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INHERITANCE OF FERTILITY RESTORATION IN WINTER TRITICALE WITH CYTOPLASM OF *TRITICUM TIMOPHEEVI*

DZIEDZICZENIE PRZYWRACANIA MĘSKIEJ PŁODNOŚCI U PSZENŻYTA OZIMEGO Z CYTOPLAZMĄ *TRITICUM TIMOPHEEVI*

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Abstract. We investigated inheritance of a male fertility restoration in winter triticale with the sterilising cytoplasm of *T. timopheevi*. Generations F_1, F_2, and BC_1 were derived from crosses between two male sterile lines with the cytoplasm *T. timopheevi* and 12 restorer inbred lines of S_3–S_{14} generations. The distribution of fertile and sterile plants in segregating progenies indicates that at least four independent nuclear genes are involved in expression of fertility restoration. Male sterility was determined by recessive genes. The simultaneous presence of at least two dominant genes in two independent loci is required for fertility restoration. The precise determination of the role of identified loci on the base of obtained phenotypic distributions is difficult due to presence of plants with intermediate fertility and variation that can not be explained by simple segregation ratios.

Słowa kluczowe: cytoplazmatyczna męska sterylność, dziedziczenie, przywracanie męskiej płodności, pszenżyto.
key words: cytoplasmic male sterility, fertility restoration, inheritance, triticale.

INTRODUCTION

System of a cytoplasm-nuclear male sterility is recommended for production of hybrid seeds of winter triticale (Nalepa 1990, 2003, Góral 2002a, Ammar et al. 2006). Although several potential sources of alien cytoplasm have ability to sterilise pollen of triticale, cytoplasm of *T. timopheevi* and *Ae. scharonensis* are considered as the most promising male sterilising systems due to lack of deleterious effects on important agronomic traits (Nalepa 1990). The drawback of the system employing CMS-*T. timpheevi* is a low frequency of genotypes maintaining male sterility (Spiss and Góral 1994, Warzecha et al. 1996, 1998, Góral 2002c, Góral and Spiss 2005, Góral et al. 2007), that are unstable in various environments (Nalepa 2003, Góral et al. 2006). The majority of lines and varieties of winter triticale incompletely restore male fertility (Góral 2002c, Góral and Spiss 2005, Góral et al. 2007). Maintaining sterility

lines in triticale must be developed by special breeding procedures owing to a low frequency of such genotypes in Polish breeding materials. Determination of genetic factors (number of genes and their interactions) that shape male sterility/fertility in triticale is prerequisite for efficient production of three key genotypes in hybrid seed production: stable CMS lines with respective maintainers and restoring lines.

Fragmentary data on the inheritance of male sterility/fertility in triticale with the CMS-*T. timopheevi* system (Cauderon et al. 1985, Góral 2002b) indicate that several nuclear genes are involved. The purpose of the present study was to analyze the inheritance of fertility restoration in 24 interline hybrids of winter triticale with cytoplasm of *T. timopheevi*.

MATERIAL AND METHODS

Fertility was recorded in progeny obtained from crosses of male sterile lines cms Salvo 15/1 B_{12} and cms Grado 2 B_{12} with 12 restorer inbred lines of S_3–S_{14} generation (Table 1). Parental lines were derived from Polish cultivars and strains in the Department of Plant Breeding and Seed Science of the Agricultural University in Cracow. F_1 generations were obtained after hand crosses of selected male-sterile plants with fertility restoring lines. Some ears of male-fertile F_1 plants were bagged and self-pollinated to obtain F_2 progenies, and the others were used for pollinating the maternal male sterile lines in order to produce BC_1 generations. Combinations of cms Salvo 15/1 × LAD 563 6/3 and cms Grado 2 × Tewo 1/1 gave mainly partially male-fertile F_1 plants which were used to derive segregating generation because no well-developed fully-fertile plants were found.

