Cytoplasmic-Genic Male-Sterility in Interspecific Matings of *Cajanus*

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ABSTRACT

The discovery of two stable male-sterile genes and the prevalence of adequate insect-aided cross-pollination led to the development and release of the first pigeonpea [*Cajanus cajan* (L.) Millsp.] hybrid in India. Commercialization of this hybrid is constrained because of the labor intensiveness of seed production and concerns about seed purity. Cytoplasmic male-steriles would effectively circumvent these constraints and revolutionize the hybrid seed industry. This paper reports the development of cytoplasmically determined male-sterility, which was accomplished by two methods: wide hybridization involving conventional backcrossing of *Cajanus sericeus* van der Maesen and *Cajanus cajan* and multiple cross genome transfer. In these matings, two forms of reversion to fertility were noticed, one influenced by low temperature and high humidity, and the other probably determined by genetic factors alone. The influence of temperature on fertility restoration as reported for *Vicia faba* L. is different from that seen in species crosses of *Cajanus*. The multiple cross genome transfer method resulted in stable cytoplasmic-genic male sterility maintainable by the pigeonpea genotypes ICPL 85030 and ICPL 90035. These male-sterile lines are in agronomically desirable backgrounds.

PIGEONPEA is unique among cultivated plants for the diversity of its mating systems, which arises from heritable alterations of the floral structures, initially adapted to self pollination. Mechanisms of partial outbreeding evolved over time and it is the norm for the species. Subsequent modification of the staminal structure from diadelphous to filamentous form led to a stable self-pollinating mechanism (Saxena et al., 1992) and the evolution of male-sterility led to complete out-breeding (Reddy et al., 1978; Wallis et al., 1980). These mating systems impart distinctly different genetic structures to populations, each having its specific use. All three systems are being used for genetic improvement of the crop. Outcrossing due to genetic male-sterility has permitted the possibility of commercial utilization of hybrids in this crop. Soloman et al. (1957) have demonstrated high F_1 heterosis for grain yield and other characters.

A review of spontaneously arisen genic male-steriles is given by Reddy (1990). Those frequently used in hybrid breeding are identifiable by their pollen morphology. Included among them is one marked by translucent anthers, which result from the non-separation of tetrads (Reddy et al., 1978), and another is characterized by brown, shrivelled, arrowhead shaped anthers devoid of pollen (Wallis et al., 1980; Dundas et al., 1982). Non-allelic monogenic recessive control was reported for these two male-sterile types (Saxena et al., 1983).

The discovery of two male-sterile genes and the prevalence of adequate outcrossing by several insect species (Williams, 1977; Onim, 1981) made it possible to develop and release the first pigeonpea hybrid in India (Gupta et al., 1983). Commercialization of this hybrid is constrained because of the labor intensiveness of seed production and seed purity concerns arising from incomplete roguing of fertile plants from the population which are used as the female parent. Pure breeding cytoplasmic male-sterile lines would effectively circumvent these constraints and revolutionize hybrid seed production. The search for spontaneous mutations for cytoplasmic male-sterility among the world pigeonpea collection was unfruitful (Reddy et al., 1978). This paper reports the development of cytoplasmic-genic male-sterility in pigeonpea. To our knowledge, this is the first report of such development in this crop.

MATERIALS AND METHODS

The experiment was conducted at ICRISAT (International Crops Research Inst. for the Semi-Arid Tropics) Center, Patancheru, Andhra Pradesh, India, during June 1991 to January 1994 in a greenhouse at 25°C, and part of the experiment was

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Abbreviation: GTS, genome transfer stage.

Table 1. Pollen sterility at different backcross generations of *C. sericeus* × *C. cajan*.

Backcross generation	Parentage	No. of plants	Range in pollen sterility
			%
BC_0F_1	*C. sericeus* × *C. cajan* (EC 121208) × (ICPX 880227-10-1)	1	37
BC_1F_1	BC_0F_1 × *C. sericeus*	2	4.9-6.7
	BC_0F_1 × ICPX 880227-10-1		
	Progeny 1	2	21.4-100
	Progeny 2	6	6.2-70
BC_2F_1	BC_1F_1 × ICPX 880227-10-1	19	11-99
BC_3F_1	BC_2F_1 × ICPX 880227-10-1	15	8-99

conducted on an Alfisol during December 1992 to August 1993.

