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Inheritance of male-fertility restoration in A_1, A_2, A_3 and $A_{4(M)}$ cytoplasmic male-sterility systems of sorghum [*Sorghum bicolor* (L.) Moench]

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Abstract

Almost all the sorghum [*Sorghum bicolor* (L.) Moench] hybrids commercially exploited to date are based on A_1 CMS (cytoplasmic-nuclear male-sterility) system. For genetic diversification and to produce more heterotic hybrids, all the available CMS systems are to be studied for genetics of male-fertility restoration preferably in iso-nuclear backgrounds. The A_1, A_2, A_3 and $A_{4(M)}$ cytoplasms present in three different nuclear backgrounds were crossed with two common restorers. The segregation of fertile and sterile plants observed in F_2 and BC_1 populations during rainy and post-rainy seasons of 2007 was tested with χ^2 for goodness of fit for monogenic, digenic and trigenic ratios. The fertility restoration of A_1 CMS system was governed by one basic gene and two duplicate complimentary genes (45F:19S in F_2) all acting in dominant fashion while the fertility restoration of A_2 and A_3 CMS systems was governed by three genes where all of the three complimentary genes in dominant condition restore fertility (27F:37S in F_2). The fertility restoration in $A_{4(M)}$ CMS system was governed by three genes where any two of the three dominant duplicate-complimentary genes restored fertility (54F:10S in F_2) in post-rainy season while two complementary genes in dominant state restored fertility (9F:7S in F_2) in rainy season in the absence of expression of the third gene.

Key words: Sorghum, Cytoplasmic-nuclear male-sterility, fertility restoration, gene action

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench], together with maize (*Zea mays* L.) and pearl millet (*Pennisetum glaucum* (L.) R. Br.], constitutes the most important cereal crops in the rainfed semi-arid tropics. The discovery of A_1 cytoplasmic nuclear male-sterility (CMS) in sorghum by Stephens and Holland [1] and its subsequent exploitation for hybrid production has revolutionized sorghum production worldwide. Effective use of CMS has made it easier to incorporate the desired characters into hybrid parents [2]. Hybrid sorghum seed production relies exclusively on CMS systems and almost all hybrid sorghum seed commercially produced is by using the *Milo* CMS (A_1) system. In addition to the A_1, several other cytoplasmic sources, like A_2 [3], A_3 [4], A_4 [5], Indian A_4 (A_{4M}, A_{4VZM}, A_{4G}) [6], A_5, A_6, 9E [7] and KS cytoplasms [8] differing from each other and from the A_1 CMS system, were identified. The inheritance of male-sterility/fertility is dependent upon the genetic make-up of cytoplasms and nuclei. Male-fertility restoration is controlled by single genes in some combinations but is polygenic when the same nuclear genotype interacts with a different cytoplasm [9]. Intra- and inter-allelic interaction and complementation influences the fertility restoration. Understanding the genetics of male-sterility and fertility restoration of these CMS systems can enhance the efficiency of selection of good restorer and maintainer parents to develop high-yielding hybrids with yield advantage based on diversified CMS seed parents [10]. However, inheritance studies involving isonuclear male-sterile lines with different sterility-inducing cytoplasms and common restorers are limited. This study was planned utilizing a set of isonuclear alloplasmic male-sterile lines crossed with a set of common restorers that restore fertility on all these cytoplasms, to determine the number of genes governing male-fertility restoration for the different CMS systems in sorghum.

