NON-MENDELIAN FEMALE STERILITY IN *DROSOPHILA MELANOGASTER*: QUANTITATIVE VARIATIONS IN THE EFFICIENCY OF INDUCER AND REACTIVE STRAINS

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SUMMARY

Crosses between various strains of *Drosophila melanogaster* lead in some cases to a quite typical female sterility which involves non-mendelian hereditary factors. On the basis of the fertility of F_1 females, strains can be divided into three classes: Inducer, Reactive and Neutral. Females showing various degrees of sterility arise when reactive strain females are crossed to inducer males. The degree of sterility depends on the particular reactive and inducer strains used in the cross. Quantitative variations in the efficiency of inducer and reactive strains to produce sterile F_1 females are studied in the present paper. The results indicate that the order which can be established within a set of reactive strains for this efficiency is largely independent of the inducer strain which is chosen for the cross.

1. INTRODUCTION

WHEN systematic crosses are made between strains of *Drosophila melanogaster*, F_1 females occasionally display a quite specific sort of incomplete sterility. We are investigating this phenomenon and although our understanding of the mechanism involved is far from complete, it clearly lies outside classical chromosomal genetics (Picard and L'Héritier, 1971; Picard *et al.*, 1972*b*).

Females showing this kind of sterility are denoted in this paper *SF* females. They lay a normal number of eggs but frequently a large proportion develop no further than migration of the nuclei (about sixth mitosis of early cleavage). Those eggs which succeed in passing this critical stage complete their development and give rise to flies displaying normal viability. Nevertheless, these surviving offspring may also show the same type of sterility (unpublished data).

SF sterility may be identified by three specific features:

1. The level of sterility is reduced with aging of the female. Even when the hatching frequency is less than 1 per cent among the first-laid eggs, it becomes almost normal some 20 or 30 days later (Picard, 1971).
2. Sterility is most frequently observed at the usual breeding temperature of 20°C. When egg-laying females are kept at a temperature of about 30°C, the egg-hatching frequency rises quickly to a nearly normal level. The effect is reversible and sterility returns, when females are returned to 20°C (Picard, 1971).

3. The death of the eggs is an entirely maternal character and its frequency does not depend on the male with which the *SF* female is crossed. Mendelian segregations remain unchanged among the surviving offspring (unpublished data).

With such characteristics, *SF* sterility may easily remain unnoticed by workers interested in other problems. This may explain why, in spite of all the genetic studies on *Drosophila*, this striking phenomenon was mentioned, as far as we know, only once in the genetic literature (Rosenfeld *et al.*, 1971).

We made a survey of a large number of *Drosophila* strains to study their behaviour concerning *SF* sterility. Some of these strains have been established with flies caught quite recently in the wild, in different countries: Europe, Africa, West Indies. The others were laboratory strains carrying different genetic markers. From this survey, three classes of strains were separated. They were termed inducer, reactive and neutral strains (Picard *et al.*, 1972a).

The only crosses which give rise to sterile females are those between reactive females and inducer males. The reciprocal crosses (inducer females by reactive males), and all the crosses between strains of the same class, or involving a neutral strain, produce normally fertile offspring.

The three classes are quite unequal in size. Inducer strains are by far the most numerous. The 71 strains established with flies caught recently in the wild and about half of the 51 laboratory strains belong to this type, which therefore may be viewed as the normal condition in *Drosophila*. The reactive condition was found only in 26 laboratory strains. However, they were obtained from several quite different laboratories and their genotypes are quite different. The neutral class includes today only one strain.

The *SF* sterility which arises when reactive and inducer strains are crossed may be reviewed as a kind of incomplete genetic barrier, which now separates some of the old laboratory strains from the normal *Drosophila melanogaster*. The appearance of the reactive condition appears therefore as a speciation process, which may occur in small isolates in laboratory conditions. The mechanism of the transformation is at present entirely unknown.

