

TESTING OF A HYPOTHESIS CONCERNING INTERACTION OF GENES WITH MUTATED CYTOPLASM CONTROLLING MALE STERILITY OF THE PAMPA TYPE IN RYE (*SECALE CEREALE L.*)¹

TADEUSZ RUEBENBAUER, LUCJA KUBARA-SZPUNAR,
KRYSTYNA PAJAK²

Institute of Plant Breeding and Seed Science, Academy of Agriculture, Kraków

Summary. The previously accepted hypothesis about the interaction of four pairs of genes $Ms_1ms_1Ms_2ms_2Ms_3ms_3Ms_4ms_4$ with mutated cytoplasm of the Pampa type in rye, out of which five single genes in a dominant form restore male fertility, has been experimentally tested. It was fully confirmed by the agreement of the observed segregations with theoretical ones and by general theoretical considerations.

The paper by Łoś, Ruebenbauer (1982) presents a hypothesis explaining a complicated mode of inheritance of male sterility. On the basis of the literature data (Geiger, Schnell 1970; Geiger 1972; Geiger, Schnell 1973; Geiger, Morgenstern 1975) and observations of the authors it was found that the action of genes restoring male sterility is weak. In consequence of that the obtaining of restorers encounters larger difficulties than the obtaining of lines maintaining male sterility. Trying to be orientated, which distribution of theoretical segregations into male-sterile and normal individuals conforms best to the experimental data, we calculated possible segregations under the assumption of a single to four pairs of genes controlling pollen formation. Part of these genes in the dominant state is necessary for restoring male fertility. Comparing the obtained empirical segregations with theoretical data, it was recognized that the most probable is the hypothesis suggesting that four pairs of genes, of which at least five single dominant genes may cause restoration of male fertility, interact with mutated cytoplasm of the Pampa type. This hypothesis called 5/8 is in agreement with the theoretical portion of sterile plants in population (67.7%) in relation to the observed portion, which additionally evidences in its favour. Having more abundant experimental material, we could test his hypothesis by comparing experimental data with theoretical calculations.

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² First author: Prof.; second: Dr.; third: M. Sc. Present address: ul. Św. Marka 37, 31-140 Kraków, Poland.



MATERIAL AND METHODS

Material for the studies consisted of backcross hybrids of six generations of the male-sterile line LN1 with inbred lines of rye. The line L1P from H. Geiger was received from the Institute of Plant Breeding and Acclimatization in Radzików. The experiments were conducted since 1974 in the experimental fields of the Prusy farm, Academy of Agriculture in Kraków. Data concerning segregation of plants into normal and male-sterile were compared with theoretical segregations obtained, when the hypothesis 5/8 was accepted. The choice of hypothesis 5/8 was made after the calculation of all possible segregation combinations resulting from the assumptions that one to four pairs of genes, of which part in a dominant state is able to restore male fertility, interact with mutated cytoplasm. All possible segregations resulting from crossing of male-sterile individuals with normal ones were obtained using CROSS generator and accompanying subprograms (K. Ruebenbauer — unpublished).

The theoretical number of pollinating plants in per cent of the population for hypothesis 5/8 are as follows: 0, 3.125, 6.25, 10.938, 12.50, 18.75, 22.656, 25, 31.25, 34.375, 36.328, 65.625, 68.75, 81.25, 87.50, 93.75, 100. When choosing theoretical figures most similar to the figures obtained from crosses between male sterile and normally pollinating individuals, we simultaneously selected genotypes for the parental forms. Among numerous pairs of the parental genotypes giving the same segregations we had to choose a pair fulfilling the following requirements;

1. Maternal form (male sterile) according to the assumption should have no more than four dominant genes, since the fifth gene restores male fertility. This requirement is fulfilled by all the observed segregations.

2. The genotype of the progeny plant in each of six generations (1976 - 1981) should arise from fertilization of possible parental gametes.

3. Taking into account that paternal forms are inbred lines performed throughout 22 inbred generations, it was assumed that they are homozygotes to a more significant extent than maternal forms. Moreover, it could be expected that the degree of their homozygosity increased from one generation to another.

The above principles of choosing parental pairs significantly limited the freedom in assigning different genotypes to particular plants. In most cases it appeared that the choice of the parental pairs fulfilling all the requirements is limited to a single theoretical case. As a result of that it may be said that genetic models in Table 1 assigned to plants are usually the only possible ones. The agreement between the distribution of the theoretical values with the experimental data obtained using the χ^2 test significantly supports the accepted hypothesis.

RESULTS AND DISCUSSION

Genetic models of Table 1 for individual male-sterile mothers and normally pollinating fathers, being inbred lines, should be recognized to be highly probable because of the fact that they often represent the only explanation of the observed

Table 1b

Tab. 1b (cont.).

(49 L1P \times 3.18) ^s \times Rogalińskie Pa	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
(49 L1P \times 3.18) ^s \times Wioszananowskie C	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
(L1P \times LN1) \times Rogalińskie Pa	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
(L1P \times LN1) \times Rogalińskie F ₁	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
(L1P \times LN1) \times Zeealandzkie E	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
[(L1P \times S ₂ 710 D. Złote) ²] \times LN1 \times Kazimierskie C ₃	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
[(L1P \times S ₂ 710 D. Złote) ²] \times LN1 \times Kazimierskie H	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
[(49 L1P \times 3.18) ^s \times 3.18 ^a] \times Kazimierskie H	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
[(49 L1P \times 3.18) ^s \times 3.18 ^a] \times Rogalińskie F ₁	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}M_{s_2}m_{s_2}M_{s_3}m_{s_3}M_{s_4}m_{s_4}$
[(L1P \times LN1) \times LN1 ^a] \times Kazimierskie C ₃	$M_{s_1}m_{s_1}m_{s_2}m_{s_2}m_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}m_{s_2}m_{s_2}m_{s_3}m_{s_3}M_{s_4}m_{s_4}$
[(L1P \times LN1) \times LN1 ^a] \times Kazimierskie D	$M_{s_1}m_{s_1}m_{s_2}m_{s_2}m_{s_3}m_{s_3}M_{s_4}m_{s_4}$	$M_{s_1}m_{s_1}m_{s_2}m_{s_2}m_{s_3}m_{s_3}M_{s_4}m_{s_4}$

