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Nuclear-cytoplasmic interactions in restoration of male fertility in the '9E' and A4 CMS-inducing cytoplasms of sorghum

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Abstract The genetics of male-fertility restoration in sorghum in the "9E" and A4 CMS-inducing cytoplasms, was studied by crossing a number of fertility restorer lines of A1 cytoplasm to CMS lines [9E]T × 398 and [A4]T × 398 and the line [9E]Milo-10, which was obtained by backcrossing Milo-10 to [9E]T × 398. It was revealed that both A4 and "9E" cytoplasms are characterized by a sporophytic mode of restoration of male fertility. Depending on the nuclear background of the male parents, fertility restoration was controlled by one or two dominant genes. Fertility-restorer genes of one of the tester lines, KVV-114, were effective in [9E]T × 398 but could not restore [9E]Milo-10. A fertile line obtained from the fertile hybrid [9E]T × 398/KVV-112, with "9E" cytoplasm, also failed to restore [9E]Milo-10. In a number of hybrid combinations with both A4 and "9E" cytoplasms a novel and unusual phenomenon of gradual restoration of male fertility in subsequent backcross generations was observed. Pollen from the fertile revertants did not transmit fertility restoration in progeny from crosses with the original CMS line and was poorly transmitted in sib-crosses. The appearance of fertile revertants and the different reactions of different CMS lines with the same cytoplasm in test-crosses may be caused by the action of recessive nuclear genes of the recurrent male parents that were accumulated during backcrossing; these may induce changes in cytoplasmic genes controlling CMS.

Key words *Sorghum bicolor* · Cytoplasmic male sterility · Cytoplasmic mutations · Fertility-restorer genes · Fertility reversions

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Introduction

The interaction of nuclear and cytoplasmic genetic systems is a key process in the expression of cytoplasmic male sterility (CMS). It has been shown that the CMS phenotype appears as a result of the activity of specific CMS-associated mitochondrial genes (Hanson 1991; Vedel et al. 1994). Certain nuclear-restorer genes, specific for a definite type of cytoplasm, influence the transcription of CMS-associated mitochondrial genes (Dewey et al. 1987; Pruitt and Hanson 1991) or process mRNA transcribed from them, which results in the restoration of male fertility (Singh and Brown 1991; Iwabuchi et al. 1993; Moneger et al. 1994; Tang et al. 1996).

A large number of genetically different types of CMS-inducing cytoplasms have been revealed in sorghum using intra- and interspecific hybridization (Schertz and Pring 1982; Pring et al. 1995). These cytoplasms differ in their response to different fertility-restorer lines, with respect to mitochondrial (mt)DNA restriction patterns, morphology and histological structure of anthers and by the stage of pollen degeneration. Based on anther morphology, different CMS-inducing cytoplasms have been subdivided into two distinct groups: those with small anthers without fertile pollen which degenerates during microsporogenesis (A1, A2, A5, A6), and those with large non-dehiscent anthers that may contain some stainable pollen (A3, A4, "9E") (Schertz et al. 1989). These groups have different restriction fragment length polymorphism (RFLP) patterns and can be clearly distinguished using specific mtDNA sequences (Xu et al. 1995). In addition, the cytoplasms belonging to the small-anthered group have a deletion in the *rpoC2* chloroplast gene which encodes the RNA polymerase subunit (Chen et al. 1995). Restoration of male fertility in the A1 (review: Kaul 1988) and A2 (Murty and Gangadhar 1990) cytoplasms is of the sporophytic mode and is

controlled by one or few dominant genes. The A3 cytoplasm is characterized by a gametophytic mode of restoration (Tang et al. 1996).

The CMS-inducing effects of the "9E" and A4 (IS7920C) cytoplasms have been described by Webster and Singh (1964) and Schertz and Ritchey (1978). According to mtDNA analyses (Pring et al. 1982; Xu et al. 1995) these cytoplasms are related but not identical. In contrast to other cytoplasms they are characterized by a rearrangement in the *cox*I mitochondrial gene, which results in the synthesis of a variant 42-kDa cytochrome *c* oxidase subunit I (instead of the 38-kDa fragment in the A1 and A2 cytoplasms) (Bailey-Serres et al. 1986). The genetics of fertility restoration in these cytoplasms is not well-characterized.