Even when assayed on a sample of the first-laid eggs and at the uniform temperature of 20°C, the hatching frequency of the eggs from *SF* females varies within broad limits. It may be very low, below 1 per cent, and, at the other end of the range, reach the level normally observed in the crosses within the same class, about 95 per cent. No thorough analysis has yet been made of all the factors responsible for this broad variation. It may be considered as the sum of three components. A first interindividuals component is observed when sisters *SF* females from the same parents are compared. The variation which arises with the choice of an inducer male and/or of a reactive female within a strain makes a second component. The choice of the strains is the third component. From the beginning of the experimental work, this inter-strain component of variation was assumed to be very important.

To demonstrate that reactive strains may show different degrees of efficiency in producing sterility, the levels of sterility of *SF* females from the crosses between females of various reactive strains and males of the same inducer strain have been compared. Similarly, when differences between various inducer strains are to be shown, females of the same reactive strain must be used in the crosses.

An experiment was conducted in which all the possible crosses were made between females of 17 reactive strains and males of 19 inducer strains. To provide control crosses without sterility, the neutral strain was also used as maternal strain with each of the inducer strains, and as paternal strain with each of the reactive strains. We report and discuss the results of the experiment in this paper.

2. MATERIALS AND METHODS

Genetic symbols are those used by Lindsley and Grell (1967). Flies were grown at the temperature of 20°C, on the axenic food described by David (1959).

(i) *Stocks of Drosophila melanogaster used in the experiments*

(a) *Reactive strains.* These belong to two groups among which a difference in internal genetic variability may be expected.

The first group includes the following strains, maintained in laboratories for many years and bearing one or two recessive markers. Their historical origin cannot be known precisely:

e, *w*, *cn*, *bw*, *se*, *cn*; *bw*, *cn*; *e* and *bw*; *st*.

A second *e* strain from different origin was designed as *e_{st}*.

The second group includes inbred families which were established in this laboratory during the last three years, dating from some original reactive strains, with selection for or against the efficiency of the reactive character following a method previously described (Picard *et al.*, 1972a):

se F₁₂, *se₂₁*, *se₂₀₁₋₁₅* and *se f₁₂* were derived in this way from the *se* strain mentioned above.

e₉₈, *e_{st28}* and *e_{st121}* were derived in the same way from the above-mentioned *e* and *e_{st}* strains.

H.J.₂₄: Stock derived by selection from the wild type *Hikon* strain which is already used in Japan for genetic work.

(b) *Inducer strains.* The 19 inducer strains can similarly be separated into two groups.

The first group includes wild type strains, originating from a small number of flies caught in the wild in different places, some years before the start of the experiment.

B.P.; *Lempdes (Le.)*; *Châteaugay (Ch.)*; *Moulins (Mo.)*; *Menetreol (Me.)*: caught in central France.

Luminy (Lu.); *Digne (Di.)*; *Hyerres (Hy.)*: caught in the South of France.

B.2'; *Saillé (Sa.)*: caught in the West of France.

Belinga (Be.): caught in Africa.

Fin.; *Br. 38*; *N.20*: originated in the same way but earlier. They have been maintained in laboratories for about ten years.

Inducer strains of the second group are, like reactive strains, old laboratory strains:

Ore. I and Ore. II are two distinct isolates, separated for many years, of the classical wild-type strain *Oregon*.

M.5 (synonymous with *Base*).

Cy/Pm.

w ct f.

(c) *Neutral strain.* The neutral strain used in the experiment is the only one which is known as neutral at present. It is called *Paris (Pa.)* and originated from flies caught in this city about 30 years ago.

(ii) *Experimental design*

Whatever their origin, all the strains used in the experiment have been kept in this laboratory in uniform conditions: mass cultures in standard bottles and temperature of 20°C, during about 10 generations. About 20 flies taken at random were used to start every new generation.

For the experiment, cultures were made of each of the 37 strains in bottles large enough to ensure that all the flies needed for breeding at the same time were reared in the same bottle.

