

Review

Implications of cytoplasmic male-sterility systems for development and deployment of pest resistant hybrids in cereals

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Abstract

The world population is increasing at an alarming rate, and there is a continued need to increase crop productivity to meet the food requirements. To meet the ever-increasing demand for food, cytoplasmic male-sterility (CMS) has been successfully exploited to develop hybrids for increasing crop production worldwide. However, large-scale cultivation of crop hybrids based on a single source of CMS may pose a serious challenge to sustainable crop production because of decreasing genetic diversity. This review analyses the potential for exploitation of different CMS systems for hybrid production, effects of CMS on various agronomic traits, and expression of resistance to insect pests and diseases in high-yielding hybrids of sorghum, maize, pearl millet, rice, wheat, and barley. Considerable information has been generated on the effects of CMS on physiology, yield, and agronomic characteristics of the plant. However, there is limited information on the effects of CMS on expression of resistance to insect pests and diseases. The available information indicates that the CMS lines are more susceptible to insect pests and diseases, and large-scale cultivation of hybrids based on a single source of CMS might result in pest outbreaks because of narrow genetic base. Therefore, there is a continuing need to evaluate various CMS systems in different genetic backgrounds for their effects on cultivar susceptibility to insect pests and diseases to develop strategies for large-scale deployment of pest-resistant hybrids on farmer's fields. Genetically engineered insect-resistant CMS lines can also be exploited to diversify the hybrid parents for sustainable crop production.

Keywords: Cytoplasmic male sterility, CMS systems, Cereals, Hybrids, Insect pests, Diseases, Resistance, Agronomic traits, Molecular characterization

Review Methodology: We searched the information from national and international journals and their cross references, newsletters, CAB Abstracts, AGRICOLA, and Web pages on the internet using the keywords such as cytoplasmic male-sterility, insect pests, diseases, sorghum, maize, rice, wheat, barley, pearl millet, cereals, hybrids, agronomic traits, molecular characterization, physiology, etc, individually or in different combinations, and analysed the information in relation to expression of resistance to insect pests, morphological and physiological traits, and development and deployment of hybrids based on CMS for sustainable crop production.

Introduction

Cytoplasmic male-sterility (CMS) results from the inability of plants to produce functional pollen because of reproductive deficiency in hermaphrodite flowers. In angiosperms, it may be the result of suppression of anthers (abortion, phyllody, petalldy, or pistillody), aberrant meiosis (where anthers do not dehisce even if viable

pollen is present), and the abortion of the androecium before pollen grains are formed (probably the result of premature dissolution of callose, and malformed androecium in which no pollen grains are formed) [1]. Male-sterility based on gametophytes results from disturbances in normal microsporogenesis, which leads to formation of non-viable microspores because of mitochondrial mutations, barriers of the tapetal layer, and improper timing of

callose activity and operon control [1]. Sporophyte-based male sterility may be conditioned by cytoplasmic, genetic, or cytoplasmic–genetic factors [1]. CMS occurs due to the mutation of mitochondria or some other cytoplasmic factors outside the nucleus, which results in the transformation of fertile cytoplasm into sterile cytoplasm. This CMS system is advantageous in ornamental species, as they tend to bloom and remain fresh longer than their fertile counterparts. The CMS is also useful for producing single/double-cross hybrids in crops where vegetative parts are the commercial product. However, it is unsuitable for hybrid seed production in crops where the fruit or seed is the commercial product. Genetic male sterility occurs in plants because of mutation at the fertility locus situated on a chromosome within the nucleus, and is usually governed by recessive genes. This type of male sterility is maintained by crossing male-sterile and male-fertile plants, and recovering the male-sterile segregants (1 sterile:1 fertile). However, this system has not been used much in practical plant breeding because of maintenance problems. Cytoplasmic–genetic male sterility arises from the interaction of nuclear genes with the sterile cytoplasm, and is essentially a cytoplasmic sterility with a provision for restoration of fertility. Cytoplasmic genes exclusively control the male sterility. The term CMS, although a misnomer, has been widely used to describe genetic CMS.

Influence of CMS on Physiology of Cereal Plants

Increased accumulations of amino acids may also be related to their increased synthesis or non-utilization by male-sterile anthers. Once amino acid composition is altered, defective proteins are formed in male-sterile anthers, resulting in disruption of carbohydrate and protein metabolism [1–4]. Asparagine and glutamine are important vehicles of nitrogen transport in higher plants, and their accumulation influences pollen development and physiology. Reduced nucleic acid content has also been reported in male-sterile anthers of sorghum [5, 6] and barley [7]. Nucleic acid content increases in male-fertile wheat anthers, and decreases in T-type CMS anthers after the tetrad stage, and in Taign CMS system after the sporogenous cell stage [8].

The activity of several enzymes is also altered in male-sterile lines. Cytochrome oxidase activity in male-sterile wheat anthers is greater than in male-fertile anthers [3], but deficient in abnormal anthers in sorghum [6], rice [1, 9], and maize [10], resulting in inefficient oxidative phosphorylation in anthers. Peroxidase activity is greater in sterile hybrids than in fertile hybrids and parents [11, 12]. Male-sterile cytoplasm also has altered levels of ribulose-bisphosphate carboxylase (RUBPcase), adenosine triphosphatase (ATPase), and the plant defence enzymes during the later stages of growth, particularly under nitrate stress. Abnormal formation or dissolution of

callose enzyme is also associated with male sterility in sorghum [13].

