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The response of maize lines to the Paraguay type of CMS

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Abstract. The development of cytosterile maize hybrids in Russia is a necessary condition for their wide implementation into production. To develop such hybrids, it's greatly relevant to be aware how the lines react to sterile cytoplasm. The study was carried out at the Agricultural Research Center "Donskoy" (ARC "Donskoy") in 2010–2021. **The purpose** of the current study was to classify the new self-pollinated maize lines according to the composition of the fertility-restoring genes of the Paraguay (C) type of CMS, to optimize the number of analyzing test-crosses. **Methods.** As initial material there have been used 45 new self-pollinated maize lines and 8 sources of sterility with different genetic structure. The method of complete top-crosses there have been identified 360 maize hybrids, used for estimation of the new lines' reaction. **Results.** According to the study results, the sterility-fixing lines KV 204, SP 286, DS 255, SP 207, DS 180, which had no fertility-restoring genes in the dominant state, belonged to the I class. As the natural complete constant fertility-restorers there has been recommended to use the lines of the VIII class KV 498, KV 272, KV 7/07, SP 357, RD 261, DS 295, SP 210, SP 197, DS 177, DS 188, having all three dominant genes Rf4, Rf5, Rf6 in the genotype. The incomplete sterility-fixing lines included the lines of the II–IV classes (KV 3, RD 245, SP 198, etc.). The incomplete fertility-restoring lines were the lines of the V–VII classes (KV 469, RD 331, KV 276, etc.). There has been found out that the most common lines were the lines of the V (24.4 %) and VIII (22.3 %) classes. **The scientific novelty** of the study was an optimal number and genetic structure of the analyzers WF 9c of the V class, Lc of the VI class and W 401c of the VII class, which are necessary for crossings and allow identifying lines according to the fertility-restoring genes.
Keywords: self-pollinated lines, test-crossing hybrids, fertility-restoring genes, dominance, recessivity.

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Introduction

Cytosterile maize hybrids should be created in Russia for introduction into production [1, p. 21]. Despite the fact that foreign breeding and seed companies grow seeds of corn hybrids on a fertile basis, they are intensively conducting research on CMS [2, p. 134; 3, p. 111]. In particular, the study of the stability of the manifestation of sterility in various types of CMS [4, p. 77; 5, p. 4322], the possibility of using a mixture of fertile and sterile plants in corn crops [6, p. 2718], the study of the genetic control of CMS in various crops [7, p. 967]. Researchers note the importance of studying CMS in corn, due to the fact that not varieties, but hybrids are used in production [8, p. 15].There was studied the effect of CMS on economically valuable traits in corn [9, p. 415; 10, p. 431] and sorghum [11, p. 55; 12, p. 21]. The use of various types of CMS helps to overcome the difficulties that arise when creating sterile analogues and reductants. Recently, the Paraguayan (C) type of CMS has been of particular interest to breeders and seed growers [13, p. 47; 14, p. 94]. A prerequisite for reliable restoration of fertility in the Paraguayan type of CMS is the presence in the genotype of three complementary genes-restorers that are in the dominant state (Rf4, Rf5, Rf6) [15, p. 22]. The efficiency of converting hybrids to a sterile basis depends on knowledge of how the lines react to sterile cytoplasm, so studies aimed at obtaining such information are relevant [16, p. 129; 17, p. 114; 18, p. 194; 19, p. 40]. Given the complexity of genetic control of the Paraguayan CMS type, the sources of sterility (analyzers) and the number of test crosses required to identify lines are of particular interest. The purpose of the research: to classify new self-pollinated maize lines according to the composition of alleles of genes-restorers of fertility of the Paraguayan type of CMS, to optimize the number of analyzing crosses.