The initial mating aimed at developing a cytoplasmic-genic system of male-sterility between *Cajanus sericeus* accession EC 121208, as a female parent, and *C. cajan* line ICPX 880227-10-1, as the male parent. *Cajanus sericeus* is an erect shrub growing to a height of 1 to 1.5 m in its natural habitat in parts of the Western and Eastern Ghats and the area near Mount Abu in India. It produces upright primary and secondary, but seldom tertiary branches. Leaflets are hairy, narrow, and grey dorsally. Flowers are borne in leaf axils and seeds are grey to black. It is a photoperiod- and temperature-sensitive species of long duration. ICPX 880227-10-1 is a short-duration determinate pure line. Hybridizations between the two species succeeded in 2 to 3% of the attempts. Ovule development was poor in the early generations, hence populations in those generations were small.

Following the initial mating, two approaches were adopted to transfer the nuclear genome of pigeonpea into *C. sericeus* cytoplasm. In the conventional backcross breeding method, ICPX 880227-10-1 was used as the recurrent parent in the BC_0F_1, BC_1F_1, and BC_2F_1 generations. The reciprocal backcross with *C. sericeus* as the male parent was done in the BC_0F_1 generation. The number of plants evaluated at each backcross generation is shown in Table 1.

Backcrossing at each stage was done on male-sterile plants which were identified during anthesis, from anthers squashed in acetocarmine. Sterile genotypes are distinguishable by the unstained clear pollen, in contrast to the deeply stained pollen of fertile genotypes. Four hundred to 600 pollen grains were examined at 10× magnification under a light microscope to estimate the pollen sterility within a plant. Pod and seed set on the sterile plants was normal, indicating that they were female-fertile.

In the second approach, the objective was to substitute the *C. sericeus* nuclear genome for that of the genomic contents of more than one pigeonpea genotype. This approach differs from conventional backcrossing where substitution of the genome of a specific genotype is the goal. It was hypothesized that reversion of male steriles to fertility and the morphological deformities frequently noticed in conventional *sericeus* × *cajanus* backcrossing could be minimized if more than one genome contributed to the expected interaction with the *C. sericeus* cytoplasm. This mode of genome transfer is referred to here as multiple cross genome transfer, and the successive mating generations as genome transfer stages (GTS). The offspring of successive matings are referred to as filial generations and not as backcross filial generations in view of the involvement of more than one genotype in the genome substitution process.

At GTS 2, the pigeonpea genotypes ICPL 87, ICPL 90035, and ICPL 9880 were used as male parents on cytoplasm donors resulting from the mating at GTS 1. From these three crosses, the F_1 resulting from the ICPL 90035 mating was selected for advancement to GTS 3 and was crossed with ICPL 87 and ICPL 85030. The F_1 progeny of the mating with ICPL 85030 consisted of 75% male-sterile plants. All the male-sterile plants of this unique progeny were mated to both ICPL 85030 and ICPL 90035. The male-fertile plant was sib mated with one of the male-sterile plants. The number of plants evaluated at each stage is shown in Table 2.

RESULTS AND DISCUSSION

Backcross Mating

The F_1 progeny of the initial mating between *C. sericeus* (EC 121208) and *C. cajan* (ICPX 880227-10-1) were pollen-fertile, except for one plant in which partial sterility (37%) was found through microscopic examination of pollen grains stained by acetocarmine (Table 1). This plant was backcrossed to both parents. Backcrossing to the pigeonpea parent was expected to increase the nuclear-cytoplasmic interaction identifiable through increased pollen sterility, whereas a backcross mating with *C. sericeus* was expected to decrease the interaction and consequently decrease pollen sterility.

Two BC_1F_1 progenies were developed from back-

Table 2. Pollen sterility at different stages of multiple cross genome transfer.

Genome transfer stage	Parentage	No. of plants	Range in pollen sterility
			%
GTS 1	*C. sericeus* × *C. cajan* (EC 121208) × (ICPX 880227-10-1)	1	37
GTS 2	(*C. sericeus* × ICPX 880227-10-1) × ICPL 87	3	6.8-47.2
	(*C. sericeus* × ICPX 880227-10-1) × ICPL 90035	5	22.7-97.0
	(*C. sericeus* × ICPX 880227-10-1) × ICP 9880	3	17.1-42.0
GTS 3	[(*C. sericeus* × ICPX 880227-10-1) × ICPL 90035] × ICPL 87	10	6.5-98.6
	[(*C. sericeus* × ICPX 880227-10-1) × ICPL 90035] × ICPL 85030	4†	4.8-100
GTS 4	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant I × Plant IV	1	100(5)
	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant II × ICPL 85030	12	7-83
	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant II × ICPL 90035	44	6-76(97)‡
	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant III × ICPL 85030	4	91-98
	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant III × ICPL 90035	2	8-99(100)
	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant IV × ICPL 85030	8	93-100
	[(*C. sericeus* × ICPX 880227-10-1 × ICPL 90035) × ICPL 85030] = Plant IV × ICPL 90035	9	97-100(98)