The CMS affects protein content and protein index [14, 15], but there is no effect of CMS on amylose content or starch viscosity [16]. The chlorophyll content is greater in CMS plants of barley, maize, rice, and wheat than in male-fertile plants [17]. The indole-3-acetic acid (IAA) content in anthers of male-sterile lines of maize is significantly lower than in the normal lines, but the zeatin content is higher in the CMS than in normal lines [18]. Murty *et al.* [19] observed substantial differences in soluble proteins, free amino acids, and peroxidase and esterase activity between CMS and maintainer lines in pearl millet. However, there were no differences in chlorophyll content and phenolics. Chhabra *et al.* [20] did not observe any differences in meiosis among isonuclear CMS lines, but chromosomal orientation and segregation were affected in the A₃ cytoplasm.

CMS Systems in Different Cereal Crops

Sorghum

CMS in sorghum was reported by Stephens and Holland [21] in crosses involving *Dwarf Yellow Milo* and *Kafir*, and *Milo* and *Blackhull Kafir*. The male-sterility resulted from introduction of *Kafir* genes into *Milo* cytoplasm. This male-sterility system is based on cytoplasmic–genetic male sterility instead of CMS, since the male sterility is based on the interaction between *Milo* cytoplasm and *Kafir* nuclear genes [21, 22]. The degree of male sterility increases with an increase in the proportion of *Kafir* genes in *Milo* cytoplasm. The recessive genes *msc*₁ and *msc*₂, present in *Milo* cytoplasm result in male sterility. In addition to *Milo* (A₁) cytoplasm, cytoplasmically male-sterile lines are also available in the A₂, A₃, A₄, A₄M, A₄VzM, A₄G₁, A₅, A₆, 9E, and Kansas (KS) cytoplasms [23–28], but their heterotic potential has not been exploited because of a lack of appropriate restorers. Changes in mitochondrial genome and in DNA clones derived from the genes of known function are responsible for male sterility [29–31], and internal mitochondrial transcription processing has been reported to be correlated with fertility restoration [32–36]. The restriction fragment length polymorphisms (RFLPs) using mitochondrial DNA (mtDNA) clones as probes and chloroplast DNA (ctDNA) restriction endonuclease fragments have been reported to be useful as molecular tools for fingerprinting sterility-inducing cytoplasms, determining CMS among germplasm accessions, and identifying new sources of cytoplasm with a potential to induce male sterility to broaden the base of CMS systems [37–46] (Table 1). Restriction endonuclease patterns of ctDNA have also been reported to distinguish fertile and male-sterile cytoplasms [47]. The A₁ (*milo*) cytoplasm has been widely deployed for producing sorghum hybrids. The A₂ cytoplasm has been deployed for

Table 1 Molecular differentiation of male-sterile and fertile cytoplasm in sorghum

Technique/gene/marker/clone	Characteristics	References
N ₁ and N ₂ plasmid-like DNAs	Differentiated A ₃ cytoplasm of IS 12563C and IS 1112C at plasmid sizes 1.7 and 2.3 kb.	[37]
Restriction endonuclease enzymes	Differentiated sterile and fertile, and A ₁ , A ₂ , A ₃ and A ₄ CMS cytoplasm.	[38]
<i>coxI</i> clone	Differentiated 9E (IS 17218) and A ₄ (IS 7920C) cytoplasm at <i>Hin</i> dIII fragment size 1.9 kb.	[39]
<i>atp6</i> probe	Differentiated 9E and A ₄ cytoplasm.	[40]
<i>rrn18</i> and <i>rrn 26</i> probes	Differentiated between KS 37 and KS 39.	[40]
<i>orf107</i> gene	Mitochondrial gene <i>orf107</i> is associated with male-sterility.	[40]
<i>atp6</i> probe	Differentiated Texas fertile and A ₃ cytoplasm at <i>orf25</i> .	[25, 41]
Restriction enzyme	The A ₁ and A ₂ cytoplasm have identical <i>Hind</i> III patterns, while <i>Bam</i> HI-digested ctDNA produced the same patterns in A ₂ , A ₃ and A ₄ , and <i>Eco</i> RI and <i>Pst</i> I produced identical patterns in all four cytoplasm.	[42]
RFLPs	Classified Indian origin CMS (<i>Maldandi</i> , <i>Guntur</i> , <i>Vizianagaram</i>) as Indian A ₄ types, and distinguished from the American A ₄ - and A ₁ -types.	[43]
RFLPs	Mitochondria of fertile 2219A have more respiring efficiency and mitochondrial electron transport (ET) rates from NADH to oxygen than CMS line, thus indicating responsible for male sterility.	[44, 45]
RFLPs	Restriction fragment locations of various mitochondrial genes and their transcripts suggest polymorphism for genes related to the ATP synthase complex between CMS and maintainer cytoplasm.	[46]

hybrid production in China [48]. Different CMS systems and the maintainer and restorer lines have also been analysed for their influence on expression of resistance to biotic and abiotic stresses and agronomic traits.

Rice

Sampath and Mohanty [49] first emphasized the role of cytoplasm in inducing male sterility in rice, and later, Japanese scientists reported several sources of CMS. The first cytoplasmically male-sterile line was developed by substituting nuclear genes of the *indica* variety, Taichung Native 1 [50]. This CMS line had poor plant type, unstable sterility, and was photoperiod-sensitive, and thus could not be used in hybrid seed production. There are three major types of CMS (HL, BT and WA), and two types of GMS systems (photoperiod-sensitive and temperature-sensitive) in rice. The BT- and HL-type CMS genes have been characterized as *orf-79* and *orfH79* [51]. However, with the advent of wild abortive (WA) cytoplasm from wild rice (*Oryza sativa* f. *spontanea* or *Oryza rufipogon* or *Oryza perennis*) in China, about 95% of the CMS lines currently used in producing rice hybrids have been derived from this source [52]. A large number of CMS lines in rice have also been developed by exploiting intra- and inter-specific cytoplasmic differences [53–56]. The genes encoding and restoring CMS have been mapped using different techniques [57–63]. The restorer allele *Rf-1* is present in some *indica* rice lines, whereas most lines of the subspecies *japonica* carry a non-restoring *Rf-1*

allele [62]. The fertility in the WA CMS system is controlled by more than two loci [63]. The fertility restorer genes *Rf-3* and *Rf-5*, have been mapped on to the short arms of chromosomes 1 and 10, respectively, while *Rf-4* and *Rf-6* genes have been mapped on the long arm of chromosome 10 [51, 64, 65]. The *Rf-1* gene encodes a PPR protein associated with functions in fertility restoration of CMS-Boro II and BT-type male-sterile cytoplasm [66–69].