Methods

Field experiments were laid in 2010–2021 at the Scientific Center "Donskoy" located in the southern zone, the climate of the zone is temperate continental. The average annual rainfall during the growing season

of corn is 200.5 mm, HTC is 0.7. Due to unstable moisture, the climate is characterized by aridity. The years of the research were contrasting in terms of moisture availability. The driest years were 2014, 2016, 2018, and 2019 with precipitation during the growing season of corn from 93.4 mm to 158.4 mm, which ranged from 46.6 to 79.0 % of the average annual norm. The years 2015, 2017, 2020 and 2021 turned out to be less arid and more favorable for the growth and development of plants with the amount of precipitation during the growing season of corn 224.1–244.6 mm (112–122 % of the average long-term norm). In the remaining years of the experiment, the amount of precipitation slightly differed from the average long-term norm. The soil of the experimental plot is ordinary black soil, 120 cm thick, humus content 3.5–4.4 % [20, p. 90].

The object of research was 45 new constant self-pollinated maize lines: KV 204, SP 286, DS 255, SP 207, DS 180, KV 3, KV 87, RD 257, DS291, SP 209, DS 176, RD 245, SP 194, DS 197, SP 198, DS 173, KV 469, KV 655, SP 275, RD 274, DS 273, SP 203, SP 195, DS 179, DS 185, DS 194, DS 199, RD 331, SP 206, DS 184, KV 276, SP 231, DS 297, SP 180, DS 192, KV 498, KV 272, KV 7/07, SP 357, RD 261, DS 295, SP 210, SP 197, DS 177, DS 188. Different sets of lines were studied in different years. 9 lines were studied in 2010–2012, 4 lines in 2012–2014, 5 lines in 2014–2015, 5 lines in 2015–2016, 10 lines in 2017–2019. The largest group of lines (12 pcs.) was studied in 2019–2021. Eight sterile sources (analyzers) of different genetic structure were taken for crossing with lines: Gb 834c, R 811c, 149c, Kr 21c, WF 9c, Lc, W 401c, V 158c. In source W 834 c, all three fertility restorer genes are present in a recessive state (rf4, rf5, rf6). One restorer gene is in the dominant state in three sources: R 811 c (Rf6), 149 c (Rf5), Kr 21 c (Rf4), the rest of the genes are recessive. One restorer gene in a recessive state is found in three other sources: WF 9 c (rf4), Lc (rf5) и W 401c (rf6), the rest are dominant. In the V 158 c source, all three fertility restorer genes of the Paraguayan CMS type are present in the dominant state (Rf4, Rf5, Rf6). Taking into account that the complete stable restoration of fertility in the sterile cytoplasm of the Paraguayan type occurs in the presence of all three genes in the dominant state, the source of V 158 c is completely fertile, despite the sterile cytoplasm.

In total for 2010–2021 by the method of topcross crossings [21, p. 5] obtained 360 corn hybrids. The level of fertility and sterility was assessed using the Gontarovskiy scale [22, p. 27].

Results

Test-cross hybrids that were obtained in 2018 from crossing 12 new early-ripening lines with sources of sterility of the Paraguayan type of CMS were evaluated in 2019–2021 by the flowering of panicles. Self-pollinated lines showed themselves differently in test crosses (Table 1).

Sterile offspring are designated as “s”, fertile – “f”. The plus sign indicates the presence in the genotype in the dominant state of the restorer gene, the minus sign indicates the absence of the gene in the dominant state.

In crosses with sources of sterility Gb 834 c, all lines had sterile offspring, with the exception of lines DS 177 and DS 138, which differ in fertile offspring. In the analyzed crosses with the source of sterility R 811c, the lines DS 192, DS 177, and DS 188 had fertile offspring, and the rest of the lines were characterized by sterile offspring. In crossing with the source of sterility 149 c, the fertility of the lines DS 184, DS 177, and DS 188 was restored. The fixation of sterility was noted in the crossing of the source Kr 21s with the lines DS 180, DS 176, DS 197, DS 173, DS 184, DS 192, and

Table 1

The flowering nature of test-cross maize hybrids and genotypic classes of fertility restoration, 2019–2021*

