	-	27
ICP 7994 X ICP 11251	18	-	-	18
ICP 7994 X BDN 1	25	-	-	25
ICP 7994 X LRG 30	19	-	-	19
ICP 7994 X ICP 8863	21	-	-	21
ICP 11251 X BDN 1	21	-	-	21
ICP 11251 X LRG 30	17	-	-	17
ICP 11251 X ICP 8863	23	-	-	23
BDN 1 X LRG 30	20	-	-	20
BDN 1 X ICP 8863	20	-	-	20
LRG 30 X ICP 8863	18	-	-	18

Table 16 Reaction of F_2 generation of resistant x resistant and susceptible x susceptible crosses to isolate 2 of pigeonpea sterility mosaic pathogen

Cross	Observed frequencies			Expected frequencies		Ratio	Probability
	Total Plants	Resistant plants (R)	Susceptible plants (S)	Resistant plants (R)	Susceptible plants (S)	R : S	
Resistant x resistant crosses							
ICP 7035 X ICP 7349	297	296	1	297	-		
ICP 7035 X ICP 8850	457	450	7	457	-		
ICP 7349 X ICP 8850	350	339	11	350	-		
Susceptible x susceptible crosses							
ICP 2376 X ICP 7994	312	-	312	-	312		
ICP 2376 X ICP 11251	287	-	287	-	287		
ICP 2376 X BDN 1	231	-	231	-	231		
ICP 2376 X LRG 30	274	3	271	-	274		
ICP 2376 X ICP 8863	293	-	293	-	293		
ICP 7994 X ICP 11251	312	-	312	-	312		
ICP 7994 X BDN 1	234	5	229	-	234		
ICP 7994 X LRG 30	323	2	321	-	323		
ICP 7994 X ICP 8863	197	2	195	-	197		
ICP 11251 X BDN 1	243	-	243	-	243		
ICP 11251 X LRG 30	212	-	212	-	212		
ICP 11251 X ICP 8863	285	-	285	-	285		
BDN 1 X LRG 30	472	9	463	-	472		
BDN 1 X ICP 8863	370	-	370	-	370		
LRG 30 X ICP 8863	271	6	265	-	271		

Table 17 Reaction of parents, F_1 and F_2 generations of resistant x susceptible crosses for isolate 3 of pigeonpea sterility mosaic pathogen

Generation	Observed frequencies			Expected frequencies		Ratio	Probability
	Total plants	Resistant plants (R)	Susceptible plants (S)	Resistant plants (R)	Susceptible plants (S)	R : S	
			ICP 7035 X ICP 8863				
ICP 7035	87	87	-	87	-	-	-
ICP 8863	95	-	95	-	95	-	-
F_1	43	-	43	-	43	-	-
F_2	911	394	517	398.56	512.44	7 : 9	0.70-0.80
			ICP 2376 X ICP 8863				
ICP 2376	93	93	-	93	-	-	-
ICP 8863	98	-	98	-	98	-	-
F_1	37	-	37	-	37	-	-
F_2	1063	271	792	265.75	797.25	1 : 3	0.70-0.80

4.3 HETEROSIS AND COMBINING ABILITY STUDY

The results obtained from line x tester trial involving ICP 2376, ICP 7035, ICP 7349, ICP 7994, ICP 8006, ICP 8136, ICP 8850, ICP 8863, BDN 1 and LRG 30 pollen parents, in combination with the two male steriles viz., ICP MS288 and ICP MS3783 are presented hereunder.

4.3.1 Analysis of variance

The analysis of variance of parents and hybrids for different characters under study is presented in Table 18. The mean sum of squares due to genotypes were highly significant for yield and all yield component characters studied. On further partitioning, parents, hybrids and parents vs. hybrids were also found significant for the various traits studied.

4.3.2 Mean performance of parents and hybrids

The *per se* performance of parents and hybrids for the yield and yield component characters studied are presented in Tables 19 and 20, respectively. The hybrids, in general were early maturing, dwarf and high yielding over parents. Further, greater variation was recorded among the hybrids for days to maturity and plant height in comparison to the parents. Among the 22 hybrids studied, 12 outyielded the checks viz., BDN 1, LRG 30 and ICP 8863. Of these, the hybrid, ICP MS3783 X LRG 30 recorded significantly higher seed yield in comparison to other hybrids and checks. In contrast, the cross, ICP MS3783 X ICP 8136 recorded minimum seed yield. Hybrids of ICP MS288 parent were early maturing, dwarf and compact in comparison to hybrids of ICP MS3783, which were late maturing, spreading and tall.

Among the parents, ICP 11251 recorded highest seed yield followed by ICP 8006 and ICP 7994 lines while, the lines, ICP MS288, ICP 7349, ICP 8863, ICP 11251 and BDN 1 were found to be early maturing.

4.3.3 Heterosis

The data on heterosis or hybrid vigor was measured as an increase or decrease over mid-parental values (relative heterosis) and better parent (heterobeltiosis) for the different traits studied. However, for seed yield, increase or decrease over the checks viz., BDN 1, LRG 30 and ICP 8863 was also estimated. The above details are presented in Tables 21 and 22 respectively. For days to 50 per cent flowering and days to maturity, the low scoring parent was considered the better parent.

Table 18 Analysis of variance (mean squares) for yield and yield component characters of parents and crosses in pigeonpea

Source	df	Days to 50 per cent flowering	Days to maturity	Plant height (cm)	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
Replications	2	1.56	3.06	12.16	4.41	7.29	8.27	0.11**	0.21	46.58
Genotypes	34	12.43**	29.42**	581.85**	39.87**	35.20**	1671.79**	0.03**	13.00**	831.92**
Parents	12	16.42**	16.79**	743.31**	51.23**	40.50**	402.17*	0.04**	20.91**	1158.30**
Hybrids	21	6.06**	28.30**	430.14**	29.32**	28.05**	2388.71**	0.02*	7.21**	563.49**
Parents vs. Hybrids	1	98.28**	204.57**	1830.33**	125.08**	121.73**	1851.93**	0.14**	39.64**	2552.42**
Error	68	1.62	2.17	68.61	2.29	2.66	194.63	0.01	0.16	136.10

**Significant at 1 per cent level

*Significant at 5 per cent level

Table 19 Mean performance of parents for yield and yield component characters of pigeonpea

Parent	Days to 50% flowering	Days to maturity	Plant Height (cm)	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
Female parent									
ICP MS228	91.00	162.00	158.20	8.90	11.90	251.10	4.20	9.30	53.80
ICP MS3783	134.00	229.00	231.90	25.10	96.20	394.40	3.00	8.30	91.20
Male parent									
ICP 2376	131.00	185.00	222.80	18.30	19.20	335.50	3.90	8.40	44.70
ICP 7035	172.00	233.00	190.80	8.90	7.50	72.60	4.20	18.50	62.90
ICP 7349	119.00	185.00	178.90	12.80	13.10	170.60	4.70	10.20	47.20
ICP 7994	133.00	185.00	223.10	13.40	25.30	409.20	4.30	11.20	123.00
ICP 8006	147.00	205.00	280.30	10.90	5.50	409.10	3.70	14.60	121.60
ICP 8136	145.00	189.00	269.00	9.30	4.70	105.70	3.10	8.10	38.90
ICP 8850	131.00	185.00	198.20	9.60	17.20	143.40	4.40	9.50	26.10
ICP 8863	116.00	155.00	215.10	16.50	21.50	324.80	3.90	10.70	66.60
ICP 11251	125.50	181.00	234.30	19.70	34.90	1199.20	3.70	7.70	221.60
BDN1	115.00	173.00	212.00	14.70	23.50	297.50	3.90	9.40	61.20
LRG 30	142.00	190.00	241.90	21.50	24.20	362.70	4.10	5.60	40.80
Mean	130.88	189.00	219.73	14.58	23.44	344.29	3.93	10.12	76.89
Range	91-172	155-233	158.2-280.3	8.9-25.1	4.7-96.2	72.6-1199.2	3-4.7	5.6-18.5	26.1-221.6
S.E ±	0.73	0.85	4.78	0.87	0.94	8.05	0.06	0.23	6.74
C.D (at 5%)	2.07	2.40	13.49	2.46	2.66	22.71	0.16	0.65	18.99

Table 20 Mean performance of hybrids for yield and yield component characters of pigeonpea

Hybrids	Days to 50% flowering	Days to maturity	Plant Height (cm)	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
ICP MS288 X ICP 2376	102.50	143.00	205.80	11.00	17.70	197.80	4.40	7.70	47.40
ICP MS288 X ICP 7035	106.00	150.00	206.40	11.30	15.80	151.60	4.90	15.20	49.70
ICP MS288 X ICP 7349	104.00	142.00	191.00	11.40	7.40	306.00	4.00	9.30	145.80
ICP MS288 X ICP 7994	104.00	142.00	200.10	11.40	16.40	239.50	4.60	9.30	54.80
ICP MS288 X ICP 8006	116.00	155.00	210.00	11.80	10.70	189.30	4.50	12.30	44.00
ICP MS288 X ICP 8136	109.00	142.00	132.25	11.75	10.00	168.50	4.00	7.30	40.80
ICP MS288 X ICP 8850	102.00	125.50	172.60	10.80	13.30	249.50	4.10	11.70	44.50
ICP MS288 X ICP 8863	108.00	125.50	206.40	14.40	17.40	184.50	4.20	10.40	42.60
ICP MS288 X ICP 11251	101.00	144.00	206.90	14.40	19.90	185.50	4.00	8.70	73.10
ICP MS288 X BDN1	108.00	127.00	190.10	14.90	17.20	218.20	4.30	9.60	45.90
ICP MS288 X LRG 30	104.00	142.00	203.10	11.80	13.50	215.50	4.10	6.60	46.00
ICP MS3783 X ICP 2376	117.00	194.00	236.40	22.80	42.90	443.60	3.90	8.90	101.20
ICP MS3783 X ICP 7035	134.00	213.00	237.40	18.50	45.20	318.30	4.10	12.90	86.30
ICP MS3783 X ICP 7349	125.50	185.00	239.10	16.90	30.20	373.80	3.90	9.30	101.00
ICP MS3783 X ICP 7994	134.00	213.00	237.10	22.90	82.70	241.10	3.80	10.30	104.20
ICP MS3783 X ICP 8006	134.00	213.00	275.40	17.40	43.70	192.10	4.00	12.30	89.50
ICP MS3783 X ICP 8136	129.00	201.00	285.70	15.70	39.50	122.00	3.00	8.70	35.80
ICP MS3783 X ICP 8850	127.00	185.00	223.00	17.70	27.00	308.90	4.20	9.30	87.40
ICP MS3783 X ICP 8863	124.00	185.00	250.10	16.60	37.60	484.60	4.00	10.30	125.40
ICP MS3783 X ICP 11251	124.00	185.00	228.60	16.50	28.60	419.40	3.80	8.60	94.30
ICP MS3783 X BDN1	125.50	185.00	225.80	17.60	52.50	568.20	4.00	10.40	137.00
ICP MS3783 X LRG 30	127.00	194.00	242.40	22.60	65.70	696.40	4.00	8.30	164.70
Mean	116.61	167.77	218.44	15.46	29.77	294.29	4.08	9.88	80.06
Range	101-134	125.5-213	132.25-285.7	10.8-22.9	7.4-82.7	122-696.4	3-4.9	6.6-15.2	35.8-164.7
S.E ±	0.73	0.85	4.78	0.87	0.94	8.05	0.06	0.23	6.74
C.D (at 5%)	2.07	2.40	13.49	2.46	2.66	22.71	0.16	0.65	18.99