Wheat

Male sterility in wheat was first reported by Kihara [70], with the discovery of male-sterile cytoplasm from *Aegilops candida*. Majority of these systems are not usable because of reduced vigour, abnormal plant morphology, zygote elimination, reduced seed set, fertility variation, and delayed maturity. Fertility restoration genes in wheat have not been discovered, and to date, only *Triticum timopheevii* has shown potential for development of a wheat fertility restoration system [71]. *Triticum aestivum* cv. Norin 26, which contains *Aegilops crassa* alloplasm, is nearly male-sterile under long-day length (>15 h), but is highly male-fertile under short-day length (<14.5 h). Ethyl-methane-sulphonate-induced mutagenesis has also been used to obtain photosensitive CMS lines [72]. Wheat cultivars with a restorer gene, *Rfv1* located on the short arm of chromosome 1B, which contains the IBL-IRS, can be used to develop wheat hybrids with SV CMS [73]. Fertility restoration for *T. timopheevii* CMS in wheat is controlled by major fertility restorer (*Rf*) and modifier genes [74]. There is considerable genotype × environment

Table 2 Molecular differentiation of male-sterile and fertile cytoplasms in maize

Technique/gene/marker/clone	Characteristics	References
<i>urf13TW</i> gene	The <i>urf13TW</i> gene, derived from the mitochondrial gene <i>T-urf13</i> responsible for Texas CMS has been expressed in <i>Saccharomyces cerevisiae</i> by targeting the <i>urf13TW</i> translation product into mitochondria.	[79]
<i>T-urf13</i> gene	The mitochondrial 35 bp open reading frame <i>T-urf13</i> shares a 165 kb sequence duplication with CMS T.	[80]
<i>orf355</i> and <i>orf77</i> genes	The mitochondrial open reading frames <i>orf355</i> and <i>orf77</i> are associated with CMS-S, and <i>orf77</i> and the mitochondrial ATP synthase subunit <i>atp9</i> share common sequence.	[81]
<i>R</i> gene	The nuclear gene <i>Rf3</i> suppresses the CMS-S phenotype, decreases the abundance of the major <i>R</i> gene transcripts, including the CMS-S-specific 1.6 kb mRNA, in mitochondria of restored plants.	[82]
<i>T-urf13</i> gene	<i>T-urf13</i> confers Texas CMS in maize plants. <i>S. cerevisiae</i> nuclei transformed with the universal code equivalent of <i>T-urf13</i> mimic <i>T-urf13</i> effects in maize and limit respiration.	[83–84]
mtDNA restriction endonuclease fragment analysis	There is heterozygosity in mtDNA among normal fertile and male-sterile cytoplasms, due to changes in ctDNA, which may affect CMS in maize.	[85–87]
<i>Rf4</i> and <i>Rf5</i> restorer genes	Fengke1 line contains <i>Rf4</i> and <i>Rf5</i> duplicating restorer genes located on 5L and 8S chromosomes, respectively.	[88–91]

(G×E) effect, which makes it difficult to develop CMS-based hybrids.

cytoplasms, suggesting that changes in ctDNA [87] may affect CMS in maize.

Maize

CMS in maize was reported by Rhodes [75], and restorer/maintainer reaction patterns have since been differentiated into three types: CMS-T (Texas), CMS-S (USDA) and CMS-C (Charrua) by Duvick [76] and Beckett [77]. Prior to 1970, CMS-T was used extensively, as it imparted full sterility in most of the inbred lines, and fertility restoration was relatively easy. However, CMS-T was not used for hybrid seed production because of susceptibility to southern corn leaf blight [*Bipolaris maydis* (Nisik. & Miyake)], which severely damaged the maize crop in the USA [78]. The epidemic resulted from a new race (T-race) of *B. maydis*, which was extremely virulent to cultivars containing the T-cytoplasm. Subsequently, molecular techniques have been deployed for differentiating male-sterile and male-fertile cytoplasms, and a number of genes responsible for CMS and restoration have been identified and used for making hybrids in maize [79–91] (Table 2). Mitochondrial gene *T-urf13* confers Texas-type CMS in maize plants [84], but some restorer genes interfere with the expression of corresponding sterility genes at development- or tissue- or organ-specific stages. The control of expression of a mitochondrial sterility gene by a nuclear restorer gene represents a valuable model for the study of interactions between nuclear and mitochondrial genomes in higher plants. However, restriction endonuclease fragment analysis of organelle DNA demonstrated the heterozygosity in mtDNA among normal fertile [85] and male-sterile [86]

Pearl Millet

Since the discovery of cytoplasmic-genetic male-sterility in Tift 23A (A₁ cytoplasm), several CMS sources have been identified [92, 93]. Tift 23A has excellent agronomic characteristics and combining ability, and has been widely used for hybrid production in India and the USA. The A₂ and A₃ cytoplasms have been identified, but have not been used in commercial hybrid production because of unstable sterility [92]. An A₄ cytoplasm from a wild subspecies of pearl millet, *Pennisetum americanum* subsp. *monodii* has been found to be stable for male-sterility, and is different from A₁, A₂ and A₃ cytoplasms [93]. Although, a very high frequency of A₄ restorer genes occurs in wild relatives of pearl millet, restorer genes for this cytoplasm occur in a low frequency in cultivated germplasm. Many unique sources of male-sterility have also been identified by using mtDNA RFLP, but there is a need to find restorers for these CMS systems [94–95].