Male-sterility of maternal lines was controlled by bagging not pollinated ears. Male-fertility of F_1 generation was evaluated during flowering and recorded in 1–5 scale (5 – male fertile, 1 – male sterile), according to Góral et al. (2006.) Classification of plants was based on seed set in bagged ears. Finally, plants without seeds were recorded as male sterile, while plants with full seed set (above 30 grains per ear) were counted as male-fertile. Restoration index (IR) was calculated with the formula:

$$IR[\%] = N_5 + 0{,}5 \times (N_4 + N_3 + N_2) \times 100,$$

where N_5, N_4, N_3 and N_2 are the number of plants in respective fertility classes.

Each of 48 segregating progenies were planted in field in wide spacing (40 × 20 cm) and evaluated for male fertility as described above. For genetic analysis all intermediate plants (group 2, 3 and 4) were included to male-fertile class (group 5). Goodness of fit of obtained segregation ratios to expected ones was tested with chi-square test.

RESULTS

The F_1 hybrids were essentially fertile but not fully phenotypicaly uniform and were characterized by the presence of plants of varying level of fertility restoration (Table 1). The majority of plants was fully male fertile but intermediate individuals were present in all progenies. Single male-sterile F_1 plants were found in 2 out of 24 progenies (crosses of cms Salvo 15/1 with Tewo 1/1 and Ugo 1/1). The lowest restoration index was found in F_1 of Tewo 1/1 and LAD 593 6/3 as male parents, irrespective of cms line used. In all other F_1 combinations restoration index surpassed 80%.

Table 1. Number of plants in different phenotypic classes (5 – male-fertile, 4 – male-fertile-intermediate, 3 – intermediate, 2 – intermediate-male-sterile, 1 – male-sterile) in F_1 hybrids from crosses of male sterile lines with fertility restoring lines, and restoration index (IR)

Tabela 1. Liczba roślin w różnych klasach fenotypowych (5 – męskopłodne, 4 – męskopłodne-pośrednie, 3 – pośrednie, 2 – pośrednie-męskosterylne, 1 – męskosterylne) u mieszańców F_1 pochodzących z krzyżowania męskosterylnych linii z liniami przywracającymi płodność i indeks restoracji (IR)

Male line Linia ojcowska	Female line – Linia mateczna											
	cms Salvo 15/1 B_{12}						cms Grado 2 B_{12}					
	5	4	3	2	1	IR[1] %	5	4	3	2	1	IR[1] %
Tornado 1/1 S_6	17	3	3	0	0	87,0	35	1	0	0	0	98,6
Pinokio 1 S_4	11	1	0	1	0	92,3	29	2	1	0	0	95,3
Prego 5/3 S_6	18	1	6	1	0	84,6	29	2	3	0	0	92,6
Nemo 4/1 S_4	26	3	0	1	0	93,3	29	2	0	0	0	96,8
Ugo 1/1 S_{12}	19	3	3	3	1	81,0	22	11	1	0	0	82,4
Ugo 2/1 S_{12}	20	8	5	0	0	80,3	17	6	3	0	0	82,7
Alzo DH S_4	20	3	4	0	0	87,0	29	7	0	0	0	90,3
Lasko 7/1/1 S_{14}	23	2	0	1	0	94,2	21	4	4	1	0	85,0
Moreno 2/4 S_6	26	0	1	3	0	93,3	35	4	2	0	0	92,7
Tewo 1/1 S_6	11	8	5	2	1	68,5	4	7	15	6	0	56,2
LAD 593 6/3 S_6	7	8	3	4	0	65,9	5	21	2	4	0	57,8
Bogo 5/3 S_6	22	2	3	0	0	90,7	23	6	2	0	0	87,1

[1]IR [%] = $(N_5 + 0,5 \times (N_4 + N_3 + N_2) \times 100$, where N_5, N_4, N_3 and N_2 are the number of plants in respective fertility classes

[1]IR [%] = $(N_5 + 0,5 \times (N_4 + N_3 + N_2) \times 100$, gdzie N_5, N_4, N_3 i N_2 są liczbami roślin w odpowiednich klasach płodności