360 different crosses were then started simultaneously. In 323 of them, virgin females from each of the 17 reactive strains are used with males of each of the 19 inducer strains. Seventeen other crosses involved males from the neutral strain *Paris* and females from each reactive strain. For the remaining 20 crosses, females from the neutral strain were used with males of each inducer strain and also with males from their own strain.

To allow a statistical analysis of the results, two independent measurements of the hatching percentage of the eggs laid by the F_1 females were made for each cross. For each measurement, a culture was made with five females from the maternal strain and five males from the paternal one. As soon as the fly progeny appeared, about 50 F_1 flies were taken at random from each culture and placed in a new vial, into which a piece of food stained with some carbon black had been introduced. A sample of about 200 eggs was collected on this food during about 24 hours. The eggs, which are easily seen on the black background, were recorded as hatched or not hatched 48 hours later. Since it is known that the hatching percentage of eggs laid by *SF* females rises when they get older, eggs samples were only collected from females under 5 days of age.

3. RESULTS

Table 1 presents the hatching percentages for the two repeats of all the crosses. For the maternal as well as the paternal strains, the adopted order is based upon the mean value of the hatching percentage measurements. Reactive strains are ordered from left to right from *strong* to *weak* and the same is true for inducer strains from top to bottom. According to this design, crosses in which the neutral strain is a partner are found in the last column and the last line.

As a first result, it can be seen that all crosses involving the neutral strain lead to high hatching percentages; nearly all of them are above 90 per cent. Furthermore, there is no difference between cases in which the *Paris* strain was used as paternal strain and those in which it was used as maternal strain. If a single pool is made with all the eggs collected from crosses of the first class (last line of table 1), the mean hatching percentage, calculated over 7013 eggs, is 95.0 per cent. The pool made with crosses of the last column (*Paris* strain used as maternal strain) rises to 6411 eggs with a hatching percentage of 94.3 per cent. The difference is not significant ($\chi^2 = 3.46$, d.f. = 1).

All the other strains lead, at least with some partners, to F_1 females which lay eggs, most of which, and some times all of which, fail to hatch. With *weak* inducer strains (bottom of table 1), this sterility is conspicuous only when *strong* reactive strains are taken as partners (left of table 1). Similarly, *weak* reactive strains (right of table 1) need *strong* inducer partners to give hatching percentages conspicuously below the control. When both strains involved in the cross are *weak*, hatching percentages may be normal or subnormal (bottom right of table 1).

With the exception of crosses involving the *Paris* strain, an analysis of variance was carried out on the figures of table 1, in order to draw a comparison between the three additive components which lead to the observed level of sterility: specific actions of both strains and interaction between them. To make the analysis, the classical angular transformation was used. Each raw percentage p was converted into the value of an angle θ in degrees, such as $\sin^2 \theta = p$. With this transformation, the component of the variance which is introduced by the sampling errors gets a uniform value. Since the harmonic mean of the sample sizes is 207, this value amounts to

$$180^2/828\pi^2 = 3.9.$$

In three of the 323 crosses, only a single measurement was available, the other one being lost accidentally. To carry on the analysis, the missing repeat was supposed to have led to the same value as the one available and, consequently, the number of degrees of freedom of the inter-repeats variance was diminished by three.

The results of the analysis of variance are presented on table 2. It can be seen first that the inter-repeats variance is greater by a factor of about 8 than the variance introduced by the fact that each measurement was made on about only 200 eggs (3.9). With the high number of degrees of freedom, this difference is, of course, highly significant. The replicate variance, rather than the sampling variance, must, therefore, be used to assess the significance of the other items.

In spite of the lack of homogeneity in the repeats, it is quite evident that the choice of the reactive strain and the inducer strain are the two most important components of the variation. Orders of magnitude of the corresponding variances and of the replicate variance are quite different. The variance of the interaction is about three times the replicate variance. This ratio is statistically significant ($P < 0.001$).

