Genetic Relationship between Pollen Fertility Restoring Genes and Cytoplasmic Factors in the Male Sterile Mutants of Sugar Beets¹⁾

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A specific relationship between the nuclear genes and the genetic factors of cytoplasm as a consequence of cytoplasmic mutation was confirmed from the genetic interaction between the pollen fertility restoring genes and the sterile cytoplasm which were induced by gamma irradiation from the normal (*N*) cytoplasm.

The two complementary genes *Rf*₄ and *Rf*₅ responsible for *S*_{*i*-2} cytoplasm were different from those for *S* cytoplasm of spontaneous origin, and *F*₃ lines having a genotype *S*_{*i*-2} *Rf*₄*Rf*₄ *Rf*₅*Rf*₅ were bred true to the pollen fertility restored types, *N* or *S.S.a*. In the pollen fertility restoration for *S*_{*i*-3} cytoplasm, an epistatic relation of two alleles (*Rf*₆ and *Rf*₇) which are different from *S* and *S*_{*i*-2} showed various segregation ratios depending on parental genotypes. Although the segregation mode of two additive genes was similar to those in *S* cytoplasm, the new genes *Rf*₈ and *Rf*₉ were responsible for *S*_{*i*-4} cytoplasm. Thus there is the specific relation between the pollen fertility restoring genes and the genetic factors of the male sterile cytoplasm.

It is probable that the cytoplasmic mutations occurred in the strain H-2002 which contains normal (*N*) cytoplasm and diverse genotypes on pollen restoration and then the combination between the altered cytoplasm and the recessive type of the specific pollen fertility restoring genes indicated male sterility. If the maintainer and fertility restorer lines for the induced cytoplasm were selected based on the inheritance mode of pollen fertility restoration, they are also available for the use of the male sterility in hybrid seed production.

Introduction

Many examples of cytoplasmic inheritance in male sterility and plastids have been found in a wide variety of plants. However, the knowledges of the nature of cytoplasmic or plasmagenes such as location, segregation, recombination and mutation are quite limited.

In the cytoplasmic male sterility, the interaction between the nuclear genes and genetic factors of cytoplasm control the diverse expression of sterility (EDWARDSON 1970). Cytoplasmic or plasmon mutations which occurred spontaneously from *S* to normal (*N*) cytoplasm were demonstrated in maize and pearl millet (SINGH and LAUGHNAN 1972, CLEMENT 1975).

The author and TAKAHASHI (1969) also induced the cytoplasmic male sterility by gamma irradiation in sugar beets. In the course of investigation on the mode of inheritance, the author proposed a hypothesis in which a specific relationship exists between the nuclear genes and the genetic factors of the male sterile cytoplasm as a probable consequence of the cytoplasmic mutation (KINOSHITA 1976). On the basis of the genic assumption the present paper deals with the identification of nuclear genes responsible for the pollen fertility

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restoration under the three types of the induced cytoplasms.

Materials and Methods

The list and description of the male sterile lines and pollen parents are given in Table 1. Test strains used as pollen parents consisted of two 0-type strains and a multigerm strain H-2002 with normal (*N*) cytoplasm. The genotype of the former strains are known as *N rf₁rf₁ rf₂rf₂* and those of the later strain were examined by test crossings with the male sterile strain W162A4 which has a known genotype *S rf₁rf₁ rf₂rf₂*. Complete sterile plants in *M*₃ generations of *r*-lines were used as female parents when crossing with the plants of the tester strains. A numeral attached to the name of the strains means the individual plant number, while hyphenated numeral indicates the family record in each of the *r*-lines.

In most of the crossings, segregation on male sterility occurred in *F*₁ populations. Therefore, the genic analyses were carried out using *F*₁ and the later generations (*F*₂ and *F*₃). It was possible to produce the seeds by self fertilization of *N* and *S.S.a* type plants in *F*₁ and *F*₂ generations in the crosses involving the strain W162-6. Plants of the segregating populations were grown in the fields of the Faculty of Agriculture, Hokkaido University.

The degrees of male sterility were classified into the four types which were applied in the previous papers, namely normal (*N*), semi-sterile type-a (*S.S.a*), semi-sterile type-b (*S.S.b*) and complete sterile (*C.S.*). *N* and *S.S.a* type plants were grouped to a male fertile type (*M.F.*) for the verification of the segregation mode.