Table 1c

Hybrids	1980		1981	
	Genotype of		Genotype of	
	mother	father	mother	father
(L1P × S ₂ 710 D. Złote) ^a × LN1] × Universalne 145	<i>M_s,m_s₁Ms₂ms₂ms₃m_s₄m_s₄</i>	<i>m_s₁m_s₂ms₂ms₃m_s₄m_s₄</i>	<i>m_s₁m_s₂ms₂ms₃m_s₄m_s₄</i>	<i>m_s₁m_s₂ms₂ms₃m_s₄m_s₄</i>
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie D	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁M_s₂ms₂ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Horton C _s	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>m_s₁m_s₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Węgierskie 1	<i>m_s₁m_s₁ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Dąbkowskie s. 231	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>
[(49 L1P × 3.18) ^a × 3.18] × Kazimierskie C _s	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>
[(49 L1P × 3.18) ^a × 3.18] × Dąbkowskie s. 231	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>
[(49 L1P × 3.18) ^a × 3.18] × Węgierskie 1	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃m_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>
(L1P × LN1) × LN1] × Universalne 145	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄m_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
(L1P × LN1) × LN1] × Włoszczowskie C	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
[(L1P × LN1) × LN1] × Horton C _s	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
[(L1P × LN1) × LN1] × Węgierskie 1	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
Dąbkowskie s. 231	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
(L1P × S ₂ 710 D. Złote) ^a] × Zeelandzkie E	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>
(L1P × S ₂ 710 D. Złote) ^a] × Rogalińskie Pa	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₂Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>	<i>M_s₁m_s₁Ms₂ms₂Ms₃ms₃M_s₄M_s₄</i>

(49 L1P × 3.18)* ×	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
Rogalinckie Pa		
(49 L1P × 3.18)* ×		
Wioszanczkie C		
(L1P × LN1) × Rogalinckie Pa	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
(L1P × LN1) × Rogalinckie F,	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
(L1P × LN1) × Zeelandzkie E	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
[(L1P × S,710 D. Złote)* × LN1] ×	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
Kazimierskie C,	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
[(L1P × S,710 D. Złote)* × LN1] ×	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
Kazimierskie H		
[[(49 L1P × 3.18)* × 3.18*] ×	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
Kazimierskie H		
[[(49 L1P × 3.18)* × 3.18*] ×	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
Rogalinckie F,		
[(L1P × LN1) × LN1*] ×	$M_{s_1}Ms_1, M_{s_2}Ms_2, M_{s_3}Ms_3, M_{s_4}Ms_4$	$M_{s_1}Ms_1, M_{s_2}Ms_2, M_{s_3}Ms_3, M_{s_4}Ms_4$
Kazimierskie C,		
[(L1P × LN1) × LN1*] ×	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$	$M_{s_1}ms_1, M_{s_2}ms_2, M_{s_3}ms_3, M_{s_4}ms_4$
Kazimierskie D		

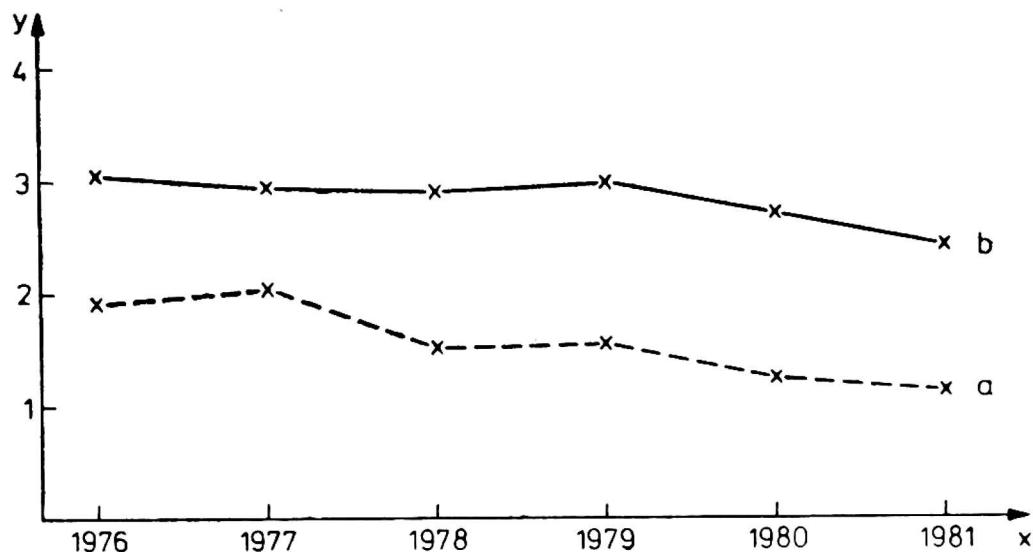


Fig. 1. Mean heterozygosity of individuals in different years
x-axis — different years, y-axis — number of heterozygous loci, a — fathers, b — mothers