Table 21 Per cent heterosis over mid-parent (MP) and better parent (BP) of few yield component characters in pigeonpea

Hybrid	Days to 50% flowering		Days to maturity		Plant Height (cm)		Number of primary branches		Number of secondary branches	
	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP
ICP MS288 X ICP 2376	-7.66**	12.64**	-17.58**	-11.73**	8.03**	-7.63**	-19.12*	-39.89**	13.83	-7.81
ICP MS288 X ICP 7035	-19.39**	16.48**	-24.05**	-7.41**	18.28**	8.18**	26.97*	26.97	62.89**	32.77**
ICP MS288 X ICP 7349	-0.95	14.29**	-18.16**	-12.35**	13.32**	6.76**	5.07	-10.94	-40.80**	-43.51**
ICP MS288 X ICP 7994	-7.14**	14.29**	-18.16**	-12.35**	4.96**	-10.31**	2.24	-14.93	-11.83	-35.18**
ICP MS288 X ICP 8006	-2.52**	27.47**	-15.53**	-4.32**	-4.22**	-25.08**	19.19	8.26	22.99	-10.08
ICP MS288 X ICP 8136	-7.63**	19.78**	-19.09**	-12.35**	-38.09**	-50.84**	29.12*	26.34	20.48	-15.97
ICP MS288 X ICP 8850	-8.11**	12.09**	-27.67**	-22.53**	-3.14**	-12.92**	16.76	12.50	-8.59	-22.67**
ICP MS288 X ICP 8863	4.35**	18.68**	-20.82**	-19.03**	10.58**	-4.04**	13.39	-12.73	4.19	-19.07**
ICP MS288 X ICP 11251	-6.70**	10.99**	-16.03**	-11.11**	5.43**	-11.69**	0.70	-26.90**	-14.96**	-42.98**
ICP MS288 X BDN1	4.85**	18.68**	-24.18**	-21.60**	2.70**	-10.33**	26.27**	1.36	-2.82	-26.81**
ICP MS288 X LRG 30	-10.73**	14.29**	-19.32**	-12.35**	1.52**	-16.04**	-22.37**	-45.12**	-25.21**	-44.21**
ICP MS3783 X ICP 2376	-11.70**	-10.69**	-6.28**	4.86**	3.98**	1.94**	5.07	-9.16	-25.65**	-55.41**
ICP MS3783 X ICP 7035	-12.42**	0.00	-7.79**	-6.99**	12.33**	2.37**	8.82	-26.29**	-12.83**	-53.01**
ICP MS3783 X ICP 7349	-0.79	5.46**	-10.63**	0.00	16.41**	3.10**	-10.82	-32.67**	-44.74**	-68.61**
ICP MS3783 X ICP 7994	0.37	0.75	2.90**	15.14**	4.22**	2.24**	18.96**	-8.76	36.13**	-14.03**
ICP MS3783 X ICP 8006	-4.63**	0.00	-1.84**	3.90**	7.54**	-1.75**	-3.33	-30.68**	-14.06**	-54.57**
ICP MS3783 X ICP 8136	-7.53**	-3.73**	-3.83**	6.35**	14.07**	6.21**	-8.72	-37.45**	-21.70**	-58.94**
ICP MS3783 X ICP 8850	-4.15**	-3.05**	-10.63**	0.00	3.70**	-3.84**	2.02	-29.48**	-52.38**	-71.93**
ICP MS3783 X ICP 8863	-0.80	6.90**	-3.65**	19.35**	11.90**	7.85**	-20.19**	-33.86**	-36.11**	-60.91**
ICP MS3783 X ICP 11251	-4.43**	-1.20	-9.76**	2.21**	-1.93**	-2.43**	-26.34**	-34.26**	-56.37**	-70.27**
ICP MS3783 X BDN1	0.80	9.13**	-7.96**	6.94**	1.73**	-2.63**	-11.56*	-29.88**	-12.28**	-45.43**
ICP MS3783 X LRG 30	-7.97**	-5.22**	-7.40**	2.11**	2.32**	0.21	-3.00	-9.96*	9.14**	-31.70**
Range	-19.39	-10.69	-27.67	-22.53	-38.09	-50.84	-26.34	-45.12	-56.37	-71.93
S.E ±	0.73		0.85		4.78		0.87		0.94	

**Significant at 1 per cent level

*Significant at 5 per cent level

Table 22 Per cent heterosis over mid-parent (MP) and better parent (BP) of yield and few yield component characters in pigeonpea

Hybrid	Pods per plant		Seeds per pod		Test weight (g)		Yield per plant (g)				
	MP	BP	MP	BP	MP	BP	MP	BP	BDN 1	LRG 30	ICP 8863
ICP MS288 X ICP 2376	-32.56**	-41.04**	8.64**	4.76*	-12.99**	-17.20**	-3.76	-11.90	-22.55	16.18	-28.83*
ICP MS288 X ICP 7035	-6.33	-39.63**	16.67**	16.67**	9.35**	-17.84**	-14.82	-20.99	-18.79	21.81	-25.38
ICP MS288 X ICP 7349	45.13**	21.86**	-10.11**	-14.89**	-4.62	-8.82**	188.71**	171.00**	138.24**	257.35**	118.92**
ICP MS288 X ICP 7994	-27.46**	-41.47**	8.24**	6.98**	-9.27**	-16.96**	-38.01**	-55.45**	-10.46	34.31	-17.72
ICP MS288 X ICP 8006	-42.65**	-53.73**	13.92**	7.14**	2.93	-15.75**	-49.83**	-63.82**	-28.10	7.84	-33.93*
ICP MS288 X ICP 8136	-5.55	-32.90**	9.59**	-4.76*	-16.09**	-21.51**	-11.97	-24.16	-33.33*	0.00	-38.74**
ICP MS288 X ICP 8850	26.49**	-0.64	-4.65**	-6.82**	24.47**	23.16**	11.39	-17.29	-27.29	9.07	-33.18*
ICP MS288 X ICP 8863	-35.93**	-43.20**	3.70*	0.00	4.00	-2.80	-29.24*	-36.04*	-30.39	4.41	-36.04*
ICP MS288 X ICP 11251	-74.42**	-84.53**	1.27	-4.76*	2.35	-6.45	-46.91**	-67.01**	19.44	79.17**	9.76
ICP MS288 X BDN1	-20.45**	-26.66**	6.17**	2.38	2.67	2.13	-20.17	-25.00	-25.00	12.50	-31.08*
ICP MS288 X LRG 30	-29.78**	-40.56**	-1.20	-2.38	-11.41**	-29.03**	-2.75	-14.50	-24.84	12.75	-30.93*
ICP MS3783 X ICP 2376	21.55**	12.47**	13.04**	0.00	6.59	5.95	48.93**	10.96	65.36**	148.04**	51.95**
ICP MS3783 X ICP 7035	36.32**	-19.30**	13.89**	-2.38	-3.73	-30.27**	12.01	-5.37	41.01*	111.52**	29.58*
ICP MS3783 X ICP 7349	32.32**	-5.22	1.30	-17.02**	0.54	-8.82**	45.95**	10.75	65.03**	147.55**	51.65**
ICP MS3783 X ICP 7994	-40.00**	-41.08**	4.11*	-11.63**	5.64	-8.04**	-2.71	-15.28	70.26**	155.39**	56.46**
ICP MS3783 X ICP 8006	-52.18**	-53.04**	19.40**	8.11**	7.42**	-15.75**	-15.88*	-26.40**	46.24**	119.36**	34.38*
ICP MS3783 X ICP 8136	-51.21**	-69.07**	-1.64	-3.23	6.10	4.82	-44.97**	-60.75**	-41.50**	-12.25	-46.25**
ICP MS3783 X ICP 8850	14.88**	-21.68**	13.51**	-4.55*	4.49	-2.11	49.02**	-4.17	42.81**	114.22**	31.23*
ICP MS3783 X ICP 8863	34.76**	22.87**	15.94**	2.56	8.42**	-3.74	58.94**	37.50**	104.90**	207.35**	88.29**
ICP MS3783 X ICP 11251	-47.36**	-65.03**	13.43**	2.70	7.50*	3.61	-39.71**	-57.45**	54.08**	131.13**	41.59**
ICP MS3783 X BDN1	64.24**	44.07**	15.94**	2.56	17.51**	10.64**	79.79**	50.22**	123.86**	235.78**	105.71**
ICP MS3783 X LRG 30	83.97**	76.57**	12.68**	-2.44	19.42**	0.00	149.55**	80.59**	169.12**	303.68**	147.30**
Range	-74.42	-84.53	-10.11	-17.02	-16.09	-30.27	-49.83	-67.01	-41.50	-12.25	-46.25
S.E ±	8.05		0.06		0.23		6.74				

**Significant at 1 per cent level

*Significant at 5 per cent level

Heterosis over mid-parent for days to 50 per cent flowering ranged from -19.39 to 4.85 while, heterobeltiosis ranged between -10.69 to 27.47. Similarly, for days to maturity, heterosis over mid-parent ranged between -27.67 to 2.90 while, heterobeltiosis recorded higher range (-22.53 to 19.35). Only four crosses (ICP MS3783 X ICP 2376, ICP MS3783 X ICP 8136, ICP MS3783 X ICP 8850 and ICP MS3783 X LRG 30) had recorded significant heterosis and heterobeltiosis in the desirable direction, for days to 50 per cent flowering. However, for days to maturity, significant heterosis and heterobeltiosis, in the desirable direction was recorded in all hybrids of ICP MS288 and the cross combination of ICP MS3783 X ICP 7035. Heterotic effects over mid and better parents for plant height were noticed in ICP MS288 X ICP 7035, ICP MS288 X ICP 7349, ICP MS3783 X ICP 2376, ICP MS3783 X ICP 7035, ICP MS3783 X ICP 7349, ICP MS3783 X ICP 7994, ICP MS3783 X ICP 8136 and ICP MS3783 X ICP 8863 hybrid combinations while, hybrid vigor, in the desirable direction was noticed for number of secondary branches in ICP MS288 X ICP 7035. Heterotic effects for pods per plant were recorded in the crosses, ICP MS288 X ICP 7349, ICP MS3783 X ICP 2376, ICP MS3783 X ICP 8863, ICP MS3783 X BDN 1 and ICP MS3783 X LRG 30 while, heterotic effects for seeds per pod were recorded in seven crosses viz., ICP MS288 X ICP 2376, ICP MS288 X ICP 7035, ICP MS288 X ICP 7994, ICP MS288 X ICP 8006, ICP MS288 X BDN 1, ICP MS3783 X ICP 8006 and ICP MS3783 X ICP 8863. Hybrid vigor for test weight was recorded in ICP MS288 X ICP 8850 and ICP MS3783 X BDN 1 crosses. Significant expression of hybrid vigor over mid-parent, better parent and the three hybrid checks, was recorded for yield per plant in the crosses, ICP MS288 X ICP 7349, ICP MS3783 X ICP 8863, ICP MS3783 X BDN 1 and ICP MS3783 X LRG 30.