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Materials and methods

Twelve A-lines (four cytoplasms *viz*., A_1, A_2, A_3 and $A_{4(M)}$; each in three different nuclear backgrounds viz., ICSB 11, ICSB 38 and ICSB 88001) were crossed with two common restorers *viz*., IS 33844-5 and M 35-1-19, that restore fertility on all the four cytoplasms, during 2005 post-rainy season to generate 24 F_1 hybrids. The B-lines used in the study were developed at ICRISAT during 1980-1990 through pedigree selection from the segregating populations derived from the crosses between improved germplasm lines [11]. Each of the four A-line versions of these different B-lines was developed at ICRISAT through backcrossing the F_1s (obtained from crossing the B-lines to the cytoplasmic sources) to their respective B-lines. The R-lines were also developed at ICRISAT through direct selection from the landraces during early 1990s. The F_1 hybrids were produced using the bulk pollen of R-lines on the A-lines. Twelve of the 24 F_1 hybrids that were completely fertile were used for the study. The restorer IS 33844-5 produced more fertile hybrids than M 35-1-19. Of the 12 F_1 hybrids, 10 hybrids were based on the restorer IS 33844-5 and two hybrids were based on the restorer M 35-1-19. The F_1s were raised in 2006 rainy season, selfed to obtain 12 F_2s and backcrossed to respective female parents to generate 12 BC_1F_1 progenies. All the generations *viz*., F_1s, F_2s and BC_1F_1s were sown during rainy and post-rainy seasons of 2007. Each generation was sown in a single row of 100 m length with a spacing of 75 × 10 cm so as to obtain a population of about 1000 plants per generation at experimental fields of ICRISAT, Patancheru, India. The experimental site is located at an altitude of 545 m above mean sea level, latitude of 17.53°N and longitude of 78.27°E. All the recommended agronomic practices were followed to raise a good crop. All the panicles in all the entries were bagged before flowering. At maturity, the bags were removed and the data were recorded on the segregation patterns of male-fertile (F) and male-sterile (S) plants i.e., the panicles with >5% seed set were scored as fertile and <5% seed set were scored as sterile. The 12 F_1 hybrids were completely fertile in both 2007 rainy and post-rainy seasons indicating that male-fertility was dominant over the male-sterility. The F_2 and BC_1 populations were tested for segregation ratios to determine the number of genes involved in the fertility restoration of cytoplasmic-genic male-sterility (CMS) systems. The χ^2 test for homogeneity of genetic ratios for a cross across the rainy and post-rainy seasons was done.

Results and discussion

Inheritance of male-fertility restoration in A_1 CMS system

For the A_1 CMS system, the inheritance of male-fertility restoration was studied in five A x R crosses involving a restorer, IS 33844-5, with A_1 lines in three diverse nuclear backgrounds; ICSB 11, ICSB 38 and ICSB 88001 and another restorer, M 35-1-19, with A_1 lines in two nuclear backgrounds; ICSB 38 and ICSB 88001.

The results obtained on the segregation pattern (Table 1) in the crosses involving the restorer parent, IS 33844-5 and A-lines in the nuclear backgrounds of ICSB 11 and ICSB 38; and the restorer parent, M 35-1-19 and the A-line in the nuclear background of ICSA 38; gave a good χ^2 fit to the expected trigenic ratio of 45F:19S in the F_2 during both rainy and post-rainy seasons and 1F:1S in the BC_1 during rainy season, that resulted from a gene action involving one basic gene and two duplicate-complimentary genes. The BC_1 population of these three crosses deviated from the expected 1:1 ratio during post-rainy season ($P < 0.01$). The main reason for this deviation is the greater number of sterile plants. Interaction of viable pollen production and/or its shedding with temperature was reported in sorghum by Stephens and Holland [1]. More specifically, when minimum temperatures go below 10°C for several days during flowering, hybrids that are otherwise male fertile show male sterility as evidenced by partial to complete absence of seed setting under bagging [12]. In sorghum, there is a tendency towards sterility/ poor seed set due to low temperature during post-rainy season [12]. The goodness of fit in the crosses involving the restorer parent IS 33844-5 with the A-line in the genetic background of ICSB 88001 gave a good fit to the expected ratio of 21F:43S in F_2 and 3F:5S in BC_1 during both rainy and post-rainy seasons that might have resulted from a gene action involving one basic and two inhibitory genes acting in dominant fashion. The goodness of fit in the crosses involving the restorer parent, M 35-1-19 with the A-line in the genetic background of ICSB 88001 gave a good fit to the expected ratio of 27F:37S in F_2 and 1F:7S in BC_1 during both rainy and post-rainy seasons that might have resulted from a gene interaction involving three non-allelic major genes acting complementarily. The crosses involving the female parent ICSA 88001 with both the restorers deviated from the expected 45F:19S ratio in the F_2 which may be due to the influence of cytoplasmic and nuclear gene interactions. These differences in the type of gene interaction could also presumably be due to the influence of female parent and/or a probable variable expression of the weaker gene in different genetic backgrounds. In mustard for *tour* cytoplasm, Pahwa *et al*. [13] has reported the influence of background genotype especially the female parent genotype in the expression of restorer genes in different backgrounds. Certain modifier genes could also be responsible for changing the segregation ratio in different generations of study as reported in rice [14] and wheat [15]. In wheat it was demonstrated that the penetrance and expressivity of the Rf gene(s) for *timopheevii* cytoplasm was affected by the parental genotype in the cross and by the genotype of the individual plant in segregating progenies. But, overall, a trigenic inheritance mechanism in which the dominant allele of a basic gene and a dominant allele of either of the two duplicate-complimentary genes might have been involved in the fertility restoration of A_1 CMS system.

