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GENES FOR POLLEN FERTILITY RESTORATION IN SUNFLOWERS

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SUMMARY

Research on 16 sources of pollen fertility restoration revealed that this character was controlled in eight cases by one single dominant gene, in three cases by two complementary genes, in four cases by three complementary genes and in one case by the cumulative action of two nonallelic dominant genes.

The presence of minor genes for restoration in the genotype of the fertile analogue B could effect partial fertility restoration in the cytoplasmic male-sterile line A, especially in late backcrosses, when its genotype becomes saturated with such polygenes.

A second major gene Rf_2 was identified among the investigated monogenic restorer sources.

INTRODUCTION

The extremely low frequency of genes for pollen fertility restoration in the present cultivated sunflowers has been one of the most important difficulties in using the sterile cytoplasm 'petiolaris' (LECLERQ, 1969) for producing commercial hybrid seed (VRÂNCEANU & STOENESCU, 1971; ANASCHENKO, 1974). As expected, such genes proved to be more common in some wild species or in the genotypes derived from them (ENNS et al., 1970; ENNS, 1972; KINMAN, 1970; LECLERQ, 1971; VRÂNCEANU & STOENESCU, 1973; FICK et al., 1974).

The first cultivated sunflowers carrying genetic factors for pollen fertility restoration were discovered by VRÂNCEANU & STOENESCU (1971, 1973) in Romania and by FERNANDEZ et al. (1974) in Argentina, SCORIĆ (1974) in Yugoslavia and VELKOV & STOYANOVA (1974) in Bulgaria.

This paper presents new data on:

- the genetic control of pollen fertility restoration in 16 sunflower cultivars;
- the appearance of partial pollen fertility restoration when converting male-fertile inbred lines into cytoplasmic male-sterile ones;
- the allelism of some *Rf* genes with varying degrees of effectiveness.

MATERIAL AND METHODS

Most of the pollen fertility restorer sources used were domestic breeding material, the others were obtained from the world germplasm collection (Table 1).

The Romanian lines MZ-1398, DV-10275, SL-71-232 and MH-5383 originate from obsolete sunflower cultivars. Our data indicate that in such cultivars the restorer factors occur in a greater frequency than in the present high-oil varieties. The inbred lines OG-817, BL-15 and BL-17 were selected by selfing within the ornamental sunflowers of our germplasm collection.

The restorer line S 11-15-72-3 was obtained at Fundulea by self-pollination and selection within the synthetic population 'Synthetic 11', which includes several interspecific hybrids of *Helianthus tuberosus* × *H. annuus*. This synthetic population contains also genes for resistance to downy mildew (*Plasmopara helianthi* NOVOT.) and white rot (*Sclerotinia sclerotiorum* (LIB.) DE BY). The Romanian inbred lines V-2618 and CF-11-73 C originate from the open pollinated variety VNIIMK 8931 and from the French hybrid CVH 61-BC 23, respectively.

Two other restorer lines, ND-7227 and ND-280 were obtained at Fundulea from the US hybrids HA 89 × Rf 7227 and HA 89 × RHA-280. The male parent of the

Table 1. Pollen fertility restorer sources used in crosses.

Restorer sources	Genetic background	Breeding centre	Authors
MZ-1398	Local cultivar Mezëhedeshy	I.C.C.P.T. Fundulea, Romania	VRÂNCEANU & STOENESCU (1971, 1973)
DV-10275	Discovolante × VNIIMK 8931	Idem	Idem
SL-71-232	Local cultivar Slovenska-siva	Idem	Idem
MH-5383	Manchurian hybrid	Idem	Idem
OG-817	Ornamental sunflower	Idem	Idem
BL-15	Ornamental sunflower	Idem	Idem
BL-17	Ornamental sunflower	Idem	Idem
S 11-15-72-3	Synthetic population	Idem	Idem
V-2618	VNIIMK 8931	Idem	Idem
CF-11-73 C	French hybrid CVH 61-BC 23	Idem	Restoration identified by LECLERCQ (1971)
ND-7227	North-American hybrid HA 89 × Rf 7227	Idem	Restoration identified by FICK et al. (1974)
ND-280	North-American hybrid HA 89 × RHA-280 (Sundak)	Idem	Restoration identified by FICK & ZIMMER (1974)
T-66006-2-1-B	Composite cross	College Station, Texas, USA	KINMAN (1970)
MO-1338	(1366 A × 1338) × Krasnodarets	Morden-Manitoba, Canada	ENNS (1972)
MO-1356	(1365 × 1356) × Krasnodarets	Idem	Idem
AGP 70-20-6-2-5	1367 A(H) × Pehuén INTA	Pergamino, Argentina	FERNANDEZ et al. (1974)

