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Hybrid dysgenesis in *Drosophila melanogaster*: the relationship between the *P–M* and *I–R* interaction systems

By MARGARET G. KIDWELL

Division of Biology and Medicine, Brown University, Providence, Rhode Island 02912, *U.S.A.*

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SUMMARY

Two systems of hybrid dysgenesis, the *P–M* system and the *I–R* system, are characterized by two different specific types of non-reciprocal hybrid sterility referred to, respectively, as *GD* and *SF* sterility. In order to determine the relationship between these two systems, strains representative of the four single-system interactive types were crossed in almost all possible combinations and tested for both types of sterility. The results suggest that the two systems are at least partially independent of one another. There are several examples of single strains that contribute the maternal component for interaction in the *P–M* system and contribute the paternal component in the *I–R* system. Using parents with the potential for the two types of interaction and appropriate temperature manipulation, both *GD* and *SF* sterility can be manifested in the same hybrid females. In other crosses, a single type of sterility is observed, or none at all, according to the dual designation of the parental strains. The evidence from a number of additional crosses suggests that most strains of this species have the potential for both types of interaction to varying degrees when mated in appropriate combinations. Some theoretical and practical implications of these results are discussed.

1. INTRODUCTION

When laboratory strain females are mated with males from the wild it is frequently observed that their F_1 progeny show one or more aberrant traits such as sterility, mutation and male recombination. Such traits are not observed at high frequencies in the reciprocal cross nor in the parental strains and their manifestation is highly dependent on external factors such as temperature. This syndrome of aberrant traits is called 'hybrid dysgenesis' (Sved, 1976; Kidwell & Kidwell, 1976).

Two systems of hybrid dysgenesis have now been described, the *P–M* system and the *I–R* system. The *P–M* system is recognized by the induction of sterility and male recombination in the progeny of crosses between *M* strain females and *P* strain males (Kidwell, Kidwell & Sved, 1977*b*). The sterility typical of this system (*GD* sterility) is the result of gonadal dysgenesis in hybrids of both sexes (Engels & Preston, 1979; Schaefer, Kidwell & Fausto-Sterling, 1979; Kidwell & Novy, 1979, and no eggs are laid by sterile females. The induction of *GD* sterility is dependent

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on high developmental temperatures applied at late embryonic or early larval stages. Associated dysgenic traits include mutation, transmission ratio distortion, non-disjunction, chromosomal aberration and increased frequencies of female recombination. A preliminary survey of North American strains suggests that most, if not all, present-day wild strains are *P* strains and long-established laboratory stocks are *M* strains (Kidwell *et al.* 1977*b*, and unpublished results.)

The *I–R* system has been identified on the basis of another specific type of sterility called *SF* sterility (Picard, 1971). When *R* (reactive) strain females are crossed with *I* (inducer) strain males, the eggs laid by their female progeny (*SF* females) show a varying degree of reduced hatchability. The embryos die during late cleavage. This type of sterility can be reversed by ageing of females and high temperature treatment 1 or 2 days prior to egglaying. Associated dysgenic traits include *X*-linked visible mutation and non-disjunction (Picard *et al.* 1978). Male fertility is not affected. A survey of strains from various parts of the world indicated that pesent-day wild strains are all, without exception, *I* strains. All three types, *R*, *I* and *N*, are found among laboratory strains (Picard *et al.* 1976).

The genetic transmission of the components of the *P–M* system provides some striking similarities with that of the *I–R* system; both involve an unusual blend of Mendelian and non-Mendelian inheritance (Engels, 1979; Picard, 1976; Bucheton & Picard, 1978). Both the *P* and *I* components appear to be multiple factors linked to any of the major chromosomes. In males, the transmission of these factors appears to be strictly Mendelian. However, in hybrid females, *I* factors can be passed interchromosomally by 'chromosomal contamination' (Picard, 1976). There is also some evidence for the transposability of *P* chromosomal factors or male recombination elements (Matthews *et al.* 1978; Slatko, 1978). The *M* and *R* components are related to the state of the cytoplasm which is ultimately dependent on the chromosomes. There is evidence for large quantitative variation among strains within a single type (i.e. within *M* or *R* strains).

With the description of these two systems of hybrid dysgenesis, and the recognition of their distinguishing traits, have come questions about their interrelationship. Are these two systems independent with respect to causality and distribution? Or are the varying dysgenic traits merely manifestations of a single complex interactive system? The purpose of this study is to investigate the relationship between the two systems by the direct crossing of representatives of the four types of strains: *P*, *M*, *I* and *R*.

2. MATERIALS AND METHODS

(*a*) *Strains employed*

(i) I–R *system*

(*a*) Strong *R* (reactive) strains: e_{st} (abbreviated E) and seF_8 (abbreviated S).

(*b*) Strong *I* (inducer) strain: Luminy (abbreviated L).

All three strains were obtained from the Laboratoire de Génetique, Université

de Clermont Ferrand where they had previously been classified and used as reference stocks for the *I–R* system (Picard *et al.*, 1977).