Based on the genetic ratios derived, the genetic constitution of A-lines could have been *rf*1a *rf*1a *Rf*1b *Rf*1b *rf*1c *rf*1c and for R-lines could have been *Rf*1a *Rf*1a *rf*1b *rf*1b *Rf*1c *Rf*1c. A three gene system governing A_1 CMS in sorghum was also reported by earlier workers [16-19]. However, monogenic modes of inheritance have been reported for A_1 (milo) CMS system [20-23] while digenic control with dominant complimentary gene action has been reported for fertility restoration [17, 22, 24-26].

Inheritance of male-fertility restoration in A_2 CMS system: The inheritance of fertility restoration in A_2 CMS system was investigated in two A x R crosses involving

Table 1. Segregation ratios for fertile and sterile plants in F_2 and backcross populations derived from crosses based on A_1 cytoplasm-based A-lines in sorghum

Cross	Generation	Season	Fertile plants (F)	Sterile plants(S)	Expected ratio (F:S)	χ^2	χ^2p	χ^2h
$ICSA_1$ 11 x IS 33844-5	F_2	Rainy	40	27	45:19	3.6 (0.06)	3.06 (0.08)	1.39 (0.53)
		Post-rainy	136	66		0.85 (0.36)		
	BC_1	Rainy	12	13	1:1	0.04 (0.84)	19.8 (<0.01)	1.91 (0.17)
		Post-rainy	65	130		21.67 (<0.01)		
$ICSA_1$ 38 x IS 33844-5	F_2	Rainy	139	45	45:19	2.4 (0.12)	0.00 (1.0)	7.01 (0.01)
		Postrainy	54	36		4.61 (0.03)		
	BC_1	Rainy	38	30	1:1	0.94 (0.33)	7.82 (0.01)	9.45 (<0.01)
		Postrainy	49	98		16.33 (<0.01)		
$ICSA_1$ 88001 x IS 33844-5	F_2	Rainy	62	117	21:43	0.28 (0.60)	0.19 (0.66)	0.09 (0.76)
		Postrainy	41	83		0.0 (1.0)		
	BC_1	Rainy	33	57	3:5	0.03 (0.86)	0.85 (0.36)	0.3 (0.58)
		Postrainy	44	89		1.12 (0.29)		
$ICSA_1$ 38 x M 35-1-19	F_2	Rainy	59	21	45:19	0.46 (0.50)	0.68 (0.498)	1.96 (0.162)
		Postrainy	108	58		2.18 (0.14)		
	BC_1	Rainy	9	18	1:1	3 (0.08)	27.02 (<0.01)	13.1 (<0.01)
		Postrainy	68	160		37.12 (<0.01)		
$ICSA_1$ 88001 x M 35-1-19	F_2	Rainy	53	64	27:37	0.45 (0.50)	0.03 (0.862)	0.56 (0.454)
		Postrainy	59	86		0.14 (0.71)		
	BC_1	Rainy	13	50	1:7	3.76 (0.05)	3.13 (0.077)	6.59 (0.010)
		Postrainy	6	152		5.96 (0.01)		

a restorer, IS 33844-5, with A_2 lines in two diverse nuclear backgrounds; ICSB 11 and ICSB 88001.

