ISSN: 2287-688X

Annals of
Plant Sciences

Volume 11, Issue 01 (2022) pp. 4561-4570

Review Article

Male Sterility in Vegetable Crop: A Mini Review

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Abstract

Male sterility is a cost-effective and efficient method of facilitating the development of hybrid seeds in a variety of vegetable crops. The development of new genomic tools, molecular markers, and sequencing technology has aided in the mapping and introduction of new male sterility in various vegetable backgrounds. For the development of cytoplasmic male sterility (CMS) and genic male sterility (GMS), male sterility is produced by interactions between mitochondrial genes and nuclear genes, or by nuclear genes alone. CMS and GMS facilitate hybrid seed production in several vegetable crops. In CMS, layers of interaction between mitochondrial and nuclear genes control its male specificity, occurrence and restoration of fertility. Environment-sensitive GMS (EGMS) mutants are controlled by non-coding RNAs and can revert to fertility under different growth conditions, making them useful breeding materials in the hybrid seed industry. Despite the fact that a great deal of study has been done, we still know very little about the biochemical and molecular basis of male sterility system inheritance in many vegetable crops. The genetical, biochemical, and molecular underpinnings of male sterility expression in several vegetable crops, as well as generic models of male sterility and fertility restoration, have been described, and the evolutionary importance of these reproductive systems examined.

Keywords: *Male sterility, Genetic and molecular basis, vegetable crops, GMS, CMS and CGMS.*

Introduction

Male sterility occurs when a plant fails to produce viable anther or pollen or male gametes. The use of hybrid varieties of different crop in agriculture has resulted in a massive improvement in food productivity due to enhanced uniformity and hybrid vigour. Koelreuter, discovered anther abortion within species and particular hybrids, was the first to document male sterility in 1763. Male sterility has always piqued the interest of academics in a variety of applied strategic and basic sciences domains. Plant breeders are particularly interested in developing more efficient and cost-effective hybrid seeds, developmental geneticists/molecular biologists are interested in studying the differential/spatial expression of male sterility genes and the interaction between the nuclear and cytoplasmic genome, and evolutionary biologists are interested in studying the end symbiotic hypothesis, which focuses on tracing the transmission mechanism of mitochondrial genes into the nuclear genome during evolution process.

Classification of Male Sterility

(Kaul. 1988) classified male sterility in two major groups, *viz.* genetic (spontaneous or induced) and non-genetic (induced) male sterility. On phenotypic basis, genetic male sterility has been classified in three classes *i.e.* sporogenous, structural and functional. Similarly non-genetic male sterility has been classified as chemical, physiological and ecological male sterility. Further on genotypic basis, genetic male sterility is grouped as

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DOI: http://dx.doi.org/10.21746/aps.2022.11.01.5

genic, cytoplasmic and gene cytoplasmic male sterility.

Phenotypic Male Sterility
Pollen Sterility
Only the lack or high paucity of functional pollen grains distinguishes male sterile from normal ones (the most common and the only one that has played a major role in plant breeding).

Structural or Staminal Male Sterility
Male flowers or stamens are malformed and non-functional or completely absent.

Functional Male Sterility
Pollen that is perfectly good and viable is stuck in an indehiscent anther and hence unable to function.

Genetic Basis of Male Sterility in Vegetable Crop
On the genetic basis, male sterility is classified in following tree groups

1) Genetic male sterility (GMS)
2) Cytoplasmic male sterility (CMS)
3) Cytoplasmic genetic male sterility (CGMS)

Genetic Male Sterility (GMS)
Male sterility is predominantly controlled by a single recessive gene, (ms), however dominant genes, such as cauliflower, are also known to influence male sterility. Male sterility alleles can appear naturally or be produced purposefully. By crossing heterozygous male fertile plants with male sterile plants, a male sterile line can be maintained. Male sterile and male fertile plants are produced in a 1:1 ratio after such a mating.