4.3.4 Combining ability analysis

4.3.4.1 *Analysis of variance and variance components*

The analysis of variance for combining ability (Table 23) revealed significant variation for all traits studied, for the hybrids. The mean squares of males were highly significant for all characters. The females also recorded significance for all traits, except seeds per pod. The interaction mean squares of males and females too were significant for days to maturity, plant height, primary branches, secondary branches, pods per plant, test weight and yield per plant. Observations for the components of genetic variation, in respect

Table 23 Analysis of variance (mean squares) for combining ability, estimates of variance components and their ratios for yield and yield component characters in pigeonpea

Source	df	Days to 50 per cent flowering	Days to maturity	Plant height (cm)	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
Hybrids	21	6.06**	28.30**	430.14**	29.32**	28.05**	2388.71**	0.02*	7.21**	563.49**
Males	10	8.74**	37.52**	620.17**	45.62**	35.77**	3014.74**	0.03**	9.08**	821.21**
Females	1	17.46**	113.70**	1087.52**	89.57**	134.69**	11167.78**	0.02	44.00**	871.65**
Males x Females	10	2.25	10.53**	174.36*	7.00**	9.66*	884.76**	0.01	1.67**	274.95*
Error	68	1.62	2.17	68.61	2.29	2.66	194.63	0.0089	0.16	136.10
$\sigma^2 gca$		0.09	0.41	5.96	0.51	0.43	34.91	0.00024	0.13	6.81
$\sigma^2 sca$		0.21	2.79	35.25	1.57	2.33	230.04	0.00037	0.50	46.28
$\sigma^2 gca/\sigma^2 sca$		0.43	0.15	0.17	0.33	0.18	0.15	0.65	0.26	0.15

**Significant at 1 per cent level

*Significant at 5 per cent level

of various characters under study (Table 23) revealed high SCA variance component for all traits studied.

4.3.4.2 *General and specific combining ability effects*

The general and specific combining ability effects of parents and crosses for yield and yield component characters of pigeonpea are presented in Tables 24 and 25, respectively.

General combining ability effects

The lines, ICP 7349, ICP 8850, ICP 11251 and ICP MS288 recorded significant and negative *gca* effects for days to 50 per cent flowering and days to maturity while, for plant height, significant and positive *gca* effects were recorded for ICP 8006, ICP 8863 and ICP MS3783. For number of branches (primary and secondary) LRG 30 and ICP MS3783 recorded significant and positive *gca* effects. However, for pods per plant and seed yield, ICP 11251, BDN 1, LRG 30 and ICP MS3783 recorded significant and positive *gca* effects. For seeds per pod, ICP 7035, ICP 8006 and ICP MS288 recorded highly significant and positive *gca* effects while, for test weight, the *gca* effects were non-significant.

In general, the female parent ICP MS3783 recorded positive and significant *gca* effects for majority of the traits including yield while, among the male parents, LRG 30 recorded positive and significant *gca* effects for most traits including yield.

Specific combining ability effects

The estimates of specific combining ability ranged from -4.18 to 5.72 for days to 50 per cent flowering and from -7.70 to 7.70 for days to maturity. Significant and negative *sca* effects were recorded in eight crosses for days to 50 per cent flowering and days to maturity. Of these, four crosses, viz., ICP MS288 X ICP 7035, ICP MS288 X ICP 8850, ICP MS 288 X ICP 7994 and ICP MS3783 X ICP 2376 recorded significant and negative *sca* effects for both days to 50 per cent flowering and days to maturity. Significant and positive *sca* effects for plant height were recorded for ICP MS3783 X ICP 8006 cross while, ICP MS288 X ICP 11251, ICP MS288 X ICP 8863, ICP MS3783 X ICP 7994 and ICP MS3783 X LRG 30 recorded positive and significant *sca* effects for number of branches (primary and secondary).

Significant and positive *sca* effects were also recorded in 10 crosses, for pods per plant and in five crosses, for yield per plant. The *sca* effects ranged from -145.00 to 115.00 for pods per plant and from

Table 24 Estimates of general combining ability effects of various parents for yield and yield component characters in pigeonpea

Parents	Days to 50 per cent flowering	Days to maturity	Plant height (cm)	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
Males									
ICP 2376	2.63**	7.30**	-0.79	1.02	14.87**	-68.89**	0.06	-0.30	-4.74**
ICP 7035	3.63**	14.10**	2.52	-0.74	0.23	-74.24**	0.27**	3.17	-16.29**
ICP 7349	-3.88**	-2.90**	-1.64	-0.19	-6.02**	-6.74	-0.24**	-1.43	-0.52**
ICP 7994	-6.63**	1.10	1.72	1.01	0.03	11.51*	0.01	-1.77	-9.94**
ICP 8006	4.93**	16.60**	18.23**	-1.04	-3.07**	-98.75**	0.11**	2.20	-17.44**
ICP 8136	3.70**	2.80**	5.08	0.96	4.41**	-19.74**	0.09*	0.83	9.97**
ICP 8850	-1.88**	-12.15**	-21.59**	-1.39*	-10.12**	-29.99**	0.01	0.42	-18.27**
ICP 8863	-0.38	-12.15**	8.87*	-0.14	-2.77**	25.36**	-0.04	0.28	-0.24
ICP 11251	-1.63**	-3.90**	-4.33	-1.49*	-11.47**	30.71**	-0.19**	-0.75	37.19**
BDN1	0.38	-11.40**	-11.44**	0.62	4.58**	84.01**	0.01	-0.05	7.23**
LRG 30	-0.88	0.60	3.37	1.37*	9.33**	146.76**	-0.09*	-2.60	13.06**
S.E ±	0.52	0.60	3.38	0.62	0.67	5.70	0.04	4.76	0.16
Females									
ICP MS288	-10.83**	-27.80**	-20.15**	-3.32**	-15.34**	-95.45**	0.17**	-0.01	-24.86**
ICP MS3783	10.83**	27.80**	20.15**	3.32**	15.34**	95.45**	-0.17**	0.01	24.86**
S.E ±	0.22	0.26	1.44	0.26	0.28	2.43	0.02	2.03	0.07

**Significant at 1 per cent level

*Significant at 5 per cent level

Table 25 Estimates of specific combining ability for yield and yield components in pigeonpea crosses

Cross	Days to 50 per cent flowering	Days to maturity	Plant height (cm)	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
ICP MS288 X ICP 7035	-3.17**	-3.70**	4.64	-0.28	0.64	12.10	0.23**	1.14**	6.56
ICP MS288 X ICP 7349	0.07	6.30**	-3.90	0.56	3.94**	61.55**	-0.12*	-0.01	47.26**
ICP MS288 X ICP 8850	-1.68*	-1.95*	-5.05	-0.14	8.49**	65.75**	-0.22**	1.16**	3.43
ICP MS288 X ICP 8006	1.82*	-1.20	-12.54*	0.52	-1.16	94.05**	0.08	-0.01	2.11
ICP MS288 X ICP 8136	0.88	-1.17	-6.41	0.12	-0.99	71.29**	0.01	-0.01	1.16
ICP MS288 X ICP 2376	3.58**	2.30**	4.84	-2.85**	2.74**	-27.45**	0.08	-0.59*	-2.04
ICP MS288 X ICP 7994	-4.18**	-7.70**	1.65	-2.44**	-17.81**	94.65**	0.23**	-0.52*	0.16
ICP MS288 X ICP 11251	-0.68	7.30**	9.29	2.27*	10.99**	-21.50**	-0.07	0.06	14.28*
ICP MS288 X BDN1	2.08**	-1.20	2.29	1.97*	-2.31*	-79.55**	-0.02	-0.41	-20.72**
ICP MS288 X LRG 30	-0.68	1.80*	0.49	-2.08*	-10.76**	-145.00**	-0.12*	-0.86**	-34.49**
ICP MS288 X ICP 8863	2.83**	-1.95*	-1.71	2.21*	5.24**	-54.60**	-0.07	0.06	-16.54*
ICP MS3783 X ICP 7035	5.72**	3.01**	-4.64	0.58	-0.64	-12.10	-0.32**	-1.45**	-8.65
ICP MS3783 X ICP 7349	-0.12	-6.78**	4.93	-0.56	-3.94**	-61.55**	0.14*	0.32	-48.29**
ICP MS3783 X ICP 8850	1.87*	2.85**	5.89	0.14	-8.49**	-65.75**	0.29**	-1.97**	-4.43
ICP MS3783 X ICP 8006	-1.83*	1.57	9.67*	-0.52	4.29**	-94.05**	-0.08	0.27	-2.11
ICP MS3783 X ICP 8136	-3.42**	1.17	6.41	-0.12	1.67	-71.29**	-0.01	0.29	-1.61
ICP MS3783 X ICP 2376	-3.58**	-2.73**	-4.84	3.15**	-2.74**	32.54**	-0.08	0.62**	5.39
ICP MS3783 X ICP 7994	4.18**	7.70**	-1.65	2.13*	13.88**	-94.65**	-0.29**	0.57*	-0.16
ICP MS3783 X ICP 11251	0.68	-7.41**	-9.29	-2.27*	-10.99**	28.41**	0.09	-0.08	-14.53*
ICP MS3783 X BDN1	-2.17**	1.64	-2.29	-1.97*	4.53**	97.55**	0.02	0.51*	20.98**
ICP MS3783 X LRG 30	0.68	-1.80*	-0.49	1.79*	8.66**	115.00**	0.14*	0.97**	35.73**
ICP MS3783 X ICP 8863	-2.88**	1.95*	2.71	-2.21*	-5.24**	54.60**	0.09	-0.06	16.51*
S.E ±	0.73	0.85	4.78	0.87	0.94	8.05	0.06	0.23	6.74

**Significant at 1 per cent level

*Significant at 5 per cent level

-48.29 to 47.26 for yield per plant. Significant and positive *sca* effects for both pods per plant and seed yield were recorded in the crosses, ICP MS288 X ICP 7349, ICP MS3783 X BDN 1, ICP MS3783 X LRG 30 and ICP MS3783 X ICP 8863. Significant and positive *sca* effects for seeds per pod and test weight were, however recorded for the crosses ICP MS288 X ICP 7035 and ICP MS3783 X LRG 30. In general, the cross ICP MS3783 X LRG 30 recorded significant *sca* effects for most traits including yield, in the desirable direction.