Line	Sources of sterility								Genotype	Class
	Gb834c	R811c	149c	Kr21c	WF9c	Lc	W401c	V158c		
	I	II	III	IV	V	VI	VII	VIII		
	– – –	– – +	– + –	+ – –	– + +	+ – +	+ + –	+ + +		
DS 180	s	s	s	s	s	s	s	f	– – –	I
DS 176	s	s	s	s	s	s	f	f	– – +	II
DS 197	s	s	s	s	s	f	s	f	– + –	III
DS 173	s	s	s	s	f	s	s	f	+ – –	IV
DS 179	s	s	s	f	s	f	f	f	– + +	V
DS 185	s	s	s	f	s	f	f	f	– + +	V
DS 194	s	s	s	f	s	f	f	f	– + +	V
DS 199	s	s	s	f	s	f	f	f	– + +	V
DS 184	s	s	f	s	f	s	f	f	+ – +	VI
DS 192	s	f	s	s	f	f	s	f	+ + –	VII
DS 177	f	f	f	f	f	f	f	f	+ + +	VIII
DS 188	f	f	f	f	f	f	f	f	+ + +	VIII

**s – sterile, f – fertile, “–” – presence of a recessive allele, “+” – presence of a dominant allele.*

the restoration - with the lines DS 197, DS 185, DS 194, DS 199, DS 177 and DS 188 Hybrids created with the participation of the source of sterility WF 9c and lines DS 173, DS 184, DS 192, DS 177 and DS 188 had full fertility, and the offspring from crossing the remaining lines with the same source were sterile. In crossing with the Lc source, only the lines DS 180, DS 176, DS 173, and DS 184 fixed sterility, the rest restored fertility. When using the W 401c as an analyzer, the fixation of sterility occurred in the offspring with the participation of the lines DS 180, DS 197, DS 173, DS 192, restoration of fertility was noted in the offspring obtained with the participation of the remaining lines.

Comparing the nature of flowering of all test-cross hybrids of the studied lines, the composition of the alleles of genes-reducing agents in all used sterile sources, the belonging of maize lines to the genotypic class was established. In the self-pollinated line DS 180, all genes that restore fertility of the Paraguayan CMS type are in a recessive state (class I). According to one gene - restoring fertility in the dominant state, three lines contain different genes: line DS 176 – gene Rf 6 (class II), line DS 197 – gene Rf 5 (class III), line DS 173 – gene Rf 4 (class IV). Six new lines have two dominant restorer genes: the Rf 5 and Rf 6 genes (class V) in the lines DS 179, DS 185, DS 194, and DS 199; Rf 4 and Rf 6 genes (class VI) in the DS 184 line, Rf4 and Rf5 genes (class VII) in the DS 192 line, Rf5, Rf6 (class VIII).

In 2017–2019, 10 new self-pollinated corn lines were evaluated by the nature of flowering of test-cross hybrids obtained from crossing with sterile sources (Table 2).

Among them, all test crosses of the SP 207 line (class I) were characterized by complete sterility, and all test crosses of the lines SP 210 and SP 197 (class VII) were characterized by fertility. The remaining lines had a different pattern of flowering depending on the source of crossing and belonged to intermediate classes (II–VII).

In 2015–2016, similar studies were carried out on 5 self-pollinated corn lines. Line DS 255 had sterile offspring in any crosses, and line DS 295 had fertile offspring. The new self-pollinated lines DS 290, DS 273, and DS 297 were characterized by different responses to flowering, depending on the source of crossing (Table 3).