Utilization of GMS in Crop Improvement
Genetic male sterility may be used in hybrid seed production. The progeny from *msms* x *Msms* crosses are used as female and are interplanted with a homozygous male fertile (*MsMs*) pollinator. The genotypes of the *ms ms* and *Ms ms* lines are identical except for the *ms* locus *i.e.,* they are isogenic and are known as male sterile (A) and maintainer (B) lines, respectively. The female line would therefore contain both male sterile and male fertile plants; the later fertile plant must be identified and removed before pollen shedding. Pollen dispersal from the male (pollinator) line should be good for a satisfactory seed set in the female line.

Status of Genetic Male Sterility (GMS) in Vegetable Crops
Tomato
There have been reports of over 55 male sterile (ms) alleles that cause sporogenous, structural, and functional sterility (Kaul. 1988). Some genes have known chromosomal locations. Flowers without stamens were produced by two stamenless mutants; stamenless-1 (sl-1) and stamenless-2 (sl-2), when cultivated at a higher temperature, but flowers with aberrant stamens and often viable pollen were produced by those maintained at a lower temperature. The insertion or deletion of a single nucleotide mutation in the poly galacturonase gene, which causes ps-2, causes recessive hereditary male sterility. The ps-2 mutation causes an alternate splicing of the pre-mRNA during maturation, resulting in an abnormal mRNA**..** The expression of male sterility was governed by various environmental factors such as temperature, photoperiod and moisture (Kaul. 1988; Greyson. 1994; Sawhney. 1997), and it has been suggested that the effects of these external agents are regulated through hormonal changes imbalance involving high ABA, and that low temperature (Singh. *et al.*, 1992). In tomato stamenless-2 (*sl-2*) is an excellent example for hormonal-environmental interaction and an effective way to utilized in hybrid seed production. Generally low temperature and gibberellic acid (GA_3) gives rise normal viable pollen instead formation of carpel in place of stamen due to occurrence of megasporogenesis instead of microsporogenesis due to treatment of high temperature and indole acetic acid (IAA) (Sawhney. 1983, 1997). (Singh. *et al.*, 1998) reported that Abscisic acid (ABA) is an effective- hormones for inducing male sterility in several vegetable crops such as tomato, brinjal and other solanaceous crops. Further extensive research has been carried to determine the impact of hormonal biosynthesis and concentration for inducing male sterility in tomato and reported that *sl-2*

in tomato can be induced by IAA and fertility can be restore by application of GA_3 (Singh. *et al*., 1998).

Table1: Genes responsible for male sterility in vegetables

Crops	Gene number/condition	Gene	Variety developed
Tomato	Single recessive gene	*ps*-2	Shalimar Tomato Hybrid-1 Shalimar Tomato Hybrid-1
Chilli	Single recessive gene	ms-12 & ms-3	CH-1, CH-3
Muskmelon	Single recessive gene	Ms-1	Punjab Hybrid-1

Chilli

The induced male sterile allele in France (mc-509) was later renamed ms-10. The ms-10 line was introduced in India at Punjab Agriculture University and recessive male sterile allele (*msms*) was introgressed into three chilli genotypes *viz*., MS12, MS13 and MS41. The male sterile line (MS-12) was developed by transferring sterility gene *ms-10* from capsicum (imported from France) into the cultivar Punjab Lal through back crossing (Singh and Kaur. 1986). By using this male sterile line (MS-12), PAU has released three chilli hybrids *viz*. CH-1 (MS-12 × LLS), CH-3 (MS- 12 × 2025) (Dhall. 2011) and CH-27 (MS-12 x S-343). A GMS line ACMS2 having monogenic recessive gene (acms2acms2) is reported (Patel. *et al*., 1998). The ms-3 line introduced from Hungary is maintained at AVRDC, Taiwan (Berke. 1999).

Okra

The Division of Vegetable Crops, IIHR, identified the Genic Male Sterile (GMS) line MS-1, which is being utilised to develop commercial F1 hybrids. Male sterility in okra has been produced by gamma radiation, which was not observed in the wild species (Dutta. 1971). When present in the homozygous (ms1ms1) condition, a pair of single recessive genes governs male sterility in okra, and these genes can be used to produce hybrid seed.