Results

1. Pollen fertility restoring genes interacting with *S_{i-2}* cytoplasm.

It is assumed that the two complementary genes are responsible for *S_{i-2}* cytoplasm and the recessive allele is epistatic to the dominant allele in the other locus. Since the pollen fertility restoration occurred in *F*₁ of the crossing between a complete sterile plant from

Table 1. List of lines or strains used

Line or strain	Type of cytoplasm	Description
<i>r</i> -60	<i>S_{i-2}</i>	Male sterile line induced by gamma irradiation from H-2002
<i>r</i> -114	<i>S_{i-4}</i>	do
<i>r</i> -130	<i>S_{i-3}</i>	do
<i>r</i> -165	<i>S_{i-3}</i>	do
W162A4	<i>S</i>	Male sterile strain, red pigmentation of leaves and roots, introduced from U.S.A.
W162-6	<i>N</i>	Type-0 plants, maintainer of W162A4, self fertile, introduced from U.S.A.
TK-81-0	<i>N</i>	Type-0 plants, maintainer of TK-81-MS, monogerm strain introduced from Hokkaido Agr. Exp. Station
H-2002	<i>N</i>	Multigerm strain selected from the variety 'Donyu-2go'

γ -60 and a type-0 plant W162-6 : 1, it appears that W162-6 : 1 possesses the dominant genes in a heterozygous state besides the homozygous condition of rf_1 and rf_2 . If the genes are postulated as Rf_4 and Rf_5 , the genotypes of W162-6 : 1 and γ -60 : 213-69 are estimated as $N Rf_4rf_4 Rf_5rf_5$ and $S_{i-2} rf_4rf_4 Rf_5rf_5$ respectively based on the segregations in F_1 and F_2 s. As shown in Table 2, segregation ratios of 3 : 1 : 4, 9 : 3 : 4 and 1 : 1 : 2 for M.F. : S.S. b : C.S. were fairly well satisfied through F_1 and F_2 generations. Thus it was ascertained that the nuclear genes Rf_4 and Rf_5 are responsible for the restoration of pollen fertility when they co-exist with S_{i-2} . In addition, the selection of pollen fertility restorers was attempted in F_3 generation. Forty-eight F_3 lines were produced from the selfing of N or S.S.a type plants which were chosen at random in F_2 and six lines bred true to N or S.S.a types although a few plants showing low fertility were occasionally seen (Table 3 and 4). It is certain that the effects of modifiers and environmental conditions affect the fertility. Segregation of F_3 lines was a close fit to the expected ratio based on the genotypes of F_2 plants.

Table 2. Segregations of male sterility in the progenies of the cross between a C. S. type plant γ -60 : 213-69 and a type-0 plant W162-6 : 1

Cross type	Generation		Phenotype			Total	Goodness of fit		
			M. F.	S. S. b	C. S.		χ^2	d. f.	P
		Genotype	Rf_4-Rf_5	$Rf_4-rf_5rf_5$	$rf_4rf_4Rf_5-Rf_4-rf_5rf_5$				
C. S. $\times$ N	F_1	Obs. Calc. (3 : 1 : 4)	38 34.88	15 11.63	40 46.50	93 93.01	2.17	2	0.3~0.5
N self.	F_2	Obs. Calc. (9 : 3 : 4)	159 181.13	63 60.38	100 80.50	322 322.01	7.54	2	0.02~0.05
N self.	F_2	Obs. Calc. (9 : 3 : 4)	268 259.88	87 86.63	107 115.50	462 462.01	0.88	2	0.5~0.7
C. S. $\times$ N	F_2	Obs. Calc. (1 : 1 : 2)	41 49.25	40 49.25	116 98.50	197 197.00	6.23	2	0.02~0.05

Genotype : γ -60 : 213-69 ($S_{i-2} rf_4rf_4 Rf_5rf_5$), W162-6 : 1 ($N Rf_4rf_4 Rf_5rf_5$),

Table 3. Selection of pollen fertility restorer lines in F_3 from selfing of male fertile plants in F_2 of the cross γ -60 : 213-69 (C. S.) $\times$ W162-6 : 1