Barley

CMS in barley was discovered from a population of alloplasmic *Hordeum jubatum* cytoplasm [96]. *Hordeum vulgare* acts as a perfect maintainer for this system, but fertility restorers have not been identified [97]. The two CMS, *msm*₁ and *msm*₂ have restorer genes [98–101], and *Rfm1a* gene restores the fertility of *msm*₁ CMS lines, but none of these are complete restorers. Locus *msg50*, with alleles

msg50gh and *msg50hm*, is responsible for the male-sterile genes *msggh* and *msggm* [102]. Several molecular markers linked to *Rfm1* locus have been identified on chromosome 6H [103].

Effects of CMS on Agronomic Traits

An understanding of cytoplasmic influences on yield and agronomic characters could have a major bearing on improving crop productivity, since cytoplasm is contributed by the seed parent to its progeny. Cereals are the major component of human diets, and the exploitation of CMS for increasing crop production, productivity, and value addition is crucial to meet the increased demand for food in future. Studies conducted on effects of CMS on various agronomic and yield traits such as plant height, unit seed weight, grain yield, leaf and panicle traits, days to 50% flowering, etc., in major cereals (sorghum, maize, pearl millet, rice, wheat and barley) in the past are given in Table 3 [104–168].

Effects of CMS on Expression of Resistance to Plant Diseases

Tan-coloured CMS lines in combination with tan restorer lines produce hybrids with high levels of resistance to rust (*Puccinia purpurea* Cooke) and head blight (*Fusarium* spp.) in sorghum. Hybrids based on red CMS lines × tan restorer lines are also resistant to these diseases, while red × red and tan × red hybrids are susceptible [169, 170], suggesting that characteristics of the restorer parent are dominant over the CMS line. Cytoplasm had no effect on head blight incidence or grain mould (*Fusarium moniliforme* J. Shield) severity [171]. The hybrids based on A₂ CMS system have 14–19% more smut (*Sporisorium reilianum* (Kuhn) Landon and Fullerton) and 6% more grain mould incidence than the hybrids based on A₁ cytoplasm [171–173].

Wheat hybrids based on *Aegilops juvenalis* cytoplasm have greater resistance to powdery mildew (*Erysiphe graminis* É.J. Marchal) and better seed germination than the hybrids based on *A. kotschyi* cytoplasm [132]. Cytoplasm accounts for 23.5% of the variance in *Puccinia recondita* Roberge resistance at the seedling stage in alloplasmic lines with bread wheat nucleus (Penjamo 62), and 17.4% at the adult stage [174]. Newly developed mt-A lines (IBL-IRS chromosome-inhibited lines) have been reported to be resistant to both *E. graminis* and *P. recondita*, but SV-A lines (SV cytoplasm-substituted lines) are susceptible to these pathogens. Mantle and Swan [175] observed >20% sclerotia of ergot (*Claviceps purpurea* (Fr.) Tul.) in threshed grain of poorly pollinated male-sterile wheat plants as compared with 0.7% sclerotia in the fertile plants.

The male-sterile barley cytoplasm (*msm*₁ and *msm*₂) have no effect on expression of resistance to barley yellow mosaic virus (BaYMV) transmitted by *Polymyxa graminis* Ledingham, but the Fusarium head blight (*Fusarium graminearum* Schwabe) damage is greater in fertile than in the sterile lines, indicating that pollen or anthers are important for infection by *F. graminearum* [176]. Male-sterile lines based on *msm*₁ cytoplasm without pollen have lower *Fusarium* head blight infestation than in the maintainer lines [176].

Male-sterile cytoplasm affects the rice plant's reaction to pathogens, as the WA male-sterile cytoplasm is less susceptible to rice blast (*Pyricularia oryzae* Cavara) and bacterial blight [*Xanthomonas campestris* pv. *oryzae* (Xoo)] than the fertile cytoplasm [177]. The *P. oryzae* resistant rice hybrids have been obtained from highly resistant A-lines × moderately resistant R-lines, while moderately resistant A-lines × highly susceptible R-lines produced moderately resistant hybrids. Susceptible A-line-susceptible R-line crosses produced susceptible hybrids [178]. Thus, resistance is required in both A- and R-lines to produce pathogen-resistant hybrids. To incorporate bacterial leaf blight (*Xanthomonas oryzae* pv. *oryzae*) resistance in rice hybrids, it is desirable to have resistance in both CMS and restorer lines, because the disease is not only affected by nuclear genes, but also by the sterile cytoplasm [179, 180]. Conversely, *Fusarium* sheath rot (*F. moniliforme*) and Karnal smut (*Tilletia barclayana* Sacc. & P. Syd.) diseases have been found to be more severe on CMS lines and hybrids as compared to that on the maintainer and restorer lines [181].

Susceptibility in Texas CMS maize lines to southern corn leaf blight [*B. maydis*] and yellow leaf blight (*Phyllosticta maydis* Arny & Nelson) are associated with the unusual mitochondrial gene *T-urf13*, which encodes a 13 kDa polypeptide (*urf13*) in comparison with normal C- or S-cytoplasm [182, 183]. Interactions between fungal toxins and *urf13* polypeptide result in inner mitochondrial membrane permeability, and account for susceptibility to these fungal pathogens. Plants with the Texas CMS are also more susceptible to the toxins from the pathogens than that of the normal fertile plants, and those with other types of CMS [184]. There are no unfavourable effects of C- and M-type CMS in maize on expression of resistance to *Ustilago zeae* (Schwein.) Unger and *Sphacelotheca reiliana* (Kühn) Clinton under natural infection, but C-type cytoplasm is susceptible to smut, and M-type to *U. zeae* and stalk rot, *Physoderma maydis* (Miyabe) Miyabe [150]. In addition, C-type CMS was resistant to *Cochliobolus heterostrophus* (Drechs.) Drechs. and *Setosphaeria turcica* (Luttrell) Leonard et Suggs [185]. The sub group CI (CMS-C) of group C is susceptible to *B. maydis* race C, but the subgroups CII (CMS-RB) and CIII (CMS-ES) are not infected seriously [186].