first cross was a wild annual sunflower species (FICK et al., 1974) and that of the second cross was isolated from the confectionary variety Sundak (FICK & ZIMMER, 1974).

The line T-66006-2-1-B comes from Texas and was selected from a 'composite' in which three rust resistance sources related to the wild annual sunflowers were included (KINMAN, 1970).

The two Canadian restorer sources MO-1338 and MO-1356 were isolated by ENNS (1972) from the wild *H. annuus* backcrossed several times to Krasnodarets.

The Argentine line AGP 70-20-6-2-5 originates from the cross 1367 A (H) × Pehuén INTA, its restorer genes coming probably from two rust resistant lines of Canadian origin included in the pedigree of Pehuén INTA (FERNANDEZ et al., 1974).

The F_1 generations were obtained by crossing the restoration sources with cytoplasmic male-sterile lines developed at Fundulea.

The same lines were used as female parents for test-crosses. Fertile F_1 plants were selfed in order to obtain the F_2 populations.

The study of the allelism of the *Rf* genes comprised ten different sources of which the genetic control of restoration was already known. All of them had been included in 'petiolaris' sterile cytoplasm and were crossed in a diallelic system. In order to obtain the F_1 generations, the female plants were emasculated by hand. In Table 7 only the segregation ratios fitting the theoretical ones with $P > 0.05$ are presented. A small number of ratios differed largely from the expected ones. These deviations may be due to some unknown genetic factors, but they could also be the results of certain errors in determining the fertility of pollen in some plants or they could be simply outcrosses.

The investigations were carried out both in a field nursery and greenhouses. Crosses and selfings were made under paper and cotton bags. Pollen fertility was estimated visually or by staining with acetocarmine, especially in the case of partially fertile plants. Plants having flowers with 0–10% stained pollen were classified as sterile, with 10–85% as partially fertile and with 85–100% as fertile. In some cases, the partially fertile plants were considered as fertile or sterile for the goodness of fit of the observed segregation ratios to the expected ones. The segregation ratios were analyzed by the chi-square method.

RESULTS AND DISCUSSION

The study of the inheritance of restoration in eight sources revealed the existence of one single dominant gene responsible for this character, at least when these sources had been crossed to the male-sterile line S-1358 A (Table 2).

The Romanian lines MZ-1398, DV-10275 and SL-71-232 proved to be of great value as they were very good restorers both under field and greenhouses conditions. The Texas line T-66006-2-1-B is a good restorer, but produces a smaller quantity of pollen under unsatisfactory illumination, especially in greenhouses. The same characteristic is present in the line CF-11-73 C obtained at Fundulea by selfing within the French hybrid CVH 61-BC 23.

A very stable restorer proved to be the US source ND-7227.

The Canadian sources MO-1338 and MO-1356 gave only partial restoration under

greenhouse conditions during the winter 1975–1976 (in the annex of Table 2 the partially fertile plants have been considered fertile). These sources also showed an increased number of sterile plants in the investigated segregation ratios under field conditions. The constancy of this phenomenon is given by the high P values for progeny homogeneity, primarily for the source MO-1356.