(ii) P–M *system*

(*a*) Strong *M* strains: Canton-S (abbreviated C) and *rucuca* (abbreviated Ru).

(*b*) Strong *P* strain: Harwich (abbreviated H)

These three strains had been maintained at Brown University where they had previously been classified and used as reference stocks for the *P–M* system (Kidwell & Kidwell, 1976; Kidwell *et al.* 1977*b*).

Additional strains were employed to test simultaneously for *SF* and *GD* sterilities. These were strains from Brown University and the Institute of Animal Genetics, Edinburgh. They are listed with the results in Tables 1 and 2.

In describing inter-strain matings the convention is adopted of always denoting the maternal strain first and the paternal strain last, e.g. E × H indicates a cross between e_{st} females and Harwich males.

(*b*) *Procotol for measuring SF sterility*

Crosses between ten males and ten females were set up in 8 dm vials. The parents were placed in a room whose temperature never exceeded 20°. F_1 females were allowed to mate with their brothers and, after 3 days, groups of 20 F_1 males and females were placed in half-pint milk bottles. Standard microscope slides covered with *Drosophila* medium and seeded with live yeast were suspended in the bottles for successive 24 h periods and egg hatchability was measured after 48 h at 20 °C. The criteria of Picard *et al.* (1976) were adopted for the classification of strains within the *I–R* system.

(*c*) *Procotol for measuring* GD *female sterility characteristic of the* P–M *system*

Crosses between 10 males and 10 females were set up in half-pint bottles. They were immediately placed in a 29 °C incubator. Parents were removed after 6 days. F_1 males and females were allowed to mate together for 3 days at 25 °C after which time individual females were separated and each mated with two unrelated males from a known fertile strain. Individual vials were examined after 4 days for the absence of eggs (as an indicator of *GD* female sterility) and after 12 days for the absence of progeny.

3. RESULTS

(*a*) *The relationship between the* I–R *and the* P–M *systems*

Two identical sets of crosses were set up, each set including all possible combinations of the six strains L, E, S, H, C and Ru, except for intrastrain and intratype matings (e.g. R × R matings). One set was used to test for *SF* sterility and the other set for *GD* sterility (see Materials and Methods).

(*b*) SF *sterility*

Mean percentages of unhatched eggs laid by females raised at 20 °C are given in Fig. 1. The low hatchability of both the known R × I crosses (i.e. E × L and S × L) confirmed the expected induction of *SF* sterility. In addition, the progeny of H, C and Ru males, mated with E and S females, produced a similar very low hatchability. This result suggests that H, C and Ru can all be classified as *I* strains

♀ \ ♂	E R	S R	L I	C M	Ru M	H P
E R			93	96	64	95
S R			99	100	97	94
L I	2	8		2	0	3
C M	3	4	3		3	15
Ru M	7	3	7	4		17
H P	16	11	2	15	14	

Fig. 1. Percentage unhatched eggs laid by F_1 females (*SF* sterility) from the indicated strain crosses. Approximately 100 eggs were tested per cross.

within the *I–R* system. *SF* sterility characteristically is reversible by ageing and heat treatment of females (Picard *et al.* 1977). In order to confirm that it was, in fact, *SF* sterility that was being observed rather than some other kind of sterility, egg-laying hybrid females from the crosses E × L, E × C and E × H were (*a*) aged for 22 days at 20 °C, (*b*) similarly aged except that the parents were placed in a 29 °C incubator between days 6 and 12. The results are presented graphically in Fig. 2. Because of large fluctuations in daily egg numbers at 20 °C, hatchability was calculated as the mean of two successive days production. At 29 °C egg production was considerably higher and daily means are plotted for this temperature.

There was a steady increase in hatchability with age of female in all three crosses maintained throughout at 20 °C and also a marked increase a day or so after the

start of the heat treatment. The pattern of increase in the E × C and E × H crosses was similar to that in the E × L cross, already known to produce *SF* sterility. One interesting minor difference was the absence of any noticeable hatchability reduction in the E × L and E × C crosses after the temperature was reduced to 20° from 29 °C. A partial reversal of the hatchability increase induced by high temperature is characteristic of *SF* sterility (Picard *et al.* 1977). The use