Starting from the usual hypothesis that each measurement is the sum of 4 components: additive actions of both parental strains, interaction and error, contributions to the total variation of each of these components can be estimated (4th column of table 2). It appears that the choice of the reactive strain is by far the most important factor, components attributable to the inducer parental strain and to interaction are of a smaller and similar magnitude.

The fact that interaction is not important with respect to the additive action of the reactive strains is brought out also by the comparison of the different orders which can be established for strains within the class. Each inducer strain, allows an ordering of the reactive strains from *strong* to *weak* on the basis of the mean of the two measurements made for each cross. The data of table 3 were obtained in making three sub-groups among the inducer strains. The first one, *strong* inducers, includes the strains *Luminy*, *Belinga*,

TABLE 1

Measurements of the hatching percentages of eggs laid by F_1 females from the cross between females from a reactive or neutral strain and males from an inducer or neutral strain. Each figure is measured on a sample of about 200 eggs. The two figures for each cross come from two independent samples

ind. ♂	react. ♀	se_{21}	se_{17}	est_{121}	$cn; bw$	est	se_{201-18}	est_{28}	cn	bw	w	H, J_{24}	se_{12}	$cn; se$	$bw; st$	e	e_{98}	Parts
Lu.		0.8	0.0	0.0	0.0	0.0	4.1	1.8	3.5	19.9	59.4	49.7	20.1	48.7	64.6	64.7	57.5	95.2
		0.9	0.0	0.0	0.0	0.2	2.1	4.6	0.0	32.9	50.0	44.8	20.7	19.3	79.7	68.0	66.1	89.4
Be.		0.0	0.4	1.1	3.1	0.0	9.1	12.5	4.2	7.5	46.2	49.7	59.1	51.2	51.5	69.4	81.7	92.9
		0.0	0.0	1.0	2.8	5.8	11.1	17.0	3.4	25.7	39.9	49.2	59.9	66.0	52.2	59.5	72.1	88.3
Le.		0.0	2.1	0.0	0.0	1.2	3.5	5.5	6.8	54.6	31.7	49.8	51.8	84.9	63.7	76.2	89.9	96.1
		0.0	0.6	0.0	0.0	0.0	16.3	6.9	28.6	10.1	26.4	66.8	56.2	77.2	61.4	69.1	89.5	95.2
Cy Pm		0.9	1.2	0.0	9.0	6.3	18.9	10.7	9.5	45.5	39.8	41.8	66.8	77.6	81.7	69.0	78.7	86.1
		0.0	0.0	2.0	2.2	6.2	19.7	17.2	15.2	45.5	27.7	42.2	65.5	72.2	82.3	69.1	81.7	86.2
Me.		5.5	1.7	0.0	3.1	6.8	6.9	3.1	3.7	36.4	30.0	67.7	55.2	74.7	69.4	80.7	91.2	90.3
		0.0	0.0	1.1	6.3	5.5	9.1	7.5	13.1	39.2	47.6	68.6	75.6	82.3	82.0	67.7	83.1	87.1
Fin		0.4	0.3	0.0	0.0	0.3	1.6	6.3	24.0	32.9	47.3	72.3	67.1	78.4	90.2	90.0	44.9	94.2
		0.0	16.6	0.0	0.4	0.4	5.7	12.7	5.7	25.4	72.9	69.8	79.6	89.0	93.6	—	89.7	97.7
Mo.		1.0	0.6	0.4	1.8	0.4	6.5	20.5	36.8	40.5	61.9	63.7	68.7	70.6	77.8	87.3	89.9	90.3
		0.0	0.0	0.5	2.5	0.9	0.0	23.8	23.6	56.2	79.5	81.2	77.9	87.1	67.6	89.3	70.0	96.1
Ore. I		0.0	0.3	0.9	0.0	1.3	8.1	12.0	18.1	34.9	60.1	65.8	82.7	73.1	93.9	86.5	84.6	96.1
		0.0	1.1	0.3	1.1	5.4	25.9	33.4	19.9	29.7	43.9	68.5	69.6	78.2	84.1	89.9	92.5	88.3
N. 20		0.0	0.9	0.0	0.0	0.0	14.7	14.6	20.9	21.6	37.3	71.0	89.3	86.7	86.6	91.9	85.2	97.6
		0.0	0.0	1.5	1.2	1.8	19.0	21.3	8.6	46.0	48.4	67.8	74.0	92.2	93.6	94.1	90.6	95.7