Table 2

The flowering nature of test-cross maize hybrids and genotypic classes of fertility restoration, 2017–2019*

Self-pollinated line	Analyzers								Genotype	Class
	I	II	III	IV	V	VI	VII	VIII		
	Gb 834c	R 811c	149c	Kr 21c	WF 9c	Lc	W 401c	V 158c		
	– – –	– – +	– + –	+ – –	– + +	+ – +	+ + –	+ + +		
SP 207	s	s	s	s	s	s	s	f	– – –	I
SP 209	s	s	s	s	s	s	f	f	– – +	II
SP 194	s	s	s	s	s	f	s	f	– + –	III
SP 198	s	s	s	s	f	s	s	f	+ – –	IV
SP 203	s	s	s	f	s	f	f	f	– + +	V
SP 195	s	s	s	f	s	f	f	f	– + +	V
SP 206	s	s	f	s	f	s	f	f	+ – +	VI
SP 180	s	f	s	s	f	f	s	f	+ + –	VII
SP 210	f	f	f	f	f	f	f	f	+ + +	VIII
SP 197	f	f	f	f	f	f	f	f	+ + +	VIII

s – sterile, f – fertile, "–" – presence of a recessive allele, "+" – presence of a dominant allele.

Table 3

The flowering nature of test-cross maize hybrids and genotypic classes of fertility restoration, 2014–2016*

Self-pollinated line	Analyzers							Genotype	Class
	I	II	III	IV	V	VI	VII		
	Gb 834c	R811c	149c	Kr 21c	WF 9c	Lc	W401c		
	– – –	– – +	– + –	+ – –	– + +	+ – +	+ + –		
DS 255	s	s	s	s	s	s	s	– – –	I
DS 291	s	s	s	s	s	s	f	– – +	II
DS 273	s	s	s	f	s	f	f	– + +	V
DS 297	s	f	s	s	f	f	f	+ + –	VII
DS 295	f	f	f	f	f	f	f	+ + +	VIII

s – sterile, f – fertile, "–" – presence of a recessive allele, "+" – presence of a dominant allele.

Table 4

The flowering nature of test-cross maize hybrids and genotypic classes of fertility restoration, 2014–2015*

Self-pollinated line	Analyzers							Genotype	Class
	Gb 834c	R 811c	149c	Kr 21c	WF 9c	Lc	W 401c		
	– – –	– – +	– + –	+ – –	– + +	+ – +	+ + –		
RD 257	s	s	s	s	s	s	f	– – +	II
RD 245	s	s	s	s	s	f	s, pf	– + –	III
RD 274	s	s	s	f	s	f	f	– + +	V
RD 231	s	s	f	s	f	s, pf	f	+ – +	VI
RD 261	f	f	f	f	f	f	f	+ + +	VIII

*s – sterile, f – fertile, pf – partially fertile, "–" – presence of a recessive allele, "+" – presence of a dominant allele.

Table 5

The flowering nature of test-cross maize hybrids and genotypic classes of fertility restoration, 2012–2014*

Self-pollinated line	Analyzers							Genotype	Class
	Gb 834c	R 811c	149c	Kr 21c	WF 9c	Lc	W 401c		
	– – –	– – +	– + –	+ – –	– + +	+ – +	+ + –		
SP 286	s	s	s	s	s	s	s	– – –	I
SP 275	s	s	s	f	s	f	f	– + +	V
SP 331	s	f	s, pf	s	pf, f	f	f	+ + –	VII
SP 375	f	f	f	f	f	f	f	+ + +	VIII

*s – sterile, f – fertile, pf – partially fertile, "–" – presence of a recessive allele, "+" – presence of a dominant allele.

Table 6

Systematization of maize lines according to the state of alleles of the fertility-restoring genes, 2010–2021

Line	Genotype	Class
KV 204, SP 286, DS 255, SP 207, DS 180	$rf_4rf_4\ rf_5rf_5\ rf_6rf_6$	I
KV 3, KV 87, RD 257, DS 291, SP 209, DS 176	$rf_4rf_4\ rf_5rf_5\ Rf_6RF_6$	II
RD 245, SP 194, DS 197	$rf_4rf_4\ Rf_5Rf_5\ rf_6rf_6$	III
SP 198, DS 173	$Rf_4Rf_4\ rf_5rf_5\ rf_6rf_6$	IV
KV 469, KV 655, SP 275, RD 274, DS 273, SP 203, SP 195, DS 179, DS 185, DS 194, DS 199	$rf_4rf_4\ Rf_5Rf_5\ Rf_6RF_6$	V
RD 331, SP 206, DS 184	$Rf_4Rf_4\ rf_5rf_5\ Rf_6RF_6$	VI
KV 276, SP 231, DS 297, SP 180, DS 192	$Rf_4Rf_4\ Rf_5Rf_5\ rf_6rf_6$	VII
KV 498, KV 272, KV 7/07, SP 357, RD 261, DS 295, SP 210, SP 197, DS 177, DS 188	$Rf_4Rf_4\ Rf_5Rf_5\ Rf_6RF_6$	VIII

