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Genetic basis of the phenomenon of male sterility and fertility restoration in maize (*Zea mays* L.) – a review

Genetyczne podstawy zjawiska męskiej sterylności i przywracania płodności u kukurydzy (*Zea mays* L.) – praca przeglądowa

Summary. The phenomenon of male sterility in higher plants is, apart from protandry (earlier maturation of stamens), protogyny (earlier maturation of pistils), heterostyly (different stigmas) and self-incompatibility, one of the evolutionarily conditioned mechanisms forcing external pollination. Due to the elimination of the time- and cost-consuming emasculation of maternal lines, male-sterile lines are an object of interest in the seed production of hybrid cultivars of many plant species, including maize. Seed production of hybrid cultivars using male-sterile lines requires the establishment of maternal lines that are male-sterile in different environments and suitable paternal lines with fertility restorer genes. This paper summarizes the findings on the genetics of male sterility and fertility restoration in maize.

Key words: fertility restoration, maize (*Zea mays* L.), male sterility

THE PHENOMENON OF MALE STERILITY IN PLANTS

Sterility, understood as the inability to produce offspring, can have many causes and manifest itself in various ways. The most important symptoms of infertility include: lack, underdevelopment or damage to reproductive cells, developmental defects of the pistil and ovule, as well as disturbances in the growth and penetration of the pollen tube into the embryo sac. Infertility may be the result of many factors affecting the sporophyte or gametophyte at different stages of development [Winiarczyk 1999]. Among the most

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important of them, Kaul [1988] includes the genetic background and the influence of the environment (plant nutrition, temperature). In higher plants, we distinguish female sterility – manifested by the inability to set seeds after pollination, and male sterility – manifested by the inability to produce/release viable pollen or male gametes [Winiarczyk 1999]. Promoting of cross-pollination improves vigor, heterozygosity and genetic diversity of offspring [Hawliczek-Strulak et al. 2011]. The feature that distinguishes all male-sterile plants from their fertile analogues is the high level of cytokinins with a simultaneous reduced level of auxins [Musgrave et al. 1986]. Inherent male sterility in higher plants is usually treated as a developmental disorder that can have many causes. It can be the result of unfavorable growing conditions, a consequence of diseases or the result of mutations. Male-sterile plants usually maintain fully normal female functions. Types of male sterility can be divided into two main groups: genetically conditioned and non-genetically conditioned (induced, for example, by chemical factors).

In 1988 Kaul proposed the following, genetically conditioned male sterility classification:

1. phenotypic (morphological):

– structural – male flower organs are underdeveloped or not developed at all;

– sporogenous – disorders of microsporogenesis or gametogenesis; sterile individuals produce little or no functional pollen;

– functional – the release of pollen is disturbed, functional pollen is trapped in the anthers;

2. genotypic:

– genic (GMS) – controlled by nuclear genes, no influence of the cytoplasm;

– cytoplasmic (CMS) – induced by sterile cytoplasm, the influence of nuclear genes is insignificant;

– cytoplasmic-genic (CGMS) – result of the cooperation of nuclear genes (*Rf*) and the cytoplasm.

The phenomenon of male sterility includes many processes leading to disturbances in microsporogenesis, which results in the formation of non-functional microspores or pollen grains. Due to its utility in the breeding process, breeders are trying to obtain systems of seed production based on the phenomenon of male sterility in various plant species. So far, this system has been successfully implemented in many species of crops, including tobacco, rapeseed, rice, sorghum, cucumber, carrot, onion, sugar beet, and sunflower [Pelletrier and Budar 2007]. Such a system may be based on the identification of sterile cytoplasm spontaneously occurring in a given species or on the introduction of cytoplasm of another species or wild form. There are several examples of spontaneous identification of sterility-inducing cytoplasm, e.g.: *pol* cytoplasm in rapeseed (identified in Polima cultivar), S cytoplasm of onion, sterility-inducing cytoplasm of bean. An example of the creation of a CMS system based on the introduction of male sterility from genetically distinct forms is the study of the CMS system in triticale based on the cytoplasm of *Triticum timopheevi* or the rye sterilizing cytoplasm of Pampa [Labudda et al. 2011]. Plants with sterility-inducing cytoplasm and fertility restoring genes do not differ phenotypically from plants with normal cytoplasm until these genes are lost through mutation or segregation. This was the case with the appearance of sterility-inducing cytoplasm in the mutagenized sunflower. For many species, sterility-inducing cytoplasms (e.g. *PET1* cytoplasm in sunflower and '*ogu*' cytoplasm in rapeseed) have been identified by distant crosses [Schnable and Wise 1998]. One of the best-known examples of cytoplasmic-genic male sterility in plants is

the system used in the seed production of hybrid maize cultivars, based on the interaction of nuclear genes with the sterility-inducing cytoplasm. In the literature, on the phenomenon of male sterility in maize, the abbreviations CMS and CGMS are sometimes used interchangeably.