<i>Br. 38</i>	0.0	0.0	1.5	2.2	0.0	0.0	13.7	15.9	19.0	33.8	68.7	77.3	75.5	71.4	86.3	91.6	78.0	96.4
	2.0	2.2	0.5	2.9	3.7	2.3	19.3	16.5	19.4	29.7	77.0	79.3	57.2	94.3	87.0	88.7	77.6	98.6
<i>B.P.</i>	0.0	0.4	4.5	1.0	0.6	4.2	4.7	5.5	40.1	34.6	78.8	84.6	82.2	59.5	83.6	85.0	84.5	92.5
	0.0	0.5	0.4	1.0	3.0	1.7	7.3	15.8	—	61.9	72.2	76.1	70.7	98.3	84.0	91.2	84.8	94.0
<i>Sa.</i>	0.0	0.3	2.3	1.4	3.1	6.4	6.6	8.7	35.5	65.3	53.4	51.6	85.0	69.1	78.2	85.9	85.0	97.4
	0.5	3.2	1.1	0.0	3.3	4.7	15.5	12.9	39.2	95.6	55.7	37.6	90.1	91.3	90.0	84.8	86.8	98.2
<i>Di.</i>	0.4	0.4	0.0	2.6	1.4	4.6	11.9	11.3	21.7	38.0	78.3	55.9	88.7	89.6	89.6	92.7	91.2	94.3
	2.5	0.0	1.3	3.1	2.7	1.3	5.4	9.5	18.3	37.5	54.4	58.1	74.6	92.8	78.7	87.4	93.4	93.9
<i>Hv.</i>	0.4	1.1	0.0	1.0	1.3	5.2	7.1	19.7	38.2	13.0	76.4	74.8	60.0	92.3	90.2	80.0	94.9	98.1
	0.0	0.0	0.0	2.6	3.8	1.4	28.5	41.9	—	21.5	57.4	71.1	82.4	92.2	85.8	80.0	95.9	95.7
<i>B.2'</i>	1.3	0.0	1.8	1.0	0.0	3.2	5.4	12.2	47.1	67.6	81.6	41.5	75.3	89.2	81.0	90.7	91.7	94.4
	0.4	0.8	0.7	7.6	2.6	15.1	7.3	18.4	50.5	47.3	77.9	53.4	78.6	73.2	81.0	94.5	98.3	89.1
<i>w cl f</i>	0.0	0.0	0.8	0.0	0.0	3.8	0.0	20.5	12.7	78.0	76.7	83.8	82.4	88.0	94.9	95.6	94.8	96.4
	16.3	0.4	1.4	0.4	0.8	0.6	5.9	22.5	11.6	80.9	54.0	55.9	71.8	93.9	92.4	96.4	84.9	95.7
<i>Ch.</i>	0.0	4.1	0.3	7.0	1.5	23.8	10.3	44.2	49.4	67.2	51.7	74.0	85.8	94.0	98.6	91.4	96.0	93.4
	0.4	0.0	1.7	6.9	9.3	20.5	17.2	48.9	32.1	86.5	57.8	76.0	65.8	79.6	95.8	97.1	97.0	94.7
<i>M.5</i>	7.3	5.1	10.6	27.8	18.4	29.4	44.8	64.5	78.6	88.6	75.3	79.7	83.3	97.5	94.3	88.9	93.7	92.3
	5.2	12.7	31.3	23.1	33.5	27.6	35.4	64.5	80.6	85.7	59.2	70.1	86.6	80.3	96.2	95.9	93.2	93.5
<i>Ora. II</i>	8.5	8.6	11.1	36.2	10.7	24.1	30.8	72.2	63.5	84.1	88.4	82.4	83.9	94.5	94.8	91.0	91.9	97.7
	5.3	19.5	8.9	63.3	21.9	18.3	41.9	59.3	46.9	88.1	79.6	98.9	89.0	98.3	94.0	95.8	95.3	95.3
<i>Paris</i>	86.7	95.4	95.6	100	92.8	94.1	96.7	93.6	98.5	94.8	90.4	94.3	95.3	97.6	96.9	98.3	95.8	99.2
	86.3	86.7	94.1	97.0	98.8	95.1	92.3	94.5	98.1	97.2	96.4	92.7	93.8	95.5	97.4	96.7	99.1	94.9