† Plant I was fertile; Plant II was initially 97% male-sterile, temperature-sensitive, partially abnormal for leaf morphology, but reverted to partial sterility at low temperature; Plant III was 100% male-sterile, had one or two branches with abnormal leaf morphology, maintained sterility throughout; and Plant IV was 98% male-sterile, morphologically normal, and retained sterility and morphology throughout.

‡ Figures in parentheses indicate sterility in female parent.

crosses to pigeonpea and in each was noticed genotypes with sharply increased pollen sterility (21.4–100% and 6.2–70%), indicative of nuclear-cytoplasmic interactions (Table 1). The variability of this interaction within and between the two progenies probably resulted from the disproportionate distribution of genomic and cytoplasmic factors due to the lack of complete chromosomal homology between the two species (Reddy, 1981). On the other hand, the backcross to *C. sericeus* showed, as expected, decreased pollen sterility (4.9–6.7%), pointing to diminished interaction between the genomic and cytoplasmic factors as a result of the genomic content approaching reversion to its original constitution. The male-sterile plant (100% sterility) from the pigeonpea backcross failed to form pods and set seeds after hand pollination or natural pollination by insects, indicating that it was both male- and female-sterile. Barrenness was observed in other backcross generations as well and often it was associated with leaf, stem, and floral deformities (Ariyanayagam and Rao, 1993). High temperature (35–40°C) tended to accentuate stem and leaf malformation. The low degree of species affinity may have also accounted for the observed abnormalities. Based on pachytene chromosome analysis, Reddy (1981) concluded that the affinity of *C. sericeus* to *C. cajan* was less than that to *C. lineatus* (W. & A.) van der Maesen. Similar conclusions were arrived at by Pundir and Singh (1985). These authors placed *C. scarabaeoides* (L.) Thouars close to *C. cajan* and in crosses with that species the abnormalities referred to here were not as frequent as in crosses with *C. sericeus* (Ariyanayagam et al., 1993).

With successive backcrosses to ICPX 880227-10-1, the expression of male-sterility, due to the interaction between cytoplasmic factors of *C. sericeus* and nuclear factors of the recurrent parental genome, was expected to increase, presumably proportionately to the expected decrease of the *C. sericeus* nuclear genome remaining after each backcross. Assuming that species affinity was of no consequence, the genomic proportions should halve with each additional backcross while homogeneity of the progeny for the male-sterile trait should increase. Mating BC_1F_1 and BC_2F_1 genotypes of high pollen sterility with the recurrent parent, ICPX 880227-10-1 did not show this trend, however (Table 1). BC_2 progenies varied in pollen sterility from 11 to 99%, and BC_3 progenies from 8 to 99%. The upper limits in both backcross generations had reached the maximum. The lower limits remained virtually unchanged from that observed in one of the BC_1 progenies (6.2%), but were substantially lower than that of the other progeny (21.4%). It was evident that instead of progress towards homogeneity for the male-sterile trait following each additional backcross mating, reversion of the male-sterile trait to fertility was occuring at each mating, probably influenced by genetic factors. The fluctuations of the pollen phenotype within a progeny class was random.

Reversion to fertility hinders stabilization of the cytoplasmic-genic male-sterility. Instability of this trait appears to be widespread among interspecific crosses of *Cajanus*, as it was also observed in substitution backcrosses between *C. scarabaeoides* × *C. cajan*, *C. cajanus* × *C. acutifolius* (F. v. Muell.) van der Maesen, *C. albicans* (W. & A.) van der Maesen × *C. cajan*, and *C. cajanifolius* × *C. cajan* (Ariyanayagam et al., 1993). Such instability, which was found in *V. faba* as well, prevents two different sterile cytoplasms so far identified from being maintained in pure form (Bond et al., 1966; Berthelem, 1966). Le Guen et al. (1983) reported that pollen phenotype and reversion to fertility were distributed randomly in progenies. The reversion in *V. faba* is more complex than that observed in pigeonpea, as the variability for the proportion of fertile pollen in that crop occurred between flowers on a plant and between plants within a progeny. The genetic background of the maintainer and temperature are cited as factors influencing reversion in *V. faba* (Duc et al., 1983).