Comparing the results of the assessment of the fertility of these lines, they are assigned to classes II, V and VII.

In 2014–2015, the response to CMS of the Paraguayan type was evaluated in 5 other self-pollinated maize lines. Not a single line has been identified that has sterile offspring from crossing with all sterile sources. Line RD 261 had fertile offspring in crosses with all sources of sterility. The remaining lines (RD 257, RD 245, RD 274, 231) were characterized by a different reaction – from complete sterility to complete fertility. Based on the results obtained, they are assigned to classes II, V and VI. The semi-fertile hybrid combination obtained from crossing the line RD 231 and the source of sterility Lc had a small number of sterile plants, which is apparently due to the incomplete constancy of this line (Table 4).

In 2012–2014, another set of new lines was evaluated according to the nature of the flowering of panicles of hybrids obtained with the participation of these lines and sterile sources. In all crossing combinations, line SP 286 had sterile offspring, line SP 375 had fertile ones, and the new self-pollinated lines SP 275 and SP 331 differed in the diversity of flowering of test cross progeny from complete sterility to complete fertility, depending on the sources of crossing (Table 5).

These lines are assigned to classes V and VII. Hybrid combinations 149 c × SP 331 and WF9c × SP 331 differed in heterogeneity in plant flowering. In the first combination, along with sterile plants, incompletely sterile ones were present (class 3). Presumably, the insufficiently complete constancy of this line was the result of splitting according to the level of fertility and the completeness of sterility.

Table 7

Identification of genotypic classes of fertility restoration based on the optimal number of analyzing test-crosses, 2019–2021*

Line	Analyzers			Genotype	Class
	V	VI	VII		
	WF 9c	Lc	W 401c		
	– + +	+ – +	+ + –		
DS 180	s	s	s	– – –	I
DS 176	s	s	f	– – +	II
DS 197	s	f	s	– + –	III
DS 173	f	s	s	+ – –	IV
DS 179	s	f	f	– + +	V
DS 184	f	s	f	+ –+	VI
DS 192	f	f	s	+ + –	VII
DS 177	f	f	f	+ + +	VIII