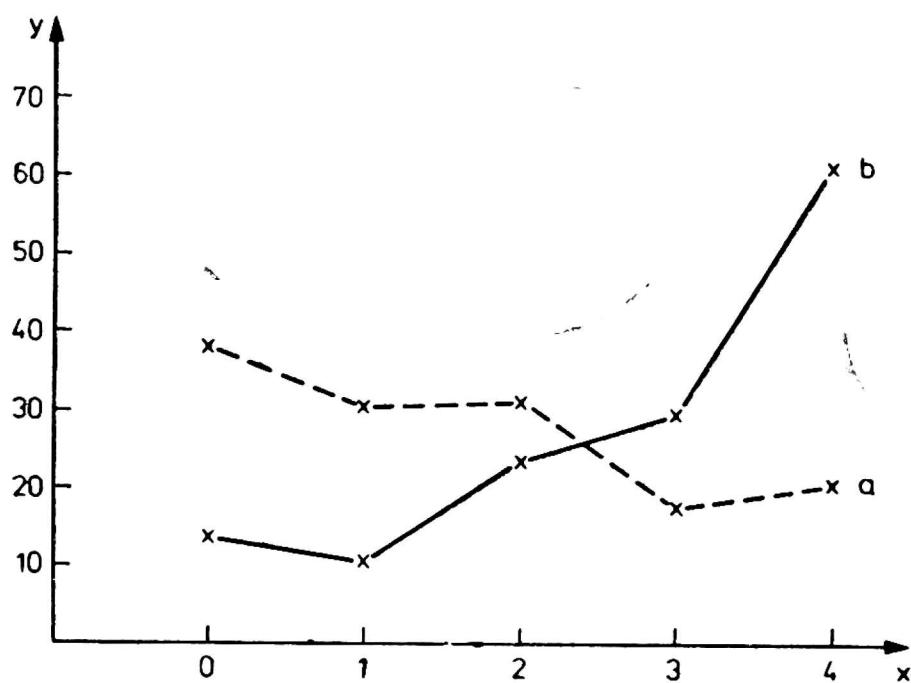


Fig. 2. Heterozygosity of all crossed individuals
x-axis — number of heterozygous loci, y-axis — number of individuals, a — fathers, b — mothers

segregation ratios. It also appeared that paternal forms despite a long-lasting inbreeding are not fully homozygotes in respect of the male sterility genes. This fact may be explained by the mode of their performance in inbreeding and by the lack of selection in this direction. Nevertheless, sib-mating as a less successful form of inbreeding leads more slowly, but also successfully, to accumulation of homozygotes, which is confirmed by data of Fig. 1. If in 1976 the mean number of heterozygous loci for fathers was 4.90, in 1981 it declined to 1.14. Mothers appeared to be heterozygous to a higher degree, however, under the influence of crossing with more homozygous fathers the degree of their heterozygosity decreased during the studied generations. In 1976 it was 3.05, whereas in 1981 — 2.45 of the heterozygous locus. As seen from the data presented in Fig. 2, the heterozygosity of mothers develops differently than that of fathers. If most fathers are homozygotes with respect to

Table 2a. Observed and theoretical numbers of male-sterile and normal plants in F_2

Hybrids	1976						1977					
	Number of plants						Number of plants					
	fertile	male-sterile	χ^2	fertile	male-sterile	χ^2	observ.	theoret.	observ.	theoret.	χ^2	P
$[(L1P \times S_2710 D. Zlote)^2 \times LN1] \times Uniwersalne 145$	8	8.355	15	14.645	0.0237	0.20 - 0.80	4	4.125	8	7.815	0.0058	0.95 - 0.90
$[(L1P \times S_2710 D. Zlote)^2 \times LN1] \times Kazimierskie D$	9	9.281	18	17.719	0.0130	0.95 - 0.90	2	2.039	7	6.981	0.0009	0.98 - 0.95
$[(L1P \times S_2710 D. Zlote)^2 \times LN1] \times Horton C_s$	11	10.937	24	24.063	0.0005	0.98 - 0.95	1	1.422	12	11.578	0.1406	0.80 - 0.70
$[(L1P \times S_2710 D. Zlote)^2 \times LN1] \times Wegierskie 1$	23	24.750	10	8.250	0.4949	0.50 - 0.30	5	5.250	3	2.750	0.0346	0.90 - 0.80
$[(L1P \times S_2710 D. Zlote)^2 \times LN1] \times Dańskowskie s. 231$	29	29.250	10	9.750	0.0085	0.95 - 0.90	5	5.000	5	5.000	0.0000	>0.99
$[(49 L1P \times 3.18)^3 \times 3.18] \times Kazimierskie C_s$	11	11.156	6	5.844	0.0083	0.95 - 0.90	0	0.000	14	14.000	0.0000	>0.99
$[(49 L1P \times 3.18)^3 \times 3.18] \times Dańskowskie s. 231$	8	7.991	14	14.010	0.0019	0.98 - 0.95	1	1.422	12	11.578	0.1406	0.80 - 0.70
$[(49 L1P \times 3.18)^3 \times 3.18] \times Wegierskie 1$	24	23.250	7	7.750	0.0968	0.80 - 0.70	3	3.281	27	26.719	0.0270	0.90 - 0.80
$[(L1P \times LN1) \times LN1] \times Uniwersalne 145$	6	6.797	24	23.203	0.1208	0.80 - 0.70	0	0.000	12	12.000	0.0000	>0.99
$[(L1P \times LN1) \times LN1] \times Włoszanowskie C$	19	19.030	10	9.970	0.0137	0.95 - 0.90	10	9.000	8	9.000	0.2222	0.70 - 0.50
$[(L1P \times LN1) \times LN1] \times Horton C_s$	17	17.000	17	17.000	0.0000	0.99	14	16.500	19	16.500	0.6576	0.50 - 0.30
$[(L1P \times LN1) \times LN1] \times Wegierskie 1$	9	8.000	23	24.000	0.1666	0.70 - 0.50	1	0.875	13	13.125	0.0190	0.90 - 0.80
$[(L1P \times LN1) \times LN1] \times Dańskowskie s. 231$	19	17.000	15	17.000	0.4706	0.50 - 0.30	1	1.312	20	19.688	0.0791	0.80 - 0.70
$[(L1P \times S_2710 D. Zlote)^2] \times Zeelandzkie E$	34	34.687	3	2.313	0.2176	0.70 - 0.50	5	4.723	8	8.277	0.0255	0.90 - 0.80
$[(L1P \times S_2710 D. Zlote)^2] \times Rogalińskie Pa$	15	16.500	18	16.500	0.2728	0.70 - 0.50	8	8.250	4	3.750	0.0243	0.90 - 0.80
$(49 L1P \times 3.18)^3 \times Rogalińskie Pa$	3	3.063	25	24.937	0.0014	0.98 - 0.95	0	0.000	10	10.000	0.0000	>0.99
$(49 L1P \times 3.18)^3 \times Włoszanowskie C$	21	21.312	10	9.688	0.0146	0.95 - 0.90	7	6.875	3	3.125	0.0073	0.95 - 0.90
$(L1P \times LN1) \times Rogalińskie Pa$	31	32.375	6	4.625	0.4672	0.50 - 0.30	1	1.062	16	15.937	0.0039	0.98 - 0.95
$(L1P \times LN1) \times Rogalińskie F_1$	28	28.125	2	1.875	0.0088	0.95 - 0.90	13	12.000	11	12.000	0.1666	0.70 - 0.50
$(L1P \times LN1) \times Zeelandzkie E$	20	17.500	15	17.500	0.7142	0.50 - 0.30	4	3.750	11	11.250	0.0222	0.95 - 0.90