All classes of plant phenotypes were observed in segregating F_2 and BC_1 populations. The male-sterile plants accounted for 11.5% and 5.7% in progenies obtained with cms Salvo 15/1 and cms Grado 2, respectively (tab. 2, 3). No male-sterile plant was found in F_2 generations from crosses cms Grado 2 × Lasko 7/71/1 and cms Grado 2 × Moreno 2/4, possibly because of too little number of plants analyzed. Segregating populations obtained with the use of 9 paternal lines were characterized with similar segregation ratios of male-sterile to male-fertile plants irrespective of maternal line. Segregation ratios in BC_1 and F_2 progenies, obtained in result of crosses of both maternal lines with Tornado 1/1, Pinokio 1 and Prego 5/3 can be explained by gene action in two independent loci. Segregations in progenies with lines Nemo 4/1, Ugo 1/1, Ugo 2/1, Lasko 7/1/1, Moreno 2/4 and DH line derived from Alzo cultivar can be explained by action of three independent loci. Segregation ratios in populations obtained with remaining paternal lines: Tewo 1/1, LAD 593 6/3 and Bogo 5/3 were different depending on maternal line. Segregation ratios in F_2 and BC_1 progenies obtained from cross cms Salvo 15/1 × Tewo 1/1 could be explained by three pairs of alleles, and in respective populations cms Grado 2 × Tewo 1/1 – with one pair. The case was reverse when LAD 593 6/3 was used. When crossed to cms Salvo 15/1 and cms Grado 2, segregations pointed to the action of one and three gene pairs, respectively. Differences in two and four pairs of alleles could be hypothesized in crosses cms Salvo 15/1 × Bogo 5/3 and cms Grado 2 × Bogo 5/3, respectively.

Based on above data we can conclude that maternal lines had different genetic determination of male sterility and both CMS lines were not recessive homozygotes in respect to all of the four proposed loci controlling male sterility. We assumed that the presence of at least two dominant alleles *Rf* in any four loci is indispensable for restoration of fertility. Male sterile plants would be recessive homozygotes in 4 loci ($rf_1rf_1rf_2rf_2rf_3rf_3rf_4rf_4$),

Table 2. Number of plants in different phenotypic classes (5 – male-fertile, 4 – male-fertile-intermediate, 3 – intermediate, 2 – intermediate-male-sterile, 1 – male-sterile) in F_2 and BC_1 hybrids from crosses of male sterile line cms Salvo 15/1 with fertility restoring lines and expected segregation ratios (SR)

Tabela 2. Liczba roślin w poszczególnych grupach fenotypowych (5 – męskopłodne, 4 – męskopłodne-pośrednie, 3 – pośrednie, 2 – pośrednie-męskosterylne, 1 – męskosterylne) u mieszańców F_2 i BC_1 pochodzących z krzyżowania męskosterylnej linii cms Salvo 15/1 z liniami przywracającymi płodność oraz oczekiwane stosunki rozszczepień (SR)

Male line	Generation	Number of plants – Liczba roślin						SR	P
Linia ojcowska	Pokolenie	5	4	3	2	1	total	(5 + 4 + 3 + 2) : 1	
Tornado 1/1	F_2	21	35	17	19	17	109	15 : 1	<0,001
	BC_1	4	13	17	10	14	58	3 : 1	0,90–0,80
Pinokio 1	F_2	60	19	8	10	4	101	15 : 1	0,50–0,30
	BC_1	19	8	7	12	14	60	3 : 1	0,80–0,70
Prego 5/3	F_2	11	58	22	7	7	105	15 : 1	0,90–0,80
	BC_1	2	0	1	0	1	4	3 : 1	>0,99
Nemo 4/1	F_2	58	26	7	9	2	102	63 : 1	0,80–0,70
	BC_1	9	5	10	9	7	40	7 : 1	0,50–0,30
Ugo 1/1	F_2	61	24	9	5	4	103	63 : 1	0,10–0,05
	BC_1	11	5	5	3	4	28	7 : 1	0,80–0,70
Ugo 2/1	F_2	19	28	42	10	1	100	63 : 1	0,70–0,50
	BC_1	0	1	0	7	2	10	7 : 1	0,50–0,30
Alzo DH	F_2	38	38	14	9	2	101	63 : 1	0,80–0,70
	BC_1	10	9	9	3	3	34	7 : 1	0,70–0,50
Lasko 7/1/1	F_2	66	24	5	1	1	97	63 : 1	0,70–0,50
	BC_1	29	11	5	7	7	59	7 : 1	0,90–0,80
Moreno 2/4	F_2	54	25	17	7	2	105	63 : 1	0,80–0,70
	BC_1	2	3	9	5	11	30	7 : 1	<0,001
Tewo 1/1	F_2	33	17	19	21	10	100	54 : 10	0,20–0,10
	BC_1	3	4	4	5	4	20	6 : 2	0,70–0,50
LAD 593 6/3	F_2	11	24	23	16	33	107	3 : 1	0,20–0,10
	BC_1	3	5	8	8	16	40	1 : 1	0,30–0,20
Bogo 5/3	F_2	31	20	14	23	16	104	15 : 1	<0,001
	BC_1	20	8	12	7	11	58	3 : 1	0,30–0,20

