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Cytoplasmic Male Sterility in *Vicia faba* L.

Part 6: Genetical Arguments for Cytoplasmic Heterogeneity

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Summary. In many higher plants, nucleo-cytoplasmic interactions lead to pollen abortion. In *Vicia faba,* cytoplasmic male sterility is unstable as the cytoplasm appears to shift from a sterile to a fertile state. In this report, five flower phenotypes are defined but the study is focussed on the progenies obtained from intermediate, semi-sterile plants with the same homozygous nuclear constitution during five successive generations. The results could be interpreted by quantitative modifications of at least four different kinds of cytoplasmic determinants.

Key words: *Vicia faba* – Cytoplasmic male sterility – Cytoplasmic inheritance – Plasmon

Introduction

Nucleo-cytoplasmic male sterility is frequently encountered in higher plants (Edwardson 1970; Laser and Lersten 1972). It was found in *Vicia faba* by Bond in 1957.

According to several authors (Bond et al. 1966; Berthelem 1970; Picard 1972; Berthelem and Le Guen 1974) the cytoplasm, known as '447', presents three peculiarities. First, some male fertile flowers may appear on male sterile plants; this is termed "somatic reversion". Second, '447' cytoplasm is unstable and gives rise to male fertile plants in the progenies of crosses between cytoplasmic male sterile (cms) and maintainer lines (maintainer for male sterility, no restorer factors in the genotype). Third, the restoration is "permanent" and is due to one dominant *Rf* major gene. One quarter male sterile plants are expected in the F2 of the hybrid between cms and restorer lines, but nearly all F2 plants are fertile with the frequency of exceptions ranging from 0 to 3 out of 700 (Bond et al. 1966).

Pollen from fertile plants or fertile sectors of plants described in the first two cases, and from about one quarter of the F2 plants in the third case, give the same offspring as a maintainer when tested on a cms line. Since this fact excludes a nuclear mutation from *rf* to *Rf,* the three peculiarities could be, therefore, interpretated as an alteration of the cytoplasm from a sterile to a fertile state.

We chose to study the instability of the male sterile phenotype in a cms line. To avoid, or at least minimize, nuclear determinants, the observations and experiments were performed with plants from a ninth back-cross, i.e. plants in a supposed homozygous nuclear state.

Previous experiments can be summarized as follows. (1) The flower phenotypes of a cms line show considerable heterogeneity. Plants may be S (male sterile), F (male fertile) or I (intermediate, neither S nor F), in addition some plants are initially only S then the I phenotype appears simultaneously on their different tillers (SVI plants) (Thiellement 1977 b). (2) This phenotypic heterogeneity reflects genetical modifications since there are differences between the proportions of the various phenotypes in the progenies from S, I or F plants, and from S or I sectors of SVI plants (Thiellement 1977 c). (3) Variability between individual offspring from plants of the same phenotypic class may be partly explained by a grandmother effect where the progeny phenotypes depend upon the phenotype of the mother plant but also upon the phenotype of the grandmother plant (Thiellement 1979 a, 1979 b). (4) Comparison of the progenies from one mother plant pollinated by different pollen sources showed no paternal effect (Thiellement 1979 b). (5) Two distinct plant phenotypes in the I class (see Material and Methods) gave different progenies (Thiellement 1980).

When rules deduced from the overall results were applied to individual progenies and genealogy, we found that there was no substantiation of a previously suggested hypothesis according to which various proportions of two plasmons, S and F, coexist in the cytoplasm of an unstable cms line of faba bean (Thiellement 1977 a, 1980).

This paper reports the observations made on the fifth generation from the ninth back-cross. By demonstrating the inheritance of new intermediate phenotypes, and taking into account the phenotypic frequencies during five generations, we propose an alternative interpretation. The flower phenotype is the reflection of a nucleocytoplasmic state which is defined, in the homozygous nuclear condition, by variable amounts of at least four genetically different kinds of cytoplasmic determinants.

Materials and Methods

See also Thiellement (1977 b, 1979 b) for more details.

Material: The ninth back-cross (BC9) of a spring type of faba bean 'Ad23', bred by Berthelem on the '447' cytoplasm, was provided by Picard (INRA).

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Classification of Flower Phenotypes: The phenotypes are defined by visual observation of the mature, unopened flowers: "S" for male-sterile with no pollen detectable and shrunken grey- brown stamens; "F" for male-fertile with abundant white pollen and usually black stamens; "I" for intermediate, semi-sterile flowers. In addition, after the F11 generation, we took into account another flower phenotype, which has black stamens with no pollen. Noted "Sn" (sterile noir), this phenotype was previously grouped in the I class since, most of the time, not every stamen was black, the others being grey-brown with few yellow pollen, i.e. "classical I" stamens (noted Ic). Alternatively, when all the stamens are black, this Sn flower is associated in the same inflorescence with Ic flowers.