Muskmelon

Five male sterile genes (*ms-1*, *ms-2*, *ms-3*, *ms4*, and *ms-5*) have been identified in melon and all of them are recessive and nonallelic. In India, male-sterile gene *ms-1* was introduced in 1978 and used to release two commercial cultivars viz; Punjab Hybrid (Nandpuri. *et al*., 1982) and Punjab Anmol (Lal. *et al*., 2007). Due to the instability of this *ms-1* gene in sub-tropical field conditions, the seed production of these hybrids has posed numerous problems consistently (Dhatt and Gill. 2000).

Table 2: Status of Genetic male sterility in different cucurbitaceous crops

Crops	Male sterile genes	Inheritance	References
Muskmelon	*ms-1*	Single recessive gene	(Bohn and Whitaker. 1949)
Muskmelon	*ms-2*	Single recessive gene	(Bohn and Principe. 1962)
Muskmelon	*ms-3*	Single recessive gene	(Mc Creight and Elmstrom. 1984)
Muskmelon	*ms-4*	Single recessive gene	(Pilrat. 1990)
Muskmelon	*ms-5*	Single recessive gene	(Lecouviour. *et al*., 1990)
Winter squash	*ms-1*	Single recessive gene	
Summer squash	*ms-2*	Single recessive gene	
Winter squash	*ms-1*	Single recessive gene	
Cucumber	*ms-2*	Single recessive gene	

Table 3: Morphological markers for male sterility identification in vegetables

Morphological markers	Vegetables
Potato leaf, green stem	Tomato
Glabrous seedling	Muskmelon
Non-lobed leaf, glabrous leaf	Water melon

Glossy foliage	Brussels sprout
Purple stem pigmentation	Cabbage
Brown seed coat colour	Onion
Bright green hypocotyls	Broccoli

Environmental Sensitive Genic Male Sterility (EGMS)

This is a hereditary male sterility system in which the expression of sterility is influenced by environmental circumstances. A specific range or concentration of environmental component at a critical time of the crop during panicle development causes total male sterility in this genic male sterility. The following are the categories of environmental sensitive genic male sterility such as Photoperiod sensitive genic male sterility (PGMS), Thermosensitive genic male sterility (TGMS) and Photo-thermo sensitive genic male sterility (PTGMS).

Table 4: Environmental sensitive genetic male sterility in vegetable crops

Vegetable	Mutant	Reference
Cabbage	TGMS, PGMS	(Rundfeldt. 1961)
Brussels sprout	TGMS	(Nieuwhof. 1968)
Broccoli	TGMS	(Dickson. 1970)
Pepper	TGMS	(Diskalov. 1972) and (shirfriss. 1977)
Carrot	TGMS	(Kaul 1988)
Tomato	TGMS	(Rick. 1948) and (sawhney. 1983)

Limitation of GMS

Due to a more tedious maintenance process and non-availability of suitable marker genes among vegetable crops, GMS has been utilized commercially only in chilli and muskmelon. More over a number of crops (e.g. tomato, brinjal and pea etc.) which are highly self-pollinated, free out crossing is prohibitive thus leading to poor seed and/or fruit set. This method could gain popularity in practice only if suitable insect pollinators or other means are found to raise the percentage of cross pollination.

Cytoplasmic Male Sterility (CMS)

This type of male sterility is determined by cytoplasm. Cytoplasmic male sterility can be transferred easily to a given strain by using that strain as a pollinator (recurrent parent) in the successive generations of the backcross programme. After six to seven backcrosses, the nuclear genotype of the male sterile line would be almost identical to that of the recurrent pollinator strain.

Utilization of CMS

Cytoplasmic male sterility can be maintained by crossing a male sterile line (A line) with the pollinator strain (maintainer line or B line) used as the recurrent parent in the backcross programme since the nuclear genotype of the pollinator is identical to that of the new male sterile line. Cytoplasmic male sterility can be utilized for producing hybrid seeds in those vegetables where the vegetative part is of economic value (e.g. onion, carrot, radish and cole crops etc.). But in those vegetables crops where seed is the economical part like tomato, chilli, melon etc., it is of no use because the hybrid progeny will be male sterile.