THE GENETIC BASIS OF THE PHENOMENON OF MALE STERILITY

Cytoplasmic male sterility (CMS) has been described in many species of flowering plants. As defined by Touzet and Budar [2004], *CMS is a maternally transmitted inability to achieve balance between the mitochondrial and nuclear genomes*. This is a specific result of a conflict between two genomes with different models of inheritance. The phenomenon of cytoplasmic male sterility is related to mitochondrial genes encoding toxic proteins. In male-sterile plants of some species, a unique, transcriptionally active type of genes has been identified – the so-called chimeric genes. They are recombinant products composed of fragments of sequences coding or flanking core mitochondrial genes and unidentified *orf* sequences. This type of genes was identified in petunia (*S-pcf* gene), rapeseed (*orf224*, *orf138* genes), sunflower (*orfH522*) and maize. Chimeric genes are responsible for the formation of proteins that disrupt the pollen production process. Typically, these proteins are encoded by a chimeric mitochondrial gene composed of rearranged mitochondrial DNA and contain a hydrophobic membrane-interacting domain [Bosacchi et al. 2015]. Chimeric genes responsible for male sterility may disrupt the functioning of mitochondrial membranes, affecting ATP synthesis. Cell death can be triggered when mitochondrial function and ATP levels are insufficient for the development of tapetum tissue, and by the production of reactive oxygen species (ROS). In male-sterile plants, the development of tapetum, a structure that plays a key role in pollen development, is disturbed [Storchova 2017]. Pollen abortion has been linked to tapetum programmed cell death initiated by ROS production in the cms Honglian rice line and in male sterile cotton [Huang et al. 2012]. The sources of male sterility are very well characterized in maize. They can be divided into groups/cytotypes according to their response to specific fertility restoring genes, cms-C, cms-S and cms-T groups. A separate mitochondrial genome representing each of the CMS cytotypes was sequenced [Allen et al., 2007], linking male sterility to the *urf13*-T gene in cms-T [Dewey et al. 1987], *atp6*-C in cms-C [Dewey et al. 1991] and with the co-transformed *orf355/orf77* in cms-S [Zabala et al. 1997]. Xiao et al. [2020] identified a transcription factor, ZmDREB1.7, that is highly expressed in sterile microspores and activates the expression of mitochondrial cms-S gene orf355. In maize mitochondrial DNA, there are sequences that were probably involved in the recombination of the mitochondrial genome. These recombinations resulted in the creation of a region containing two reading frames: *urf13* and *orf221*, responsible for cms-T type. The *urf13* chimeric gene contains fragments of the 3' flanking and coding sequence of the 26S rRNA gene, ATPase subunit 6 and a sequence of unknown origin. T-*urf13*, a mitochondrial gene with unique chimeric sequences, is present only in T-cytoplasmic mitochondria. The 13 kDa mitochondrial polypeptide (URF13) encoded by the T-*urf13* gene has been shown to confer sensitivity to the T-toxin produced by *Bipolaris (Helminthosporium) maydis race T* [Dewey et al. 1987], a fungal pathogen, that causes the Southern Corn Leaf Blight (SCLB). Dangerous to cultivars with cytoplasm T, the race *Bipolaris maydis race T* was first identified in a winter nursery of maize in the Philippines in 1961, and appeared for the first time in maize