Table 3 presents three cases in which the restoration of pollen fertility seems to be determined by the action of two complementary genes. In the first case (S 11-15-72-3) the restorer source, represented by the selfed male-parent, was homozygous for the two *Rf* genes and consequently the F_1 generation was entirely fertile. In the second case (ND-280), the ratio 1 fertile : 1 sterile in F_1, as well as the segregation of the selfed male plant indicate that one of the complementary genes was heterozygous and the other homozygous. In order to draw this conclusion a Yates' correction for continuity within the F_1 segregation was calculated. In the third case (AGP 70-20-6-2-5) the plant under cross was double heterozygous, the F_1 generation containing 25%

Table 2. Segregation ratios of crosses between the cytoplasmic male-sterile line S-1358 A and various pollen fertility restorers controlled by one single dominant gene (Fundulea, 1971–1975).

Restorers	Generation	Number of progenies	Ratio fertile:sterile plants		P %	
			observed	theoretical	for segregating progenies	for progeny homogeneity
MZ-1398	F_2	19	527:166	3:1	0.5–0.7	0.5–0.7
	sterile × F_1	13	178:185	1:1	0.8–0.9	0.5–0.7
DV-10275	F_2	8	260: 86	3:1	>0.9	0.1–0.3
	sterile × F_1	3	113:126	1:1	0.3–0.5	0.5–0.7
SL-71-232	F_2	5	161: 50	3:1	0.5–0.7	0.5–0.7
	sterile × F_1	5	127:139	1:1	0.3–0.5	0.1–0.3
T-66006-2-	F_2	3	106: 40	3:1	0.5–0.7	>0.05
-1-B	sterile × F_1	4	154:141	1:1	0.3–0.5	>0.9
CF-11-73 C	F_2	2	38:22	3:1	>0.05[1]	0.7–0.9
	sterile × F_1	3	61:69	1:1	0.3–0.5	0.3–0.5
MO-1338	F_2	3	69:28	3:1	0.3–0.5	0.7–0.9
	sterile × F_1	3	67:82	1:1	0.1–0.3	0.3–0.5
MO-1356	F_2	3	76:36	3:1	>0.05	0.7–0.9
	sterile × F_1	3	54:61	1:1	0.5–0.7	>0.9
ND-7227	F_2	2	76:23	3:1	0.5–0.7	0.3–0.5
	sterile × F_1	1	26:26	1:1	>0.99	–

[1] P for χ^2 corrected (Yates' correction for continuity).

Annex to Table 2. Segregation ratios of the lines MO-1338 and MO-1356 in greenhouses, 1975–1976.

MO-1338	F_2	1	[9:11]: 8[2]	3:1	0.5–0.7	–
	sterile × F_1	1	[7: 3]:14[2]	1:1	0.3–0.5	–
MO-1356	F_2	1	[11:11]:12[2]	3:1	0.1–0.3	–
	sterile × F_1	1	[5:10]:15[2]	1:1	>0.9	–

[2] Segregation ratio = fertile: partially fertile: sterile plants.

Table 3. Segregation ratios of crosses between the cytoplasmic male-sterile line S-1358 A and pollen fertility restorers controlled by two complementary genes. Fundulea, 1975 (field) and 1975–1976 (greenhouses).