In the crosses involving the A_2 CMS system, the nuclear background of the A-line was found to influence the inheritance pattern. The restorer parent IS 33844-5 gave a good χ^2 fit to the digenic ratio 9F:7S in F_2 and 1F:3S in BC_1 with the A-line in the nuclear background of ICSB 11 during both rainy and post-rainy seasons that might have resulted from the gene action involving two complimentary genes in dominant state. In the nuclear background of ICSB 88001, the restorer IS 33844-5 gave a trigenic ratio 27F:37S in F_2 during both rainy and post-rainy seasons and 1F:7S in BC_1 during rainy season. The BC_1 population of this cross deviated from the expected ratio during post-rainy season ($P <$ 0.01) due to excess of fertile plants.

The manifestation of digenic ratios along with trigenic ratios in A_2 CMS system suggests the likely involvement of three genes in the inheritance of fertility restoration. The trigenic F_2 ratio of 27F:37S and the BC_1 ratio of 1F:7S is likely with the genetic constitution of female parent 'aaBBcc' and the male parent 'AAbbCC' but with a gene interaction in which a plant will be fertile if it possesses dominant allele of all three complementary genes (A_B_C_). All other genotypes will produce sterile plants. Even in a three-gene mechanism, there is a possibility of getting a two-gene ratio depending on the number of genes segregating and the genetic background of the female and male parents. The digenic ratio of 9F:7S in the F_2 and 1F:3S in the BC_1 is possible with the 'AAbbcc' genotype of the male parent and is a result of dominant alleles of two complimentary genes.

However, overall, all the three complementary genes in dominant state seemed to be influencing the fertility restoration in A_2 CMS system. Based on the Mendelian ratios obtained, the postulated genotypes of the A-lines are *rf*2a *rf*2a *Rf*2b *Rf*2b *rf*2c *rf*2c; and the R-lines are *Rf*2a *Rf*2a *rf*2b *rf*2b *Rf*2c *Rf*2c (where trigenic ratio fits) and *Rf*2a *Rf*2a *rf*2b *rf*2b *rf*2c *rf*2c or *rf*2a *rf*2a *Rf*2b *Rf*2b *Rf*2c *Rf*2c (where digenic ratio fits). Tripathi *et al.* [19] and Lonkar and Borikar [26] reported a trigenic inheritance for A_2 CMS system while digenic control was reported by Murty and Gangadhar [23].

Inheritance of male-fertility restoration in A_3 CMS system: The inheritance of fertility restoration in A_3 CMS system was investigated based on the segregation pattern of F_2 and BC_1 plants in three A x R crosses involving a restorer, IS 33844-5, with A_3 lines in three diverse nuclear backgrounds; ICSB 11, ICSB 38 and ICSB 88001.

For the A_3 CMS system, the restorer parent IS 33844-5 gave a good χ^2 fit to the digenic ratio of 13F:3S in F_2 and 3F:1S in BC_1 with the A-line in the nuclear backgrounds of ICSB 11 during rainy season and ICSB 88001 during postrainy season; The same restorer line gave a trigenic ratio of 27F:37S in F_2 and 1F:7S in BC_1 with the A-line in the nuclear background of ICSB 38 during both rainy and postrainy seasons. This showed that the genetic background of the female parent and its interaction with the season influenced the inheritance pattern of the A_3 CMS system. The trigenic F_2 ratio of 27F:37S and the corresponding BC_1 ratio of 1F:1S is

Table 2. Segregation ratios for fertile and sterile plants in F_2 and backcross populations derived from crosses based on A_2 cytoplasm based A-lines in sorghum