crops in the USA in 1969 [Burns 2017]. The interactions of URF13 with mitochondria and toxins produced by *Bipolaris maydis race T* have been extensively studied. The URF13 polypeptide is associated with the inner mitochondrial membrane. The oligomers bind to the toxins of fungal pathogens, leading to the formation of hydrophilic pores [Rhoads et al. 1995]. URF13 has three membranes spanning alpha helices, and the oligomers conform in the presence of fungal toxins, allowing the inner mitochondrial membrane to become permeable rapidly [Kempken and Pring 1999]. Further studies also showed the susceptibility of T-cytoplasmic plants to the cause of gray leaf spot, *Mycosphaerella zea-maydis*. In the presence of the *Rf1* gene that restores fertility to the T cytoplasm, the amount of URF13 polypeptide decreases significantly [Dewey et al. 1987]. When only the *Rf2* gene is present, the amount of URF13 polypeptide does not decrease. Research by Liu et al. [2001] showed that the *Rf2* gene encodes the production of aldehyde dehydrogenase (ALDH), a protein needed for anther development. Male sterility of the sporophytic type occurs in the T and C cytoplasm – as a result of the collapse of the tapetum cells, the release of pollen is prevented or disturbed. In this type of sterility, the genotype of the plant (sporophyte) plays a decisive role in the production of normal, viable pollen. Cytoplasm S is characterized by a gametophytic type of sterility – the produced pollen is non-viable. In this case, it is the pollen genotype that determines the production of viable or non-viable pollen [Hanson and Bentolia 2004]. Therefore, if an S-cytoplasmic plant is heterozygous for *Rf3rf3*, the pollen it produces is half viable and half aborted [Xiao et al. 2020]. The stability of male sterility is of highest importance from the point of view of the practical application of the CMS system in the seed production of hybrid cultivars. In the C and S cytoplasms, there are cases of spontaneous restoration of male fertility. Currently, in the seed production of maize hybrid cultivars, based on the CMS system, mainly the C cytoplasm is used. It provides the possibility of efficient production of seeds of hybrid cultivars, however, its implementation in seed production has been difficult due to the incomplete understanding of the process of fertility restoration in cms-C, which underlines the importance elucidation of the mechanism underlying the spontaneous restoration of fertility in this cytoplasm [Jaqueth et al. 2020]. A genomic shift is responsible for the spontaneous restoration of fertility, which, through recombination, can rapidly reduce the copy number of the DNA molecule carrying the mutation related to male sterility, leaving the rest of the mitochondrial genome essentially unchanged. In this way, the CMS mutation is silenced and the plant shows male fertility. The frequency of spontaneous fertility restoration in the majority of CMS systems studied is influenced by the nuclear genetic background. Therefore, a breeder wishing to create a seed production system using the CMS trait must test the stability of this system in the widest possible range of germplasm used in the breeding program [Mackenzie 2012].

GENETIC BASIS OF FERTILITY RESTORATION

In parallel with the discovery of sterile cytoplasms, fertility restoring genes (*Rf*) have been identified, enabling the restoration of the lost harmony between the nuclear and mitochondrial genomes [Bohra et al. 2016]. Due to the wide use of male sterile lines in the breeding of hybrid cultivars, the fertility of the F_1 generation is of high importance. Restoring pollen fertility in plants with sterility-inducing cytoplasm (restoration) is possible with the appropriate cooperation of the mitochondrial genome and nuclear genes. This

process occurs with the participation of dominant restoring genes (*Rf* – restorer of fertility genes), it may be the result of suppression or compensation of the sterile mitochondrial genome. Most of the *Rf* genes cloned so far (e.g. the *Rf1* gene in sorghum) encode proteins belonging to the PPR (pentatricopeptide repeat) family, the RFL (restorer of fertility-like) subfamily [Storchova 2017]. PPR genes form one of the largest gene families among land plant genomes. It is believed that in most cases PPR proteins are imported into mitochondria or plastids [Gaborieau et al. 2016]. Most are believed to function as sequence-specific RNA-binding proteins that modulate mitochondrial and chloroplast gene expression through post-transcriptional processes including editing, splicing and nuclease cleavage [Qin et al. 2014]. These proteins, as RNA binding factors, often play a significant role in post-transcriptional regulation during embryogenesis and plant development. The PPR proteins involved in restoring fertility target the mitochondria and reduce the effect of chimeric mitochondrial *orf* sequences. The action of these proteins can be considered as the response of the nuclear genome to the discrepancy in optimizing the reproductive success of the mitochondrial and nuclear genomes [Piątkowski 2016]. Several non-PPR family *Rf* genes have also been cloned, all of which encode proteins that interact with mitochondria, e.g. the *Rf2* (maize) gene encoding aldehyde dehydrogenase, as well as the *Rf17* (rice) and *bvORF20* (sugar beet) genes [Kotchoni et al. 2010, Jaqueth et al. 2020]. The *Rf2* gene encodes the RF2A/ALDH2B2 protein that binds proteins interfering with pollen development in male sterile plants [Jimenez-Lopez et al. 2010]. An important aspect is also the availability of *Rf* genes in the gene pool. For example, the *Rf1* gene involved in restoring fertility in T-cytoplasm maize is very rare in maize lines, while the other restorer for T-cytoplasm, the *Rf2* gene, is common [Schnable and Wise 1998]. Fertility restoration is a complex process, often conditioned by the presence of several cooperating *Rf* genes, and also largely dependent on environmental conditions. For different types of maize sterility-inducing cytoplasm with distinct mtDNA types, different *Rf* genes are required to restore fertility (tab. 1). The complexity of the fertility restoration process is related to the rare occurrence of *Rf* genes in the gene pool, as well as the cooperation of many complementary genes, which, in the absence of the main *Rf* gene, only partially restore fertility