In pearl millet, incidence of downy mildew [*Sclerospora graminicola* (Sacc.) Schroet.] was similar in hybrids carrying either A₁ male-sterile or B-cytoplasm [187], and there

Table 3 Influence of male-sterile/male fertile cytoplasm on agronomic traits in different cereal crops

Crop/traits	Cytoplasm	Effect	References
Sorghum			
Grain yield, seeds/panicle, 100-seed weight, panicles per plant, leaf length and area, leaves per plant, and days to flowering.	MS ¹ versus MF ²	Yes	[104]
Grain yield components	MS versus MS	No	[104]
Grain yield, plant height, panicle length and excretion, flowering, and grain moisture	MS versus MS	No	[104–108]
Plant height and days to 50% flowering	MS versus MS and MS versus MF	Yes	[109–110]
Grain yield and other agronomic traits	MS versus MS	No	[111–112]
Grain size, yield and yield components	MS versus MS	Yes	[113–114]
GCA and SCA of morphological traits	MS versus MS	Yes	[114]
Days to flowering, inflorescence length and plant height	MS versus MS	No	[115]
Agronomic and morphological traits, pollen fertility and seed set	MS versus MS	Yes	[116–118]
Heterosis for yield	MS versus MF	Yes	[119]
Days to flowering, plant height, grain yield and forage quality	MS versus MF	No	[120]
Seed setting	MS versus MS	Yes	[120]
Wheat			
Grain weight and texture	MS versus MF	Yes	[121]
Agronomic traits	MS versus MF	No	[122–123]
	MS versus MS	Yes	[122–123]
Number of tillers, ear length, seed setting, days to maturity, yield/panicle, and grain yield	MS versus MF	Yes	[124–126]
1000-grain weight, ear density, flag leaf length, and winter hardiness	MS versus MF	No	[126]
Agronomic traits, except ear length	MS versus MS	No	[124]
Panicle emergence, spikelet number, kernel texture, germination rate, and grain weight/plant	MS versus MF	Yes	[127]
Grain quality	MS versus MF	No	[127]
Internodes length and plant height	MS versus MF	Yes	[128]
Bread making, and agronomic or yield traits	MS versus MS	No	[129]
Grain yield, panicle emergence, days to flowering, and height	MS versus MF	Yes	[130]
Grain yield	MS versus MF	Yes	[131]
Agronomic characters	MS versus MS	No	[132]
Seed germination		Yes	[132]
Barley			
1000-grain weight, effective panicles/plant, grains/panicle, plant height, length of peduncle and total grain weight/plant	MS versus MF	Yes	[133]
Morphological and yield characteristics	MS versus MF	No	[134]
Rice			
Grain yield	MS versus MF	Yes	[135–142]
Panicle number, panicle length and grain yield	MS versus MS and MS versus MF	Yes	[143]
Pollen and spikelet sterility	MS versus MS	Yes	[144]
Dry matter in early growth stages and yield	MS versus MF	Yes	[145–146]
Maize			
Stability and phenotypic expression of growth	MS versus MF	No	[147]
Stem breakage/lodging and grain yield	MS versus MF	Yes	[148–149]
Hybrid heterosis	MS versus MF	Yes	[150–151]
Grain moisture content and stem breakage at harvest	MS versus MS	No	[152–153]
Grain yield	MS versus MF	Yes	[154]
Plant height, tassel length, branches/tassel, and yield	MS versus MS	Yes	[155]
Grain yield, ears per plant, grains per ear, tassel length, and tassel branches	MS versus MF	No	[156]
Yield and morphological traits	MS versus MF	No	[157–158]
Pearl millet			
Grain yield, and leaf and peduncle lengths	MS versus MS	Yes	[159]
Grain yield, and leaf and peduncle lengths, and commercial hybrid production	MS versus MS	No	[160–161]
Grain yield	MS versus MS	Yes	[162–165]
Dry matter production	MS versus MS and MS versus MF	No	[162–165]
Plant height, days to flowering, dry matter yield, and grain yield	MS versus MF	Yes	[166]
Stability of male-sterility	MS versus MS	Yes	[167]
Earliness, panicle weight, length and girth, number of tillers, and grain yield	MS versus MS	Yes	[168]

¹MS = male-sterile cytoplasm.²MF = male-fertile cytoplasm.