Cross	Generation	Season	Fertile plants (F)	Sterile plants(S)	Expected ratio (F:S)	χ^2	χ^2p	χ^2h
ICSA$_2$ 11 x IS 33844-5	F_2	Rainy	92	95	9:7	3.78 (0.052)	1.41 (0.235)	2.4 (0.121)
		Post-rainy	130	99		0.03 (0.862)		
	BC_1	Rainy	69	273	1:3	4.24 (0.039)	2.03 (0.154)	2.46 (0.117)
		Post-rainy	42	115		0.25 (0.617)		
ICSA$_2$ 88001 x IS 33844-5	F_2	Rainy	83	52	27:37	0.76 (0.383)	6.52 (0.011)	-4.42 (0.036)
		Post-rainy	42	72		1.34 (0.247)		
	BC_1	Rainy	28	134	1:7	3.35 (0.07)	12.48 (<0.01)	1.04 (0.308)
		Post-rainy	32	120		10.17 (<0.01)		

possible when the genotype of the female parent is 'aaBBcc' and the genotype of the restorer parent is 'AAbbCC' and all three genes acting complimentarily in restoring fertility and the fertile plants have a genetic constitution A_B_C_ . The digenic F_2 ratio of 13F:3S and the BC_1 ratio of 3F:1S in the BC_1 is likely with the same genetic constitution of the female parent 'aaBBcc' and the genetic constitution of male parent being 'AABBCC' but with a gene interaction in which dominant allele 'C' causes sterility in the absence of dominant allele of gene 'A' i.e., C-gene exhibits inhibitory action. The different genetic constitution of male parent is likely due to the residual heterozygosity for fertility restoration. On the whole, all the three complementary genes in dominant state seemed to be influencing the A_3 CMS system. Digenic control for A_3 was reported by a few workers [27-28]. Based on the Mendelian ratios obtained, the postulated genotypes of the A-lines could be *rf*3a *rf*3a *Rf*3b *Rf*3b *rf*3c *rf*3c and the R-lines could be *Rf*3a *Rf*3a *rf*3b *rf*3b *Rf*3c *Rf*3c (where trigenic ratio fits) and *Rf*3a *Rf*3a *Rf*3b *Rf*3b *Rf*3c *Rf*3c (where digenic ratio fits).

Inheritance of male-fertility restoration in $A_{4(M)}$ CMS system

The inheritance of fertility restoration in $A_{4(M)}$ CMS system was investigated based on the segregation pattern of F_2 and BC_1 plants in two A x R crosses involving a restorer, IS 33844-5, with $A_{4(M)}$ lines in two diverse nuclear backgrounds; ICSB 11 and ICSB 38.

For $A_{4(M)}$ CMS system, the restorer parent IS 33844-5 gave a good χ^2 fit to the digenic ratio 9F:7S in F_2 and poor fit to 1F:3S in BC_1 during rainy season and trigenic ratio 54F:10S in F_2 and 3F:1S in BC_1 (that must have resulted from a gene action involving any two of the three dominant duplicate-complimentary genes) during post-rainy season with the A-lines in both the nuclear backgrounds of ICSB 11 and ICSB 38. The good fit of digenic ratio in rainy season and trigenic ratio during postrainy season for $A_{4(M)}$ cytoplasm indicates active role of more number of genes in post-rainy season. Considering 'A', 'B' and 'C' as the three genes involved in the fertility restoration of the $A_{4(M)}$ CMS system, the trigenic F_2 ratio of 54F:10S and the BC_1 ratio of 3F:1S in post-rainy season is likely with the genetic constitution of female parent 'aaBBcc' and the male parent 'AAbbCC' but with a gene interaction in which a plant will be fertile if it possesses dominant allele of at least two of the any three duplicate-complimentary genes (A_B_C_, A_B_cc, A_bbC_ and aaB_C_). But a digenic ratio of 9F:7S in the F_2 in the rainy season could result from dominant alleles of two complimentary genes. The

Table 3. Segregation ratios for fertile and sterile plants in F_2 and backcross populations derived from crosses based on A_3 cytoplasm based A-lines in sorghum