Limitations of CMS

Cytoplasmic male sterility (CMS) is sensitive to environmental factors e.g. a line may be completely male sterile in one environment and may have partial fertility in another. This phenomenon may lead to mixture of selfed seed in an otherwise hybrid seed. Certain diseases or disorders are associated with a particular type of cytoplasm which leads to genetic vulnerability e.g. T-cytoplasm is associated with southern corn leaf blight in corn. Continuous incorporation of a small amount of male parent cytoplasm through each backcross during maintenance may lead to a partial or complete breakdown of male sterility.

Status of Cytoplasmic Male Sterility (CMS) in Vegetable Crops

Onion

First ms plant was reported in the progenies of cultivar Italian Red (Jones and Emsweller. 1936). It was due to 2 recessive genes *ms1*and *ms2*. Two types of sterile cytoplasm, *viz.*, S and T are reported among which S-cytoplasm is exploited most widely (Pelletier. *et al*., 1995). Arka Kirtiman (IIHR. Bangalore), Arka Lalima (IIHR. Bangalore), Hybrid-63 (IARI. New Delhi) and Hybrid-35 (IARI. New Delhi) are hybrids developed in onion through use of male sterility.

Radish

Japanese scientist (Ogura. 1968) has discovered CMS in a Japanese radish cultivar, and the first alloplasm was transferred into the *Brassica oleraceae* genome by repeated backcrosses with broccoli (Bannerot. *et al*., 1974). IARI regional station Katrain in India used cytoplasmic male sterility to generate two cabbage hybrids, H-64 and KCH-4.

Anand Cytoplasm

The Anand cytoplasm derives from the wild species *B. tournefortii*. It was transferred from *B. rapa* to *B. oleraceae* through cybridization process. The presence of Anand chloroplasts with a *B. oleracea* nucleus did not result in cold temperature chlorosis as seen in ogura CMS plants (Cardi and Earle. 1997).

Cytoplasmic Genetic Male Sterility (CGMS)

It is caused by an interaction between genetic factor (s) present in cytoplasm and the nucleus. Absence of a sterility inducing factor either in the cytoplasm or in the nucleus makes a line male fertile. The cytoplasmic genetic male sterility system involves male sterility CMS (A) line, maintainer (B) line and restorer (R) line respectively. A-line and B-line are exactly same genetically but they differ only in respect of cytoplasm content. The cytoplasm of A-line causes sterility, while that of B-line is normal. The R-line has a dominant form of the fertility restorer gene. Regardless of whether the R-line is sterile or fertile, it will always be fertile in cytoplasm. In intervarietal reciprocal crosses and interspecific crosses, the CMS source can be established.

Utilization of CGMS in Crop Improvement

A triple cross may be produced by crossing single cross with a fertility restoring inbred so that all the plants in the triple cross would be male fertile. In this case, the sterility is transmitted only through the female and all progeny will be sterile. This is not a problem for crops such as onions or carrots where the commodity harvested from the F_1 generation is produced during vegetative growth.

Limitation of CGMS

Although the CGMS system is the most widely used male sterility system, it is limited to a few species due to limitations such as the lack of CGMS in many crops and wild relatives, the need for a fertility restorer allele in fruit-producing vegetables, the undesirable pleiotropic effect of sterile cytoplasm on horticultural qualities, the breakdown of male sterility in specific environments, and the highly unstable sterile cytoplasm in certain species.

Cytoplasmic Genetic Male Sterility (CGMS) in Vegetable Crops

Chilli

The World Vegetable Centre, Taiwan identified two CGMS lines (A lines) in chilli *i.e.* CCA-4759 and CCA-4757 which were found to be reliably sterile under conditions of night temperatures less than 15 degree Centigrade (Liu and Gniffke. 2004). CGMS lines (CCA4261) of chilli introduced at the IIVR from AVRDC are utilized to produce hybrid- Kashi Surkh (CCH-2). Three CGMS based hybrids i.e. Arka Meghna (MSH-172), Arka Harita (MSH-149) and Arka Sweta (MSH-96) have been developed at IIHR, Bangalore.