Table 1. Nuclear restorer genes for different types of cms in maize

Cytoplasm type restored	Restorer gene	Mode of action	Chromosome	References
cms-T	Rf1	I	3	Schnable and Wise 1994
	Rf2		9	Duvick 1968
	Rf8	III	2	Meyer 2010
cms-S	Rf3	II	2	Levings 1993
	Rf9			
cms-C	Rf4	I	8	Duvick 1965, Levings 1993, Gabay-Laughnan et al. 2004, Sofi et al. 2007
	Rf5			
	Rf6			

I – cooperation of restorer genes; II – one main restorer gene required to restor male fertility; III – partial restoration of fertility

[Kohls et al. 2011]. In the case of the C cytoplasm, partial restoration of fertility is common, as well as the phenomenon of "late brake of sterility" [Kheyr-Pour 1981]. The phenomenon of partial restoration of fertility is caused by QTLs identified on chromosomes 3, 4, 5, 6 and 8 [Kohls et al. 2011]. An additional problem is also the presence of inhibitory genes that abolish the effect of restoring genes. For the *Rf5* gene (C-cytoplasm restorer), a gene that inhibits *Rf*-I has been identified [Hu et al. 2006].

Due to the genetic complexity of the restoration phenomenon, the reaction of an inbred line to the type of cytoplasm does not give a clear answer to the question of which genes are responsible for it in a given line. An example of this is research on the genetic background responsible for restoring fertility in the A619 line. This line is considered an example of a strong fertility restorer for cytoplasm C [Zheng et al. 2020]. In the case of this line, there are many scientific reports on the presence of various genes that restore fertility in the C cytoplasm. In 1991, Sisco, studying the A619 line, mapped the *Rf4* gene on chromosome 8 and its duplicate on chromosome 3 [Sisco 1991]. Some reports suggest that only the *Rf4* gene, located on chromosome 8, is responsible for restoring fertility in the A619 line [Tang et al. 2001, Yongming et al. 2016]. There are also reports of the presence of a restoring gene other than *Rf4* in the A619 lineage on chromosome 7 [Huang et al. 2012]. In 2016, research conducted by Yongming and his team led to the identification of a new gene in the A619 line that restores fertility in the C cytoplasm, *Rf*-A619*. The latest reports on the genetic basis of the A619 restoration [Zheng et al. 2020] suggest the presence of the QTL, qRf8-1, on the long arm of chromosome 8, whose cooperation with the *Rf4* gene is responsible for restoring fertility in the C cytoplasm. In 2019, Mou and his team identified in two inbred lines: Z16 and 7250-14-1, two restoring genes for cytoplasm C, on the short arm of chromosome 8 [Mou et al. 2019]. Research conducted by Luo et al. [2001] showed that genes restoring fertility in the C or S cytoplasm are more common in sweet corn (*Zea mays* var. *saccharata* Kórn) and waxy corn (*Zea mays* var. *ceratina* Kul.). However, the use of these types of maize as sources of restoring genes may be difficult due to changes in grain quality characteristics obtained by crossing common maize with sweet or waxy maize [Luo et al. 2001].

IMPORTANCE OF MALE STERILITY AND FERTILITY RESTORATION IN BREEDING

The phenomenon of heterosis plays a key role in many plant breeding programs. F_1 offspring obtained by crossing between two (usually inbred) lines show better yields, higher resistance to diseases and adverse environmental effects. The phenomenon of intensification of positive features in the F_1 generation is referred to as the vigor of hybrids. In order to produce the F_1 generation, pollen from the paternal line must be used to fertilize the maternal line. To avoid self-pollination of the maternal line, it is necessary to prevent it from producing pollen by removing the male flower (emasculation), or by interfering with the development of these structures. In the case of maize, emasculation can be done manually or mechanically. However, these procedures may result in reduced F_1 seed yield due to plant damage [Hunter et al. 1972, Wise et al. 1999]. In research conducted by Czepak and his team [2019], it was proved that the removal of leaves, which often takes place during mechanical emasculation of maize plants, negatively affects the number of kernels in a row in the cob and the weight of a thousand kernels. Due to the key importance of hybrid cultivars for biological progress in modern crop breeding, the possibility of eliminating the mechanical emasculation of maternal lines, which is offered by the use of