Classification of Plant Phenotypes: Flowers on each tiller of each plant were observed approximately once each week during the flowering period. Since one plant can present different phenotypes we recorded: (1) an "S", "I", or "F" for a plant showing the same flower phenotype on all the tillers throughout the flowering period. (2) "SVI" for a plant showing a sterile to intermediate phenotype for all the tillers simultaneously. (3) "IVF" for plants with intermediate to fertile flowers and (4) an "X" for plants with different tillers having different phenotypes, eg. "S/F" denotes a plant with an S main tiller and an F for one or more secondary tillers. Among I plants and since the F11 generation, the plants showing frequent Sn stamens are recorded as "SnI" and those showing only Sn stamens are denoted "Sn". "Classical I" plants are noted "Ic".

Growth Conditions: The seeds are sterilized then sown in multipots. The plantlets are pricked out in a greenhouse and spaced 0.6 m between rows and 0.4 m within a row, allowing

Table 1. F_{13}: Progenies from F_{12} Sn, SnI, and I sister plants

F_{12} mother plants (phenotype)	Phenotypes					Number of plants
	SVI	I (Sn/SnI/Ic)	IVF	F	X	
(1) $C_2Z_2E_4D_3$ (Sn)	0	4 (0/ 3/ 1)	1	20	2	27
(2) $C_2Z_2E_4E_3$ (Sn)	0	10 (0/ 8/ 2)	0	16	4	30
(3) $C_2Z_2E_4F_1$ (Sn)	0	18 (1/16/ 1)	0	3	6	27
(4) $C_2Z_2E_4F_5$ (Ic)	0	13 (0/ 9/ 4)	0	13	1	27
(5) $F_1XI_6J_6B_4$ (Sn)	0	17 (4/13/ 0)	1	11	1	27
(6) $F_1XI_6J_6C_3$ (SnI)	0	7 (0/ 7/ 0)	0	13	0	20
(7) $F_1XI_6J_6E_1$ (SnI)	0	19 (0/ 9/10)	0	9	2	30
(8) $G_5H_2N_3G_2$ (Sn)	0	14 (3/ 9/ 2)	0	6	3	23
(9) $G_5H_2N_3H_1$ (Sn)	0	8 (0/ 7/ 1)	0	6	1	15
(10) $G_5H_2N_3C_4$ (Ic)	0	13 (0/ 3/10)	0	10	0	23
(11) $G_5H_2N_3D_6$ (Ic)	0	14 (0/ 0/14)	0	14	3	31
Total Sn	0	71 (8/56/ 7)	2	62	17	152
Total SnI	0	26 (0/16/10)	0	22	2	50
Total Ic	0	40 (0/12/28)	0	37	4	81
Frequencies Sn	0.00	0.47 (0.11/0.79/0.10)	0.01	0.41	0.11	152
Frequencies SnI	0.00	0.52 (0.00/0.62/0.38)	0.00	0.44	0.04	50
Frequencies Ic	0.00	0.49 (0.00/0.30/0.70)	0.00	0.46	0.05	81

individual observations and favouring the tillering of the plants. The photoperiod of the greenhouse is 16 hours.

Generations: The F 10 was obtained by open pollination of the BC 9 in isolation. F 11 I plants were obtained from the F 10 I plants able to give seeds from open pollination as well as from self pollination. The Ic and SnI plants of the F 11 gave the F 12 generation by open pollination. We found in this F 12 three distinct I plant phenotypes, Ic, SnI and Sn. The F 13 generation was obtained from open pollinated Sn, SnI or Ic sister plants.

Table 2. F_{13}: Progenies from F_{12}Ic plants chosen according to the segregation pattern of F_{11}Ic plants. Number of plants

Genealogy			F_{13} phenotypes		
F_{11}	F_{12} plants		I	F	X
$C_2Z_2E_1$	1 SVI	$C_2Z_2E_1A_5$ (Ic)	17	3	0
	16 I	$C_2Z_2E_1A_2$ (Ic)	10	3	1
	1 X				
$F_3N_1D_5$	7 I				
	7 F	$F_3N_1D_5C_1$ (Ic)	9	6	1
	2 X				
$F_1XI_6J_2$	6 I				
	10 F	$F_1XI_6J_2C_6$ (Ic)	9	9	0
	2 X				

Results

Inheritance of the Sn-Phenotype

To obtain information about heritability and stability of the new Sn phenotype, we sowed the progenies of the 6 F 12 Sn plants and compared them to those furnished by their F 12 SnI or Ic sister plants. The results are reported in Table 1.