**s – sterile, f – fertile, "–" – presence of a recessive allele, "+" – presence of a dominant allele.*

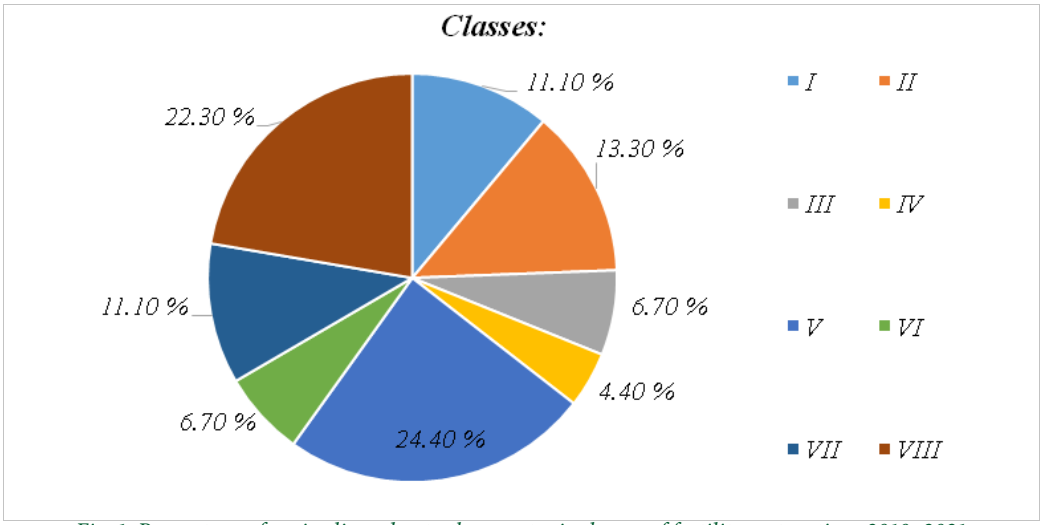

Fig. 1. Percentage of maize lines due to the genotypic classes of fertility restoration, 2010–2021

Based on the results of evaluating the reaction of 9 lines in 2010-2012, a complete fixer of sterility was identified – KV 204 (class I) and constant restorers of fertility: KV 498, KV 272, KV 7/07 (class VIII). Lines KV 3 and KV 87 (class II) turned out to be incomplete fixers of sterility, KV 469, KV 655, KV 276 (classes V, VII) were variable restorers.

In total, for the period from 2010 to 2021, there were studied 45 new self-pollinated maize lines, which allowed them to be systematized (assigned to certain classes) according to their genotype, depending on the dominant or recessive state in which the genes restoring the fertility of the Paraguayan CMS type are present (Table 6).

Among them, CV 204, SP 286, DS 255, SP 207, and DS 180 belonging to class I and having the genotype rf4rf4 rf5rf5 rf6rf6 should be considered the most valuable among them for the creation of sterile analogues and use as sterility fixers of the Paraguayan type of CMS. These lines, in crossing with any sterile forms, fix the sterility of the Paraguayan type of CMS.

For use as natural fertility restorers of the Paraguayan type CMS, the following lines are recommended: KV 498, KV 272, KV 7/07, SP 357, RD 261, DS 295, SP 210, SP 197, DS 177, DS 188, belonging to class VIII (genotype Rf4Rf4 Rf5Rf5 Rf6RF6). These lines completely restore fertility in crosses with any sterile forms.

An intermediate position is occupied by self-pollinated lines belonging to classes II-VII. Lines II - IV classes should be characterized as incomplete fixers of sterility. In lines belonging to the second class CV 3, CV 87, RD 257, DS 291, SP 209, DS 179 (genotype rf4rf4 rf5rf5 Rf6RF6), sterility is fixed in crosses with sterile forms in which the genes that restore fertility are absent in the genotype in the dominant state Rf 4 and Rf 5. In lines of the third class RD245, SP 194, DS 197 (rf4rf4 Rf5Rf5 rf6rf6), sterility is fixed in crossing with sterile forms that do not have the genes Rf 4 and Rf 6 in the dominant state. Lines of the fourth class RD 245, SP 194, DS 197 (Rf4Rf4 rf5rf5 rf6rf6) are fixatives in relation to sterile forms in the genotype of which the rf 4 and rf 6 genes are in a recessive state.

Lines of classes V–VII are characterized as variable fertility restorers, that is, in crossing with not all sterile forms, they restore fertility. Lines of the fifth class: KV 469, KV 655, SP 275, RD 274, DS 273, SP 203, SP 195, DS 197, DS 185, DS 194, DS 199 (genotype rf4rf4 Rf5Rf5 Rf6RF6) restore fertility with sterile forms that have the gene – reducing agent Rf 4 in the dominant state. The sixth class includes lines RD 331, SP 206, DS 184 (genotype Rf4Rf4 rf5rf5 Rf6RF6). To restore fertility, the Rf 4 gene is additionally required. Lines of the seventh class KV 276, SP 231, DS 297, SP 180, DS 192 (genotype Rf4Rf4 Rf5Rf5 rf6rf6) are fertility restorers in relation to sterile sources that have the Rf 6 gene in the genotype in the dominant state.

