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A Study on Comparative Fertility Restoration in A_2 and A_4 Cytoplasms and Its Implication in Breeding Hybrid Pigeonpea [*Cajanus cajan* (L.) Millspaugh]

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Abstract

Exploitation of hybrid vigour has been visualized as the most efficient option for increasing productivity in pigeonpea [*Cajanus cajan* (L.) Millspaugh]. Cytoplasms from various wild relatives of pigeonpea have been transferred to develop CMS lines in the background of cultivated pigeonpea. However, A_2 (*Cajanus scarabaeoides*) and A_4 (*Cajanus cajanifolius*) cytoplasms have been utilized most frequently. In order to study fertility restoration efficiency in F_1 hybrids having either A_2 or A_4 cytoplasms, an experiment was conducted at the Indian Institute of Pulses Research (IIPR), Kanpur during 2008-2012. Four CMS lines namely Hy4A, H28A (each with A_2 cytoplasm), ICP 2039A and ICP 2043A (both with A_4 cytoplasm) were crossed with ten genotypes/restorers of long duration pigeonpea for two years. The F_1 hybrids so-obtained were assessed in the succeeding years for pollen fertility and pod setting. All the pollinators except IPA 203 restored fertility in F_1 hybrids derived from ICP 2039A and ICP 2043A (both having A_4 cytoplasm). However, none of the restorers were effective in restoring fertility in hybrids derived from Hy4A and H28A (each with A_2 cytoplasm). This could be ascribed to undesirable linkage drag still present in these two CMS lines having A_2 cytoplasm. The F_2 progenies derived from 4 hybrids (ICP 2039A × NA-1, ICP 2039A × Bahar, ICP 2043A × NA-1 and ICP 2043A × Bahar) segregated approximately into 3 *fertile*: 1 *sterile* plants. However, 2 F_2 progenies having Pusa 9 as the restorer revealed approximately 15 *fertile*:1 *sterile* ratio. Thus monogenic and digenic duplicate gene action with complete dominance for fertility restoration was observed in F_1 hybrids derived from CMS lines having A_4 cytoplasm. F_3 progenies from individual F_2 plants of these crosses also confirmed the same pattern of fertility restoration. This study indicated that CMS lines based on A_4 cytoplasm would be more desirable as these might have more number of restorers compared to those having A_2 cytoplasm.

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Keywords

***Cajanus cajan*, CMS Lines, A_4 Cytoplasm, Fertility Restoration, Hybrid Pigeonpea**

1. Introduction

Heterosis breeding was resorted to improve productivity of pigeonpea which has been static for the last three decades the world over [1]. Pigeonpea fulfils several pre-requisites including higher outcrossing percentage for exploitation of hybrid vigour. Several cytoplasmic nuclear male sterility (CMS) systems are available in pigeonpea. However, CMS lines derived from *Cajanus scarabaeoides* [2] (A_2 cytoplasm) and *C. cajanifolius* [3] (A_4 cytoplasm) have been widely utilized to develop commercial hybrids. Despite release of a few hybrids from both sources, hybrids did not gain ground on farmers' fields due to several factors including partial fertility restoration and high genotype-environment interaction [4].

According to De [5], *C. cajanifolius* resembles cultivated types in most morphological traits. The CMS lines containing A_4 cytoplasm have been reported to be highly stable across environments and years without showing any morphological deformity [6]. However, a comparative picture of hybrids derived from both A_2 and A_4 cytoplasm is scanty and also not well-documented. The present study reports a comparative assessment of fertility restoration in hybrids containing individually either A_2 or A_4 cytoplasm and their significance in breeding hybrid pigeonpea. In order to take advantage of this CMS hybrid technology, it is essential to breed high-yielding hybrids based on diverse genetic backgrounds. To achieve this, breeding of promising hybrid parents and knowledge of the inheritance of fertility restoration are also essential [7]. Therefore, in addition to the F_1, F_2 and F_3 generations were also generated from A_4 CMS lines to determine the nature of gene action in the F_1 generation, the segregation pattern in F_2 generation and its confirmation through F_3 generation in pigeonpea.