Table 3. Number of plants in different phenotypic classes (5 – male-fertile, 4 – male-fertile-intermediate, 3 – intermediate, 2 – intermediate-male-sterile, 1 – male-sterile) in F_2 and BC_1 hybrids from crosses of male sterile line cms Grado 2 with fertility restoring lines and expected segregation ratios (SR)

Tabela 3. Liczba roślin w poszczególnych grupach fenotypowych (5 – męskopłodne, 4 – męskopłodne--pośrednie, 3 – pośrednie, 2 – pośrednie-męskosterylne, 1 – męskosterylne) u mieszańców F_2 i BC_1 pochodzących z krzyżowania męskosterylnej linii cms Grado 2 z liniami przywracającymi płodność oraz oczekiwane stosunki rozszczepień (SR)

Male line	Generation	Number of plants – Liczba roślin						SR	P
Linia ojcowska	Pokolenie	5	4	3	2	1	total	(5 + 4 + 3 + 2) : 1	
Tornado 1/1	F_2	56	32	8	5	4	105	15 : 1	0,50–0,30
	BC_1	18	14	9	7	11	59	3 : 1	0,30–0,20
Pinokio 1	F_2	80	10	10	3	5	108	15 : 1	0,50–0,30
	BC_1	15	10	9	14	11	59	3 : 1	0,30–0,20
Prego 5/3	F_2	63	18	11	5	6	103	15 : 1	0,90–0,80
	BC_1	15	8	10	6	0	39	3 : 1	<0,001
Nemo 4/1	F_2	65	21	11	8	2	107	63 : 1	0,80–0,70
	BC_1	20	9	3	4	1	37	7 : 1	0,10–0,05
Ugo 1/1	F_2	70	18	4	11	1	104	63 : 1	0,70–0,50
	BC_1	11	5	5	0	2	23	7 : 1	0,70–0,50
Ugo 2/1	F_2	39	30	20	18	2	109	63 : 1	0,90–0,80
	BC_1	1	5	8	5	0	19	7 : 1	0,10–0,05
Alzo DH	F_2	38	39	20	3	2	102	63 : 1	0,80–0,70
	BC_1	2	6	6	1	1	16	7 : 1	0,50–0,30
Lasko 7/1/1	F_2	33	13	1	1	0	48	63 : 1	0,50–0,30
	BC_1	28	17	7	5	2	59	7 : 1	0,05–0,02
Moreno 2/4	F_2	63	27	10	4	0	104	63 : 1	0,20–0,10
	BC_1	11	19	20	3	4	57	7 : 1	0,20–0,10
Tewo 1/1	F_2	14	5	3	11	12	45	3 : 1	0,80–0,70
	BC_1	8	7	6	5	8	34	1 : 1	0,01–0,001
LAD 593 6/3	F_2	36	22	23	9	4	94	54 : 10	<0,001
	BC_1	5	4	0	5	1	15	6 : 2	0,20–0,10
Bogo 5/3	F_2	45	19	10	18	8	100	243 : 13	0,20–0,10
	BC_1	26	12	13	4	4	59	14 : 2	0,20–0,10