4.4 VARIABILITY, HERITABILITY AND GENETIC ADVANCE

The differences among genotypes were highly significant for all traits studied (Table 18). The range, phenotypic co-efficient of variation, and genotypic co-efficient of variation were highest for pods per plant followed by seed yield per plant and plant height (Table 26). However, they were low for seeds per pod, test weight, days to 50 per cent flowering and days to maturity.

The estimates of heritability for various traits are presented in Table 26. Heritability was considered low, when it was less than 20 per cent. moderate at 20 to 50 per cent and high, when more than 50 per cent. The heritability estimates for the traits under study, thus ranged between moderate to high. High heritability was noticed for test weight (96.40), followed by number of primary branches (84.54), days to maturity (80.72), number of secondary branches (80.31), pods per plant (71.67), plant height (71.38), days to 50 per cent flowering (68.99) and yield per plant (63.02) while, the heritability was moderate for seeds per pod (40.00).

The results on genetic advance and genetic advance as per cent of mean for the various traits are also presented in Table 26. Maximum genetic advance was recorded for pods per plant (38.70) followed by yield per plant (24.91) and plant height (22.76) while, it was minimal for seeds per pod (0.11), days to 50 per cent flowering (3.25), test weight (4.18) and days to maturity (5.58).

4.5 CHARACTER ASSOCIATIONS AND PATH CO-EFFICIENT ANALYSIS

Simple correlations among the various traits studied are presented in Table 27. Significant and

Table 26 Range, mean, coefficient of variability, heritability and genetic advance for yield and yield component traits in pigeonpea

Character	Range	Mean ± SEm	Phenotypic coefficient of variation (PCV)	Genotypic coefficient of variation (GCV)	Heritability	Genetic Advance	Genetic advance as % of mean
Days to 50 per cent flowering	91-172	121 91 ± 0 73	1 87	1.56	68 99	3 25	2 66
Days to maturity	125.5-233	175 65 ± 0 85	2 75	2.47	80 72	5 58	4 58
Plant height	132 25-285 7	218.91 ± 4 78	12 70	10.73	71 38	22.76	18 67
Number of primary branches	8 9-25 1	15 13 ± 0.87	3 16	2.90	84 54	6 70	5.50
Number of secondary branches	4 7-96 2	27 41 ± 0 94	3.01	2.70	80 31	6 08	4 99
Pods per plant	72.6-1199 2	312 86 ± 8 05	21.50	18 20	71 67	38.70	31 74
Seeds per pod	3-4 9	4 02 ± 0 06	0 11	0 07	40 00	0 11	0 09
Test weight	5 6-18 5	9 96 ± 0 23	1 73	1.70	96 40	4 18	3 43
Yield per plant	26 1-221.6	78 88 ± 6 74	15 74	12 49	63 02	24 91	20 43

Table 27 Character associations for yield and yield component characters in pigeonpea

Character	Days to 50 per cent flowering	Days to maturity	Plant height (cm)	Primary branches	Secondary branches	Pods per plant	Seeds per pod	Test weight (g)	Yield per plant (g)
Days to 50 per cent flowering		0.745**	0.176	0.043	0.088	0.018	0.069	0.474	0.155
Days to maturity			0.332**	0.219*	0.328**	0.022	-0.093	0.339**	0.133
Plant height (cm)				0.503**	0.390**	0.179	-0.297**	-0.052	0.276**
Number of primary branches					0.762**	0.463**	-0.595**	-0.357**	0.382**
Number of secondary branches						0.407**	-0.476**	-0.245*	0.412**
Pods per plant							-0.479**	-0.380**	0.857**
Seeds per pod								0.440**	-0.293**
Test weight (g)									-0.101

**Significant at 1 per cent level *Significant at 5 per cent level

positive association of plant height, number of primary branches, number of secondary branches and pods per plant was noticed with yield per plant while seeds per pod recorded significant negative association with yield per plant. The association of days to 50 per cent flowering, days to maturity and test weight with seed yield was however non significant.

Positive and significant associations were also noticed for days to 50 per cent flowering with days to maturity; days to maturity with plant height, primary branches, secondary branches and test weight; plant height with primary branches and secondary branches; primary branches with secondary branches and pods per plant; secondary branches with pods per plant, and seeds per pod with test weight. However, significant and negative associations were recorded between plant height and seeds per pod; primary branches with seeds per pod and test weight; secondary branches with seeds per pod and test weight; and pods per plant with seeds per pod and test weight.

The direct and indirect effects of path matrix for seed yield are presented in Table 28. Pods per plant recorded the largest direct effect on seed yield followed by plant height and number of secondary branches. Days to maturity and number of primary branches recorded negative direct effects. However, correlation of number of primary branches with yield was positive. It had recorded high positive indirect effects via number of secondary branches and pods per plant and negative indirect effects via days to maturity, seeds per pod and test weight. On the other hand, seeds per pod and test weight recorded positive direct effects, while their association with seed yield was negative.

Table 28 Direct and indirect effects of yield component characters on grain yield in pigeonpea

Character	Days to 50 per cent flowering	Days to maturity	Plant height	Number of primary branches	Number of secondary branches	Pods per plant	Seeds per pod	Test weight	Correlation with yield
Days to 50 per cent flowering	**0.0305**	-0.0471	0.0268	-0.0043	0.0152	0.0168	0.0085	0.1088	0.1553
Days to maturity	0.0227	**-0.0631**	0.0505	-0.0220	0.0571	0.0209	-0.014	0.0778	0.1326
Plant height	0.0054	-0.0209	**0.2294**	-0.0505	0.0678	0.1709	-0.0365	-0.0120	0.2765**
Number of primary branches	0.0013	-0.0138	0.0765	**-0.1005**	0.1325	0.4413	-0.0732	-0.0818	0.3823**
Number of secondary branches	0.0027	-0.0207	0.0594	-0.0765	**0.1739**	0.3875	-0.0585	-0.0561	0.4115*
Pods per plant	0.0005	-0.0014	0.0273	-0.0465	0.0707	**0.8526**	-0.0589	-0.0873	0.8572**
Seeds per pod	0.0021	0.0059	-0.0598	0.0598	-0.0828	-0.4562	**0.1229**	0.1009	-0.2926**
Test weight	0.0145	-0.0214	0.0358	0.0358	-0.0425	-0.3624	0.0541	**0.01523**	-0.1006

Residual effect = 0.4623 Direct - Diagonal Indirect - Non-diagonal **Significant at 1 per cent level *Significant at 5 per cent level

DISCUSSION

CHAPTER V

DISCUSSION

Pigeonpea (*Cajanus cajan* (L.) Millsp.) is an important pulse crop, grown widely in the Indian sub-continent. However, its yields are relatively low in India, owing to lack of proper crop management and susceptibility to diseases and pests. Sterility mosaic disease has been considered one of the major constraints for low productivity of pigeonpea in India. The disease is known to occur in all major pigeonpea growing areas of the country. Resistance breeding for the disease has received much emphasis in India, as chemical control has been considered uneconomical (Nene *et al.*, 1989)

The existence of resistance for sterility mosaic disease of pigeonpea has long been known. Alam (1933) was the first to report Sabour 2E and some other Sabour types of pigeonpea to be resistant to sterility mosaic. However, systematic screening efforts for resistance sources were initiated only in 1975 at ICRISAT, India. Thousands of accessions were screened (Nene and Reddy, 1976a,b; Nene *et al.*, 1980) and several resistant and tolerant sources were identified. However, in view of the reported genetic plasticity of the sterility mosaic pathogen in India (Nene *et al.*, 1989; Reddy *et al.*, 1991; Reddy *et al.*, 1993; Khare *et al.*, 1994), the need for screening against specific strains of the sterility mosaic pathogen became apparent.

The phenomenon of "pathogen variation" for sterility mosaic disease was conceptualized and demonstrated, beginning with the observation of large genotype x location interactions for several lines, tested in multi-location trials (Nene *et al.*, 1989; Amin *et al.*, 1993). Later on, five different variants of the sterility mosaic pathogen were reported to occur in India (Reddy *et al.*, 1993). In this context, characterization of resistance sources against specific strains has become essential for precise genetic studies and effective resistance breeding for the disease.

SCREENING FOR DIFFERENT ISOLATES OF PIGEONPEA STERILITY MOSAIC PATHOGEN

Several pigeonpea lines reported resistant/tolerant earlier (Nene *et al.*, 1980) were screened in the

present investigation, against two isolates of the sterility mosaic pathogen. Breakdown of resistance was noticed in several lines. Among the 152 lines evaluated against isolate 1, 37 recorded resistance while, 83 lines showed tolerance. While, for isolate 2 of the 410 lines screened, 161 were resistant and 53 were tolerant.

Screening for isolate 2 included the 152 lines tested against isolate 1. A comparison of the disease reaction of these lines, revealed a breakdown of resistance/tolerance observed for isolate 1, in several lines, to isolate 2. Many lines (37) had recorded resistance against isolate 1, in contrast to few (17) against isolate 2. Similarly, 83 lines (29 ring spot and 54 mild mosaic) had exhibited tolerance for isolate 1, as against 28 (4 ring spot and 24 mild mosaic) for isolate 2. However, two lines (ICP 8852 and ICP 11276), found resistant to isolate 2 had recorded greater disease for isolate 1 indicating a variation in the disease reaction with the strain involved. These findings are in agreement with earlier reports of breakdown of resistance and variation in disease reaction of pigeonpea lines with the location (Nene *et al.*, 1989; Amin *et al.*, 1993; Reddy *et al.*, 1993)

Several lines resistant/tolerant to both isolates were also observed. Hence, a thorough screening of all available lines for their reaction to the strains of sterility mosaic pathogen is essential, for identification of strain-specific/non-specific resistant/tolerant sources

INHERITANCE OF STRAIN-SPECIFIC RESISTANCE

Inheritance of resistance to sterility mosaic disease has been studied since early eighties (Singh *et al.*, 1983; Sivasubramanian *et al.*, 1983; Sharma *et al.*, 1984; Amala Balu and Rathnaswamy, *Personal Communication*) with no precise knowledge of pathogenic variability. Studies carried out at Pantnagar, Uttar Pradesh (Singh *et al.*, 1983) revealed resistance for sterility mosaic disease to be under the control of four independent non-allelic genes while, studies at Coimbatore, Tamil Nadu indicated the governance of resistance trait by non-allelic interaction of two factors (Sivasubramanian *et al.*, 1983; Amala Balu and Rathnaswamy, *Personal Communication*). In contrast, the findings of Sharma *et al.* (1984) at Patancheru, Andhra Pradesh revealed the role of multiple-alleles for resistance reaction to sterility mosaic disease.