F_3 group	Type of segregation	No. of lines observed	Expected No. (1 : 2 : 2 : 4)
	M. F. : S. S. b : C. S.		
Fert. restored	1 : 0 : 0	6	5.33
Seg. (M. F. : C. S.)	3 : 0 : 1	7	10.67
" (M. F. : S. S. b)	3 : 1 : 0	12	10.67
" (M. F. : S. S. b : C. S.)	9 : 3 : 4	23	21.33
	Total	48	48.00

$\chi^2=1.64$, d. f.=3, $P=0.5-0.7$.

Table 4. Frequency distribution of pollen fertility in six F_3 lines bred true to N or S.S.a types

F_3 line	Pollen fertility (%)										Total	Average (%)
	95	85	75	65	55	45	35	25	15	5		
131	33	3	1	2	0	1	0	0	0	0	40	91.0
182	15	3	3	5	2	3	3	1	0	1	36	72.5
185	17	0	1	0	0	0	0	0	0	0	18	93.9
191	13	3	2	1	0	0	1	0	0	1	21	83.1
195	15	4	3	4	2	0	0	0	1	1	30	79.3
230	18	3	3	1	0	0	0	0	0	0	25	90.2

 $F_3 : \gamma-60 : 213-69(C.S.) \times W162-6 : 1$ **2. Pollen fertility restoring genes interacting with S_{i-3} cytoplasm.**

When the pollen parent W162-6 : 1 is crossed with a complete sterile plant from $\gamma-165$, pollen fertility restoration occurred in F_1 plants because of the participation of a dominant gene which is different with rf_1 and rf_2 . As the segregation of F_1 plants was monogenic, the dominant gene differed from Rf_4 and Rf_5 which segregated in the former cross (Table 5). The monogenic ratio, 1 : 1 was also indicated in F_2 from the crossing C.S. $\times$ N when S.S.b type was grouped with N or S.S.a types. It is estimated that the segregation occurred in one of the fundamental genes, Rf_6 or Rf_7 .

Table 5. Segregations of male sterility in the progenies of the cross $\gamma-165 : 461-203$ (C.S.) $\times$ W162-6 : 1 (N)

Cross type	Generation		Phenotype			Total	Goodness of fit		
			M. F.	S. S. b	C. S.		χ^2	d. f.	P
C. S. $\times$ N	F_1	Genotype	$Rf_6-rf_7rf_7$ rf_6rf_6 rf_7rf_7			49 49.00	0.51	1	0.3~0.5
		Obs.	26	1					
		Calc. (1 : 0 : 1)	27 24.50		22 24.50				
C. S. $\times$ N	F_2	Genotype	$Rf_6-rf_7rf_7$ rf_6rf_6 rf_7rf_7			252 252.00	0.14	1	0.7~0.8
		Obs.	112	17					
		Calc. (1 : 0 : 1)	129 126.00		123 126.00				

Genotype : $\gamma-165 : 461-203$ (S_{i-3} rf_6rf_6 rf_7rf_7), W162-6 : 1 (N Rf_6rf_6 rf_7rf_7).Table 6. Estimation of genotype of pollen parents by the test crosses with the complete sterile strain W162A : 4 having a known genotype, S rf_1rf_1 rf_2rf_2

Cross combi.		Phenotype			Total	Goodness of fit		
		M. F.	S. S. b	C. S.		χ^2	d. f.	P
W162A : 4 $\times$ H-2002 : 5	Genotype	Rf_1rf_1 rf_2rf_2 rf_1rf_1 rf_2rf_2			115 115.00	4.60	1	0.02~0.05
	Obs.	2	67					
	Calc. (1 : 1)	69 57.5		46 57.5				
W162A : 4 $\times$ H-2002 : 6	Genotype	Rf_1rf_1 rf_2rf_2 rf_1rf_1 rf_2rf_2			49 49.0	1.00	1	0.3~0.5
	Obs.	5	23					
	Calc. (1 : 1)	28 24.5		21 24.5				

Genotype : H-2002 : 5 and H-2002 : 6 (N Rf_1rf_1 rf_2rf_2).