2. Materials and Methods

For the present study, a set of 4 CMS lines were taken. Two CMS lines namely ICP 2039A and ICP 2043A containing A_4 cytoplasm (*C. cajanifolius*) were procured from International Crops Research Institute for Semi-Arid Tropics (ICRISAT), Hyderabad. These two CMS lines belong to medium maturity group, which behave as long-duration type in North-East Plain Zone (NEPZ) of India due to low temperature during winter months (December-January). The other two CMS lines "H28A" and "Hy4A" were developed at Indian Institute of Pulses Research (IIPR), Kanpur using the accession "GT 288A" having A_2 cytoplasm (*Cajanus scarabaeboides*). These two CMS lines are long-duration types with non-determinate (NDT) growth habit. For fertility restoration, 10 genotypes "NA-1", "Bahar", "T 7", "Pusa 9", "MA 6", "IPA 203", "IPA 234", "IPA 7-2", "IPA 7-6" and "Kudrat 3" were selected randomly (**Table 1**). Out of these, the first six are released varieties of long-duration pigeonpea for cultivation in NEPZ.

During the first year of experiment (2008), the two A_4 CMS lines (ICP 2039A and ICP 2043A) were crossed with all the 10 restorers. F_1 seeds were harvested separately, and grown during the next cropping season. All the F_1 plants were put under nylon net to observe pod setting. Pollen fertility reaction was also assessed with 2% acetocarmine. The same set of crosses was made again to observe the stability of fertility restoration in the ensuing season. Besides, the other two A_2 CMS lines (H28A and Hy4A) were also crossed with the same set of 10 testers to observe differences (if any) for fertility restoration. During the cropping season 2010, all the 20 F_1's and 20 F_2's derived from CMS lines ICP 2039A and ICP 2043A (A_4 cytoplasm) were grown in addition to 20 F_1's descended from the two CMS lines containing A_2 cytoplasm. Pollen fertility was again assayed by the same procedures. Data were also recorded for segregation pattern on fertility restoration in F_2 generation for six crosses (ICP 2039A × NA-1, ICP 2039A × Bahar, ICP 2039A × Pusa 9, ICP 2043A × NA-1, ICP 2043A × Bahar and ICP 2043A × Pusa 9). All the F_2 plants were bagged under nylon net to observe pod setting. 20 crosses involving the two CMS lines (H28A and Hy4A) with the same set of 10 testers were repeated again to observe stability of performance in the next generation. F_3 seeds from randomly chosen 10 F_2 plants from all the six crosses were grown during the year 2011-12. Data were recorded for the number of fertile and sterile plants in selected F_3 families. In addition to this, the 20 F_1's of the previous season were also grown to observe the breeding behaviour. The same procedure was followed to observe fertility reaction in F_1 hybrids derived from

Table 1. Description of pigeonpea genotypes (parents)*.