Restorers	Generation	Testing place and year	Number of progenies	Ratio fertile:partially-fertile sterile plants		P %	
				observed	theoretical	for segregating progenies	for progeny homogeneity
S 11-15-72-3	F_1	field, greenhouses 1975–1976	4	82:0:0	–	–	–
	♂ ⊗	field, 1975–1976	4	86:0:0	–	–	–
	F_2	field, greenhouses 1975–1976	5	164:0:109	9:7	0.1–0.3	0.3–0.5
	sterile × F_1	field, greenhouses 1975–1976	4	[52:3]:181	1:3	0.5–0.7	0.5–0.7
ND-280	F_1	field, 1975	1	16:0:30	1:1	>0.05[1]	–
	♂ ⊗	field, 1975 greenhouses, 1975–1976	2	80:0:21	3:1	0.3–0.5	0.1–0.3
	F_2	greenhouses, 1975–1976	2	66:0:40	9:7	0.1–0.3	0.1–0.3
AGP 70-20--6-2-5	F_1	field, 1975	3	37:0:100	1:3	0.5–0.7	0.1–0.3
		greenhouses, 1975–1976	1	[11:5]:71	1:3	0.1–0.3	
	$♂_1$ ⊗	field, 1975	2	37:0:36	9:7	0.1–0.3	0.3–0.5
	F_2	greenhouses, 1975–1976	1	[13:19]:32	9:7	0.1–0.3	–
		field, 1976	1	[7:20]:24	9:7	0.3–0.5	–
	sterile × F_1	greenhouses, 1975–1976	1	[6:4]:30	1:3	>0.9	–

[1] P for χ^2 corrected (Yates' correction for continuity); the partially fertile plants have been considered sterile.

fertile and 75% sterile plants, both under field and greenhouse conditions, and the selfed male plant giving the segregation ratio 9 : 7. The F_2 generations were obtained by selfing individually the F_1 plants and the test-cross generations by crossing them to the male-sterile line S 1358 A.

Restoration provided by S 11-15-72-3 and ND-280 was very stable. It was very much affected in the Argentine line AGP 70-20-6-2-5 by the greenhouse conditions of the 1975–1976 winter. The partially fertile plants were considered fertile in all cases, in order to get the observed segregation ratios closer to the expected ones. In fact, the fertile plants of this line as well as those of its segregating generations, produced a quantity of pollen which was twice smaller than that of the other two lines.

The restoration of pollen fertility seems to be in some cases the result of the complementary action of more than two genes. The segregation ratios presented in Table 4 suggest the existence of three complementary genes which assure the fertility of pollen only when they all occur in a dominant state (*Rfa-Rfb-Rf-*). When a monoheterozygote participates in the cross, the ratios 3 fertile : 1 sterile for the selfed male plant and 1 : 1 for F_1 are obtained. For a double heterozygote, these ratios are 9 : 7 and 1 : 3 and for the triple-heterozygote 27 : 37 and 1 : 7. When a plant which is homozygous for all the three *Rf* genes is used in crosses, the offspring of the selfed plant and of the F_1 generation are entirely fertile and the F_2 generation presents the ratio 27 fertile : 37 sterile plants.

Some of the segregating ratios in Table 4 could not be interpreted, because they differed too much from the expected proportions. Such ratios as well as the high frequency of the partially fertile plants, particularly under unfavourable conditions, indicate also the existence of certain modifiers which are very susceptible to environmental variations. It is likely that some of the complementary genes play also the role of modifiers.

Data in Table 5 point out another category of genetic control of pollen fertility restoration in the line MH-5383, namely the cumulative action of two nonallelic dominant genes. The first generation, entirely fertile, indicates the homozygosity of this line for the *Rf* genes. The clear-cut ratios 9 : 6 : 1 and 1 : 2 : 1 between fertile, partially fertile and sterile plants obtained in the two segregating generations (F_2 and test-cross), both under field and greenhouse conditions, suggest that the partial restoration in this case is determined by a single dominant gene (*Rfa-rfbrfb*) but for the complete restoration the existence of the dominant alleles of both genes (*Rfa-Rfb-*) is necessary.

The results presented in this paper confirm our previous findings that the genes for pollen fertility restoration are present in a greater frequency in wild *Helianthus* species, in their related hybrids or in the old sunflower cultivars with low oil content than in the present high-oil varieties.

Polygenic restorers, which have more than two *Rf* genes, should be avoided in practical breeding work because of their susceptibility to various environmental conditions and because they require more complicated breeding and seed production methods.

When such minor genes for restoration occur in the genotype of the fertile analogue B, the cytoplasmic male-sterile line A is completely sterile in the first generations of back-crossing, but as its genotype becomes saturated with such polygenes, the

Table 4. Segregation ratios of crosses between cytoplasmic male sterile lines and pollen fertility restorers controlled by more than two complementary genes (Fundulea, 1972–1976).