Table 2b

Hybrids	1978						1979					
	Number of plants			χ^2	P	fertile observ. theor.	Number of plants			χ^2	P	
	fertile observ.	male-sterile observ.	male-sterile theoret.				fertile observ. theor.	male-sterile observ. theor.				
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Universalne 145	4	4.125	18	17.875	0.0047	0.95 - 0.90	0	0.000	46	46.000	0.0000	> 0.99
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie D	0	0.000	32	32.000	0.0000	> 0.99	0	0.000	46	46.000	0.0000	> 0.99
[(L1P × S ₃ 710 D. Złote) ^a × LN1] × Horton C _s	1	1.125	35	34.875	0.0143	0.95 - 0.90	1	1.500	47	46.500	0.1721	0.70 - 0.50
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Węgierskie 1	14	13.850	24	24.195	0.0043	0.95 - 0.90	0	0.000	24	24.000	0.0000	> 0.99
[(L1P × S ₄ 710 D. Złote) ^a × LN1] × Dańkowskie s. 231	15	17.500	20	17.500	0.7142	0.50 - 0.30	16	14.187	23	24.813	0.3642	0.70 - 0.50
[(49 L1P × 3.18) ^a × 3.18] × Kazimierskie C _s	4	4.875	35	34.125	0.1794	0.70 - 0.50	8	8.383	29	28.817	0.0226	0.90 - 0.80
[(49 L1P × 3.18) ^a × 3.18] × Dańkowskie s. 231	18	19.000	20	19.000	0.1053	0.80 - 0.70	1	1.406	44	43.594	0.1210	0.80 - 0.70
[(49 L1P × 3.18) ^a × 3.18] × Węgierskie 1	9	8.750	26	26.250	0.0095	0.95 - 0.90	0	0.000	35	35.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Universalne 145	6	4.625	32	32.375	0.0347	0.90 - 0.80	0	0.000	42	42.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Włoszanowskie C	7	6.875	3	3.125	0.0073	0.95 - 0.90	—	—	—	—	—	—
[(L1P × LN1) × LN1] × Horton C _s	1	1.125	35	34.875	0.0143	0.95 - 0.90	23	21.500	20	21.500	0.2093	0.70 - 0.50
[(L1P × LN1) × LN1] × Węgierskie 1	0	0.000	30	30.000	0.0000	> 0.99	1	0.906	28	28.094	0.0100	0.95 - 0.90
[(L1P × LN1) × LN1] × Dańkowskie s. 231	—	—	—	—	—	—	—	—	—	—	—	—
[(L1P × S ₂ 710 D. Złote) ^a] × Zeelandzkie E	25	25.594	14	13.406	0.0401	0.90 - 0.80	2	1.687	25	25.313	0.0619	0.90 - 0.80
[(L1P × S ₂ 710 D. Złote) ^a] × Rogalińskie Pa	11	11.344	21	20.656	0.0161	0.90 - 0.80	1	1.375	43	42.625	0.1056	0.80 - 0.70
(49 L1P × 3.18) ^a × Rogalińskie Pa	2	1.969	16	16.031	0.0005	0.99 - 0.98	0	0.000	25	25.000	0.0000	> 0.99
(49 L1P × 3.18) ^a × Włoszanowskie C	5	4.812	2	2.188	0.0234	0.90 - 0.80	34	33.312	7	7.688	0.0758	0.80 - 0.70
(L1P × LN1) × Rogalińskie Pa	0	0.000	32	32.000	0.0000	> 0.99	0	0.000	34	34.000	0.0000	> 0.99
(L1P × LN1) × Rogalińskie F ₁	25	24.062	10	10.938	0.1168	0.80 - 0.70	18	20.000	22	20.000	0.4000	0.70 - 0.50
(L1P × LN1) × Zeelandzkie E	6	6.25	19	18.750	0.0133	0.95 - 0.90	0	0.000	41	41.000	0.0000	> 0.99
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie C _s	15	13.805	23	24.195	0.1624	0.70 - 0.50	1	0.749	23	23.251	0.0868	0.80 - 0.70
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie H	26	26.125	12	11.875	0.0019	0.98 - 0.95	22	23.000	24	23.000	0.0869	0.80 - 0.70
[(49 L1P × 3.18) ^a × 3.18] × Kazimierskie H	34	34.887	3	2.313	0.2176	0.70 - 0.50	0	0.000	43	43.000	0.0000	> 0.99
[(49 L1P × 3.18) ^a × 3.18] × Rogalińskie F ₁	29	29.000	0	0.000	0.0000	> 0.99	32	30.625	3	4.375	0.4938	0.50 - 0.30
[(L1P × LN1) × LN1] × Kazimierskie C _s	7	6.500	19	19.500	0.0978	0.80 - 0.70	3	2.437	36	36.563	0.1388	0.80 - 0.70
[(L1P × LN1) × LN1] × Kazimierskie D	0	0.000	33	33.000	0.0000	> 0.99	1	1.469	46	45.531	0.1545	0.70 - 0.50