Carrot

Brown anther type

The brown anther (*ba*) male sterility was first discovered in the cultivar Tender Sweet and reported by Welch and Grimbal in 1947. Brown anther type male sterility is due to the interaction of "*sa* cytoplasm" with at least two independent recessive nuclear genes.

Petaloid Male Sterility

Petaloid sterility is commercially used for hybrid seed production in the world. According to (Morelock. 1974) the pt type of male sterility is due to interaction between "*Sp* cytoplasm" and two independent dominant genes (*M1* and *M2*). In India, at IARI, petaloid CGMS was transferred to nantes type and crossed with the indigenous variety "Pusa yamdagini to develop hybrid Pusa Nayanjyoti in 2009.

Chemically Induced Male Sterility

Chemical hybridizing agent (CHA) is the chemicals that induce male sterility in plants. The most important general feature revealed from the literatures is that the earlier developed compounds (e.g. FW-450, ethephon, RH-531 and PPX 3778) can induce a range of specific effects that are dependent upon treatment time and dosage interaction.

Table no 5: Potential gametocide used for induction male sterility in vegetable crops

Gametocides	Concentration	Vegetable crops
GA_3	2000-3000 ppm	Onion, lettuce
M.H	0.4-0.5%	Chilli, muskmelon
	2400-2600 ppm	carrot
	100-500 ppm	Tomato
	400-500 ppm	Okra
FW -450 (Mendok)	0.2-0.4%	Tomato
	0.4%	okra
	0.2%	Brinjal
	0.3%	Muskmelon
Phosphon –D	750-1000 ppm	Onion
2-4D	50 ppm	Tomato
	20 ppm	Brinjal
TIBA	50-100ppm	Watermelon,
		Tomato
GA3	1000ppm	Capsicum
Ethrel		Brinjal.

Biochemical Basis of Male Sterility

Expression of male sterility trait is associated with a large number of morphological, physiological, histological, cytological, biochemical and molecular changes in male reproductive tissues at various stages of micro-sporogenesis and micro-gametogenesis. Male sterility is accompanied by qualitative and quantitative changes in amino acids, proteins and enzymes in developing anthers. The Amino acids such as proline, leucine, isoleucine, and phenylalanine is reduced but valine, glycine, arginine and aspartic acid is increased. In radish mature male sterile anthers contain one-eighth amount of proline in comparison to the fertile anthers (Kakihara. *et al.*, 1988). Soluble proteins amount in male sterile anthers contains lower proteins and fewer polypeptide bonds. Decreased activity of esterase in male sterile plants has been observed in tomato (Bhadula and Sawhney. 1987) and radish (Zhou and Zhang. 1994).The Enzyme activity of amylases is decreased and it corresponds with high starch content and reduced levels of soluble sugars. Accumulation of adenine due to the decrease of adenine phosphoribosyl transferase (APRT) activity may be toxic to the development of microspores.

Role of PGSs

Endogenous plant growth substances (PGSs) play very important role in stamen and pollen development. Male sterility has been reported to be associated with changes in a number of PGSs, rather than any specific substance. Reduced level of cytokinins and increased level of abscisic acid associated with rape seed (*Brassica napus*) of GMS and CMS plants, indicates that both kind of male sterility system probably involve some common pathways. The exogenous supply of reduced substances in several male sterile lines has been found to restore fertility tomato (Sawhney. 1997).

Molecular Basis of Male Sterility

Marker assisted selection (MAS) is a method of selecting a genetic determinant or determinants of a trait of interest (such as productivity, disease resistance, abiotic stress tolerance, and/or quality) by using a marker (morphological, biochemical, or based on DNA/RNA variation). In plant and animal breeding, this method is utilised. Pollen development is a very complicated process involving many genes. If a certain gene expression in pollen development is inhibited artificially, male sterility may be caused. As an inherent sequence-specific RNA degradation mechanism, post-transcriptional gene silencing can silence target genes in plants. Antisense RNA and RNA interference (RNAi) can both specifically reduce or silence the expression of target genes and thus produce individual plant losing the gene function.