Previously, when investigating different nuclear-cytoplasmic combinations by the transfer of genomes of several restorer lines of A1 cytoplasm to other CMS-inducing cytoplasms, we observed an unusual gradual restoration of male fertility in subsequent backcross generations (Elkonin et al. 1995). Moreover, different CMS lines with the same type of cytoplasm manifested different reactions in the test-crosses. In this paper we present a description and genetic characterization of these phenomena in the "9E" and A4 cytoplasms.

Materials and methods

Isonuclear alloplasmic lines with the T × 398 genome and A4 (IS7920C) and "9E" (IS17218) cytoplasms were used as female parents (the seeds were kindly supplied by Dr. K. F. Schertz). Milo-10, Feterita-14, Hegari k-2342, Guineyskoe k-2974, Pishchevoe-1, Volgogradskoe-26, S-723, and KVV-28, − 52, − 112, − 114, − 181 were used as male parents. These male parents are pure lines selected from hybrid populations obtained by the crossing of different varieties of grain sorghum belonging to the *cafir*, *caudatum*, *durra* and *guinea* races of *Sorghum bicolor* (L.) Moench. All these lines are restorers of A1 cytoplasm.

The F_1 hybrids with [9E]T × 398 and [A4]T × 398 as female parents were grown in the greenhouse. The F_1 hybrids with [9E]Milo-10 and BC1-BC8 hybrids and progenies of self-pollinated fertile segregants were grown in the field in 5- to 10-m-long rows. Fertility was determined by the seed setting on panicles bagged before blooming. All plants in each generation were classified on the extent of seed setting as sterile (s) (0% of seed setting), partially sterile (ps) (<25%), partially fertile (pf) (25–75%) and fertile (f) (>75%). For Chi-square tests, plants were scored as "restored" (r) (f, pf, ps) or "sterile" (s). To select plants for crosses we observed the panicles at 3 days after anthesis of the panicle base; plants with "fresh" stigmas on all of the panicle were defined as male sterile and used as females in the production of BC generations and in the sib-crosses with fertile siblings.

Results

Restoration of male fertility of different CMS lines with "9E" cytoplasm

The results of crosses of CMS line [9E]T × 398 with different male parents are presented in Table 1. Complete restoration of male fertility was observed in two of five hybrid combinations tested. The number of fertile and sterile plants of the F_2 of the hybrid [9E]T × 398/Feterita-14 corresponded to a segregation ratio of 15 : 1, which indicates the presence of two duplicate dominant genes in the genome of Feterita-14 being responsible for the restoration of male fertility. In the combination [9E]T × 398/KVV-114, segregation in the F_2 for restored (fertile, partially fertile and partially sterile) versus non-restored (sterile) plants corresponded to a 3 : 1 ratio. This ratio indicated that restoration of male fertility in this hybrid combination might be controlled by one dominant gene.

A complete and stable maintenance of male sterility was observed in the F_1 and in subsequent backcross generations in the combinations [9E]T × 398/Milo-10 and [9E]T × 398/Pishchevoe-1. The nearly isogenic CMS line [9E]Milo-10 (BC9), which differed from the paternal line by the type of cytoplasm, was obtained after nine subsequent backcrosses. This line was used in subsequent crosses.

The line [9E]Milo-10 when crossed with Feterita-14 also yielded fertile F_1 hybrids (Table 1). However, when this CMS line was crossed with KVV-114, the latter being defined as a fertility restorer for "9E" cytoplasm by hybridization with [9E]T × 398, only sterile and partially restored F_1 hybrids were obtained. Fully fertile hybrids were also not found in the BC_1 obtained by the pollination of sterile F_1 hybrids with KVV-114 (Table 1). These data illustrate the different interactions of the [9E]T × 398 and [9E]Milo-10 CMS lines with KVV-114 genome.