The diverse reports on genetics of resistance for sterility mosaic disease could be due to a variation in the pathogenic strain involved. Several workers (Roane *et al.*, 1986; Sun *et al.*, 1990; Poehlman, 1991; Browers *et al.*, 1992; Suh *et al.*, 1995) had reported a variation in inheritance of resistance with the strain involved. The studies of Reddy *et al.* (1993) and results of multi-location trials of earlier workers (Nene *et al.*, 1989; Amin *et al.*, 1993) had also clearly established the occurrence of different variants of sterility mosaic pathogen at these locations i.e., Uttar Pradesh, Tamil Nadu and Andhra Pradesh. The present investigation was undertaken in this context, to elucidate the genetics of strain-specific resistance for different strains of pigeonpea sterility mosaic pathogen. This is the first systematic and comprehensive report of genetics of sterility mosaic resistance, based on strain-specificity.

Inheritance of resistance to isolate 1

Genetic analysis of resistance pertaining to isolate 1 of the pigeonpea sterility mosaic pathogen was studied in crosses of ICP 8863 with five different resistant parents viz., ICP 7035, ICP 7349, ICP 8006, ICP 8136 and ICP 8850. Susceptibility was found dominant over resistance. The observation is in conformity with earlier reports on inheritance of resistance for the disease (Singh *et al.*, 1983; Sharma *et al.*, 1984). The segregation pattern (Table 11) of F_2 and backcrosses (resistant x susceptible) suggested that the susceptible parent, ICP 8863 and the resistant parents ICP 7035, ICP 7349 and ICP 8006 differed in respect of two genes pairs, while ICP 8863 and the resistant parents, ICP 8136 and ICP 8850 differed at least, in respect of one gene pair. Similar variation among different crosses, in the number of genes governing resistance trait for sterility mosaic disease was also reported earlier (Singh *et al.*, 1983; Sharma *et al.*, 1984).

The 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 in the present study, 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. A monogenic ratio of 3 susceptible : 1 resistant was obtained when the resistant parent involved, differed for one of the genes. However, when the parents differed by two genes, a digenic ratio of 9 susceptible : 7 resistant was obtained, indicating the complementary nature of two genes for susceptibility.

Reactions of F_1, F_2 and backcross generations of the tolerant x susceptible cross (Tables 10 and 11) indicated the recessive nature of tolerance over susceptibility. F_2 segregation ratio of 7 tolerant : 9 susceptible, indicated the control of tolerance reaction by two independent and non-allelic gene pairs, exhibiting complementary gene action. Similar inferences for inheritance of tolerance reaction to sterility mosaic disease, were also drawn earlier (Sharma *et al.*, 1984).

It is therefore postulated that resistance/tolerance to isolate 1 of pigeonpea sterility mosaic pathogen is under the control of two independent loci exhibiting complementary gene action. If locus 1 or 2 or both occurred in homozygous recessive state, resistance or tolerance reaction occurred, while dominant condition at both loci invariably resulted in susceptibility. Accordingly, resistance or tolerance is dependent on the presence of recessive alleles at least at one locus.

Inheritance of resistance for isolate 2

The study on inheritance of resistance for isolate 2 of pigeonpea sterility mosaic pathogen (Tables 12-14) revealed a variation in the dominance relationships of the disease reaction with the cross involved. F_1's of the resistant x susceptible crosses involving ICP 7035 and ICP 7349 parents were resistant while, susceptibility was dominant in crosses involving the resistant parent, ICP 8850. The findings are in broad agreement with the results of Sharma *et al* (1984).

The F_2 segregation ratios of the resistant x susceptible crosses (Table 14) suggested that ICP 7035, ICP 7349 and ICP 8850 differed with the susceptibles, ICP 2376, BDN 1 and ICP 8863, in respect of a single gene pair, while with ICP 7994, ICP 11251 and LRG 30, they differed in respect of at least two gene pairs. A similar variation in the number of genes governing resistance was also reported earlier (Singh *et al.*, 1983; Sharma *et al.*, 1984).

The F_2 segregation ratios of 9 resistant : 7 susceptible, in the resistant x susceptible crosses involving the resistant parents, ICP 7035 and ICP 7349 with ICP 7994, ICP 11251 and LRG 30 and 3 resistant : 13 susceptible, in cross combinations of ICP 8850 with ICP 7994, ICP 11251 and LRG 30 indicated the presence of two independent non-allelic gene pairs.

The various F_2 segregation ratios observed for the resistant x susceptible crosses coupled with the variation in disease reaction of F_1's with the cross involved, may be explained on the assumption of

existence of multiple alleles and duplicate genes governing resistance trait for the isolate. The hypothesis of duplicate genes and multiple alleles is combined to explain the diverse reactions observed in F_1 combinations and segregation in F_2. At least three allelic forms are inferred to be present at one of the loci with the dominance relationships of $a_1>a_2>a_3$. The alleles, a_1 and a_3 are assumed to be responsible for resistance reaction, while allele a_2 results in susceptible reaction. Thus, ICP 7035 and ICP 7349 appear to possess the a_1 allele for resistance (a_1a_1BB), while ICP 8850 possesses a_3 allele for resistance (a_3a_3BB). The susceptible parents, ICP 2376, BDN 1 and ICP 8863 appear to possess the a_2 allele for susceptibility, with the genetic constitution a_2a_2BB, while ICP 7994, ICP 11251 and LRG 30 appeared to have $a_2a_2$bb genotypic constitution. This would explain the differential reactions of the F_1's and F_2's observed in the resistant x susceptible crosses. The above genotypes of the resistant and susceptible parents were further confirmed in the study of resistant x resistant and susceptible x susceptible cross combinations (Tables 15 and 16). Segregation was not observed in the F_2 generation of either resistant x resistant or susceptible x susceptible crosses indicating the presence of same genes for resistance and susceptibility in the parents.

Inheritance of resistance for isolate 3

Studies on genetics of resistance for isolate 3 of pigeonpea sterility mosaic pathogen was carried out with two resistant parents, ICP 7035 and ICP 2376 crossed with the susceptible, ICP 8863 (Table 17). Susceptible reaction was found dominant over resistance. Similar observations on dominance of susceptibility over resistance have been reported in earlier studies (Singh *et al.*, 1983; Sharma *et al.*, 1984) for the disease. Further, digenic inheritance of resistance (7 resistant : 9 susceptible) was noticed for the cross, ICP 7035 X ICP 8863 while, monogenic inheritance of resistance was recorded for ICP 2376 X ICP 8863. Similar variation in the number of genes governing resistance trait for sterility mosaic disease with the cross involved was also reported (Singh *et al.*, 1983; Sharma *et al.*, 1984).

The F_2 segregation ratios (7:9 and 1:3) observed in the crosses, for the isolate, might have resulted from two recessive genes governing resistance. Either pair of alleles governing resistance was however observed sufficient to confer resistance for the isolate. Resistance reaction appeared to occur when locus 1 or 2 or both occurred in homozygous recessive state, while dominant condition at both loci invariably resulted in susceptible reaction. When a cross involving a resistant parent (ICP 2376) differed

for one of the genes, a monogenic ratio of 3 susceptible : 1 resistant was obtained. However, when the parents differed by two genes (ICP 7035 and ICP 8863), a digenic ratio of 9 susceptible : 7 resistant was obtained.

Comparative study of inheritance of resistance for isolates of pigeonpea sterility mosaic pathogen

The resistance trait for pigeonpea sterility mosaic disease, thus appeared to be governed by two independent non-allelic genes for isolates 1, 2 and 3. However, for isolate 2, existence of multiple alleles was noticed at one of the locus. The inheritance pattern of resistance was also observed to vary with the parent involved. Monogenic and digenic ratios were obtained depending on the resistant/susceptible parent combinations studied. Variation in the inheritance of resistance with the strain involved was thus complicated with variation in the material. Hence, a comparative study of the same cross combinations for inheritance of resistance to the three isolates was taken up, to elucidate variation in strain-specific inheritance patterns (Table 29).

The results revealed a variation in the inheritance of resistance with the strain involved. The F_1's of ICP 7035 X ICP 8863 cross were susceptible to isolates 1 and 3. However, they were resistant for isolate 2. Susceptible reaction was also observed dominant for isolate 1, in the cross, ICP 7349 X ICP 8863 while, for isolate 2, resistance reaction was dominant over susceptibility. However, for ICP 8850 X ICP 8863 cross, resistance reaction was observed recessive to susceptibility for both isolates 1 and 2. A similar variation in F_1 reaction of the same cross with the strain involved has been reported (Finlay, 1953; Browers *et al.*, 1992) in studies on inheritance of resistance to viral diseases of other crops. The F_2 generation of crosses involving ICP 7035 and ICP 8863 parents segregated in a digenic ratio of 7 resistant : 9 susceptible, indicating presence of two independent non-allelic genes exhibiting complementary gene action, for isolates 1 and 3. 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 resistance reaction. Similar, digenic inheritance for isolate 1 and monogenic inheritance for isolate 2 was also noticed for ICP 7349 X ICP 8863 cross. A similar variation in the number of genes governing disease reaction in the same cross, with the strain involved has been reported in chinese cabbage with turnip mosaic viral strains (Suh *et al.*, 1995). The cross between inbred chinese cabbage lines, 'SSD31' and 'O-2' resulted in digenic inheritance of

Table 29 Comparative study of inheritance of resistance to three isolates of pigeonpea sterility mosaic pathogen

Resistant x Susceptible cross	Strain of pigeonpea sterility mosaic pathogen	F_1 reaction	F_2 segregation ratio
			Resistant : Susceptible
ICP 7035 X ICP 8863	Isolate 1	Susceptible	7 : 9
	Isolate 2	Resistant	3 : 1
	Isolate 3	Susceptible	7 : 9
ICP 7349 X ICP 8863	Isolate 1	Susceptible	7 : 9
	Isolate 2	Resistant	3 : 1
ICP 8850 X ICP 8863	Isolate 1	Susceptible	1 : 3
	Isolate 2	Susceptible	1 : 3

resistance to C_1 and monogenic inheritance of resistance to strains C_4 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 noticed for both isolates. The inheritance of resistance in chinese cabbage to C_4 and C_5 strains in crosses 'O-2 X E-9' and 'O-2 X FL-9' (Yoon *et al.*, 1993) and to C_2, C_3 and C_5 strains in the cross, 'Seoul X O-2' (Suh *et al.*, 1995) also did not vary with the strain of turnip mosaic virus.