In summing the progenies from Sn, SnI and Ic F 12 mother plants (three last lines of Table 1), two main remarks should be made: (1) no difference appears between the three groups of mother plants concerning the proportions of I, F, and X classes, in contrast with the F 12 observations (Thiellement 1980) and (2) the three phenotypic classes of mother plants gave different proportions of Sn, SnI and Ic plants in F 13 (within the I class), providing evidence for the heritability of these phenotypes. This inheritance is of the same unstable kind as the other (I, S) phenotypes.

However, as in the previous generations, when looking at individual progenies, a large variation is seen within each phenotypic class. One can, for instances note the numerous F plants arising from Sn plant 1, as compared with the very few F plants derived from sister Sn plant 3.

A Grandmother Effect in F13

We also investigated whether F 12 classical I plants, chosen in progenies of F 11 classical I plants differing by their segregation pattern could also be differentiated in F 13 i.e. whether the grand mother effect reoccurred. For this purpose, we compared two F 12 I plants from F 11 I plants which gave approximately the same number of I and F plants with two F 12 I plants arising from an F 11 I plant with no F progeny. The results obtained are described in Table 2. When the two types of progeny (C2 Z2 E1 A5 + C2 Z2 E1 A2 versus F3 N1 D5 C1 + F1 XI6 J2 C6) are compared for I and F classes, they appear to be different ($.05 > p > .01$). Thus, there is again a grandmother effect which determines in part the heterogeneity existing within the I class and within the "classical I" phenotypes.

Evolution of Phenotypic Frequencies

Table 3 presents the phenotypic frequencies obtained in F 10, F 11, F 12 and F 13 which show the evolution of the different progenies in the "classical I" genealogy. Table 4 shows the phenotypic frequencies obtained in the I genealogy, i.e. grouping Ic, SnI and Sn plants. In both tables, the SVI class decreases then disappears. The F class shows a relative stability or a small decrease and the I class of phenotype increases.

Table 3. Evolution of phenotypic frequencies in the genealogy of "classical I" plants

Generation (number of mother plants)	Phenotypes						Number of daughter plants
	S	SVI	I	IVF	F	X	
BC_9 (5)	0.00	0.11	0.28	0.05	0.52	0.04	80
F_{10} (9)	0.00	0.07	0.32	0.01	0.48	0.12	142
F_{11} (5)	0.00	0.01	0.37	0.00	0.56	0.06	104
F_{12} (7)	0.00	0.00	0.57	0.00	0.39	0.04	149

Table 4. Evolution of phenotypic frequencies in the genealogy of I plants (Ic + SnI + Sn)

Generation (number of mother plants)	Phenotypes						Number of daughter plants
	S	SVI	I	IVF	F	X	
BC_9 (6)	0.00	0.10	0.33	0.04	0.50	0.03	90
F_{10} (9)	0.00	0.07	0.32	0.01	0.48	0.12	142
F_{11} (11)	0.00	0.07	0.43	e	0.41	0.09	294
F_{12} (15)	0.00	0.00	0.52	e	0.41	0.07	349

Discussion

Instability of cms has been described in other higher plants such as maize (Singh and Laughnan 1972; Laughnan and Gabay 1973), pearl millet (Burton 1972, 1977; Clement 1975) and sunflower (Leclercq 1971, 1979; Vear 1980). For cms-S in maize as for the *Heliantus petiolaris* source in sunflower, the genetical analysis, dealing mostly with newly arisen restored condition, lead the authors (Laughnan and Gabay 1975; Vear 1980) to hypothesize the involvement of an episomial element. This F-episome, free in the cytoplasm (male sterile form) may move both into organellar DNA (mt-DNA) as suggested by biochemical analysis (Levings et al. 1980) and into nuclear DNA, defining two different patterns of genetical determinism, cytoplasmic, and mendelian.

In *Vicia faba,* the occurence of intermediate phenotypes as well as the phenotypic modification occuring simultaneously on different tillers of one plant (the SVI and IVF plants) lead us to prefer a working hypothesis of cytoplasmic heterogeneity (Thiellement 1977 a). This kind of hypothesis has also been developped by Demarly (1974).

As in other plant species, the pollen phenotype is defined in faba beans by nucleo-cytoplasmic interactions. To eliminate the effects of the nuclear part of this determination, we chose to work with supposedly homozygous plants of a ninth back-cross.