Lempdes, *Cy/Pm*, *Ménétreol*, and *Fin*. The strains *Châteaugay*, *M-5* and *Ore. II* form the third sub-group. The rest make up the second sub-group, *mild* inducers. This grouping is justified by the existence of exceptionally large gaps between the strains concerned. Thus, each reactive strain can be given a figure which is the mean of its ranks in the orders established with the

TABLE 2

Analysis of variance and estimation of the components of mean square of the hatching percentages measured on samples of about 200 eggs, laid by SF females, bred from the crosses of females from 17 reactive strains by males from 19 inducer strains. To make the analysis, percentages were transformed into angular values. The sampling variance of individual measurements is 3.9. (See text)

	Sums of squares	Degrees of freedom	Variance	Components of mean square
Total	458,309	642		
Between two repeats	10,192	320	32	32
Between inducer strains	30,436	18	1,691	47
Between reactive strains	391,976	16	24,498	642
Interaction inducer/reactive	25,705	288	93	37

inducers of the sub-group. These figures, which of course fall between 1 and 17, are presented in table 3. Correlation coefficients between these mean ranks are quite high: they rise to 0.99 between *strong* and *mild* inducers, to 0.98 between *mild* and *weak* and to 0.97 between *strong* and *weak*. The order of a set of reactive strains is therefore largely independent of the particular inducer strain which is used in the cross.

TABLE 3

Means of the ranks of the reactive strains in the orders established with each inducer strain of three subgroups. (See text)

	Strong inducers	Mild inducers	Weak inducers
<i>se</i>	2.5	2.3	1.0
<i>se</i> ₂₁	2.3	1.9	2.7
<i>seF</i> ₁₂	2.2	3.4	2.3
<i>est</i> ₁₂₁	2.7	3.8	5.3
<i>cn; bw</i>	3.7	4.2	4.3
<i>est</i>	4.7	5.5	6.0
<i>se</i> ₂₀₁₋₁₅	8.0	6.9	6.3
<i>est</i> ₂₈	7.7	8.1	8.7
<i>cn</i>	7.8	8.7	9.0
<i>bw</i>	10.6	10.4	12.3
<i>w</i>	11.1	11.3	9.6
<i>Hf</i> ₂₄	12.3	11.7	12.3
<i>sef</i> ₁₂	12.5	12.9	12.0
<i>cn; e</i>	14.7	15.0	15.0
<i>bw; st</i>	15.5	14.7	16.3
<i>e</i>	15.1	15.7	14.3
<i>e</i> ₉₈	16.0	15.5	15.0

The order which can be attributed to inducer strains is made more variable by two causes. First, many of the differences between inducer strains, chiefly within the sub-group *mild* inducers, are not significant and, therefore, their ranks are random. Second, some inducer strains are somewhat more sensitive (*w ctf*) or less sensitive (*Cy/Pm* and *Me.*) than the majority to changes

in the degree of efficiency of the reactive strain. The behaviour of these strains accounts for the most part of the interaction. In spite of the importance of interaction with respect to the additive action of inducer strains, the variance between inducer strains is statistically higher than the interaction variance ($P < 0.001$). Indeed, *strong* and *weak* inducers can easily be recognised as such, whatever may be the reactive strain used in the cross.