The restorer genes of another line, KVV-112, which is genetically related to KVV-114, also restored fertility of the F_1 hybrids with the CMS line [9E]T × 398 and in subsequent generations (Fig. 1). However, the F_1 of [9E]Milo-10/KVV-112 consisted of predominately sterile and partially restored (partially sterile and partially fertile) plants. After constant selection of fertile plants in each subsequent generation from the [9E]T × 398/KVV-112 cross, a fertile line (#263) was obtained in the "9E" cytoplasm. However, when fertile plants of this line, which should be homozygous for the restorer genes for the "9E" cytoplasm, were crossed with CMS line [9E]Milo-10 only sterile and partially sterile F_1 hybrids were found. Selfed progeny of the male plants grown in the same year were fertile. Thus, the dominant gene restorers of KVV-112 which were effective for [9E]T × 398 could not restore [9E]Milo-10.

All other lines crossed to [9E]Milo-10 (Hegari k-2342, KVV-52, KVV-181, Volzhskoe-4w) maintained sterility of this CMS line in the F_1 generation, except for line Guineyskoe k-2974 which produced partially restored F_1 hybrids (Table 1).

We obtained rather unexpected results when the KVV-28, KVV-181 and Hegari k-2342 genomes were transferred to cytoplasm "9E". The F_1s of hybrids

Table 1 Inheritance of male-fertility restoration in the "9E" cytoplasm in crosses between different female parents with nuclear genomes of T × 398 and Milo-10 and several male parents

Male parent	Generation	Number of plants[a]						Ratio	*P*
		f	pf	ps	s	r	s		
		[9E]T × 398							
Feterita-14	F_1	4	–	–	–	4	0		
	F_2	58	–	–	4	58	4	15:1	0.95–0.99
KVV-114	F_1	3	1	–	–	4	0		
	F_2	22	9	8	12	39	12	3:1	0.50–0.75
Milo-10	F_1	–	–	–	5	0	5		
	BC_1[b]	–	–	–	8	0	8		
	…								
	BC_8	–	–	–	17	0	17		
Pishchevoe-1	F_1	–	–	–	10	0	10		
	BC_1	–	–	–	19	0	19		
	…								
	BC_5	–	–	–	10	0	10		
KVV-28	F_1	–	–	–	4	0	4		
	BC_1[b]	1	3	–	13	4	13		
	BC_3[b]	1	4	8	1	13	1		
		[9E]Milo-10							
Feterita-14	F_1	8	–	–	–	8	0		
Guineyskoe k-2974	F_1	–	6	–	–	6	0		
KVV-114	F_1	–	2	13	30	15	30		
	BC_1[b]	–	2	6	14	8	14		
KVV-181	F_1	–	–	–	16	0	16		
	BC_1	3	12	9	9	24	9		
	BC_2[b]	8	7	14	3	29	3		
Hegari k-2342	F_1	–	–	–	9	0	9		
	BC_1[b]	–	–	2	5	2	5		
	BC_2[b]	2	1	5	–	8	0		
Volzhskoe-4w	F_1	–	–	–	9	0	9		
KVV-52	F_1	–	–	1	39	1	39		

[a] The plants in each generation were classified on the extent of seed setting as sterile (s) (0% seed set), partially sterile (ps) (<25%), partially fertile (pf) (25–75%), fertile (f) (>75%); for Chi-square tests f, pf and ps plants were bulked as restored (r).
[b] BC_1–BC_3 hybrids were obtained by crossing sterile plants, which were selected in each generation, to recurrent male parents