In the previous paper (KINOSHITA 1976), two dominant genes were found to be responsible for S_{i-3} cytoplasm and the dominant allele in one locus was epistatic to the recessive in the other locus showing a ratio of 12 : 3 : 1 in F_2 . Crossing experiments were carried out using the sterile plants from γ -130 and γ -165 and the pollen parents, H-2002 : 5 and H-2002 : 6. First, the genotype of pollen parents was examined by the crossing with the male sterile line having a known genotype $S\ rf_1rf_1\ rf_2rf_2$. As shown in Table 6, the segregation modes of F_1 were readily explained if a genotype of $N\ Rf_1rf_1\ rf_2rf_2$ or $N\ rf_1rf_1\ Rf_2rf_2$ is given for H-2002 : 5 and H-2002 : 6. In the crosses γ -130 : 419-581 $\times$ H-2002 : 5 and γ -165 : 465-473 $\times$ H-2002 : 5, the segregation mode in F_1 was monogenic and an F_2 population indicated a digenic segregation showing a ratio of N, S.S.a : S.S.b : C.S. = 12 : 3 : 1 (Table 7). Assuming that the genotype of the pollen parent is $N\ Rf_6rf_6\ Rf_7Rf_7$, then the above ratios are expected based on the assumption of the allelic interaction. In contrast with this, digenic segregation ratios were obtained through F_1 and F_2 generations when H-2002 : 6 was used as a pollen parent (Table 8). If H-2002 : 6 possesses the genotype of

Table 7. Segregations of male sterility in the progenies of the crosses between C.S. type plants from γ -130 and γ -165 and the pollen parent H-2002 : 5

Cross combi	Cross type	Generation		Phenotype			Total	Goodness of fit		
				M. F.	S. S. b	C. S.		χ^2	d. f.	P
γ -130 : 419-581 $\times$ H-2002 : 5	C. S. $\times$ N	F_1	Genotype	Rf_6-Rf_7- $Rf_6-rf_7rf_7$	$rf_6rf_6-Rf_7-$ $rf_6rf_6\ rf_7rf_7$	$rf_6rf_6\ rf_7rf_7$				
			Obs.	39	33	0	72			
			Calc.	36.00	36.00	0	72.00	0.50	1	0.3~0.5
			(1 : 1 : 0)							
	N $\times$ N	F_2	Obs.	35	10	4	49			
			Calc.	36.75	9.19	3.06	49.00	0.33	1*	0.5~0.7
			(12 : 3 : 1)							
γ -165 : 465-473 $\times$ H-2002 : 5	C. S. $\times$ N	F_1	Obs.	30	26	0	56			
			Calc.	28.00	28.00	0	56.00	0.29	1	0.5~0.7
			(1 : 1 : 0)							

Genotype : γ -130 : 419-581 and γ -165 : 465-473 ($S_{i-3}\ rf_6rf_6\ rf_7rf_7$), H-2002 : 5 ($N\ Rf_6rf_6\ Rf_7Rf_7$).

* C. S. type was included in S. S. b in the calculation of chi-square.

Table 8. Segregations of male sterility in the progenies of the cross γ -130 : 419-544 (C. S.) $\times$ H-2002 : 6

Cross type	Generation		Phenotype			Total	Goodness of fit		
			M. F.	S. S. b	C. S.		χ^2	d. f.	P
C. S. $\times$ N	F_1	Genotype	Rf_6-Rf_7- $Rf_6-rf_7rf_7$	$rf_6rf_6-Rf_7-$ $rf_6rf_6\ rf_7rf_7$	$rf_6rf_6\ rf_7rf_7$				
		Obs.	72	31	14	117			
		Calc.	58.50	29.25	29.25	117.00	11.17	2	0.001~0.01
		(2 : 1 : 1)							
C. S. $\times$ N	F_2	Obs.	79	47	56	182			
		Calc.	91.00	45.50	45.50	182.00	4.05	2	0.1~0.2
		(2 : 1 : 1)							
N $\times$ N	F_2	Obs.	85	41	10	136			
		Calc.	102.00	25.50	8.50	136.00	12.52	2	0.001~0.01
		(12 : 3 : 1)							

Genotype : γ -130 : 419-544 ($S_{i-3}\ rf_6rf_6\ rf_7rf_7$), H-2002 : 6 ($N\ Rf_6rf_6\ Rf_7rf_7$).