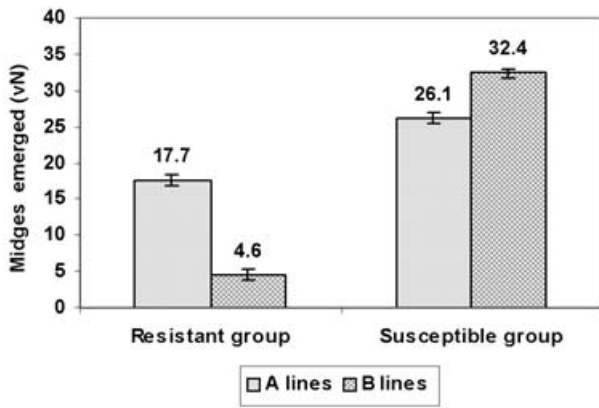


Figure 1 Effect of CMS on midge, *Stenodiplosis sorghicola* adult emergence in resistant and susceptible groups of CMS (A) and maintainer (B) lines of sorghum [198]

was no effect of different CMS systems on expression of resistance to downy mildew [188]. The A_1 cytoplasm confers moderate susceptibility to smut (*Tolyposporium penicillariae* Brefeld), downy mildew, and leaf blight (*Xanthomonas* spp.) in A_1 -based pearl millet hybrids [189]. In the case of *T. penicillariae*, pollination affects disease development [190], and susceptibility to smut may be attributed to cytoplasmic×nuclear interaction effects [191]. High ergot (*Claviceps fusiformis* Loveless) susceptibility in pearl millet hybrids has been associated with the A_1 cytoplasm, but highly resistant hybrids have been obtained from the crosses of highly resistant A- and R-lines [192]. The A-lines are more susceptible to smut than the B- and R-lines. Thakur et al. [193] noted that open-pollinated varieties are less susceptible to ergot than the F_1 hybrids. Pearl millet hybrids based on A_1 cytoplasm are also more susceptible to smut than the open-pollinated varieties [194]. The A-line-based hybrids had higher smut severity than the hybrids based on B-lines, indicating that CMS rather than the A_1 cytoplasm *per se* resulted in greater smut severity in A-line hybrids. However, the hybrids based on smut-resistant A- and R-lines were as resistant as the hybrids based on B-lines. The A_2 , A_3 , and A_4 cytoplasm are not linked to downy mildew susceptibility, and can be exploited commercially for hybrid production [195]. Hybrids based on A_2 , A_3 and *Violaceum* CMS systems have better downy mildew, ergot and smut resistance, and can be exploited commercially for hybrid production [161].

Effects of CMS on Expression of Resistance to Insect Pests

Most of the sorghum hybrids grown in India are based on the A_1 cytoplasm, which is highly susceptible to insect pests [196, 197]. Ross and Kofoed [105] reported that the Kansas lines KS 34 to KS 39 based on Kansas CMS system are as susceptible as CKA (Combine Kafir-based CMS

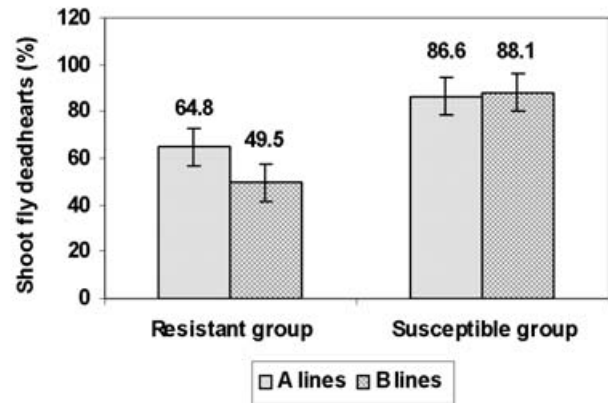


Figure 2 Effect of CMS on expression of resistance to shoot fly, *Atherigona soccata* in resistant and susceptible groups of CMS (A) and maintainer (B) lines of sorghum [203]

lines) to the greenbug, *Schizaphis graminum* (Rondani). Sharma et al. [198] recorded low damage by the sorghum midge, *Contarinia sorghicola* (Coquillett), and reduced midge emergence on midge-resistant B-lines as compared with corresponding A-lines (Figure 1). However, there were no differences in midge damage or adult emergence between midge-resistant and -susceptible A-lines. Midge-resistant CMS×susceptible restorer-based hybrids are less susceptible to *C. sorghicola* damage than susceptible CMS×susceptible restorer-based hybrids [199–201].

The expression of non-preference and antibiosis components of resistance to southwestern corn borer, *Diatraea grandiosella* Dyar and sugarcane borer, *Diatraea saccharalis* Fab. was better in resistant inbred lines based hybrids CML 67×CML 135 and CML 139×CML 135 than the inbreds [202]. These hybrids also suffered low leaf and stalk damage, and grain yield loss (3–4%) in comparison with the susceptible hybrid Ki 3×CML 131 (35–40%). The oviposition and deadheart formation on main plants and tillers by the sorghum shoot fly, *Atherigona soccata* (Rondani), are significantly lower on maintainer lines compared with the CMS lines [203] (Figure 2). Larval development was prolonged and pupal mortality was greater on maintainer lines than on the CMS lines, whereas pupal weights and fecundity were greater on the CMS lines [203]. The maintainer lines showed better recovery resistance than the CMS lines, but such differences were more apparent in the shoot fly-resistant CMS and maintainer lines as compared to shoot fly-susceptible CMS and maintainer lines. Expression of morphological traits such as leaf glossiness, trichomes, and leaf surface wetness (which are associated with resistance to shoot fly) was better in the maintainer lines as compared to the CMS lines [204]. The shoot bug (*Peregrinus maidis* Ashmead)- and sugarcane aphid [*Melanaphis sacchari* (Zehntner)]-resistant CMS lines suffered more damage than the B-lines, whereas such

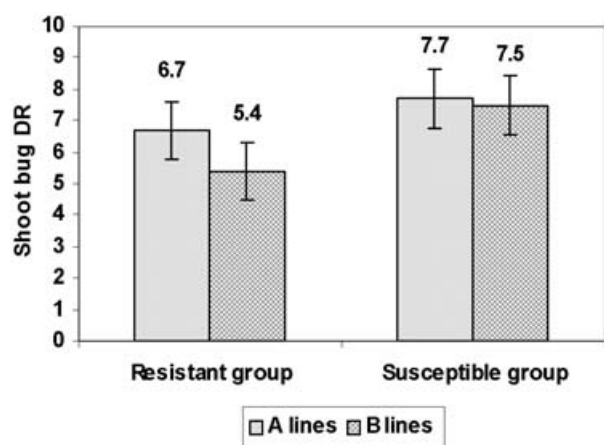


Figure 3 Effect of CMS on shoot bug, *Peregrinus maidis* damage in resistant and susceptible groups of CMS (A) and maintainer (B) lines of sorghum. DR= damage rating (1–9) [205]