Genotypes	Pedigree/origin	Distinguishing (marker) characters
ICP 2039A	A CMS line having A_4 cytoplasm (*Cajanus cajanifolius*)	Determinate growth habit, medium maturity (170 - 180 days); matures late in NEPZ due to low temperature during winter months (November-January)
ICP 2043A	A CMS line having A_4 cytoplasm (*Cajanus cajanifolius*)	Non-determinate (NDT) growth habit, medium maturity (170 - 180 days); matures late in NEPZ due to low temperature during winter months (November-January)
Hy4A	A CMS line having A_2 cytoplasm (*Cajanus scaraeboides*)	Mid-late, stable male sterility with fusarium wilt (FW) and sterility mosaic (SM) resistance
H28A	A CMS line having A_2 cytoplasm (*Cajanus scaraeboides*)	Late, SM resistance and FW tolerance, stable expression of male sterility
NA-1	Selection from a land race of *Faizabad* district of U.P. (India)	A long-duration variety with dense red streaks on outer surface of standard petal with green pods
Bahar	Selection from a land race of *Motihari* district in Bihar (India)	Compact plant type with golden yellow colour of *standard* petal and purple pods (unripe)
T 7	Selection from a land race belonging to the Lucknow district in U.P. (India)	A very late (280 - 300 days) and tall (2.5 - 3.0 m) variety of long-duration pigeonpea with semi-compact plant type and green stem colour
MA 6	MA 2 × Bahar	Spreading plant type, late maturity, SM resistance
Pusa 9	UPAS 120 × 3673	NDT, resistant to SM and Alternaria blight, suitable for pre-rabi cultivation, sensitive to Al toxicity
Kudrat 3	A local land race, selected from Varanasi area of U.P. (India)	Medium height and compact, semi-determinate (SDT), pink coloured standard petal
IPA 234	T 7 × WRP 1	loose canopy, NDT, green stem colour, yellow standard (petal) colour, green pods with thin black stripes, FW and SM resistant
IPA 7-2	Selection from Kudrat 3	Compact plant type, SDT, large seed size (14 g/100seeds), dark red petal colour
IPA 7-6	Selection from Kudrat 3	Medium plant height, semi-compact plant type, NDT, yellow petal colour
IPA 203	Bahar × Ac 314-314	A released long-duration pigeonpea variety for NEPZ, compact plant type and large seed size, resistance to FW, SM and PSB

*Modified after Choudhary *et al.* [8].

CMS lines having A_2 cytoplasm.

For determining pollen fertility in each generation, five fully developed floral buds were taken randomly from each plant and the anthers were squashed in 2% aceto-carmine solution. The pollen fertility of each plant was studied under light microscope. The densely stained pollen grains were considered as fertile, while the empty or partially stained pollen grains were assessed as sterile. The chi-square test was applied for the goodness of fit to different expected ratios in F_2 and F_3 generations. The entire experimentation was performed during 2008-12 at IIPR, Kanpur.

3. Results

Pollens of all F_1 hybrids (having A_4 cytoplasm) except "ICP 2039A × IPA 203 and ICP 2043A × IPA 203 were observed densely stained with 2% acetocarmine, and hence showed fertile pollen reaction during the year 2009. All such pollen fertile F_1 hybrids were observed to have normal pod setting under nylon net (**Table 2(a)**). The same fertility reaction was noticed in the next year also (2010), confirming the results of previous year. This indicated that all pollinators (except IPA 203) efficiently restored fertility in F_1 hybrids, and thus these crosses could be assessed for yield and other attributes. When hybrids containing A_2 cytoplasm were analysed for fertility reaction, pollens did not take stain at all. None of the hybrids set pods under nylon net (**Table 2(b)**), revealing that none of the 10 pollinators was able to restore fertility in any one of F_1 hybrids during the year 2010. The same set of F_1 hybrids having A_2 cytoplasm was assessed further for fertility reaction during 2011. It again showed the same results, showing consistency of performance for fertility restoration. Thus it was obvious that a total of 9 pollinators (out of 10) were able to restore fertility in F_1 hybrids having A_4 cytoplasm; however, none

Table 2. (a) Fertility restoration in A_4 cytoplasm based pigeonpea hybrids; (b) Fertility restoration in A_2 cytoplasm based pigeonpea hybrids.

(a)