The study thus revealed strain-specific inheritance patterns of resistance for pigeonpea sterility mosaic pathogen. Hence, a clear knowledge on the mode of inheritance of resistance for both the strain and the line involved is essential in breeding pigeonpea cultivars resistant to the disease. Further, a detailed study involving all possible cross combinations is needed to classify the parents based on allelic relationship for different isolates.

Screening of available germplasm against different strains of the pigeonpea sterility mosaic pathogen, followed by characterization of resistance sources for their allelic compositions with regards to the isolates would be of immense value in breeding of diverse sterility mosaic resistant cultivars with broad genetic base. Attempts should be made to combine different alleles to diversify genetic composition of the lines with regards to the resistance genes.

HETEROSIS AND COMBINING ABILITY STUDIES

Pigeonpea improvement programs aimed at evolving high yielding, disease resistant varieties may be carried out effectively, only if information is available on combining ability of the recipient and donor parents. This is more so, in the case of sterility mosaic disease, since most of the donors are poor yielders. The present investigation was, therefore, undertaken to gather information on the combining ability of few pigeonpea lines comprising of resistant, tolerant and susceptible types. These were involved in a line x tester mating design and the parents along with the hybrids were evaluated for their heterosis and combining ability effects. Arunachalam (1974) however, argued against inclusion of parents along with the hybrids for combining ability studies. In contrast, Griffing (1956) found it necessary to include parents in the same experimental area as the hybrids, so that the hybrids may be compared directly with their parents

grown in the same environment. The use of data from such a design, to determine combining ability was also recommended by Simmonds (1979). He concluded that the results obtained could provide useful guidance with regards to choice of parents and crosses for economic exploitation.

Analysis of mean and variance

The analysis of variance (Table 18) revealed significant differences among genotypes, parents and hybrids for all traits studied, indicating the existence of sufficient variation for effective selection. The average performance of hybrids (Table 20) was different from that of parents (Table 19), as evident from the significance of parent vs. hybrid source of variation for all characters. The hybrids, in general were early maturing, dwarf and high yielding over parents. Significant differences were also noticed among the males, females and hybrids. Among the 22 hybrids studied, 12 outyielded the checks viz., BDN 1, LRG 30 and ICP 8863 (Table 30). The use of medium duration pollen parents, was in general observed to result in productive crosses. Further, the hybrids of ICP MS288, the early maturing female parent, were all early maturing, in comparison to hybrids of ICP MS3783 and the checks. These hybrids were also relatively dwarf and compact in growth habit, compared to the checks and hybrids of ICP MS3783. Significant variation was also recorded among females (Table 23) for all traits, except seeds per pod. However, the variation among males was found significant for all the traits.

Analysis of Heterosis

Commercial exploitation of heterosis in crop plants is regarded, a major breakthrough in the realm of plant breeding. Heterosis breeding had led to considerable yield improvement of several cereal and other crops (Rai, 1979). A substantial degree of heterosis for yield and related traits over mid-parent, better parent and standard check variety has been reported in pigeonpea hybrids based on male sterile lines (Gupta *et al.*, 1983; Saxena *et al.*, 1986; Patel, 1988; Saxena *et al.*, 1989; Zaveri *et al.*, 1989). The present investigation also revealed significant levels of heterosis for yield and yield component characters.

The aim of heterosis analysis in the present study was to identify the best combination of parents giving high degree of useful heterosis. The existence of overall heterosis was evident by the significance of parents vs. hybrids in the analysis of variance (Table 18) for all characters under study. The expression of heterosis was most evident for yield per plant, pods per plant and number of secondary branches (Table

Table 30 Details of high yielding pigeonpea crosses for seed yield per plant

Hybrid	Maturity groups of parents	*Per se* performance	Heterosis (%) over			*sca* effects
			BDN 1	LRG 30	ICP 8863	
ICP MS288 X ICP 7349	Early x Medium	145 80	138.24**	257.35**	118.92**	47.26**
ICP MS288 X ICP 11251	Early x Medium	73.10	19.44	79.17**	9.76	14.28*
ICP MS3783 X ICP 2376	Mid-late x Medium	101 20	65 36**	148.04**	51 95**	5.39
ICP MS3783 X ICP 7035	Mid-late x Mid-late	86 30	41 01*	111 52**	29.58*	-8 65
ICP MS3783 X ICP 7349	Mid-late x Medium	101.00	65.03**	147 55**	51.65**	-48.29**
ICP MS3783 X ICP 7994	Mid-late x Late	104 20	70.26**	155 39**	56.46**	-0 16
ICP MS3783 X ICP 8006	Mid-late x Late	89.50	46 24*	119.36**	34.38*	-2 11
ICP MS3783 X ICP 8850	Mid-late x Late	87.40	42.81**	114.22**	31 23*	-4 43
ICP MS3783 X ICP 8863	Mid-late x Medium	125.40	104.90**	207.35**	88.29**	16.51*
ICP MS3783 X ICP 11251	Mid-late x Medium	94.30	54.08**	131.13**	41.59**	-14.52*
ICP MS3783 X BDN 1	Mid-late x Medium	137.00	123.86**	235 78**	105.71**	20 98**
ICP MS3783 X LRG 30	Mid-late x Medium	164.70	169 12**	303.68**	147 30**	35.73**

**Significant at 1% level *Significant at 5% level

21). Several workers have also reported the presence of considerable degree of heterosis for seed yield in pigeonpea (Morbad and Solanki, 1957; Sharma *et al.*, 1973a; Shrivastava *et al.*, 1976; Saxena, 1977; Marekar, 1981; Gupta *et al.*, 1983; Mohammed Sheriff and Subramanian, 1983; Singh *et al.*, 1983; Jadhav and Nerkar, 1983; Omanga, 1984; Marekar, 1985; Patel, 1985; Saxena *et al.*, 1986; Patel *et al.*, 1987; Kumar Surya, 1987; Patel, 1988; Saxena *et al.*, 1989; Zaveri *et al.*, 1989; Patel and Patel, 1992). The high heterosis for pods per plant observed in the present study is akin to the findings of Singh (1971), Shrivastava *et al.* (1976), Saxena *et al.* (1986), Sinha *et al.* (1986), Patel *et al.* (1987), Kumar Surya (1987), Patel (1988), Zaveri *et al.* (1989) and Patel and Patel (1992). The high manifestation of heterosis in different crosses for seed yield per plant in the present study was found associated with higher expression of heterosis for pods per plant and plant height. Rana (1990) also reported association of heterosis for seed yield with greater amount of heterosis for component characters like number of pods per plant, branches per plant and per day production. High heterosis for seed yield per plant due to high heterosis for pods per plant, plant height and branches per plant was reported by Patel *et al.* (1991)

Higher levels of heterosis in desired direction was observed in several crosses for various traits under study (Table 31). Majority of the crosses (18) recorded positive and significant heterosis (over mid-parent) for plant height and seeds per pod while negative heterosis was observed for days to 50 per cent flowering (15) and days to maturity (21). Veeraswamy *et al.* (1973b), Chaudhary (1979) and Marekar (1981) also reported positive heterosis for plant height. Singh *et al.* (1989) also reported positive heterosis for plant height and seeds per pod in 15 medium duration hybrids obtained from crosses between male sterile 3783 and 15 advanced breeding lines. Negative heterosis was also recorded over better parent for days to maturity, plant height, primary branches, secondary branches, pods per plant, seeds per pod, test weight and yield per plant in majority of the crosses studied in the present investigation. Reddy *et al.* (1979) also indicated negative heterosis over better parent for plant height, days to maturity and seed weight.

Yield as well as heterosis were noticed higher in the present investigation, in mid-late x medium, followed by early x medium crosses. Mid-late x medium crosses also recorded greater heterotic effects for yield component characters such as pods per plant and test weight in comparison to crosses of other maturity groups. In addition, all (six) mid-late x medium crosses studied had recorded heterosis greater than

Table 31 Pigeonpea crosses with substantial useful heterosis for yield and yield component characters

Character	Number of hybrids with significant heterosis in the desirable direction	
	Over mid-parent	Over better parent
Days to 50 per cent flowering	15	5
Days to maturity	21	12
Plant height	18	8
Primary branches	4	-
Secondary branches	3	1
Pods per plant	9	5
Seeds per pod	16	5
Test weight	7	2
Yield per plant	7	4

Table 32 Details of promising hybrids identified for different maturity groups

Maturity group	Cross	Seed yield per plant						High *per se* performance for component characters	Significant heterosis for component characters		Characterization for *gca* of parents	Characterization with regards to maturity group of parents
		Per se performance	Heterosis over				*sca* effects		Over mid parent	Over better parent		
			Better parent	BDN 1	LRG 30	ICP 8863						
Medium	ICP MS288 x ICP 7349	145.80	171.00**	138.24**	257.35**	118.92**	47.26**	D50, DM, P/P	DM, PH, P/P	DM, PH, P/P	Low x Low	Early x Medium
Mid-late	ICP MS3783 X BDN 1	137.00	50.22**	123.86**	235.78**	105.71**	20.98**	PH, PB, SB, P/P, TW	DM, PH, P/P, S/P, TW	P/P, TW	High x High	Mid-late x Medium
	ICP MS3783 X ICP 8863	125.40	37.50*	104.90**	207.35**	88.29	16.51	PH, PB, SB, P/P, TW	DM, PH, P/P, S/P, TW	PH, P/P	High x High	Mid-late x Medium
	ICP MS3783 X LRG 30	164.00	80.59**	169.12**	303.68**	147.30**	35.73**	PH, PB, SB, P/P	D50, DM, PH, SB, P/P, S/P, TW	D50, P/P	High x High	Mid-late x Medium

**Significant at 5 per cent level *Significant at 1 per cent level

D50-Days to 50 per cent flowering, DM-Days to maturity, PH-Plant height, PB-Primary branches, SB-Secondary branches, P/P-Pods per plant, S/P-Seeds per pod, TW-Test weight

20 per cent for seed yield, over the checks (Table 30), indicating their potential in hybrid breeding programs. Crosses involving mid-late female (ICP MS3783), in general recorded high heterosis for seed yield and yield component characters, particularly, pods per plant and plant height. Similar results were also obtained in the studies of Patel (1988). Greater hybrid vigor in hybrids based on mid-late females compared to those based on early females was also reported (Rao, 1989). However, the findings of Omanga (1984) are contrary. A greater degree of heterosis for seed yield and other traits in crosses involving early parents was reported. The variation may probably be due to the water stress to which the mid-late parents were subjected in the investigations of Omanga (1984), resulting in poor performance of the mid-late parents and their hybrids with regards to seed yield and other traits.