Table 2c

1981

Hybrids	1980						1981					
	Number of plants			P			Number of plants			P		
	fertile observ.	male-sterile observ.	theoret.	fertile observ.	male-sterile observ.	theoret.	fertile observ.	male-sterile observ.	theoret.	χ^2	χ^2	P
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Universalne 145	0	0.000	50	50.000	0.0000	> 0.99	0	0.000	37	37.000	0.0000	> 0.99
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie D	0	0.000	46	46.000	0.0000	> 0.99	0	0.000	24	24.000	0.0000	> 0.99
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Horton C _s	25	22.000	19	22.000	0.8182	0.50 - 0.30	11	12.187	28	26.813	0.1683	0.70 - 0.50
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Węgierskie 1	0	0.000	41	41.000	0.0000	> 0.99	0	0.000	14	14.000	0.0000	> 0.99
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Dańkowskie s. 231	35	3.609	20	18.906	0.0964	0.80 - 0.70	16	18.500	21	18.500	0.6756	0.50 - 0.30
[(49 L1P × 3.18) ^a × 3.18] × Kazimierskie C _s	5	4.813	39	39.187	0.0081	0.95 - 0.90	2	2.187	33	32.813	0.0172	0.90 - 0.80
[(49 L1P × 3.18) ^a × 3.18] × Dańkowskie s. 231	25	25.000	25	25.000	0.0000	> 0.99	11	10.535	18	18.465	0.0322	0.90 - 0.80
[(49 L1P × 3.18) ^a × 3.18] × Węgierskie 1	3	3.187	48	47.813	0.0117	0.95 - 0.90	0	0.000	29	29.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Universalne 145	0	0.000	54	54.000	0.0000	> 0.99	0	0.000	37	37.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Włoszanowskie C	—	—	—	—	—	—	—	—	—	—	—	—
[(L1P × LN1) × LN1] × Horton C _s	25	23.000	21	23.000	0.3532	0.70 - 0.50	—	—	—	—	—	—
[(L1P × LN1) × LN1] × Węgierskie 1	2	1.469	45	45.531	0.1981	0.70 - 0.50	0	0.000	27	27.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Dańkowskie s. 231	—	—	—	—	—	—	—	—	—	—	—	—
[(L1P × S ₂ 710 D. Złote) ^a] × Zeelandzkie E	13	13.750	42	41.250	0.0545	0.90 - 0.80	19	18.000	17	18.000	0.1111	0.80 - 0.70
[(L1P × S ₂ 710 D. Złote) ^a] × Rogalińskie Pa	1	1.656	52	51.344	0.2683	0.70 - 0.50	2	2.734	23	22.266	0.2212	0.70 - 0.50
(49 L1P × 3.18) ^a × Rogalińskie Pa	0	0.000	40	40.000	0.0000	> 0.99	0	0.000	31	31.000	0.0000	> 0.99
(49 L1P × 3.18) ^a × Włoszanowskie C	12	12.000	0	0.000	0.0000	> 0.99	39	39.000	0	0.000	0.0000	> 0.99
(L1P × LN1) × Rogalińskie Pa	4	5.250	44	42.750	0.3341	0.70 - 0.50	0	0.000	22	22.000	0.0000	> 0.99
(L1P × LN1) × Rogalińskie F ₁	24	25.594	15	13.406	0.2888	0.70 - 0.50	8	7.000	6	7.000	0.2857	0.70 - 0.50
(L1P × LN1) × Zeelandzkie E	26	26.000	26	26.000	0.0000	> 0.99	8	8.437	19	18.563	0.0830	0.90 - 0.80
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie C _s	0	0.000	51	51.000	0.0000	> 0.99	0	0.000	20	26.000	0.0000	> 0.99
[(L1P × S ₂ 710 D. Złote) ^a × LN1] × Kazimierskie H	36	30.562	3	2.438	0.1381	0.80 - 0.70	26	26.000	0	0.000	0.0000	> 0.99
[(49 L1P × 3.18) ^a × 3.18] × Kazimierskie H	42	42.875	7	0.125	0.1428	0.80 - 0.70	—	—	—	—	—	—
[(49 L1P × 3.18) ^a × 3.18] × Rogalińskie F ₁	47	46.875	3	3.125	0.0053	0.95 - 0.90	2	2.000	6	0.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Kazimierskie C _s	0	0.000	56	56.000	0.0000	> 0.99	0	0.000	34	34.000	0.0000	> 0.99
[(L1P × LN1) × LN1] × Kazimierskie D	0	0.000	35	35.000	0.0000	> 0.99	0	0.000	32	32.000	0.0000	> 0.99

four loci, a significant majority of mothers are heterozygotes in respect of four loci. Before 1975 mothers were crossed with fathers originating from the population. During the next years male sterility was introduced into inbred lines by backcrosses.