$N Rf_6rf_6 Rf_7rf_7$, a segregation ratio, 2:1:1 is expected from the crossing between $S_{i-3} rf_6rf_6 rf_7rf_7$ and $N Rf_6rf_6 Rf_7rf_7$. An F_2 ratio of 12:3:1 was also found in the inter-crossings of N type plants although the fitness was somewhat awry. Thus, two genes Rf_6 and Rf_7 which are different with the pollen fertility restoring genes for S and S_{i-2} were responsible for S_{i-3} cytoplasm.

3. Pollen fertility restoration interacting with S_{i-4} cytoplasm.

In F_1 plants of the cross $r-114:778:1 \times TK-81-0:1$, pollen fertility restored types, N and S.S.a were produced by the segregation of the genes other than rf_1 and rf_2 . If $TK-81-0:1$ possesses the genes Rf_8 and Rf_9 in a heterozygous state, namely $N Rf_8rf_8 Rf_9rf_9$, the digenic segregation ratios such as 1:2:1 and 9:6:1 are expected in F_1 and F_2 families.

Table 9. Segregations of male sterility in the progenies of the cross $r-114:778-1$ (C.S.) $\times$ $TK-81-0:1$ (N)

Cross type	Generation		Phenotype			Total	Goodness of fit		
			M. F.	S. S. b	C. S.		χ^2	d. f.	P
		Genotype	Rf_8-Rf_9-	$Rf_8-rf_9rf_9$ $rf_8rf_8Rf_9-$	$rf_8rf_8rf_9rf_9$				
C. S. $\times$ N	F_1	Obs.	32	68	60	160			
		Calc.	40.00	80.00	40.00	160.00	13.40	2	0.001~0.01
		(1:2:1)							
N $\times$ N	F_2	Obs.	26	16	6	48			
		Calc.	27.00	18.00	3.00	48.00	0.08	1*	0.7~0.8
		(9:6:1)							
C. S. $\times$ N	F_2	Obs.	36	65	40	141			
		Calc.	35.25	70.50	35.25	141.00	1.09	2	0.5~0.7
		(1:2:1)							
C. S. $\times$ N	F_2	Obs.	14	27	16	57			
		Calc.	14.25	28.50	14.25	57.00	0.30	2	0.8~0.9
		(1:2:1)							

Genotype: $r-114:778:1$ ($S_{i-4} rf_8rf_8rf_9rf_9$), $TK-81-0:1$ ($N Rf_8rf_8 Rf_9rf_9$).

* C. S. type was included in S. S. b in the calculation of chi-square.

Table 10. Independent relation between the genes for plant coloration and pollen fertility restoration

Cross combi.	Cross type		Colored		Colorless		Total	Recombination value (%)	Goodness of fit		
			M. F.	C. S.	M. F.	C. S.			χ^2	d. f.	P
$r-60:213-69$ $\times$ $W162-6:1$ F_2	N Self.	Obs.	161	78	61	22	322				
		Calc.	181.13	60.38	60.38	20.13	322.02	54.2	7.56	3	0.05~0.1
		(9:3:3:1)									
	N Self.	Obs.	252	78	103	29	462				
		Calc.	259.88	86.63	86.63	28.88	462.02	51.3	4.19	3	0.2~0.3
		(9:3:3:1)									
	C. S. $\times$ N	Obs.	64	90	17	26	197				
		Calc.	73.88	73.88	24.63	24.63	197.02	48.4	7.28	3	0.05~0.1
		(3:3:1:1)									
$r-165:461-203$ $\times$ $W162-6:1$ F_2	N Self.	Obs.	192	76	42	21	331				
		Calc.	186.19	62.06	62.06	20.69	331.00	46.7	9.80	3	0.02~0.05
		(9:3:3:1)									
	C. S. $\times$ N	Obs.	104	100	25	23	252				
		Calc.	94.50	94.50	31.50	31.50	252.00	50.8	4.91	3	0.1~0.2
		(3:3:1:1)									

Table 11. Independent relation between the genes for monogerm and pollen fertility restoration