Crosses	Year	No. of plants	Pollen reaction	Pod set under nylon net
ICP 2039A × NA-1	2009	59	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2039A × Bahar	2009	60	Fertile	Normal pod setting
	2010	57	Fertile	Normal pod setting
ICP 2039A × T 7	2009	57	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2039A × MA 6	2009	60	Fertile	Normal pod setting
	2010	61	Fertile	Normal pod setting
ICP 2039A × Pusa 9	2009	59	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2039A × Kudrat 3	2009	56	Fertile	Normal pod setting
	2010	55	Fertile	Normal pod setting
ICP 2039A × IPA 234	2009	57	Fertile	Normal pod setting
	2010	57	Fertile	Normal pod setting
ICP 2039A × IPA 7-2	2009	55	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2039A × IPA 7-6	2009	56	Fertile	Normal pod setting
	2010	57	Fertile	Normal pod setting
ICP 2039A × IPA 203	2009	60	No restoration	No pod setting
	2010	61	No restoration	No pod setting
ICP 2043A × NA-1	2009	59	Fertile	Normal pod setting
	2010	60	Fertile	Normal pod setting
ICP 2043A × Bahar	2009	56	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2043A × T 7	2009	55	Fertile	Normal pod setting
	2010	54	Fertile	Normal pod setting
ICP 2043A × MA 6	2009	60	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2043A × Pusa 9	2009	56	Fertile	Normal pod setting
	2010	57	Fertile	Normal pod setting
ICP 2043A × Kudrat 3	2009	59	Fertile	Normal pod setting
	2010	59	Fertile	Normal pod setting
ICP 2043A × IPA 234	2009	57	Fertile	Normal pod setting
	2010	58	Fertile	Normal pod setting
ICP 2043A × IPA 7-2	2009	55	Fertile	Normal pod setting
	2010	54	Fertile	Normal pod setting
ICP 2043A × IPA 7-6	2009	58	Fertile	Normal pod setting
	2010	55	Fertile	Normal pod setting
ICP 2043A × IPA 203	2009	59	No restoration	No pod setting
	2010	61	No restoration	No pod setting

(b)

Crosses	Year	No. of plants	Pollen reaction	Pod set under nylon net
H28A × NA-1	2010	59	No restoration	No pod setting
	2011	56	No restoration	No pod setting
H28A × Bahar	2010	58	No restoration	No pod setting
	2011	60	No restoration	No pod setting
H28A × T 7	2010	61	No restoration	No pod setting
	2011	60	No restoration	No pod setting

Continued

H28A × MA 6	2010	59	No restoration	No pod setting
	2011	56	No restoration	No pod setting
H28A × Pusa 9	2010	58	No restoration	No pod setting
	2011	59	No restoration	No pod setting
H28A × Kudrat 3	2010	56	No restoration	No pod setting
	2011	55	No restoration	No pod setting
H28A × IPA 234	2010	57	No restoration	No pod setting
	2011	60	No restoration	No pod setting
H28A × IPA 7 - 2	2010	59	No restoration	No pod setting
	2011	55	No restoration	No pod setting
H28A × IPA 7 - 6	2010	54	No restoration	No pod setting
	2011	59	No restoration	No pod setting
H28A × IPA 203	2010	60	No restoration	No pod setting
	2011	57	No restoration	No pod setting
Hy4A × NA-1	2010	56	No restoration	No pod setting
	2011	57	No restoration	No pod setting
Hy4A × Bahar	2010	58	No restoration	No pod setting
	2011	54	No restoration	No pod setting
Hy4A × T 7	2010	59	No restoration	No pod setting
	2011	60	No restoration	No pod setting
Hy4A × MA 6	2010	60	No restoration	No pod setting
	2011	61	No restoration	No pod setting
Hy4A × Pusa 9	2010	59	No restoration	No pod setting
	2011	59	No restoration	No pod setting
Hy4A × Kudrat 3	2010	56	No restoration	No pod setting
	2011	55	No restoration	No pod setting
Hy4A × IPA 234	2010	60	No restoration	No pod setting
	2011	59	No restoration	No pod setting
Hy4A × IPA 7 - 2	2010	59	No restoration	No pod setting
	2011	58	No restoration	No pod setting
Hy4A × IPA 7 - 6	2010	59	No restoration	No pod setting
	2011	59	No restoration	No pod setting
Hy4A × IPA 203	2010	59	No restoration	No pod setting
	2011	60	No restoration	No pod setting

of them was able to produce fertile hybrids with CMS containing A_2 cytoplasm.