Table 2 contains the actual segregations into male sterile and normal plants observed in individual generations of reciprocal hybrids. Besides these figures, the table gives theoretical segregations resulting from genetic composition assigned to the parental forms. The calculated values of the Chi^2 in all the cases show an agreement between the observed segregations and the accepted theoretical assumptions. The distribution of most probabilities supporting to a greater or lesser degree the validity of the accepted hypothesis has basically a random character, the cases of very high probabilities supporting the correctness of the accepted hypothesis being more frequent (Fig. 3). Considering the size of theoretical segregations, it may be noticed that intervals between individual values are not similar and that they are particularly large about a 50% value. This raises a question whether larger deviations of the observed segregations as compared to the most similar theoretical values are associated with larger differences between the neighbouring theoretical values.

Dependences between the values of theoretical segregation differences and those of Chi^2 presented in Fig. 4 suggest the existence of correlation ($r=0.48$). However, rather a random distribution of the Chi^2 values conforms to the corresponding values on the x -axis. Taking into account the value of the correlation coefficient and the random distribution of the Chi^2 values, it may be assumed that the size of differences between the most similar theoretical values determined to a small degree the distribution of the Chi^2 values.

Now we should think to what degree hypothesis 5/8 agrees with the assumptions concerning domination of relations in panmictic population, controlled by the action of four pairs of genes. Accepting the hypothesis about the action of four pairs of genes of male sterility, we simultaneously assume that the fusion of 16 different female gametes with 16 male gametes gives rise to 256 individuals, one of which is a fourfold dominant homozygote and only one individual is a fourfold recessive homozygote. According to our observations the chance of choosing a good paternal line, both retaining male sterility in the progeny and restoring plant fertility, is small. Theoretically it is about 0.4%. However, as far as pollinating plants, independently of the genetic composition of mothers, cannot occur in their progeny after crossing with a fully homozygotously recessive father, so in the progeny of father, which is a fourfold dominant homozygote, there may occur male-sterile plants in the ratio 1/16, i.e. 6.25%. This case will take place in the progeny of the parents:

$Ms_1ms_1Ms_2ms_2Ms_3ms_3Ms_4ms_4 \times Ms_1Ms_1Ms_2Ms_2Ms_3Ms_3Ms_4Ms_4$. A question arises, to what degree the ratio of dominant genes to the whole of genes determines the portion of pollinating or nonpollinating plants in panmictic population. The ratio of nonpollinating to pollinating progenies in panmictic population according to theoretical assumptions for hypothesis 5/8 should be 163: 93, i.e. 63.7% nonpollinating to 36.3% pollinating. The number 63.7 is similar to the number of cases observed in our studies within 81 - 58%, which confirms the acceptance of hypothesis 5/8.