Hybrid breeding programs involve the identification of highly heterotic and useful combinations. In this direction, heterosis over best varieties available for general cultivation, important from commercial view point, was estimated over BDN 1, LRG 30 and ICP 8863 (Maruthi) varieties, with regards to seed yield. Eleven hybrids had recorded more than 20 per cent heterosis over the checks, BDN 1, LRG 30 and ICP 8863 (Table 30) for seed yield. Of these, four promising hybrid combinations were identified based on their *per se* performance, heterosis (over mid-parent, better parent and checks) and *sca* effects (Table 32). The component characters, showing significant and useful heterosis are also mentioned for each hybrid. The cross involving ICP MS3783 (MS 3A) as female and LRG 30 as male parent was adjudged the best hybrid combination.

Analysis of Combining Ability

The main objective of this part of study was to identify parents with better potential to transmit desirable characteristics to the progenies and identify the best specific crosses for seed yield and yield components. The analysis of quantitative inheritance was also an equally important objective to gain knowledge regarding the nature and magnitude of gene action, which has an important bearing concerning choice of most appropriate and efficient breeding procedures.

The average performance of the hybrids was different from that of the parents as evident from the significance of parents vs. hybrid source of variation for all characters. This indicated the importance of additive genetic variation as well as heterosis in the material investigated. Further, the mean sum of

squares attributed to the male and female parents of the hybrids, that provide a measure of their general combining ability and the interaction between male and female parents that provide a measure of specific combining ability (Rojas, 1951) were significant for days to maturity, plant height, number of primary branches, secondary branches, pods per plant, test weight and yield per plant, in the present study indicating the importance of both additive and non-additive gene effects for these traits. However, for seeds per pod, the mean squares for females and male x female interaction were non-significant. This indicated the possibility for adequate prediction of performance for the character in the hybrids, on the basis of general combining ability i.e., the best performing hybrid may be produced by crossing two parents having the highest general combining abilities. These observations were found true for the trait, in the present investigation, wherein, the best hybrid for seeds per pod (ICP MS288 x ICP 7035) was the resultant of parents (ICP 7035 and ICP MS288) with the highest general combining abilities for the trait (Table 24).

Estimates of the relative contribution of general and specific combining ability within the genetic variability present in a population are of interest to plant breeders as, breeding methods differ appreciably depending upon the type of gene action. The estimates of components of variance (Table 23) and their ratio (σ^2gca/σ^2sca) indicated the pre-ponderance of non-additive gene action for all traits studied. The significance of heterosis in majority of the crosses (Tables 21 and 22) and parent vs. hybrid comparison (Table 18) strengthened this observation. The findings are also in conformity with the results of earlier workers. Pre-ponderance of non-additive gene action for days to 50 per cent flowering (Dahiya and Brar, 1977; Patel, 1990), days to maturity (Patel, 1990), plant height (Pandey, 1972; Patel, 1988; Patel, 1990), primary and secondary branches (Patel, 1988; Patel 1990), pods per plant (Reddy *et al.*, 1979; Patel, 1988; Patel, 1990), seeds per pod (Patel, 1988), test weight (Reddy *et al.*, 1979; Singh *et al.*, 1983) and yield per plant (Laxman Singh and Pandey, 1974; Reddy *et al.*, 1979; Singh *et al.*, 1983; Patel *et al.*, 1992) observed in the present investigation had been reported earlier.

Among the females, ICP MS288 was found to be a good combiner for early maturity, dwarf and compact growth habit. Hybrids based on ICP MS288 were also observed to be early maturing, dwarf and compact (Table 20). Hence, ICP MS288 may be used in crop improvement programs for imparting

earliness, dwarf and compact growth habit to pigeonpea hybrids for adoption in multiple cropping systems. MS Prabhat, the male sterile source of ICP MS288 was also reported to be a good combiner and ideal parent for imparting earliness by other workers (Omanga, 1984; Patel, 1988; Patel, 1990). The use of this female was further reported to result in high heterosis for earliness, seed yield and other traits in studies conducted by Gupta *et al.* (1983). However, undesirable *gca* effects for seed yield and majority of the yield component characters (Table 24) was noticed for the parent in the present study. In contrast, ICP MS3783 was found to be a good combiner for seed yield, pods per plant, test weight, primary and secondary branches. The hybrids based on ICP MS3783 parent were also high yielding, indicating its potential in hybrid breeding programs. However, owing to late maturing and spreading nature of the hybrids produced, they would be appropriate for sole pigeonpea cropping system. MS 3A, the male sterile source of ICP MS3783, was also reported to be a good combiner for seed yield in earlier studies (Omanga, 1984; Patel, 1988; Patel, 1990). Considerable degree of heterosis for seed yield using MS 3A was also reported by Saxena *et al.* (1985), similar to the findings of the present investigation

Among the male parents, LRG 30 proved to be the best general combiner for yield and majority of the yield components. Similar high *gca* effects of LRG 30 for yield and yield components was also noticed by Cheralu *et al.* (1989). ICP 7035, a vegetable type, was found to be best combiner for seeds per pod and test weight. Similar results were also observed by Venkateshwarlu and Singh (1982). In general, the *gca* effects for most characters were negative for early and medium maturing parents while, they were positive for mid-late parents. The present findings are in conformity with the reports of Reddy *et al.* (1979).

The parents were further characterized with regards to their *per se* performance and general combining ability effects (Table 33) as per the procedure outlined by Reddy and Arunachalam (1981). The ranking of parents based on *per se* performance in general agreed fairly with their ranking based on *gca* effects. Similar results were recorded in pigeonpea (Sharma *et al.*, 1973b; Venkateshwarlu and Singh, 1982). The sterility mosaic resistant parents (ICP 7035, ICP 7349 and ICP 8850) were found to be poor combiners for seed yield and other yield component characters. ICP 2376 parent, resistant to isolate 3 of sterility mosaic pathogen was also found to be a poor combiner. However, ICP MS3783, tolerant to isolate

Table 33 Characterization of parents for *per se* performance and general combining ability effects

Category	Parental lines	
	Per se performance	*gca* effects
High	ICP MS3783, ICP 7994 ICP11251, LRG 30	ICP MS3783, ICP 7994, ICP 8863, ICP 11251, LRG 30, BDN 1
Low	ICP MS288, ICP 2376, ICP 7035, ICP 7349, ICP 8006, ICP 8136, ICP 8850, ICP 8863, BDN 1	ICP MS288, ICP 2376, ICP 7035, ICP 7349, ICP 8006, ICP 8136, ICP 8850

1 of pigeonpea sterility mosaic pathogen was found to be a good combiner for seed yield and majority of yield component traits and hence, may be used in breeding programs aimed at developing high yielding resistant varieties.

The study of *sca* effects (Table 25) revealed significant and desirable effects, in several hybrids for days to 50 per cent flowering (8), days to maturity (8), plant height (1), primary branches (6), secondary branches (9), pods per plant (10), seeds per pod (5), test weight (6) and yield per plant (5). The crosses with high *sca* effects for yield were also associated with high and desirable *sca* effects for some component characters. For example, ICP MS3783 X LRG 30 was associated with significant *sca* effects in desirable direction for days to maturity, number of primary branches, secondary branches, pods per plant, seeds per pod and test weight. Similarly, ICP MS3783 X BDN 1 also, a heterotic hybrid had significant *sca* effects in the desirable direction for days to 50 per cent flowering, number of secondary branches, pods per plant and test weight.

The high degree of non-additive gene effects coupled with high heterosis for seed yield and related traits, observed in the present study favors a hybrid breeding program. The evaluation of hybrids have also suggested the availability of a substantial degree of hybrid vigor over better parent and checks in several crosses. Of these, few (four) promising hybrids were identified based on their *per se* performance, heterosis and *sca* effects (Table 32). The stability of these hybrids across environments and production systems needs to be evaluated for commercial cultivation.

Among the promising hybrids, only ICP MS288 X ICP 7349 hybrid combination belonged to the medium maturity group. Further, the cross involved both parents with low *gca* effects indicating a dominance x dominance type of gene action. However, the crosses, ICP MS3783 X ICP 8863, ICP MS3783 X BDN 1 and ICP MS3783 X LRG 30 were mid-late in maturity and involved parents with high *gca* effects indicating the presence of complementary gene action, and hence the possibility of better segregants in advanced generations.

VARIABILITY, HERITABILITY AND GENETIC ADVANCE

The information on genetic parameters of variability for different characters of economic importance

is pre-requisite for a plant breeder to work with any crop improvement program. Further, heritability has to be considered in conjunction with genetic advance, for an idea about the expected genetic gain in the next generation.

A wide range of variability has been reported for virtually all important agronomic characters in pigeonpea (Sharma and Green, 1977). In the present study also, differences among genotypes were highly significant for all traits (Table 18). Variability was the highest for pods per plant followed by seed yield per plant and plant height (Table 26), as observed by other workers (Joshi, 1973; Gupta *et al.*, 1975; Malik *et al.*, 1981; Sidhu *et al.*, 1985). The genotypic coefficient of variability was maximum for pods per plant followed by seed yield per plant and plant height (Table 26). However, it was the lowest for seeds per pod, days to 50 per cent flowering and test weight. The difference between genotypic and phenotypic co-efficients of variability for days to 50 per cent flowering and days to maturity were small. But seed yield, pods per plant and plant height were found to be more influenced by environment.

Heritability (broad sense) was high for all traits except seeds per pod as reported by other workers (Hiramath and Talwar, 1971; Kumar and Haque, 1973; Malik *et al.*, 1981; Sidhu *et al.*, 1985). The genetic advance as per cent of mean was maximum for pods per plant due to its high heritability, but was negligible for seeds per pod (Table 26). Low genetic advance coupled with low heritability, as for seeds per pod, is indicative of non-additive gene effects resulting in limited genetic gain from selection. The ranges, co-efficients of variability and heritability estimates suggest better scope for improvement of seed yield, pods per plant and plant height in pigeonpea.

CHARACTER ASSOCIATIONS AND PATH ANALYSIS

Correlations and path co-efficients provide a realistic basis for allocation of weightage to each of the contributing characters in deciding upon a suitable selection criteria for genetic improvement of complex characters like yield. Hence, correlation and path analysis were studied in the present investigation to assess the relationships among yield and its components through association and path analysis for enhancing the usefulness of selection.

Yield was found to be positively associated with plant height, number of primary branches, number

of secondary branches and pods per plant. Similar positive association of seed yield with plant height (Sidhu *et al.*, 1985; Patil *et al.*, 1989; Natarajan *et al.*, 1990; Patel and Patel, 1992); primary branches (Wakankar and Yadav, 1975); secondary branches (Sharma *et al.*, 1971; Singh and Malhotra, 1973; Wakankar and Yadav, 1975) and pods per plant (Sidhu *et al.*, 1985; Patil *et al.*, 1989; Natarajan *et al.*, 1990; Patel and Patel, 1992) were also reported earlier. However, seed yield recorded negative association with seeds per pod in the present investigation while, the association of yield with days to 50 per cent flowering, days to maturity and test-weight was non-significant. Similar non-significant association of days to flowering and days to maturity with seed yield was reported by several workers (Pankaj Reddy *et al.*, 1975; Dahiya *et al.*, 1978; Sidhu *et al.*, 1985).