Genetics of fertility restoration in A_4 cytoplasm (ICP 2039A and ICP 2043A) was also studied using three pollinators (NA-1, Bahar and Pusa 9). The results showed that all the F_1 plants in the six crosses were male-fertile, indicating dominance of the fertility restoring genes over the CMS system. As expected, F_2 populations derived from all these six crosses segregated for male sterility and male fertility (**Table 3**). 6 F_2 populations from the respective F_1 hybrids (ICP 2039A × NA-1, ICP 2039A × Bahar, ICP 2039A × Pusa 9, ICP 2043A × NA-1, ICP 2043A × Bahar and ICP 2043A × Pusa 9) were observed for segregation into fertile and sterile plants during 2010. It was interesting to notice that the segregation pattern was obviously fitting into 3:1 ratio for 4 crosses (ICP 2039A × NA-1, ICP 2039A × Bahar, ICP 2043A × NA-1 and ICP 2043A × Bahar) in which "NA-1" and "Bahar" had been utilized as restorers (fertile/sterile, P = 0.95 - 0.50). For the remaining 2 crosses (ICP 2039A × Pusa 9 and ICP 2043A × Pusa 9), a ratio of 15 fertile: 1 sterile plant was observed (fertile/sterile, P = 0.90 - 0.70). Randomly selected 2 F_3 progenies (descended from individual fertile F_2 plants) from each of 4 crosses (ICP 2039A × NA-1, ICP 2039A × Bahar, ICP 2043A × NA-1 and ICP 2043A × Bahar) were also assessed for segregation pattern into fertile and sterile plants. The 3: 1 ratio of fertility restoration was again confirmed (fertile/sterile, P = 0.95 - 0.05). 8 F_3 progenies from each F_2 population derived by utilizing "Pusa 9" as the pollinator parent were also observed for fertility restoration. 2 progenies from each population followed 15:1 segregation pattern (fertile/sterile, P = 0.90 - 0.70). The segregation patterns observed in these two crosses (ICP 2039A × Pusa 9 and ICP 2043A × Pusa 9) suggested the presence of two duplicate dominant genes in controlling the pollen fertility.

Table 3. Segregation pattern for male-sterile and male-fertile plants in F_1, F_2 & F_3 generation of crosses involving A_4 cytoplasm.

Crosses	Generation	No. of plants			Expected	χ2 probability
		Total	Male fertile	Male sterile		
ICP 2039A × NA-1	F_1	58	58	--	--	--
	F_2	84	62	22	3:1	P > 0.95
	F_3	174	137	37	3:1	P = 0.30 - 0.25
ICP 2039A × Bahar	F_1	60	60	--	--	--
	F_2	80	61	19	3:1	P = 0.70 - 0.50
	F_3	170	138	32	3:1	P = 0.10 - 0.05
ICP 2039A × Pusa 9	F_1	59	59	--	--	--
	F_2	82	76	06	15:1	P = 0.90 - 0.70
	F_3	94	88	06	15:1	P = 0.90 - 0.70
ICP 2043A × NA-1	F_1	60	60	--	--	--
	F_2	120	93	27	3:1	P = 0.70 - 0.50
	F_3	176	131	45	3:1	P > 0.95
ICP 2043A × Bahar	F_1	58	58	--	--	--
	F_2	114	84	30	3:1	P = 0.90 - 0.70
	F_3	113	87	26	3:1	P = 0.90 - 0.70
ICP 2043A × Pusa 9	F_1	57	57	--	--	--
	F_2	94	87	07	15:1	P = 0.90 - 0.70
	F_3	65	60	05	15:1	P = 0.90 - 0.70