The frequency of occurrence of lines of different classes varies greatly (Fig. 1).

The fifth (24.4 %) and eighth (22.3 %) classes turned out to be the most numerous, the lines belonging to the fourth class (4.4 %) are the least common. The first class (complete sterility fixers) includes 11.1 % of the lines.

The use of eight sterile sources, and the evaluation of test cross hybrids obtained with their participation, makes it possible to classify maize lines according to fertility restoring genes. Such information is useful for targeted and efficient work on the creation of maize cytosterile hybrids.

However, the use of all sources of sterility requires a large amount of work. Therefore, reducing the number of analyzers without distorting the evaluation results is of practical interest. Analyzing the results of the studies, we came to the conclusion that the use of three out of eight sterile sources allows us to obtain sufficiently complete information to determine the state of the genes that restore fertility. In this case, it is necessary to select sources of certain classes: the fifth (WF 9c), the sixth (Lc) and the seventh (W 401c) (Table 7).

Lines belonging to different classes will have different flowering patterns of testcross hybrids depending on the analyzer used. By these differences it is possible to identify the belonging of each line to a certain class. Thus, by arranging the sources of sterility in ascending order of classes from the fifth to the seventh, we obtain the following combination of sterile (s) and fertile (f) test crosses by class: the first (c – c – c), the second (s – s – f), the third (s – f – s), fourth (f – s – s), fifth (s – f – f), sixth (f – s – f) seventh (f – f – s), eighth (f – f – f). The combination of sterile and fertile test crosses is individual for each class of lines, which allows them to be identified.

Only constant lines should be taken to assess response to CMS. The use of non-constant lines can make their evaluation difficult. Test cross progeny of such lines are often split by flowering into sterile, fertile and semi-fertile plants. Presumably, the reason for the separation of semi-fertile plants can be not only the genetic unevenness of the lines, but also the presence of modifier genes in their genotype. Therefore, in these cases, three analyzers may not be enough to evaluate the response of lines to CMS. For example, additional crosses involving the source of sterility of the fourth group (Kr 21c) with the dominant Rf4 gene, which makes it possible to identify the lines belonging to the most numerous fifth group, may be appropriate.

Discussion and Conclusion

Using specially selected sources of sterility, in 2010–2021, 45 self-pollinated maize lines were systematized by genes that restore fertility.

The first class includes the lines KV 204, SP 286, DS 255, SP 207, DS 180, they are the most valuable for creating sterile analogues, as they completely fix sterility. The second class includes the lines of incomplete fixers of sterility KV 3, KV 87, RD 257, DS 291, SP 209, DS 176, having the Rf6 gene in the genotype in the dominant state, the third class includes the lines: RD 245, SP 194, DS 197 are incomplete sterility fixers with the dominant Rf5 gene, and the fourth one contains SP 198 and DS 173 with the dominant Rf4 gene. Variable restorers of fertility are lines of the fifth class (KV 469, KV 655, SP 275, RD 274, DS 273, SP 203, SP 195, DS 179, DS 185, DS 194, DS 199) with genes Rf5, Rf6 in the dominant , lines of the sixth class RD 331, SP 206, DS 184 with genes Rf4, Rf6 in the dominant state and lines of the seventh class KV 276, SP 231, DS 297, SP 180, DS 192 with dominant genes Rf4, Rf6. The largest of interest in the creation of cytosterile hybrids are the lines of the eighth class (KV 498, KV 227, KV 7/07, SP 357, etc.), which belong to the natural constant fertility restorers of the Paraguayan type of CMS.

Information about the behavior of lines in sterile cytoplasm allows efficient and purposeful work on the creation of cytosterile hybrids. It was revealed that the most numerous classes are the fifth (24.4 %) and eighth (23.3 %), the least is the fourth (4.4 %).

The optimal number of analyzers to obtain information about the behavior of lines in the sterile cytoplasm is three (WF 9c, Lc, W 401c).

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