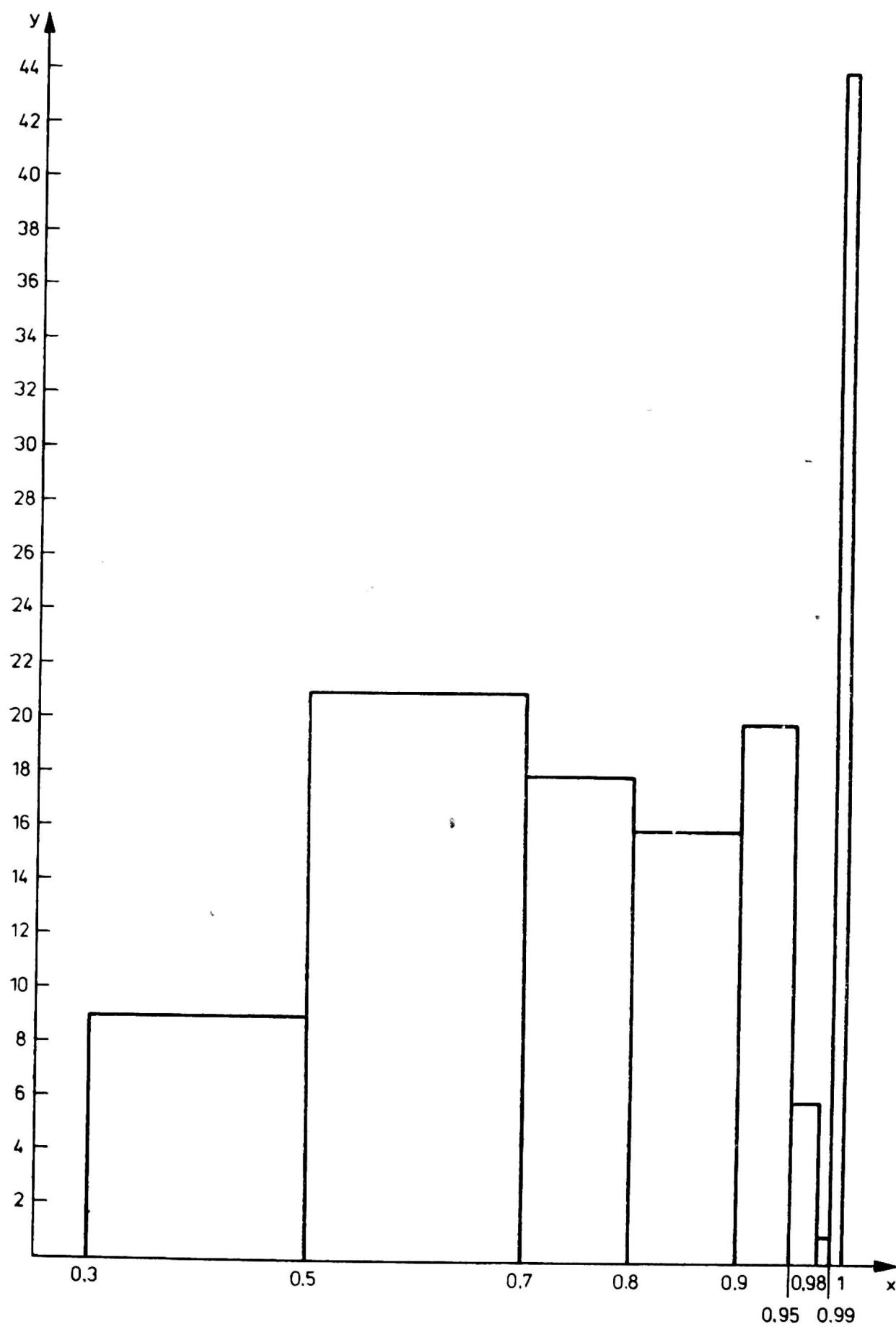


Fig. 3. Frequency of probabilities supporting validity of the accepted hypothesis 5/8
 x-axis — probabilities, y-axis — frequency

Though this ratio is also similar at hypothesis 4/6 — 66.7, hypothesis 5/8 makes possible better comparison of the experimental data with theoretical assumption. It should be mentioned that the ratio of non-pollinating to pollinating plants is determined by the ratio of recessive genes to the whole of genes, whereas the number of genes changes this ratio only to small a degree (Fig. 5).

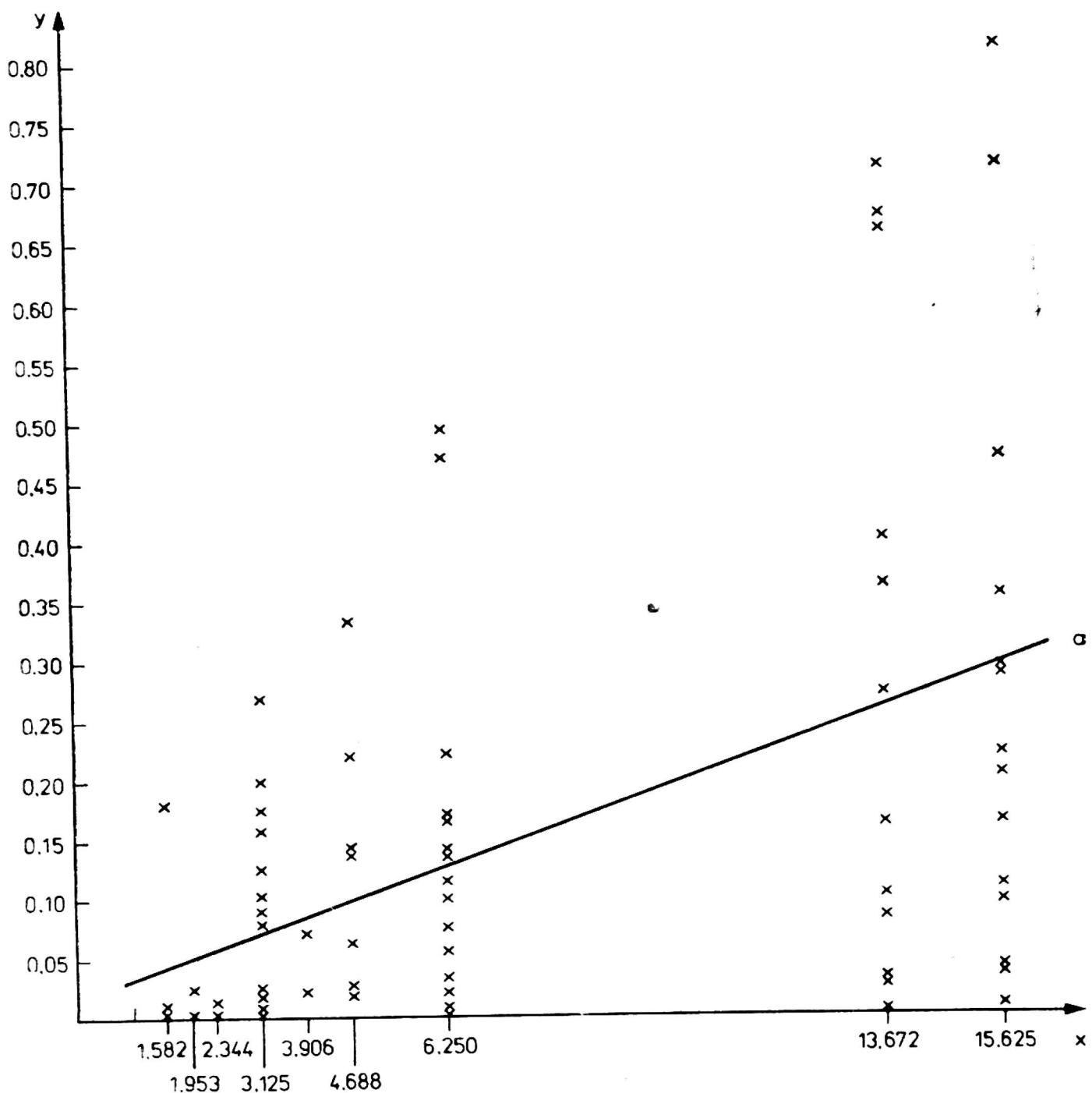


Fig. 4. Dependence of the χ^2 value on the size of differences between the values of theoretical segregations

x-axis — values of differences between the values of theoretical segregations, y-axis — χ^2 values, a — a straight line of regression

Moreover, contemplations on the plant ratios in populations substantiate the agreement of the accepted hypothesis 5/8 with results of the studies and confirm the validity of that hypothesis concerning the control of cytoplasmatic male sterility of the Pampa type by four pairs of genes, five of which in a dominant state are necessary to restore male fertility. This hypothesis suggests some conclusions concerning the breeding method of male sterile lines. The process of attaining the homozygosity of maternal lines, as well as that of paternal lines, requires inbreeding with a simultaneous testing of the progeny by the division of the progeny population into non-pollinating and pollinating plants. The accepted hypothesis 5/8 is very helpful in a conscious choice of lines retaining and eliminating male sterility.