Restorers	The female sterile line	Testing place and year	Ratios fertile : partially fertile : sterile plants					
			selfed male plant		F_1		F_2	
			observed	theoretical	observed	theoretical	observed	theoretical
		field, 1972	31:0:36	27:37	–	–	–	–
OG-817	V-3319 A	field, 1973	27:[9:19]	27:37	5:[12:28]	1:7	–	–
		greenhouses, 1973–1974	2:9:36		0:3:32			
		field, 1974	[57:1]:21	3:1	2:1:29			
		field, 1976	40:0:29	9:7	[11:3]:53	1:3	[74:2]:115	27:37
		field, 1972	48:0:40	9:7				
BL-15	SV-1679 A	field, 1974	47:[8:7]	3:1	27:14:20	1:1		
		field, 1976	51:0:0		[43:2]:0		[47:4]:76	27:37
BL-17	P–1380 A	greenhouses, 1973–1974	[19:6]:29	27:37	0:4:38			
V-2618	P-1380 A	field, 1973	60:[4:41]	9:7	21:[3:59]	1:3		
		greenhouses, 1974–1975	3:5:38					

The partially fertile plants have been considered either fertile or sterile, depending upon the intensity of the phenomenon.

Table 5. Segregation ratios of crosses between the cytoplasmic male sterile line SP-4559 A and the pollen fertility restorer MH-5383 (Fundulea, 1974–1976).

Generation	Testing place and year	Number of progenies	Ratio fertile : partially fertile : sterile plants		P %	
			observed	theoretical	for segregating progenies	for progeny homogeneity
F_1	field, 1974–1975	4	87:0:0	–	–	–
	greenhouses, 1974–1975	1	29:1[1]:0	–	–	–
Male parent ⊗	field, 1974	2	43:0:0	–	–	–
	greenhouses, 1974–1975	1	26:2[1]:0	–	–	–
F_2	field, 1975	3	43:34:3	9:6:1	0.5–0.7	0.1–0.3
	greenhouses, 1975–1976	1	12:12:0	9:6:1	0.1–0.5	–
Sterile × F_1	field, 1975	2	13:45:16	1:2:1	0.1–0.3	⩾0.05
	greenhouses, 1975–1976	1	6:16:4	1:2:1	0.3–0.5	–

[1] The partially fertile plants have been considered fertile.

Table 6. The frequency of partial fertility restoration in cytoplasmic male-sterile lines developed at Fundulea.

Inbred lines	Backcross generations with the analogue B							
	F_1	BC_1	BC_2	BC_3	BC_4	BC_5	BC_6	BC_7
Total number of cytoplasmic male-sterile lines	728	635	512	409	327	241	155	83
% inbred lines with partial pollen fertility	0	0	0.6	1.5	3.2	1.2	0.7	0

phenomenon of pollen fertility restoration appears, in most cases as a partial fertility (Table 6), especially in the third to fifth backcrosses.

Eight sources, the restoration capacity of which is known to be controlled by one single dominant gene, were included in a system of diallelic crosses in order to test the allelism of the *Rf* major genes (Table 7). All these restorers contain sterile 'petiolaris' cytoplasm, being homozygous for the *Rf* genes, except for CF-11-73 C and ND-7227. The F_1 generations were entirely fertile.

When both parents with monogenic restoration have the same gene in a homozygous state, the F_2 and test-cross generations are entirely fertile. This is the case with the lines MZ-1398, DV-10275, SL-71-232 and ND-7227 on one hand and T-66006-2-1-B and MO-1338 on the other hand.