The extent of the phenotypic heterogeneity from the BC 9 onwards, together with the features of the somatic reversion (the SVI phenomenon) do not appear to be related to a reverse mutation from *rf* to *Rf*. Indirect evidence is also provided in F 11 (Thiellement 1979 b) since no pollen effect was observed, which excludes an unstable nuclear system. We assume that we are dealing here with genetical modifications occuring in the cytoplasm. We define three, then five, pollen phenotypes permitting a genetical analysis, but the phenomenon is quantitative. For this reason, we suggest that cytoplasmic states leading to pollen phenotypes are due to relative quantities of cytoplasmic determinants, plasmons, among which a selection pressure is acting towards male fertility.

According to the two plasmon hypothesis (Thiellement 1977 a), since SnI and Ic F 11 plants differ by their F 12 progeny (Thiellement 1980), one may admit that in SnI plants the S/F ratio is higher that in sister Ic plants. This is contradicted by individual progenies since an SnI plant can provide numerous F progenies and an Ic plant none. This is also in contradiction to the F 13 results reported above (Table 1) where Sn, SnI and Ic F 12 plants gave the same proportions of SVI, I, F and X progenies.

Looking at the evolution of phenotypic frequencies in I genealogy (Tables 3 and 4), the progressive decrease of the SVI class is not correlated with an increase of the F class. Therefore, fewer *S* plasmons do not mean more *F* plasmons. With the assumption, provided by data presented in Table 1, that the pollen phenotypes Sn and SnI are inherited, we suggest that two additional plasmons are involved: (1) *Sr,* for remodeled *S* plasmon with a selective value close to that of the *F* and higher that the *S;* and (2) *Srn,* with the same characteristic of selective value and which is involved in the manifestation of the Sn and SnI phenotypes.

According to these considerations, the I phenotype may result from different cytoplasmic mixtures such as [*S, F*], [*S, Sr, F*], [*S, Srn, Sr, F*], [*Srn, Sr, F*], [*Sr, F*]. This could explain the great variability between progenies from I plants. During the I generations (Table 3 and 4), the *Sr* and *Srn* plasmons increase in quantity, overcoming the *S* plasmons; SVI decrease, I increase and F remain the same. The grandmother effect is explained by the fact that I from SVI plants as well as X from S plants (Thiellement 1979 a, 1979 b) are mostly [*S, F*] mixtures, in which *F* plasmons easily overcome the *S*. Accordingly, I from I plants and X from I plants have, most of the time, a [*S, Sr, F*] cytoplasmic constitution in which selection pressure is weak on *Sr* and not so strong on *S* since more plasmons are involved. F 11 SnI plants may have [*S, Sr, Srn, F*] cytoplasmic components whereas F 11 Ic plants have mostly [*Sr, F*] with no more SVI progenies (Thiellement 1980). One generation later, F 12 SnI and F 12 Sn plants can be described as [*Sr, Srn, F*] while Ic plants are [*Sr, F*] with no SVI progeny either from Ic or from SnI and Sn (Table 1). The selection towards elimination of *S* plasmons is supposed less easy when more plasmons are involved.

What can be the molecular basis of those plasmons? This point is still puzzling, even in the best studied cases of cms. Arguments have been developed which suggest the involvement

of mitochondria in maize (Miller and Koeppe 1971; Warmke and Lee 1977; Forde et al. 1978; and others) and more precisely mt-DNA in maize (Levings and Pring 1976, 1978), in wheat (Quetier and Vedel 1977), in *Nicotiana* (Belliard et al. 1979) and in sorghum (Pring et al. 1980). Other arguments indicate a chloroplastic localisation as in barley (Ahokas 1978) or in *Gossypium* and *Nicotiana* (Chen and Meyer 1979). In other systems, as suggested for *Vicia faba* (Edwardson et al. 1976), a virus may be the cause of male sterility. With these few examples, no clear cut evidence is yet available and it seems likely that different mechanisms may be involved between or even within species. It has been suggested that cytoplasmic inheritance can be sometimes the result of the chromosomal state in the female gamete, i.e. of nuclear genes, the activity of which is dependant upon their own product in the cytoplasm (L'Heritier 1975). This implies strict maternal heredity, which is not the case in our results.

To suggest cytoplasmic heterogeneity, which accounts for all the so far observed results, does not appear a contradiction to our present knowledge of cytoplasmic heredity. Interesting analogies can be suggested dealing with other Eucaryotes, as hybrid dysgenesis in *Drosophila* (Picard 1971, 1976; Bucheton 1978; Kidwell and Kidwell 1975), or the incompatibility system in *Culex* (French 1970, 1978; Subbarao et al. 1977). In higher plants, recent data indeed suggest cytoplasmic molecular heterogeneity, for instance, in mt-DNA of maize (Levings et al. 1979) and soybean (Synenki et al. 1978) where amplification of one or several of the supposed "mitochromosomes" (Spruyll et al. 1980) may be involved.

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