recessive homozygotes in 3 out of 4 loci, and dominant homozygotes/heterozygotes in respect to one pair of alleles ($Rf_1Rf_1rf_2rf_2rf_3rf_3rf_4rf_4$, $rf_1rf_1Rf_2Rf_2rf_3rf_3rf_4rf_4$, $rf_1rf_1rf_2rf_2Rf_3Rf_3rf_4rf_4$, $rf_1rf_1rf_2rf_2rf_3rf_3Rf_4Rf_4$, $Rf_1rf_1rf_2rf_2rf_3rf_3rf_4rf_4$, $rf_1rf_1Rf_2rf_2rf_3rf_3rf_4rf_4$, $rf_1rf_1rf_2rf_2Rf_3rf_3rf_4rf_4$, $rf_1rf_1rf_2rf_2rf_3rf_3Rf_4rf_4$). The remaining genotypes exhibit varying level of fertility restoration. Based on this assumption 85% of segregation ratios were in accordance with expectations (Table 2, 3). In 7 out of 48 populations a significant deviations from expected segregation ratios were found. Based on above assumption we propose the genotypes of the female and male lines as presented in table 4.

Table 4. Putative genotypes of male-sterile and male-fertile lines
Tabela 4. Prawdopodobne genotypy linii męskosterylnych i przywracających płodność

Female line Linia mateczna	Male line – Linia ojcowska	
	genotype – genotyp	line – linia
Salvo 15/1 $rf_1rf_1rf_2rf_2rf_3rf_3Rf_4Rf_4$	$Rf_1Rf_1rf_2rf_2Rf_3Rf_3Rf_4Rf_4$	Tornado 1/1, Pinokio 1, Prego 5/3
	$Rf_1Rf_1Rf_2Rf_2Rf_3Rf_3Rf_4Rf_4$	Nemo 4/1, Ugo 1/1, Ugo 2/1, Alzo DH, Lasko 7/1/1, Moreno 2/4
	$Rf_1Rf_1rf_2rf_2rR_3Rf_3rf_4rf_4$	Tewo 1/1
Grado 2 $rf_1rf_1rf_2rf_2Rf_3Rf_3rf_4rf_4$	$Rf_1Rf_1rf_2rf_2rf_3rf_3Rf_4Rf_4$	LAD 593 6/3
	$Rf_1Rf_1Rf_2Rf_2rf_3rf_3Rf_4Rf_4$	Bogo 5/3

DISCUSSION

Determination of the number of nuclear genes cooperating with sterilising cytoplasm depends on the source of investigated cytoplasm and genetic composition of both male sterile lines and fertility restorers. Cauderon et al. (1985) suggest that in triticale with cytoplasm of *T. timopheevi* male sterility is determined by three recessive, independent, additive genes. Also Góral (2002b) studying F_2 and BC_1 of cms Salvo 15/1 × Bolero 14/1 suggested that three loci with recessive alleles determined pollen sterility. According to Nalepa (2003) restoration of male fertility in the system of CMS-*Ae. sharonensis* depends on two loci.

Restoration of fertility may depend on variable number and effects of fertility restoring genes, intra- and inter-allelic interaction, genetic background of female form, and environmental factors (Sage 1972, Scoles and Evans 1979). In wheat with *T. timopheevi* cytoplasm and rye with *Pampa* cytoplasm several major *Rf* genes were identified, as well as genes of minor effects and gene modificators (Maan et al. 1984, Miedaner et al. 2000). Probably similar situation occurs in the case of triticale with cytoplasm of *T. timopheevi*. Low frequency of genotypes restoring male fertility in wheat with cytoplasm of *T. timopheevi* and high frequency of genotypes restoring fertility in triticale indicate that triticale *Rf* genes are derived from the rye R genome. These suggestions are supported by results of Curtis and Lukaszewski (1993) who found that genes restoring fertility in F_1 of hexaploid wheat with *T. timopheevi* cytoplasm are located on the long arms of rye chromosomes 6R and 4R. However, it cannot be excluded that genetic determination of male sterility/fertility in triticale

is more complicated than in rye and wheat, as triticale comprises genomes of both genera and genetic diversity may result from inter- and intra-allelic interactions of wheat and rye genes.