Multiple Cross Genome Transfer

Taking into consideration the frequent reversion, the factors responsible for such reversion, and the abnormal morphological developments observed, the multiple cross genome transfer procedure shown in Table 2 was adopted.

The F_1 arising from the GTS 1 mating (Table 2) was used as the cytoplasm donor in matings with ICPL 87, ICP 9880, and ICPL 90035 (GTS 2). The progeny resulting from the ICPL 87 cross showed variability (6.8–47.2%) among genotypes for pollen sterility. The genotypes of the mating with ICP 9880 varied from 17.1 to 42.0%, and the progeny of the ICPL 90035 mating from 22.7 to 97.0%. The matings with ICPL 87 and ICP 9880 resulted in reversion to fertility, probably genetically influenced, as in the case of the backcross matings. The cross with ICPL 90035 produced male-sterile plants and such plants were mated as the cytoplasm donor to ICPL 87 and ICPL 85030 (GTS 3). The resulting progenies were sown on an Alfisol at ICRISAT Center, Patancheru on 15 Dec. 1992. Flowering commenced in March 1993 and continued into August 1993.

The progeny of the mating with ICPL 87 displayed a pollen sterility range of 6.5 to 98.6%. There was only one male-sterile plant, while the rest showed reversion to fertility as in the case of the backcrosses of *C. sericeus* × ICPX 880227-10-1.

The mating with ICPL 85030 on the other hand resulted in a unique progeny array consisting of four plants of which three were male-sterile (Table 2). The phenotypic features of the four plants are described below.

Plant I. A morphologically normal plant which was fully fertile. It resembled the recurrent parent ICPL 85030 for leaf, stem, maturity, and pod characteristics, and was of determinate habit.

Plant II. A chimeric plant with some of its leaves deformed. At the commencement of flowering it was male-sterile (97%) and continued as such during the greater part of its flowering period, but reverted to partial sterility when it approached maturity, at which time environmental changes also occurred. The change from sterility to partial sterility might have been influenced by the ambient temperature and humidity. During the

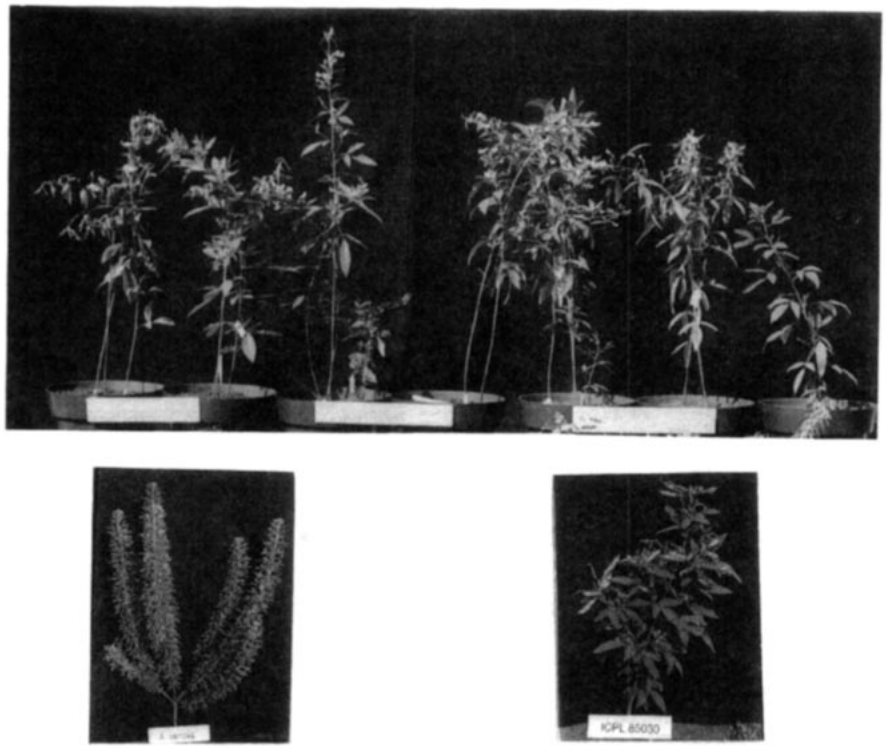

Fig. 1. Cytoplasmic-genic male-sterile progenies developed from *C. sericeus* × *C. cajan*, female parent *C. sericeus* and the maintainer ICPL 85030. Bottom left – *Cajanus sericeus*, Bottom right – *Cajanus cajan* cultivar ICPL 85030, and Top row – Cytoplasmic-genic male-sterile progenies.

male-sterile period, which lasted from the commencement of flowering in March to early June, the ambient temperature was high (mean day temperature 37.8°C, night temperature 23.1°C) and the humidity was low (mean 26.7% at 14 h). With the onset of rains in June the temperature dropped (mean day temperature 32.0°C, night temperature 23.1°C), humidity increased (57.5% at 14 h), and coinciding with these changes, reversion from male-sterility to partial sterility became apparent.