Positive and significant associations were also recorded between several yield component traits. Days to 50 per cent flowering was positively associated with days to maturity; days to maturity with primary branches, secondary branches, test weight and plant height; plant height with primary branches and secondary branches; primary branches with secondary branches and pods per plant; secondary branches with pods per plant; and seeds per pod with test weight. However, significant and negative associations were recorded between plant height and seeds per pod; primary branches with seeds per pod and test weight; secondary branches with seeds per pod and test weight; and pods per plant with seeds per pod and test weight. Such negative correlations arise primarily from competition for a common possibility, such as nutrient supply. If one component gets advantage over the other, a negative correlation may arise (Adams, 1967; Adams and Grafius, 1971).

Path co-efficient analysis revealed the largest direct effect of pods per plant on seed yield followed by plant height and number of secondary branches. Dumbre and Deshmukh (1985) also reported high positive direct effect of pods per plant on yield. The importance of pod number was also reported by Sharma and Asawa (1977). The high direct effect appeared to be the main factor for its strong positive correlation with seed yield (Wakankar and Yadav, 1975). Hence, a direct selection for the trait would be effective. Further, the direct effect of seeds per pod was found positive, while its association with yield was negative. Hence, a restricted selection model (Singh and Kakar, 1977) is suggested for the trait, for utilizing the direct effects noticed. The indirect effects of all characters via pod number were also observed to be

much higher. Primary branches appeared to contribute mostly via pods per plant. The indirect effects of primary branches via number of secondary branches; and days to 50 per cent flowering and seeds per pod via test weight were also high.

The results indicate that for obtaining higher seed yield, selection should be based on a plant type having higher number of pods per plant, greater plant height and higher number of secondary branches, since these were found to be the important contributors for yield in pigeonpea as indicated by other workers (Sidhu *et al.*, 1985; Natarajan *et al.*, 1990).

CONCLUSIONS AND FUTURE STRATEGIES

A variation in the disease reaction of lines with the isolate involved, was noticed in the present investigation, indicating the need for screening and characterization of all available lines for their reaction against different strains/isolates of the pathogen. Further, the inheritance pattern of resistance varied, both with the isolate and the material involved. Hence, a prior knowledge on the mode of inheritance of resistance for the isolate and the donor parent involved, is essential in breeding resistant cultivars. For this, characterization of resistance sources for their allelic compositions with regards to the strains of the pathogen is necessary. In this direction, it would be desirable to develop a series with various allelic combinations in a common genetic background to be used as a tester, to facilitate the proper identification of alleles in different genotypes.

The study on heterosis and combining ability, involving resistant, tolerant and susceptible types revealed poor combining ability of the resistant parents studied, for seed yield and yield component characters. However, the tolerant line, ICP MS3783, also reported resistant to wilt disease, recorded high *per se* performance and combining ability for yield and component characters. Hence, it would be desirable to study all available resistance sources, in combination with ICP MS3783, for production of high yielding, resistant hybrids/varieties. Further, in the present investigation, few promising crosses belonging to medium and mid-late maturity groups were identified. Testing of these hybrids over a range of environments is suggested to establish their stability in performance. The role of fixable additive gene interaction was observed in three of these hybrids (ICP MS3783 X ICP 8863, ICP MS3783 X BDN 1 and ICP MS3783 X

LRG 30). Hence, advanced generation progenies of these crosses may be obtained to derive lines with high yield potential and tolerance to isolate 1 of the pigeonpea sterility mosaic pathogen. Further, studies on variability, heritability and genetic advance revealed scope for improvement of seed yield, pods per plant and plant height. The character associations and path analysis also emphasized the need for selection based on higher number of pods per plant and greater plant height, for isolation of high yielding pigeonpea lines. Hence, the crosses, ICP MS3783 X ICP BDN 1, ICP MS3783 X LRG 30 and ICP MS3783 X ICP 8863 may be advanced through conventional breeding procedures with screening at each generation for resistance to different isolates of sterility mosaic pathogen, coupled with selection for pods per plant and plant height among the resistant lines, towards development of high yielding disease resistant varieties.

SUMMARY

CHAPTER VI

SUMMARY

The present investigations were undertaken to elucidate genetics of strain-specific resistance for three isolates of pigeonpea sterility mosaic pathogen and to study the combining ability of few resistant and tolerant lines. In this direction, the available resistant/tolerant lines were screened against two different isolates (isolate 1 and 2) of the sterility mosaic pathogen. Breakdown of resistance was noticed for several lines, against isolate 2 of the pathogen. However, few lines were found resistant (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) and tolerant (ICP 999, ICP 7201, ICP 7873, ICP 8125, ICP 8266, ICP 8857, ICP 11245, ICP 11249 and ICP 11283) to both the isolates.

Inheritance of resistance to the strains of sterility mosaic disease was investigated in few resistant and tolerant lines selected from the above screening experiment. Five resistant (ICP 7035, ICP 7349, ICP 8006, ICP 8136 and ICP 8850) and one tolerant (ICP MS3783) line, crossed with a susceptible (ICP 8863), constituted the material for study on mode of inheritance of resistance/tolerance for isolate 1. Parents, F_1, F_2 and backcross generations were studied for their disease reaction against this isolate. Screening was carried out in pots using leaf-stapling technique. Resistance/tolerance was observed recessive for the isolate. Further, monogenic (1 resistant : 3 susceptible) and digenic (7 resistant : 9 susceptible) segregation ratios were obtained in the F_2 generation, indicating the role of two independent, non-allelic genes. The resistance/tolerance reaction appeared to be dependent on the presence of recessive alleles, at least at one locus.

Genetics of resistance for isolate 2, was studied in 18 resistant x susceptible cross combinations, involving three resistant (ICP 7035, ICP 7349 and ICP 8850) and six susceptible lines (ICP 2376, ICP 7994, ICP 11251, BDN 1, LRG 30 and ICP 8863). The resistant x resistant and susceptible x susceptible crosses were also studied to obtain information on the allelic relationships of the resistant and susceptible lines. Parents, F_1 and F_2 were screened in pots, using infector-hedge technique. The disease reaction of F_1's

varied with the cross involved. Resistance was dominant in crosses involving ICP 7035 and ICP 7349 parents while, susceptibility was dominant in crosses involving ICP 8850 resistant parent. Further, monogenic and digenic segregation ratios were obtained in the F_2 generation. The resistant parents, differed with the susceptibles, ICP 2376, BDN 1 and ICP 8863, in respect of a single gene pair and in respect of at least two gene pairs, with the susceptibles, ICP 7994, ICP 11251 and LRG 30. Disease reaction appeared to be governed by two independent non-allelic genes, with at least three multiple alleles, at one of the loci. Further, resistant and susceptible parents studied, did not differ with regards to genes, for disease reaction, against isolate 2 of the pathogen

Studies on genetics of resistance for isolate 3 of pigeonpea sterility mosaic pathogen was carried out with two resistant parents, ICP 7035 and ICP 2376, crossed with a susceptible, ICP 8863. Parents, F_1 and F_2 generations of these crosses were studied for their disease reaction. Screening was carried out in pots using leaf-stapling technique. Susceptibility was found dominant over resistance. Further, monogenic inheritance of resistance (1 resistant : 3 susceptible) was recorded for ICP 2376 X ICP 8863, while digenic inheritance of resistance (7 resistant : 9 susceptible) was noticed for the cross, ICP 7035 X ICP 8863, indicating the role of two independent non-allelic genes. However, presence of either pair of recessive alleles, governing resistance, appeared enough to confer resistance for this isolate.

Combining ability studies of resistant, tolerant and susceptible lines were carried out to aid pigeonpea improvement programs, directed at evolving high yielding, disease resistant varieties. The resistant, tolerant and susceptible lines, included in the inheritance studies, were used in a line x tester mating design and were evaluated for heterosis and combining ability effects.

Analysis of variance revealed significant differences among the genotypes, parents and hybrids for yield and all yield attributes studied, indicating the presence of ample variation for effective selection. The parents vs. hybrid source of variation was also significant for all characters, indicating the existence of heterosis. Further, estimates of components of variance and their ratios ($\sigma^2 gca/\sigma^2 sca$) indicated the preponderance of non-additive gene action for all traits. The expression of heterosis was most evident for yield per plant, pods per plant and number of secondary branches per plant. Significant heterosis in desired

direction was also observed in several crosses for various traits under study. Heterosis for yield and its component characters was maximum for mid-late x medium, followed by early x medium crosses. The mid-late x medium combinations also recorded heterosis greater than 20 per cent for seed yield, over the checks viz., BDN 1, LRG 30 and ICP 8863, indicating their potential in hybrid breeding programs. The study of *sca* effects also revealed significant and desirable effects in several hybrids for various traits studied. Crosses with high *sca* effects for yield were also found associated with high and desirable *sca* effects for most component characters. Studies on variability, heritability, genetic advance, character associations and path analysis also emphasized the need for selection based on component characters, such as, higher number of pods per plant and greater plant height. The high degree of non-additive gene effects coupled with high heterosis for seed yield and related traits, observed in the present study favored a hybrid breeding program. Four promising hybrids (ICP MS288 X ICP 7349, ICP MS3783 X BDN 1, ICP MS3783 X LRG 30 and ICP MS3783 X ICP 8863) were identified based on their *per se* performance, heterosis and *sca* effects. The crosses, ICP MS3783 X ICP 8863, ICP MS3783 X BDN 1 and ICP MS3783 X LRG 30, involved parents with high *gca* effects, indicating the role of fixable additive x additive gene interaction. Hence, they may be advanced through conventional breeding procedures coupled with screening and selection for isolation of high yielding, disease resistant cultivars.

Among the parents, ICP MS288 female, was found to be a good combiner for early maturity, dwarf and compact growth habit, while ICP MS3783 was observed to be a better combiner for seed yield, pods per plant, test weight, primary and secondary branches per plant. The crosses involving ICP MS3783 (mid-late female) also recorded high heterosis for seed yield and component characters. Further, among the male parents, LRG 30, proved to be the best general combiner for yield and majority of yield components. Sterility mosaic resistant parents were found to be poor combiners, in general, for yield and component characters. However, in contrast, ICP MS3783, tolerant to isolate 1 of pigeonpea sterility mosaic pathogen, was found to be superior combiner for yield and other component traits and hence, may be involved in pigeonpea improvement programs.

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