F₂: γ -114 : 778 : 1 (C. S.) $\times$ TK-81-0 : 1 (N) : repulsion

Cross type		Multigerm		Monogerm		Total	Recombination value (%)	Goodness of fit		
		M. F.	M. S.	M. F.	M. S.			χ^2	d. f.	P
N $\times$ N	Obs.	17	14	9	8	48	51.9	2.91	3	0.3~0.5
	Calc. (27 : 21 : 9 : 7)	20.25	15.75	6.75	5.25	48.00				
C. S. $\times$ N	Obs.	70	28	31	12	141	49.5	3.13	3	0.3~0.5
	Calc. (9 : 3 : 3 : 1)	79.31	26.44	26.44	8.81	141.00				
C. S. $\times$ N	Obs.	28	12	13	4	57	45.3	1.21	2*	0.5~0.7
	Calc. (9 : 3 : 3 : 1)	32.06	10.69	10.69	3.56	57.00				

M. F. ... Male fertile type; M. S. ... Male sterile type. In the first cross, M. S. contains S. S. b and C. S., while S. S. b is included in M. F. in the other crosses.

* M. S. and M. F. in 'Monogerm' were put together in the calculation of chi-square.

As shown in Table 9, the observed numbers of four populations were a close fit to the calculated numbers. Although the segregation mode caused by the two additive genes was similar to those in S cytoplasm, the new genes Rf_8 and Rf_9 were responsible for S_{i-4} cytoplasm.

4. Genetic association between pollen fertility restoration and other characters.

In F₂ populations of the cross γ -60 : 213-69 $\times$ W162-6 : 1, an independent relation was recognized between the genes for pollen restoration and pigmentation of root and leaves (Table 10). A similar relation was obtained in the cross γ -165 : 461-203 $\times$ W162-6 : 1. As reported in the previous paper (KINOSHITA 1976), the pollen restoring genes Rf_8 and Rf_9 showed an independent relation with the gene m for monogerm character in the cross γ -114 : 778 : 1 $\times$ TK-81-0 : 1 (Table 11). Therefore, the results support the assumption that the genes other than Rf_1 locus are responsible for the pollen fertility restoration under S_{i-4} cytoplasm.

Discussion

In the previous paper (KINOSHITA and TAKAHASHI 1969), it was reported that a single gene Rf_3 was responsible for the pollen fertility restoration when it co-existed with the cytoplasmic factor S_{i-1} , which was named as S' formerly. In this paper, it was indicated that six kinds of pollen fertility restoring genes which are allotted two at one cytoplasm were estimated from the genic analyses on the pollen fertility restoration under three different cytoplasm. The specific relation between the pollen fertility restoring genes and the cytoplasmic factors is shown diagrammatically in Fig. 1. The set of pollen restoring genes which acts to one out of the four sterile cytoplasm does not act effectively to the other cytoplasm. In the pollen fertility restoring genes for S_{i-2} cytoplasm, the recessive gene rf_4 was epistatic to the dominant gene Rf_5 , while the dominant gene Rf_6 was epistatic to the recessive gene rf_7 for S_{i-3} cytoplasm. The genes Rf_8 and Rf_9 for S_{i-4} showed an

Fig.1. "One set of pollen fertility restoring genes for one cytoplasm" relation in the male sterile mutants. S_{i-2} , S_{i-3} and S_{i-4} were induced by gamma irradiation from normal (N) cytoplasm and S occurred spontaneously.

—X— showing different cytoplasm and pollen fertility restoring genes.

additive effect as well as Rf_1 and Rf_2 for S cytoplasm. It is probable that the cytoplasmic mutations occurred in the strain H-2002 which consisted of normal (N) cytoplasm and diverse genotypes on pollen fertility restoration, and a specific combination between the altered cytoplasm and the recessive type of pollen fertility restoring genes corresponding to the induced cytoplasm indicated male sterility. Therefore, it may be possible to select the maintainer and fertility restorer lines with normal (N) cytoplasm from the original populations and other strains. They are available for production of the double-cross hybrid seeds according to the method proposed by THEURER (1969).