the CMS system, made this system a very useful breeding tool. Male-sterile lines are used as components of hybrid cultivars. The inability to produce functional pollen eliminates the need for manual or mechanical castration, and is a guarantee that the seeds obtained as a result of crossing do not come from self-pollination. The first successful example of using the CMS phenomenon in hybrid breeding was the onion cultivar Calred (California Hybrid Red no. 1) grown in 1947 at the University of California, based on the source of sterility identified in the cultivar Italian Red 13-53 by Jones and Emsweller in 1937 [Duvick 1959, Yen 1959]. Currently, seed production of F_1 cultivars based on the CMS system is carried out in the case of onions, beets (sugar, edible and fodder), sunflower, rape, sorghum, rice, rye, tobacco [Duvick 1959, Budar and Pelletier 2001, Stojałowski and Łapiński 2001]. Intensive research and breeding work is also carried out on the use of male cytoplasmic-gene sterility based on the cytoplasm of *Triticum timopheevi* in the breeding of wheat and triticale hybrid cultivars [Góral et al. 2009]. Research on the practical use of the CMS system, based on Pampa sterile cytoplasm, in the seed production of hybrid cultivars of winter rye has been conducted for many years at various research institutions [Miedaner et al. 2000, Kolasińska 2014]. The first attempts to use the phenomenon of male sterility in maize breeding were carried out independently, but with the same result, by two breeders – D.F. Richey and H.A. Walace. In their work to eliminate manual castration of plants, they relied on the sterile cytoplasm discovered by Rhodes. They assumed that all breeding lines after crossing with a source of sterility will give sterile progeny, so in the F_1 cultivar, it will be necessary to admix seeds with normal cytoplasm, giving fertile plants as a source of pollen. In their studies, they did not take into account the genetic interaction of inbred lines with the source of cytoplasm. Due to the varying stability of male sterility, after initial enthusiasm for the use of this phenomenon in maize breeding, work was abandoned for a few years, and the source of sterile cytoplasm discovered by Rhodes was irretrievably lost. The results of this work have also not been published in detail anywhere [Duvick 1959]. Subsequent attempts at breeding work on the use of the CMS phenomenon in maize breeding were related to the discovery of a new source of sterility by Rogers and Edwardson in 1944. The discovery of sources of male sterility in maize made it possible to improve and reduce the costs associated with seed production of hybrid cultivars, and also enabled more effective use of the potential of heterosis [Su et al. 2017]. Currently, cytoplasm C is a main source of male-sterility used in seed production of commercially important hybrid maize varieties in many European countries; however, detailed data on the reproduction area of varieties using cms-C are lacking [Kohls 2010]. In the case of sweet maize, the use of CMS system in seed production is limited by the relatively short life (three to five years) of a specific hybrid [Harvey 2004]. One example of the use of cytoplasmic-genic male sterility in maize seed production is the "Plus-hybrid system". Studies conducted by Weingartner et al. [2004] on the effects of male sterility and the xenia effect on the yield and grain quality of maize hybrids, as well as studies by Stamp and his team [2000], which showed a positive effect of cytoplasm T on the yield of hybrids, led to the concept called the "Plus-hybrid system". The Plus-hybrid system refers to the commercial production of two hybrids in a mixture, one of which is male-sterile and the other acts as a fertile pollinator. A potential Plus-hybrid mix consists of 75–80% sterile hybrid and 20–25% fertile hybrid [Jovanović et al. 2018]. The best Plus-hybrid combinations achieved significantly higher grain yields than their component parts, without any reduction in grain quality parameters [Bozinović et al. 2010].

CONCLUDING REMARKS

Years of research conducted by many authors have brought us closer to understanding the genetic basis of the phenomenon of male sterility and fertility restoration, and allowed us to identify the positive and negative aspects related to the use of the CMS system in seed production. Identification of *Rf* genes is only one of the components of the CMS system. It is also important to identify and verify potential complementary genes as well as inhibitory genes in relation to *Rf* genes and to determine the stability of fertility restoration depending on environmental conditions. Determining the interaction of inbred lines with sterility-inducing cytoplasms is one of the most important elements of the implication of the CMS system for seed production. Only lines with a stable interaction, resulting in complete restoration of fertility or maintaining of sterility, can be successfully used as paternal or maternal components.

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