Example 1

Anti-gene CYP86MF encoding cytochrome P450 associated with the nuclear male sterility into Chinese cabbage-*pak-choi* and broccoli, obtaining transgenic male sterile plants whose hypogenetic stamina or ungerminated pollen was observed. The transgenic male sterile plants could set seeds if artificially pollinated with normal pollen (Yu. *et al*., 2004).

Example 2

antisense RNA and RNAi with male sterility related gene BcMF3 and BcMF4 from Chinese cabbage-pakchoi to inhibit the expression of related genes of flowering Chinese cabbage, resulting in poor development of some pollen and low germination rate in vitro (Liu. *et al*., 2006).

Other Approaches

Other approaches of creating male sterility through genetic transformation include fusing the specific promoter with a toxinic gene of chemical-inducible expression by simulating chemical hybridizing to transform plants, obtaining male sterile lines through double transgenic lines hybridization, and transpose on mutation. But these approaches are rarely applied in vegetable crops.

Table 6: Characterization of CMS and Fertility restoration (Rf) genes in different vegetable crops

Crops	CMS type	Associated ORF	Rf locus	References
Brassica (*B. napus*)	*CMS-Ogu (S)*	*orf138-atp8*	Rfo (P)	(Brown. *et al*., 2003), (Uyttewaal. *et al*., 2010)
	CMS-Pol (S)	*orf224-atp6*	Rfp (R	(Menassa. *et al*., 1999)
Brassica (*B. juncea*)	*CMS-Hau (S)*	*atp6-orf288 (T)*	UK	Jing. *et al*., 2012)
	CMS-orf220	*orf220 (T)*	UK	(Yang. *et al*., 2010)
Brassica (*B. tournefortii*)	*CMS-Tour (S)*	*atp6-orf263*	UK	(Landgren. *et al*., 1996)
Radish	*CMS-Kos (S)*	*orf125-atp8*	Rfk1 (P)	(Iwabuchi. *et al*., 2012)
Common bean	*CMS-Sprite (S)*	*atp1- orf98-orf239 (T)*	Fr (G), Fr2 (P)	(Abad. *et al*., 1995); (He. *et al*., 1996).
Pepper	*CMS-Peterson*	*cox2-orf456 (T), cox2-orf507*	U. K	(Gulyas. *et al*., 2010)
Carrot	*CMS-Petaloid*	*orfB*	U. K	(Nakajima. *et al*., 2001)

Conclusion

Inspite of the detailed studies and understanding about the male sterility systems, still the phenomenon is not being widely used for hybrid seed production in many vegetable crops. The main reason for such under exploitation of this mechanism is non-availability of stable male sterile lines, whereas in case of genetic male sterility seed multiplication of male sterile lines remains a problem. The use of biotechnology, molecular markers and transgenic can provide an aid for overcoming such obstacles. Development of practically feasible molecular markers may provide appropriate cost-effective selection strategy to discard 50% male fertile sister plants at seedling stage, which may open the way to exploit monogenic recessive male sterile lines in several vegetables. Identification of functional male sterile and EGMS lines also have great potential for being utilized in commercial hybrid seed production due to presence of functional pollen grains unlike genetic male sterility in which pollen grains are non-functional.

Acknowledgement
The author is grateful to our colleagues, senior, junior, and scientists from the Division of Vegetable Science, IARI New Delhi, for their assistance in planning and executing this review, as well as for giving all recent articles, books, and newsletters throughout the composition of this publication.

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Source of support: Nil; **Conflict of interest:** Nil.

Cite this article as:

Singh, S and Singh, A. " Male Sterility in Vegetable Crop: A Mini Review." *Annals of Plant Sciences*.11.1 (2022): pp. 4561-4570.

DOI: http://dx.doi.org/10.21746/aps.2022.11.1.5