Reversion to fertility because of temperature influences occurs frequently in *V. faba* (Le Guen et al., 1983). In that crop, low temperatures at meiosis permit the expression of the sterile phenotype of pollen, whereas high temperatures lead to the fertile pollen phenotype. The reverse situation prevailed in the pigeonpea genotype, where high temperatures permitted the expression of male-sterility and low temperatures caused a reversion to partial sterility.

Plant III. A chimeric plant in which a few branches tended to elongate abnormally and produced deformed leaves. The plant was male-sterile (100%) and maintained the male-sterile character until its maturity.

Plant IV. A plant which was normal for all morphological characteristics, but was male-sterile (98%). It retained these characters all through its duration and appeared agronomically the most desirable plant among the progeny.

The fertile plant (Plant I) was sib-mated with Plant IV. From seven seeds only one plant survived to maturity, and it was male-sterile. The male-sterile plants (II, III, and IV) were mated with ICPL 85030 and ICPL 90035. The pollen sterility of the progeny of Plant II had a range of 7–83% in the mating to ICPL 85030, and a range of 6–76% in the mating to ICPL 90035. All the plants of both progenies had inherited the leaf morphology of the maternal parent, and the tendency for reversion to fertility, indicating cytoplasmic inheritance of leaf morphology.

Plant III (male-sterile plant), when mated to ICPL 90035 produced two plants, of which one was male-sterile and the other showed reversion to fertility. The morphological characters, e.g., leaf and stem deformities had been cytoplasmically inherited. The mating of Plant III to ICPL 85030 resulted in a progeny of four male-sterile plants (91–98%) with stem and leaf deformities. Although these deformities would preclude the use of this progeny in agriculture, there was unambiguous indication of cytoplasmic inheritance for both characters.

Plant IV was a male-sterile genotype that was free of morphological defects when examined in the field after its planting in December 1993. When mated with ICPL 85030, one of these plants produced a progeny consisting of eight plants. In May 1993 sowing in greenhouse, one plant showed 93.1% pollen sterility, and the rest above 98% sterility. The cross with ICPL 90035 as the male parent resulted in a progeny of nine plants, all of which were defect-free and showed pollen sterility exceeding 97% in a May 1993 sowing in greenhouse. This indicated that the *C. sericeus*-cytoplasmic factors of the maternal parent had interacted with the nuclear genomic factors of ICPL 85030 and ICPL 90035, and as a consequence of these interactions the male-sterile trait had been transmitted through the *C. sericeus* cytoplasm. Inheritance of male-sterility and other traits discussed here show

that intra-mother plant variation is maternally transmitted to the progenies, as has been reported in *V. faba* (Duc et al., 1983; Thiellement, 1977).

A preliminary cytological investigation of male-meiosis in these cytoplasmic male-sterile lines indicated that meiosis proceeded normally until the release of microspores. Soon after the release, vacuolation and degeneration of the protoplasm was seen. In contrast, in the genetic male-steriles, meiotic failure occurs at pollen mother cell or at early to late tetrad stages.

The sterile cytoplasm, in combination with the maintainers ICPL 85030 and ICPL 90035, is a promising cytoplasmic-genic system of male-sterility. The plant types associated with the male-sterile cytoplasm resemble the maintainer parents ICPL 85030 and ICPL 90035 in maturity, growth habit, flower, pod, and seed characteristics (Fig. 1).

Male-sterile Plant IV at GTS-3, when crossed with ICPL 85030 and ICPL 90035, produced progenies that had 93 to 100% pollen sterility, indicating that ICPL 85030 and ICPL 90035 were good maintainers. The nuclear genome of Plant IV, and male-sterile plants derived from it, still differ from those of the two ICPL parents, and also are not pure lines. Therefore, we postulate that further plant-to-row selection within the two ICPL parents, coupled with additional backcrossing to the male-sterile plants derived from Plant IV, should produce lines that will be completely male-sterile. This program is currently underway at ICRISAT Center.