4. Discussion

It is known that CMS system is a maternally inherited trait governed by specific (mitochondrial) genes which do not affect otherwise other properties of the plant [9]. The fertility restorer (Rf or Fr) genes in the nucleus suppress the expression of male-sterile phenotype, leading to commercial exploitation of the CMS system for the production of hybrid seeds. Commercially exploitable CMS system has not been found in cultivated pigeonpea. Therefore, various wild relatives have been utilized to develop CMS system. The CMS system containing A_2 cytoplasm appears to reduce reproductive fitness of plants due to presence of several undesirable wild genes from *C. scarabaeoides*. This has been empirically observed in GTH-1, the first CMS based hybrid in pigeonpea. On the other hand, *C. cajanifolius*, which is the immediate progenitor of pigeonpea, resembles cultivated types in most morphological and agronomic traits [5]. The male-sterile lines derived from A_4 cytoplasm are the best as they do not show morphological deformity and other fitness-reducing traits across environments and years [10]. All these accounted for discrepancies in fertility restoration in F_1 hybrids containing A_2 and A_4 cytoplasm.

The knowledge of inheritance pattern of fertility restoration is indispensable for the transfer of restorer genes from one genotype to another. In the present study, it was observed that two restorers "NA-1" and "Bahar" showed monogenic inheritance (3:1) when crossed each with ICP 2039A and ICP 2043A, while "Pusa 9" revealed digenic inheritance of fertility restoration with both the CMS lines. The similar pattern of fertility restoration has also been reported in three diverse early maturing lines of pigeonpea [11]. Variable restoration patterns among a common set of restorer lines (male parents) within a single cytoplasmic source of pigeonpea has been reported by Nadarajan *et al*. [12]. In another study, it has been observed that the fertility restoration in A_4 CMS lines of pigeonpea may be controlled by either one or two fertility-restoring genes [13]. In the present study, one fertility restorer line "Pusa 9" produced different results compared to "NA-1" and "Bahar" when crossed with the same set of A_4 CMS lines. The variable expression of fertility restoration can be attributed to different genetic backgrounds of the F_1 plants, arising from male parents of different genetic constitution. Alternatively, differences observed in segregation patterns also could be due to the presence of some modifier genes that influence the process of penetrance and expressivity of the fertility-restoring genes [14]. On the contrary, the same pollinator (restorer) may also produce variable results if crossed with different A_4 CMS lines [7].

5. Conclusions

Pigeonpea is an important source of dietary protein especially for vegetarians of India as well as East Africa. Despite its global importance, the increase in its productivity has not been significant as it still possesses several

wild traits including its perennial nature. Hybrid technology has been envisaged as one of the technological interventions to realise quantum jump in its productivity. For successful exploitation of hybrid vigour, CMS lines from various wild relatives have been developed. However, CMS lines containing A_2 (*C. scarabaeoides*) and A_4 (*C. cajanifolius*) cytoplasms have been widely used to develop high-yielding stable hybrids of pigeonpea. Although some CMS based hybrids have been made available for cultivation, these are yet to find commercial worth at farmers' fields. In this paper, we have examined a relative worth of A_2 and A_4 CMS lines for producing specific cross combinations and genetics of fertility restoration in A_4 CMS lines. The results indicated that A_4 CMS lines could provide larger number of cross combinations that could be assessed across years and locations as more number of pollinators could restore fertility in F_1 hybrids. As such, A_4 cytoplasm (derived from immediate progenitor of pigeonpea, *C. cajanifolius*) had displayed unconditional advantages over A_2 cytoplasm. In the present study, fertility restoration in A_4 CMS lines of pigeonpea was found to be cross-specific and influenced by the nuclear background of fertility-restoring lines. In 4 crosses (ICP 2039A × NA-1, ICP 2039A × Bahar, ICP 2043A × NA-1 and ICP 2043A × Bahar), fertility restoration was governed by a single dominant gene; while in 2 crosses (ICP 2039 × Pusa 9 and ICP 2043 × Pusa 9), it was controlled by two duplicate dominant genes. The differential behaviour of the two A_4 CMS lines (ICP 2039A and ICP 2043A) in crosses with "NA-1" and/or "Bahar" and "Pusa 9" could be ascribed to the interactions of different nuclear genes of the restorer male parents.

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