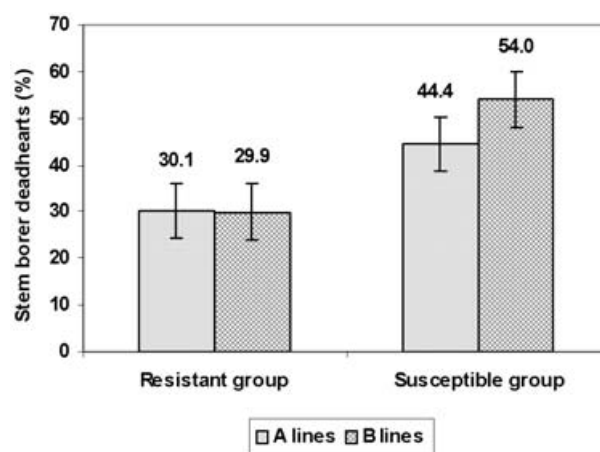


Figure 5 Effect of CMS on expression of resistance to spotted stem borer, *Chilo partellus* in resistant and susceptible groups of CMS (A) and maintainer (B) lines of sorghum [205]

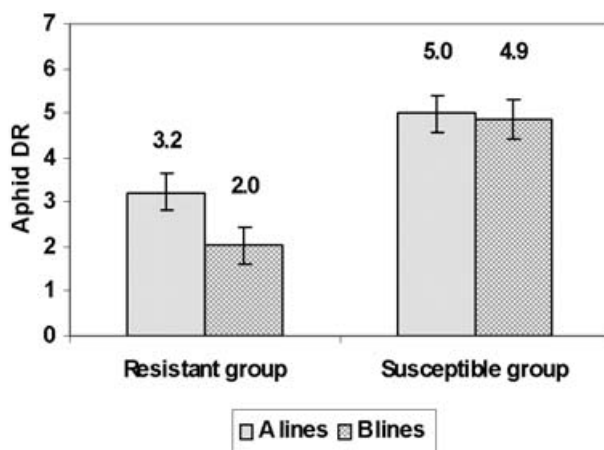


Figure 4 Effect of CMS on sugarcane aphid, *Melanaphis sacchari* damage in resistant and susceptible groups of CMS (A) and maintainer (B) lines of sorghum. DR= damage rating (1–9) [205]

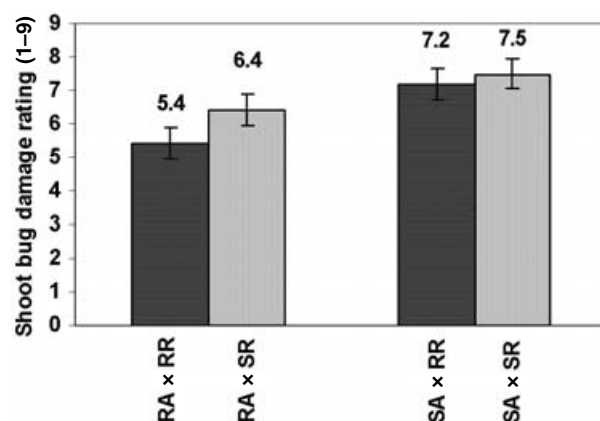


Figure 6 Influence of CMS on expression of resistance to shoot bug, *P. maidis* in sorghum hybrids based on insect-resistant or -susceptible CMS and restorer lines. RA= resistant CMS (A) lines; SA= susceptible CMS (A) lines; RR= resistant restorer lines; SR= susceptible restorer lines [197, 201, 205]

differences were not apparent in the case of susceptible CMS and the maintainers [205] (Figures 3 and 4). The A-lines, in general, suffered greater damage than the corresponding B-lines (except in the case of stem borer), suggesting that factors in the cytoplasm of the maintainer line influence the expression of resistance to insects. The stem borer, *Chilo partellus* (Swinhoe)-resistant CMS and maintainer lines had a similar level of deadheart formation, while the stem borer-susceptible maintainers suffered more damage than the CMS lines (Figure 5) [205]. Expression of resistance may also be influenced by the interaction of factors in the cytoplasm of maintainer lines with the nuclear genes. Hybrids based on shoot bug (Figure 6), sugarcane aphid (Figure 7), sorghum midge (Figure 8), and shoot fly (Figure 9)-resistant CMS and restorer lines suffer less damage than the hybrids based

on susceptible CMS and resistant or susceptible restorer lines, suggesting that the expression of resistance to these insects is influenced by the genetic background of the CMS lines [197, 201, 206, 207]. However, the hybrids based on stem borer-resistant or susceptible CMS lines with resistant restorers showed significantly lower deadheart formation as compared with the hybrids based on stem borer-resistant or -susceptible CMS lines and -susceptible restorers (Figure 10), suggesting that restorer lines exercised a greater influence on expression of resistance to stem borer in sorghum [205]. Similar results have also been reported for expression of resistance to stem borers, *C. partellus* and *Busseola fusca* (Fuller) in maize [208]. The A₄M cytoplasm has been found to be comparatively resistant to *A. soccata* damage than the A₁, A₂, A₃ or A₄G, A₄VzM cytoplasm [28, 109].