[9E]T × 398/KVV-28, [9E]Milo-10/KVV-181 and [9E]Milo-10/Hegari k-2342 were completely male sterile (Table 1). However, a few fertile and/or partially fertile plants appeared in the BC_1 generation obtained by crossing these sterile plants with recurrent male parents. In the next backcross generation (BC_2), which was obtained by backcrossing sterile BC_1 plants with the recurrent parent, the percentage of fertile plants significantly increased. For example, in the combination [9E]Milo-10/KVV-181, the number of fertile plants in the BC_2 generation exceeded the number of sterile plants. No sterile plants were observed in the BC_2 generation of the [9E]Milo-10/Hegari k-2342 combination. The same increase in the number of restored plants was observed in the combination [9E]T × 398/KVV-28 in the BC_3 (obtained by pollination of sterile BC_2 plants with KVV-28 pollen) relative to the BC_1. Thus, in these combinations a gradual restoration of male fertility took place during genome substitution in subsequent backcross generations.

To reveal the genetic nature of these fertile segregants we crossed them with the original CMS line [9E]Milo-10 and analyzed both the F_1 hybrids and the self-pollinated progenies of the same paternal plants. Only 21 sterile plants were observed in the F_1 in all three crosses [9E]Milo-10/BC_2. At the same time, in the selfed progeny of the BC_2 paternal parents grown in the same year, we observed restored and partially restored plants (Table 2). These data show that fertility in the backcross generation in this combination was not transmitted through the pollen to the F_1 hybrids and, hence, it was not caused by dominant fertility restorer gene.

Restoration of male fertility in the A4 cytoplasm

The results of crosses of different fertile lines with CMS-line [A4]T × 398 are summarized in Table 3. Two lines (Feterita-14 and KVV-181) among the six

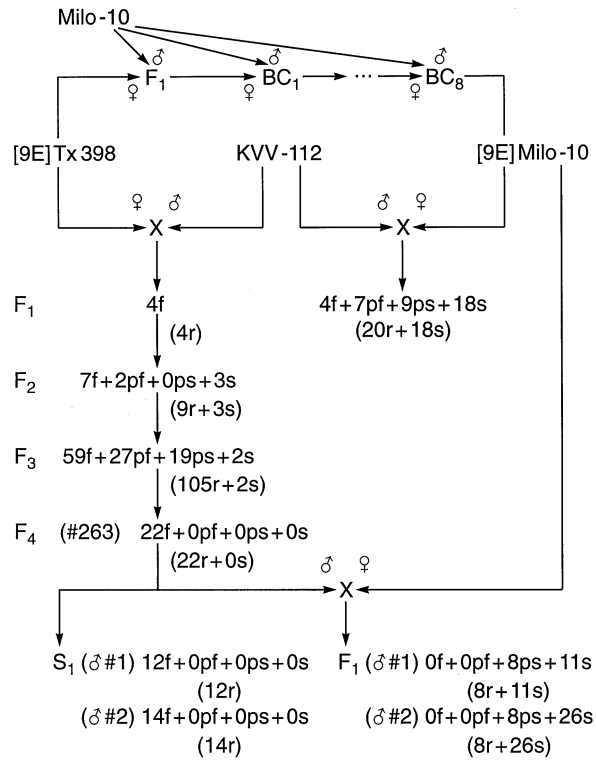

Fig. 1 Expression of gene restorers of the line KVV-112 in test-crosses with CMS lines [9E]T × 398 and [9E]Milo-10. *s* Sterile (0% seed set), *ps* partially sterile (<25%), *pf* partially fertile (25–75%), *f* fertile (>75%), *r* restored

Table 2 Data of the test- and sib-crosses of fertile plants from backcross generations in the "9E" and A4 cytoplasms