The evidences for genetic difference of cytoplasm are shown in the cytoplasmic male sterilities of maize (BECKETT 1971). Through the studies of the cytoplasm substitution lines

of wheat, the effects of alien cytoplasm are detected on various characters (TSUNEWAKI and ENDO 1973, ENDO and TSUNEWAKI 1975). MICHAELIS (1966) emphasized that the proofs of the cytoplasmic inheritance should not be the final result, for it is only the basis for the real investigation of the genetic nature of cytoplasmic units. CLEMENT (1975) also pointed out that it is possible to obtain the isoplasmic lines which have the same genotype except for the difference of cytoplasm by a plasmon mutation. Thus, it is promising to utilize the cytoplasmic mutants which are induced by artificial mutagens, not only for the studies of cytoplasmic inheritance, but also for the practical breeding such as the use of multiplasms (GROGAN 1971).

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てん菜の雄性不稔突然変異における細胞質 因子と花粉稔性回復遺伝子の関係

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ガンマー線照射によって、正常型細胞質 (N) より誘発された3種の不稔細胞質 (S_{i-2} , S_{i-3} および S_{i-4}) にそれぞれ対応する花粉稔性回復核遺伝子について遺伝子分析を行うと共に、細胞質因子と核遺伝子の相互作用について検討した。

検定花粉親系統には、 S 細胞質 (自然起源の不稔細胞質) に対する O 型 ($N\ rf_1\ rf_1\ rf_2\ rf_2$) である W162-6 および TK-81-0 の2系統とあらかじめ完全不稔型検定系統 W162A4 ($S\ rf_1\ rf_1\ rf_2\ rf_2$) との交雑実験により遺伝子型を明らかにした正常細胞質系統2個体、H-2002 : 5 および H-2002 : 6 を用いた。3種の突然変異系統 (r -系統) からの完全不稔個体を母本として交雑実験を行ない、 F_1 および F_2 における花粉稔性回復型の分離を調べ、各花粉親系統がガンマー線誘発の不稔細胞質に対応する花粉稔性回復遺伝子をヘテロに保有する事を明らかにした。また、 S_{i-2} 細胞質には、 S 細胞質に対する Rf_1 および Rf_2 と異なる2種の稔性回復遺伝子 (Rf_4 および Rf_5) が関与し、 rf_4 は Rf_5 に対して上位性を示した。 S_{i-3} 細胞質には Rf_6 および Rf_7 の2種の稔性回復遺伝子が関与し、 Rf_6 は rf_7 に対し上位に働き、それらは S あるいは S_{i-2} 細胞質に働く稔性回復遺伝子と異なる遺伝子であった。 S_{i-4} 細胞質に作用する稔性回復遺伝子の F_2 分離様式は S 細胞質における場合と同一であったが、 S に対する O 型系統を交配すると、 F_1 には正常型や半不稔-a 型を分離し、 Rf_1 および Rf_2 とは異なる遺伝子、 Rf_8 および Rf_9 が稔性回復にそれぞれ相加的に作用していた。

この様に不稔細胞質にはそれぞれ特有の花粉稔性回復遺伝子組が対応し (Fig. 1), 各不稔細胞質に対する稔性回復機構は、すべて前報における遺伝仮説 (木下 1976) に従っていた。H-2002 および2種の O 型系統はいずれも新しい不稔細胞質に対する稔性回復遺伝子をヘテロに保有していたので、それらの後代では各不稔細胞質に対応する不稔維持系統ならびに稔性回復系統を育成する事も可能であると考えられる。

細胞質突然変異の機構については、ガンマー線照射によって、まず、原系統 H-2002 の N 細胞質に何らかの変化を生じて、 S_{i-2} , S_{i-3} および S_{i-4} なる不稔細胞質型が誘起され、それらの不稔細胞質と特定の関係にある稔性回復遺伝子について2重劣性や単純劣性である個体が M_2 あるいは M_3 代で不稔性を示したと考えられる。

人為的な細胞質突然変異の誘発は、細胞質遺伝に関する基礎的な問題の解明に寄与するのみならず、遺伝的に多様な不稔細胞質型を作出できることから、トウモロコシで提唱されているような複数種の不稔細胞質を混合して利用する様な育種方式には極めて有用であると考えられる。