As the *Rf* gene of the line ND-7227 comes from a wild ecotype of *H. annuus*, one can assume that the obsolete open-pollinated varieties such as Mezëhedeshy, Discovolante and Slovenska-siva still possess this gene having derived it from their wild ancestor species *H. annuus*. MO-1338, which resulted from a cross between wild and cultivated sunflowers turned out to possess the same fertility restorer gene as T-66006-2-1-B, designated by KINMAN (1970) as *Rf*. This confirms also the assumption (VRÂNCEANU & STOENESCU, 1971) that the Rf_1 gene comes from wild sunflowers carrying rust-resistance genes.

If the sources with monogenic restoration have different *Rf* genes in a homozygous state, the F_2 and test-cross generations will segregate 15:1 and 3:1, respectively. In the cross CF-11-73 C × SL-71-232, the ratios 3:1 in F_2 and 1:1 in test-cross are due to the fact that the plant of the line CF-11-73 C, which was utilized in crosses, was heterozygous (*Rfa rfa*) and the F_1 self-pollinated plant had the genotype *rfa rfa Rfb Rfb*. The fertility restorer genes of the lines MO-1338, MO-1356 and CF-11-73 C were also affected in this case by the greenhouse environment (lack of artificial illumination) during the winter 1975–1976, producing a significant proportion of partially fertile plants. In some cases, these plants were considered as fertile, so as to bring the observed segregating ratios nearer to the expected ones.

Since the gene of the line T-66006-2-1-B was already named Rf_1, we propose the symbol Rf_2 for the other gene existing in the genotype of the lines MZ-1398, DV-10275, SL-71-232 and ND-7227. The restoration capacity of the gene Rf_2 under field conditions is similar to that of Rf_1, both quantitatively and qualitatively, but the gene Rf_2 is less influenced by greenhouse conditions.

Table 7. Segregation ratios of fertile and sterile plants in F_2 and test-cross (sterile × F_1) generations of diallelic crosses between eight pollen fertility restorer lines (Fundulea, greenhouses 1975, field 1976).

Restorers	Testing place	DV-10275		SL-7-1-232		T-66006-2-1B		CF-11-73C MO-1338			ND-7227	
		F_2	t. cross	F_2	t. cross	F_2	t. cross	F_2	F_2	t. cross	F_2	t. cross
MZ-1398	greenhouses	47:0	58:0	39:0	73:0						47:0	
	field		41:0[1]	61:0	22:0	19:0 (15:1)	74:20 (3:1)		81:10 (15:1)		45:13[2] (3:1)	38:1
DV-10275	greenhouses			33:0	53:0			41:2[1] (15:1)	23:2[1] (3:1)	34:14[1]	36:0	70:0
	field				42:2	80:9 (15:1)	86:36 (3:1)	68:4 (15:1)	31:2 (15:1)		40:0	
SL-71-232	greenhouses					37:3 (15:1)	68:16 (3:1)					
	field	48:0	84:1				94:24 (3:1)			51:20 (3:1)	51:12[2] (3:1)	36:21[2] (1:1)
T-66006-2-1-B	greenhouses	41:2 (15:1)	71:23 (3:1)									
	field		68:26 (3:1)	74:7 (15:1)	99:38 (3:1)				46:0	29:0	37:1 (15:1)	77:36 (3:1)
CF-11-73 C	greenhouses			46:20[2] (3:1)	18:14[2] (1:1)							
	field	40:2[1] (15:1)			14:8 (1:1)	34:3 (15:1)	53:13 (3:1)					79:34 (3:1)
MO-1356	greenhouses	28:3[1] (15:1)	21:9 (3:1)	19:0 (15:1)	38:20 (3:1)							
	field		63:18 (3:1)	41:2 (15:1)	43:23 (3:1)	19:0 (15:1)	69:27 (3:1)		51:4[1] (15:1)			

[1] The partially fertile plants have been considered fertile.
[2] The plant used in F_1 was heterozygous for one *Rf* gene.
Gene Rf_2, Gene Rf_1

The lines CF-11-73-C and MO-1356 seem to carry another *Rf* gene causing to assume the existence of more than two independent major genes for pollen fertility restoration.

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