Crosses	Number of plants					
	f	pf	ps	s	r	s
[9E]Milo-10/KVV-181(BC2)						
[9E]Milo-10/mf # 1	–	–	–	6	0	6
mf # 1, selfed	4	4	4	1	12	1
[9E]Milo-10/mf # 2	–	–	–	8	0	8
mf # 2, selfed	8	6	–	–	14	0
[9E]Milo-10/mf # 3	–	–	–	7	0	7
[A4]T × 398/S-723(BC3)						
ms # 1/mf # 1	–	1	6	26	7	26
mf # 1, selfed	2	9	23	19	34	19
ms # 2/mf # 2	–	–	5	20	5	20
mf # 2, selfed	8	13	17	18	39	18
ms # 3/mf # 3	–	5	5	19	10	19
mf # 3, selfed	–	4	26	26	30	26

tested possessed the ability for fertility restoration in this cytoplasm. In both cases the segregation of sterile plants in the F_2 generations indicated a sporophytic mode of fertility restoration. Segregation in the F_2 of both combinations ([A4]T × 398/KVV-181 and [A4]T × 398/Feterita-14) fit a 15:1 ratio, suggesting the presence of two duplicate dominant fertility-restorer genes in the KVV-181 and Feterita-14 genomes.

In the combinations [A4]T × 398/Milo-10 and [A4]T × 398/KVV-52 complete and stable maintanance of male sterility was observed except for 1 fertile plant in the BC_1 with Milo-10 as male. At the same time, it should be noted that a gradual restoration of male fertility was observed in subsequent backcross generations of [A4]T × 398/S-723, [A4]T × 398/Hegari k-2342 and [A4]T × 398/Volgogradskoe-26. All the F_1 hybrids in these combinations were sterile, whereas fertile and partially restored plants appeared in the BC_1 generation. The BC_3 population of [A4]T × 398/S-723 consisted of 85% restored plants; in the BC_2 of [A4]T × 398/Hegari k-2342 no sterile plants were observed. Similar results were observed in the "9E" cytoplasm (Table 1).

To examine the genetic nature of the fertile plants that appeared in backcross generations, we crossed sterile and fertile siblings from the BC_3 of [A4]T × 398/S-723. As in the combination [9E]Milo-10/KVV-181, the fertility of fertile siblings was poorly transmitted through the pollen: the F_1 of sib-crosses consisted of sterile and a few partially restored plants (Table 2). Remarkably, in the self-pollinated progenies of fertile siblings, fertile plants were few, and partially sterile plants predominated. The ratio of different phenotypic groups differed significantly from any Mendelian segregation.

Discussion

Our data show that different line restorers of A1 cytoplasm were able to restore male fertility in the A4 and "9E" cytoplasms in the F_1 generation, gradually restore fertility in subsequent backcross generations or stably maintain male sterility. The maintenance of male sterility by A1 restorers demonstrates the differences among gene restorers for the A1 and A4 and "9E" cytoplasms. Restoration of male fertility in the F_1 in some hybrid combinations and segregation of sterile plants in the F_2 generation testifies to the dominant nature and the sporophytic mode of action of fertility-restorer genes. The number of these genes varied depending on the genotype of the male parent, from one or two for "9E" cytoplasm (Table 1), and identical (two genes) in both male parents for the A4 cytoplasm (Table 3).

The sporophytic mode of fertility restoration should be expected because the male-sterile phenotype of these cytoplasms is induced by the specific structure of the sporophytic tissues of mature anthers ("strongly developed endothecium and thick-walled epidermis and persistence of the septum between loculi of anther halves", Webster and Singh 1964), which results in their non-dehiscence. In our preliminary cytological observations the "9E" and A4 cytoplasms were also

Table 3 Inheritance of male-fertility restoration in the A4 cytoplasm in crosses of [A4]T × 398 with different male parents

Male parent	Generation	Number of plants						Ratio	*P*
		f	pf	ps	s	r	s		
Feterita-14	F_1	4	–	–	–	4	0		
	F_2	43	5	3	3	51	3	15:1	0.75–0.90
KVV-181	F_1[a]	2	9	3	1	14	1		
	F_2	74	48	29	17	151	17	15:1	0.05–0.10
Milo-10	F_1	–	–	–	3	0	3		
	BC_1	1	–	–	5	1	5		
	BC_2	–	–	–	25	0	25		
	BC_3	–	–	–	43	0	43		
KVV-52	F_1	–	–	–	6	0	6		
	BC_1	–	–	–	5	0	5		
	BC_2	–	–	–	12	0	12		
	BC_3	–	–	–	20	0	20		
	BC_4	–	–	–	8	0	8		
S-723	F_1	–	–	–	3	0	3		
	BC_1	2	7	1	13	10	13		
	BC_2	–	1	–	8	1	8		
	BC_3	9	30	11	9	50	9		
Hegari k-2342	F_1[a]	–	–	–	6	0	6		
	BC_1	–	–	1	7	1	7		
	BC_2	1	2	4	–	7	0		
Volgogradskoe-26	F_1[a]	–	–	–	11	0	11		
	BC_1	4	3	5	16	12	16		