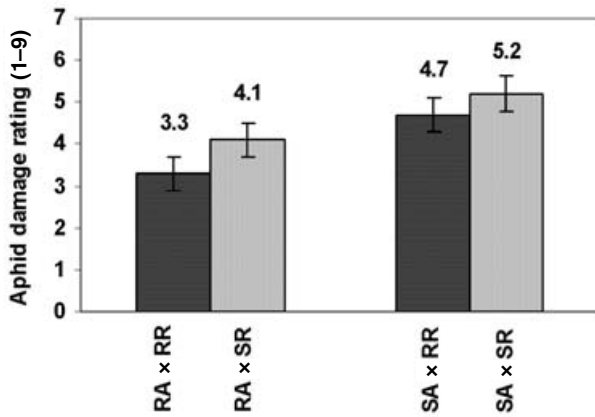


Figure 7 Influence of CMS on expression of resistance to sugarcane aphid, *M. sacchari* in sorghum hybrids based on insect-resistant or -susceptible CMS and restorer lines. RA=resistant CMS (A) lines; SA=Susceptible CMS (A) lines; RR=resistant restorer lines; SR=susceptible restorer lines [197, 201, 205]

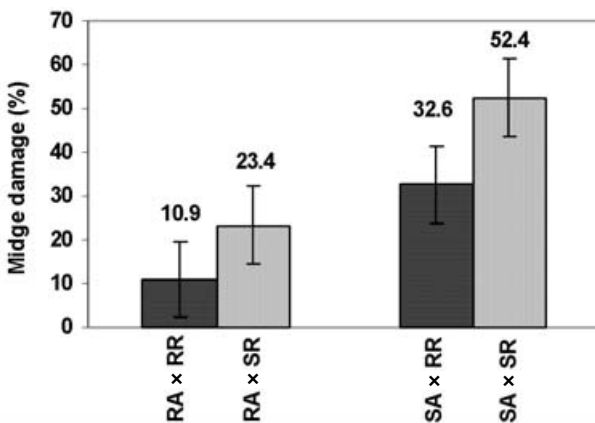


Figure 8 Influence of CMS on expression of resistance to midge, *S. sorghicola* in sorghum hybrids based on insect-resistant or -susceptible CMS and restorer lines. RA=resistant CMS (A) lines; SA=susceptible CMS (A) lines; RR=resistant restorer lines; SR=susceptible restorer lines [197, 201, 205]

The A₄M (*Maldandi*) cytoplasm in combination with shoot fly-resistant restorers can be used to produce sorghum hybrids with high levels of resistance to this pest [28].

Conclusions

Considerable information has been generated on effects of CMS on morphological and physiological characteristics in different crop plants, and on the influence of CMS on expression of resistance to insect pests and plant pathogens. There is a continuing need to evaluate different cytoplasmic systems for their effects on cultivar susceptibility to pest insects and diseases. The analyses of literature

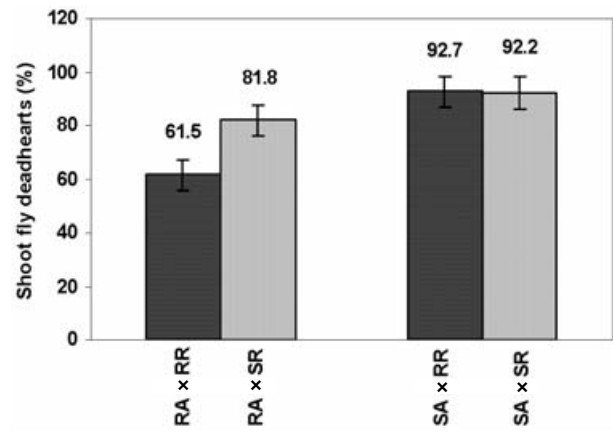


Figure 9 Influence of CMS on expression of resistance to shoot fly, *A. soccata* in sorghum hybrids based on insect-resistant or -susceptible CMS and restorer lines. RA=resistant CMS (A) lines; SA=susceptible CMS (A) lines; RR=resistant restorer lines; SR=susceptible restorer lines [197, 201, 205, 207]

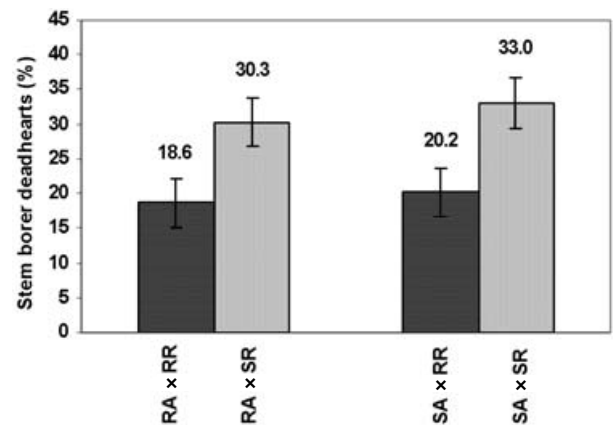


Figure 10 Influence of CMS on expression of resistance to spotted stem borer, *C. partellus* in sorghum hybrids based on insect-resistant or -susceptible CMS and restorer lines. RA=resistant CMS (A) lines; SA=susceptible CMS (A) lines; RR=resistant restorer lines; SR=susceptible restorer lines [205]

available on different CMS systems in cereals suggested that the genetic background of CMS, cytoplasmic factors, the interactions of the factors in the cytoplasm of maintainer lines with the nuclear genes, and the restoration abilities of the restorers influence the expression of resistance to insect pests and diseases. Therefore, it will be desirable to use more than one source of CMS in different genetic backgrounds as a safeguard against outbreaks of major pest insects and diseases in different crops. There is an urgent need to convert various sources of resistance to insect pests and diseases into CMS, maintainer, and restorer lines, so as to be able to develop hybrids with increased levels and diverse mechanisms of resistance to the target pests.

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