The presence of single male-sterile and intermediate plants with different levels of anther degeneration in F_1 generation (Table 1) indicates that alleles responsible for sterility restoration in pollinator lines were not complete or heterozygous. Partially fertile plants with sterilising cytoplasm may result from environmental factors or modificator genes but these genotypes are male-fertile (Kaul 1988). In case of a low number of intermediate plants they are usually classified as male-fertile. However, we found a relatively high number of intermediate plants. Establishing for them a separate class did not allow to explain the observed ratios by additive effects of genes from four postulated loci and by inter-allelic interactions (data not shown). When only two phenotypic classes are considered (male-fertile and male-sterile), the simplest hypothesis is that four independent nuclear genes affect fertility restoration in the CMS-*T. timopheevi* system. At least two dominant alleles in two independent loci are necessary to restore male fertility. In the most cases we obtained a good agreement with this assumption.

Segregations in generation BC_1 obtained from crosses of cms Salvo with Moreno 2/4 and cms Grado 2 with Tewo 1/1, Prego 5/3 and Lasko 7/1/1 did not confirm hypothetic segregation ratios in respective F_2 progenies. Segregations in generation F_2 of cross cms Salvo 15/1 × Tornado 1/1 and Bogo 5/3 did not fit the expected 15 : 1 ratio of male-fertile to male-sterile plants but showed a good fit to the 13 : 3 ratio (P = 0,50 – 0,30). Similarly, the F_2 generation from cms Grado 2 × LAD 593 6/3 cross showed a good fit to 61 : 3 (P = 0,90 – 0,80) instead to the expected 54 : 10 ratio. In each of these three combinations in BC_1 generation we obtained a good agreement with expected segregations (Table 2, 3). Inconsistent conclusions arising from the analysis of these F_2 and BC_1 generations are difficult to explain. It is possible, that inheritance of male fertility restoration in the system of CMS *T. timopheevi* is more complicated than we assumed. Observed deviations from assumptions may come out from involvement of additive alleles in segregation, varying allelic effects derived from different loci, presence of specific modificators in parental lines, or differences in chromosome composition. Presence of modificators may increase sensitivity of some genotypes to the environment (Kaul 1988) and can further affect the proper phenotypic classification of plants. Additionally, male lines, although developed by inbreeding, might have not been homozygous in respect to all restorer genes and therefore could produce unexpected segregation ratios in segregating progenies from crosses with two different male sterile lines.

SUMMARY

Our results indicated that at least four independent, nuclear genes are involved in expression of male sterility/fertility in triticale with cytoplasm of *T. timopheevi*. Male sterility is determined by recessive genes. Restoration of male fertility depends on the presence of at least two dominant alleles in 2 independent loci out of 4 possible. Mode of action of these genes in the material studied was not fully explained.

Complex, multi-genic determination of male sterility/fertility in the CMS-*T. timopheevi* system makes significant difficulties in the development of male sterile lines and their male-fertile

analogues. Introduction of male sterility into selected lines or cultivars will require reduction of size of back-crossed populations by the use of doubled haploid lines and prior identification of non-restoring genotypes with molecular markers.

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Streszczenie. Przeprowadzono analizę dziedziczenia przywracania męskiej płodności u pszenżyta ozimego z cytoplazmą *T. timopheevi*. Oceniono pokolenia F_1, F_2 i BC_1, otrzymane w wyniku krzyżowań dwóch linii męskosterylnych z cytoplazmą *T. timopheevi* z 12 restorującymi liniami wsobnymi w pokoleniach S_3–S_{14}. Rozszczepienia w pokoleniach segregujących wskazują, że nie mniej niż cztery niezależne geny jądrowe są zaangażowane w ekspresję przywracania męskiej płodności. Męska sterylność jest cechą recesywną. Do przywrócenia męskiej płodności konieczne są przynajmniej dwa dominujące allele, obecne jednocześnie w dwóch z czterech postulowanych loci. Precyzyjne określenie sposobu działania tych genów na podstawie otrzymanych rozszczepień fenotypowych jest trudne ze względu na występowanie stosunkowo dużej liczby roślin pośrednich i zmienność nie dającą się wytłumaczyć prostymi stosunkami rozszczepień.