[a] The F_1s in these combinations as well as the BC hybrids were grown in the field

non-dehiscent. [A4]T × 398, [9E]T × 398 and [9E]Milo-10 all contained more than 70% stainable pollen, but their anthers did not dehisce. The presence of stainable pollen in the anthers of A4 cytoplasm was also reported by Worstell et al. (1984).

The different segregation patterns in crosses of the same CMS line with different male parents that were observed in our experiments show that restoration of male fertility on one and the same type of cytoplasm in sorghum may be conditioned by different genes. Evidently, this phenomenon is characteristic not only of the "9E" cytoplasm but also of other CMS-inducing cytoplasms because different segregation patterns were also observed in crosses between the same CMS A1 lines with different restorers, which indicates the action of different fertility-restorer genes (Nagur and Menon 1974; Schertz et al. 1989).

Together with fertility restoration in the F_1 hybrids, we observed a novel and unusual phenomenon of maintenance of male sterilty in the F_1 generation and gradual restoration of male fertility during genome substitution in subsequent backcross generations. This phenomenon was observed in crosses of both [9E]T × 398, [9E]Milo-10 and [A4]T × 398 with different male parents (Tables 1 and 3).

Theoretically, the appearance of fertile plants in backcross generations may result from: (1) heterozygosity of the recurrent male parental line that may consist of plants bearing dominant fertility-restorer gene(s) and plants without this gene; (2) the presence of recessive fertility-restorer genes or recessive gene modifiers in the recurrent parent that pass in the homozygous state to backcross generations; (3) cytoplasmic mutations.

If one assumes that the male parental line was heterozygous (contained *Rf*/*rf* and *rf*/*rf* plants) and that sterility of the F_1 was the result of pollinating a CMS line with an *rf*/*rf* plant, while fertile plants in backcross generations appeared after pollinating sterile F_1 hybrids with an *Rf*/*rf* plant, then such fertile plants from backcross generations should bear a dominant *Rf* allele and should restore the original CMS line or sterile siblings in the test-crosses. This was not observed in the [9E]Milo-10/KVV-181 combination; in the [A4]T × 398/S-723 combination only few partially restored plants were observed in sib-crosses, which also excludes this supposition.

The hypothesis of recessive restorer genes may be a possible explanation for our data. In this case the fertile plants from the backcross generations, which should be homozygous for recessive fertility-restorer genes, would not segregate sterile plants under self-pollination. This was observed in the [9E]Milo-10/KVV-181 combination except for a single sterile plant in 1 of the selfed progenies. However, in the progenies of fertile plants from the [A4]T × 398/S-723 (BC_3) a large number of sterile plants were observed (Table 2).

At the same time, the absence of fertility transmission through the pollen in the test-crosses of fertile plants from backcross generations conforms to the hypothesis that these fertile plants may be cytoplasmic revertants. However, such reversions could occur under the influence of certain recessive nuclear genes because the number of revertants increased in subsequent backcross generations. Hence, this supposition may be one explanation of the mode of action of the recessive fertility-restorer genes which may be responsible for fertility restoration in backcross generations. This phenomenon may be similar to the appearance of fertile cytoplasmic revertants of CMS-*S* maize in certain nuclear genomes (Laughnan and Gabay-Laughnan 1982) or in CMS *Phaseolus vulgaris* under the influence of the *Fr* gene (Mackenzie and Chase 1990). Segregation in the progeny of fertile revertants may be explained by their cytoplasmic heterogeneity. It is possible that such reversions may only take place in some sectors of the panicles (such fertile sectors were observed in partially sterile plants) or only in anthers, resulting in maintenance of "sterile" cytoplasmic genes in the majority of egg cells on the panicle and a predominance of semisterile and sterile plants in the progeny of revertants.