4. CONCLUSIONS AND DISCUSSION

Two conclusions can be drawn from the experimental data which are reported in this paper.

1. Among the factors which are responsible for the wide variation observed in the degree of sterility of individual *SF* females, the choice of the reactive strain and, to a minor degree, the choice of the inducer strain stand out as the most important. The two main classes, into which the *Drosophila melanogaster* strains which have been studied can be distributed, are therefore not homogeneous. Among strains of the same class there are differences which are actually genetic characters. So, the actual nature of the *Paris* strain may be viewed also as the extreme *weak* type of either of the two main classes. Some recent results which will not be reported here, seem to indicate that the *Paris* strain is a very *weak* reactive strain.

2. As the component of the variation attributable to interaction is weak with respect to the additive action of the reactive strains, a degree of efficiency can be defined for each strain within this class, on the basis of the level of sterility observed in *SF* females. This degree is independent of the inducer strain taken as partner. Differences between inducer strains are less important and are more dependent upon the choice of the partner strain. Nevertheless, a degree of efficiency can also be attributed to each inducer strain, though in a far less precise way. Addition of the degrees of both parental strains accounts for the most part of the variation observed between the crosses.

The sterility of *SF* females may be taken as the result of an interaction between two factors. That brought by the paternal strain may be called *I* factor and the other brought by the maternal strain, *R* factor. It is clear that experimental facts reported in this paper do not lead by themselves to any precise view about the nature of these factors. However, any hypothesis that can be made about this point must take into account the conclusions mentioned above.

The second conclusion, indeed, appears to make rather unlikely a hypothesis, which, on other grounds, had to be taken into consideration. It assumes that death of the eggs is the outcome of some sort of complementation, or perhaps recombination, between genetic elements, brought together by the cross. These elements might be of a symbiotic nature. The observed differences between strains within a class might reflect qualitative genetic variations of these elements. With such a hypothesis, one should expect the level of sterility of *SF* females to depend strongly upon the way the variations present in both parental strains fit one another. Pairs of strains should be found which, crossed together, would breed highly sterile females, while, in other associations, they would appear as *weak* reactive or inducer and, statistically, interaction would be found important with respect to the additive actions of both parental strains. Within the available experimental data, such a situation was not observed.

The existence of degrees of efficiency in both factors suggests a way to obtain information about their nature, since it is possible to investigate how these differences are inherited in crosses between strains of the same class. This work is in progress in our laboratory. Some preliminary results are available in the case of *R* factor. The degree of efficiency of *R* factor is essentially maternally transmitted and is independent of chromosomal segregations in the short term. However, in crosses between reactive strains, a minor effect of the paternal strain is regularly met (Bucheton, 1973) and a belated effect of the genotype may be observed after two or more generations. Generally speaking it looks as if *R* factor degree of efficiency is dependent on (at the time of the cross) the frequency in the oocyte, within a heterogeneous population, of a specific genetic type of cytoplasmic particles. At the present state of the investigations, the nature of these particles is purely a matter of guess and the different possible hypotheses will not be discussed in this paper.

Non-mendelian female sterility in *Drosophila* bears, at first sight, some similarity with a number of genetic phenomena, involving non-chromosomal factors, in which a loss of viability or of fertility is observed in the offspring from crosses between different strains of a species or between related species. Cytoplasmic male sterility in higher plants is the best known and the most thoroughly investigated of these phenomena (Edwardson, 1970). The experimental results which have been presented in this paper do not allow by themselves any precise discussion of this similarity and it seems advisable to postpone this discussion until the results of the work which is presently being done in our laboratory to elucidate the nature of what have been called the *I* and the *R* factors are available.

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