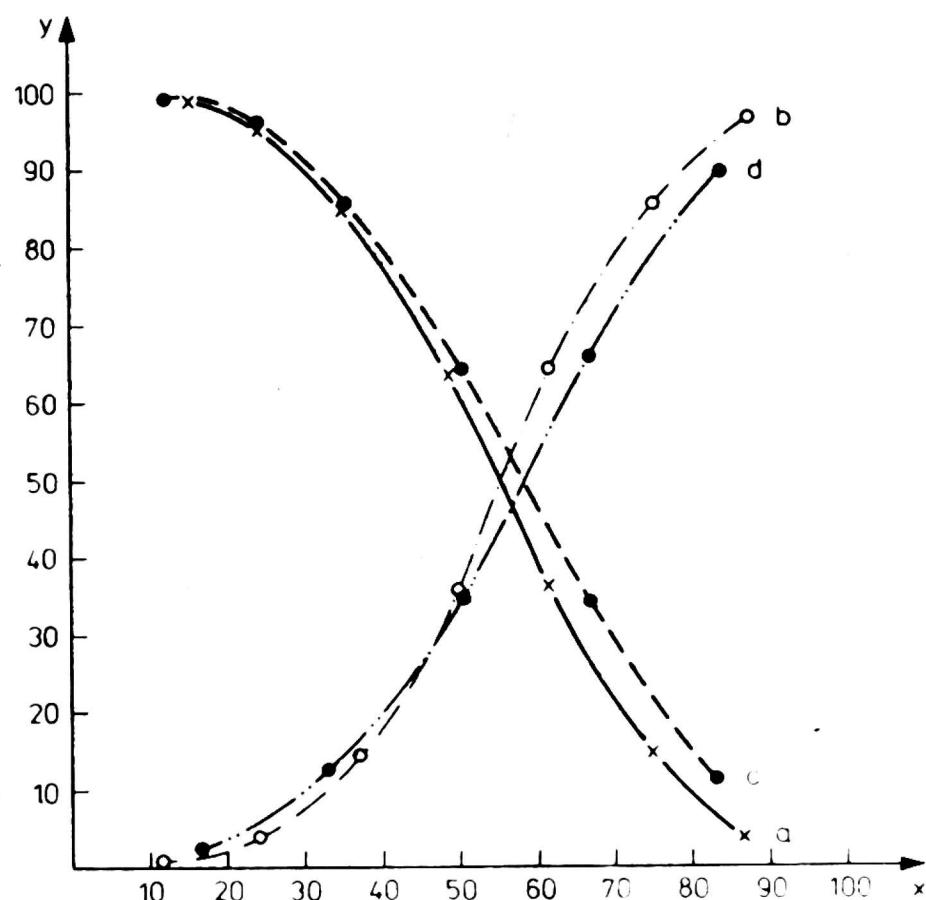


Fig. 5. The influence of the ratio of dominant genes to the whole of genes expressed in per cent of the number of male-sterile plants and normal plants at the assumption of the interaction of 3 and 4 pairs of genes with mutated cytoplasm

x-axis — ratio of dominant genes to the whole of genes in per cent, y-axis — percentage of pollinating or male-sterile plants
 a — for pollinating plants — hypothesis of 4 gene pairs, b — for sterile plants — hypothesis of 4 gene pairs, c — for pollinating plants — hypothesis of 3 gene pairs, d — for sterile plants — hypothesis of 3 gene pairs

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SPRAWDZENIE HIPOTEZY DOTYCZĄcej WSPÓŁDZIAŁANIA GENÓW ZE ZMUTOWANĄ CYTOPLAZMĄ KONTROLUJĄCYCH MĘSKĄ JAŁOWOŚĆ TYPU PAMPA U ŻYTA (*SECALE CEREALE* L.)

Streszczenie

Przyjęta poprzednio hipoteza współdziałania czterech par genów, $Ms_1ms_1Ms_2ms_2Ms_3ms_3Ms_4ms_4$ ze zmutowaną cytoplazmą typu Pampa u żyta, z których pięć pojedynczych genów

w formie dominującej przywraca męską płodność, została sprawdzona eksperimentalnie. Znajduje ona pełne uzasadnienie zarówno na podstawie zgodności rozszczepień obserwowanych z rozszczepieniami teoretycznymi jak i na podstawie ogólnych rozważań teoretycznych.

**ПРОВЕРКА ГИПОТЕЗЫ ОТНОСИТЕЛЬНО ВЗАИМОДЕЙСТВИЯ ГЕНОВ С МУТИРОВАННОЙ ЦИТОПЛАЗМОЙ КОНТРОЛИРУЮЩИХ МУЖСКУЮ БЕСПЛОДНОСТЬ ТИПА РАМПА У РЖИ
(*SECALE CEREALE L.*)**

Резюме

В настоящей работе экспериментально проверена ранее принятая гипотеза о взаимодействии 4-х пар генов $Ms_1ms_1Ms_2ms_2Ms_3ms_3Ms_4ms_4$, с мутированной цитоплазмой типа Рампа у ржи, из которых 5 отдельных генов в доминирующей форме восстанавливают мужскую плодность. Эта гипотеза получила полное подтверждение в соответствии наблюдаемых и теоретических расщеплений, а также в общих теоретических рассуждениях.