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REFERENCES

Ariyanayagam, R.P., and A. Nageshwar Rao. 1993. Pleiotropism or linkage in crosses involving pigeonpea and its wild relatives. Intl. Pigeonpea Newsl. 18:15–16.

Ariyanayagam, R.P., A. Nageshwar Rao, and P.P. Zaveri. 1993. Cytoplasmic-genic male-sterility in pigeonpea. Intl. Pigeonpea Newsl. 18:7–11.

Berthelem, P. 1966. Rapport d'activité de la station d'amelioration des plantes de rennes. 1965-1966. INRA, Le Rheu, France.

Bond, D.A., J.C. Fyfe, and G. Joynbee-Clark. 1966. Male-sterility with a cytoplasmic type of inheritance in field bean. J. Agric. Sci. (Cambridge) 66:359–367.

Duc, G., R. Scalla, and L. Lefebre. 1983. New developments in cytoplasmic male-sterility in Vicia faba. p. 255–260. *In* Agronomy, physiology and breeding. Proceeding of Seminar on Plant Protein Improvement, University of Nottingham, UK.

Dundas, I.S., K.B. Saxena, and D.E. Byth. 1982. Pollen mother cell and anther wall development in a photoperiod-insensitive male-sterile mutant of pigeonpea, *Cajanus cajan* (L.) Millsp. Euphytica 31:371–375.

Gupta, S.C., L.J. Reddy, and D.G. Faris. 1983. Early maturing pigeonpea hybrids. Intl. Pigeonpea Newsl 2:19–20.

Le Guen, J., P. Berthelem, and F. Ronsselle. 1983. Instability of cytoplasmic male-sterility in *Vicia faba*: role of temperature at meiosis in *Vicia faba*. Agronomy, physiology and breeding. p. 261-270. *In* Proc. of a Seminar on Plant Protein Improvement, University of Nottingham, UK.

Onim, J.F.M. 1981. Pigeonpea improvement in Kenya. p. 427–436. *In* Y.L. Nene and V. Kumble (ed.) Intl. crops research institute for the semi-arid tropics, Vol. 1. Proc. Intl. Workshop on Pigeonpeas, ICRISAT Center, Patancheru, India. 15-19 Dec. 1980. ICRISAT, Patancheru, India.

Pundir, R.P.S., and R.B. Singh. 1985. Biosystematic relationships among *Cajanus*, *Atylosia* and *Rhynchosia* species and evolution of pigeonpea (*Cajanus cajan* (L.) Millsp.). Theor. Appl. Genet. 69: 531–534.

Reddy, B.V.S., J.M. Green, and S.S. Bisen. 1978. Genetic male-sterility in pigeonpea. Crop Sci. 18: 362–364.

Reddy, L.J. 1981. Pachytene analysis in *Atylosia sericea* and *Cajanus cajan* × *A. sericea* hybrid. Cytologia 46:567–577.

Reddy, L.J. 1990. Pigeonpea: morphology. p. 47-84. *In* Y.L. Nene et al. (ed.) The Pigeonpea, CAB International, Oxon, Wallingford, England.

Saxena, K.B., E.S. Wallis, and D.E. Byth. 1983. A new gene for male sterility in pigeonpea (*Cajanus cajan* (L.). Millsp.). Heredity 51:419–421.

Saxena, K.B., R.P. Ariyanayagam, and L.J. Reddy. 1992. Genetics of a high selfing trait in pigeonpea. Euphytica 59:125–127.

Soloman, S., G.P. Argikar, M.S. Solanki, and I.R. Morbad. 1957. A study of heterosis in *Cajanus cajan* (L.) Millsp. Ind. J. Genet. 17:90–95.

Thiellement, H. 1977. La Sterilité male-cytoplasmique chez *Vicia faba* L. III. Heredité des phenotypes polliniques. Ann. Amelior. Plantes 27:555–562.

Wallis, E.S., K.B. Saxena, and D.E. Byth. 1980. A new source of genetic male-sterility in pigeonpea. p. 105-108. *In* Y.L. Nene and V. Kumble (ed.) Intl. crops research institute for the semi-arid tropics, Vol. 2. Proc. Intl. Workshop on Pigeonpeas, ICRISAT Center, Patancheru, India. 15-19 Dec. 1980. ICRISAT, Patancheru, India.

Williams, I.H. 1977. Behaviour of insects foraging on pigeonpea [*Cajanus cajan* (L.) Millsp.] in India. Trop. Agri. (Trinidad) 54: 353–363.