Cross	Generation	Season	Fertile plants (F)	Sterile plants(S)	Expected ratio (F:S)	χ^2	χ^2p	χ^2h
ICSA$_3$ 11 x IS 33844-5	F_2	Rainy	102	26	13:3	0.2 (0.655)	34.13 (<0.01)	20.27 (<0.01)
		Post-rainy	100	69		54.2 (<0.01)		
	BC_1	Rainy	53	27	3:1	3.26 (0.071)	0.11 (0.74)	7.15 (0.007)
		Post-rainy	90	18		4 (0.046)		
ICSA$_3$ 38 x IS 33844-5	F_2	Rainy	50	58	27:37	0.73 (0.393)	0.04 (0.345)	0.89 (0.841)
		Post-rainy	66	97		0.2 (0.655)		
	BC_1	Rainy	63	46	1:7	205.2 (<0.01)	48.23 (<0.01)	158.9 (<0.01)
		Post-rainy	22	210		1.93 (0.16)		
ICSA$_3$ 88001 x IS 33844-5	F_2	Rainy	90	40	13:3	12.28 (<0.01)	1.13 (0.288)	12.1 (<0.01)
		Post-rainy	266	53		0.95 (0.330)		
	BC_1	Rainy	85	54	3:1	14.16 (<0.01)	0.35 (0.554)	22.63 (<0.01)
		Post-rainy	117	19		8.82 (0.003)		

Table 4. Segregation ratios for male-fertility restoration (%) of F_2 and backcross sorghum populations derived from crosses based on $A_{4(M)}$ cytoplasm based A-lines

Cross	Generation	Season	Fertile plants (F)	Sterile plants(S)	Expected ratio (F:S)	χ^2
$ICSA_{4(M)}$ 11 x IS 33844-5	F_2	Rainy	129	110	9:7	0.5 (0.48)
		Post-rainy	172	30	54:10	0.09 (0.76)
	BC_1	Rainy	77	177	1:3	3.82 (0.051)
		Post-rainy	28	8	3:1	0.15 (0.699)
$ICSA_{4(M)}$ 38 x IS 33844-5	F_2	Rainy	135	86	9:7	2.11 (0.15)
		Post-rainy	245	48	54:10	0.13 (0.718)
	BC_1	Rainy	48	86	1:3	8.7 (<0.01)
		Post-rainy	25	5	3:1	1.11 (0.292)

digenic ratio of 9F:7S in the F_2 and 1F:3S in the BC_1 is also possible with 'AAbbCC' genotype of male parent. Even in a three-gene mechanism, there is a possibility of getting a two-gene ratio depending on the genotype of the male and female parents and hence the number of genes segregating in the F_2 and BC_1 populations.

The postulated genotypes of A-lines could be *rf*4a *rf*4a *Rf*4b *Rf*4b *rf*4c *rf*4c and the R-lines could be *Rf*1a *Rf*1a *rf*1b *rf*1b *Rf*1c *Rf*1c. Tripathi *et al.* [19] postulated a four-gene model, with a possibility of a fifth gene, controlling male-fertility restoration for sorghum male-sterile cytoplasms VZM2A and G1A (cytoplasms belonging to A_4 Indian group) while Elkonin *et al.* [29] reported a digenic inheritance mechanism.

Commercially exploitable heterotic combinations depend on the inheritance of fertility restorer gene(s) and their consistent expression across various genotypic backgrounds. From the F_2 segregation behaviour of the hybrid combinations in the present study, it is apparent that the fertility restoration in the A_1, A_2, A_3 during rainy and post-rainy seasons and $A_{4(M)}$ CMS systems during rainy season in sorghum is governed by a trigenic inheritance mechanism though the gene action varied among the CMS systems. The fertility restoration of A_1 CMS systems was governed by one basic gene and two duplicate complimentary genes all acting in dominant fashion while the fertility restoration of A_2 and A_3 CMS systems was governed by three genes where all of the three complimentary genes in dominant condition restore fertility. The inheritance of fertility restoration in $A_{4(M)}$ CMS system during post-rainy season was governed by trigenic mechanism in which any two of the three dominant duplicate-complimentary genes restore fertility while only two complementary genes in dominant state restored fertility in rainy season. Also the involvement of the background genotype on the expression of restorer genes in F_1 hybrid combinations was strongly indicated.

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