Another example of unusual specific interactions of nuclear and cytoplasmic genes controlling CMS on the "9E" cytoplasm is the difference in the fertility restoration of CMS lines [9E]T × 398 and [9E]Milo-10. Fertility restorer genes of KVV-114 restored the male fertility of [9E]T × 398 but failed to restore [9E]Milo-10, which was obtained by backcrossing Milo-10 to [9E]T × 398. An important observation is the absence of fertility restoration in hybrids between [9E]Milo-10 and a fertile line in the same cytoplasm ([9E] #263), which was selected from the restored F_1 hybrid [9E]T × 398/KVV-112. These data indicate that dominant genes that restored [9E]T × 398 could not restore [9E]Milo-10.

These results cannot be explained by different environmental conditions (F_1 hybrids with [9E]T × 398 were grown in the greenhouse while F_1 hybrids with [9E]Milo-10 were grown in the field) because restorer genes of KVV-114 were also expressed in the F_2 generation of the hybrid [9E]T × 398/KVV-114 grown in the field. Fertile line #263 was obtained in field conditions after several generations of self-pollination of fertile plants.

These data may be explained by the action of one or several dominant gene inhibitors that may be present in the genome of Milo-10 which suppress the action of restorer genes of KVV-114 and KVV-112. A dominant gene inhibitor of restoration of male fertility in the cytoplasm of *Triticum timopheevi* Zhuk. has been described in wheat (*Tr. aestivum* L.) (Du and Maan 1992). However, this explanation seems less convincing because fertile plants without gene inhibitor(s) should appear in the BC_1 as a result of recombination during meiosis in the F_1 plants. Nevertheless, the proportion of partially restored plants did not increase in the BC_1 relative to the F_1.

An alternative explanation of this phenomenon may be that cytoplasmic genes controlling CMS in [9E]T × 398 and [9E]Milo-10 are different. Perhaps changes (such as selective replication, loss or rearrangement of the sequences participating in CMS control) might occur in the "9E" cytoplasmic genes during substitution of the T × 398 nuclear genome by the Milo-10 genome. As a result of these processes, the nuclear restorer genes regulating the expression of these CMS-associated genes in [9E]T × 398 became inefficient in [9E]Milo-10 and could not restore fertile phenotype.

The hypothesis of induction of mutations in the cytoplasmic (mitochondrial) genes under the influence of a novel nuclear genome arising as a result of backcrossing is speculative but not without precedent. The influence of nuclear genes on the structure of mtDNA has been described in higher plants. A specific nuclear locus that promotes rearrangements in the mitochondrial genome, resulting in a variegated phenotype, was described in *Arabidopsis* (Martinez-Zapater et al. 1992). In *Phaseolus vulgaris* the nuclear gene *Fr* induces the selective elimination of a specific CMS-associated mitochondrial sequence, *pvs*, thus restoring male fertility, and the fertility level gradually increases from the F_1 to the F_2 (Mackenzie and Chase 1990). In maize, the nuclear genotype influences the frequency of cytoplasmic reversions to male fertility in *S*-cytoplasm (Laughnan and Gabay-Laughnan 1982) and mitochondrial genome organization of these revertants (Gabay-Laughnan et al. 1995), and rearrangements of the mitochondrial genome in non-chromosomal stripe (NCS) mutants (Newton 1995). Perhaps the interaction of nuclear and cytoplasmic genes of distantly related representatives of the highly polymorphous genus *Sorghum* may also induce changes in the mitochondrial genome and, thus, may be a factor in mitochondrial genome evolution.

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