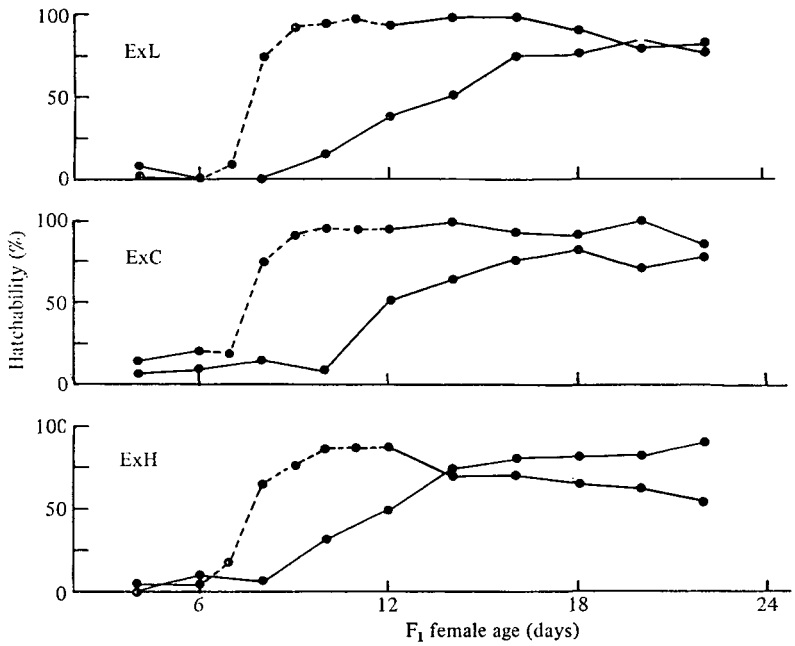

Fig. 2. Percent egg hatchability with increasing F_1 female age for three parental crosses. Solid lines indicate a 20 °C maintenance temperature and dashed lines one of 29 °C.

of live yeast in the present tests but not in those of Picard is a possible explanation. There were also differences in the constitution of the food medium. In any case, the similarity of the patterns of increase in hatchability with ageing and heat treatment in the three crosses confirms the presence of *SF* sterility.

(c) *Test for GD female sterility*

The frequencies of F_1 females that laid no eggs after being raised at 29 °C (*GD* sterility) are given in Fig. 3. As expected, the known $M \times P$ crosses (C × H and Ru × H) produced high frequencies of this type of sterility. In addition, both E and S females mated with H males produced a high frequency of non-egglaying female progeny, suggesting that the E and S strains can also be classified as *M* strains within the *GD* system. No other crosses produced a high level of *GD* sterility. The L strain, therefore, cannot be classified as either *M* or *P*. This suggests the existence of a third type of strain within the *P–M* system analogous to the neutral (*N*) type of the *I–R* system. This third category is hereafter referred

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to as the *Q* type . The existence of other *Q* strains has subsequently been confirmed in both the laboratory and the wild.

(*d*) *Frequency of females producing no progeny*

In addition to observing the number of females that laid no eggs under the *GD* sterility protocol, the number of females producing no progeny was also observed. These data are presented in Fig. 4. It appears that this measure of sterility can indicate the presence of both *SF* and *GD* types of sterility both

♀ \ ♂	E R	S R	L I	C M	Ru M	H P
E R			0	3	3	80
S R			7	0	0	50
L I	0	0		0	0	3
C M	0	0	0		0	87
Ru M	0	0	0	0		47
H P	0	0	0	0	0	

Fig. 3. Percent F_1 females laying no eggs (*GD* sterility) from the indicated strain crosses. Approximately 30 females were tested per cross.

separately and together (compare Fig. 4 with Figs. 1 and 3 together). This suggests that high F_1 developmental temperatures do not suppress and may, in fact, enhance *SF* sterility. Thus, the tested crosses can be divided into four groups: (*a*) those showing only *SF* sterility (E × L, E × C, E × Ru, S × L, S × C, S × Ru), (*b*) those showing only *GD* sterility (C × H and Ru × H), (*c*) those showing both *SF* and *GD* sterilities (E × H, S × H) and (*d*) those showing no sterility (the remaining crosses). It is concluded that the use of 'absence of progeny' alone as a measure of sterility may be difficult to interpret in terms of different underlying types of sterility.

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(e) *Test for male sterility*

As mentioned earlier, hybrid male sterility has previously been found to be associated with *GD* female sterility (Kidwell & Kidwell, 1975) but never with *SF* sterility. In order to provide confirmation of the correct indentification of the two types of sterility, F_1 male sterility was measured in a group of 11 crosses which included all those crosses showing a significant frequency of female sterility

♀ \ ♂	E R	S R	L I	C M	Ru M	H P
E R			57	17	3	100
S R			93	33	13	100
L I	0	0		0	0	3
C M	0	0	3		0	87
Ru M	0	0	0	0		53
H P	0	0	0	0	0	

Fig. 4. Percent F_1 females producing no adult progeny from the indicated strain crosses. Approximately 30 females were tested per cross.

(see Fig. 4). Five-day-old, F_1 hybrid males raised under the protocol described for *GD* sterility were individually mated with three virgin females of a highly fertile strain. The percentage of males producing no progeny is given in Fig. 5. Four crosses produced high frequencies of male sterility and the remainder none at all. These four corresponed exactly with the four *GD* female sterile crosses (see Fig. 3). These results provide reassurance for the correct identification of the type of sterility involved.

The results described above suggest that most strains have the potential for interstrain interaction with respect to both the *P–M* and the *I–R* systems and that the two types of potential occur independently of one another. In order to test this idea of dual classification, two additional groups of strains were tested: (i) five strains from Brown University, whose classification in the *P–M* system

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is well documented, (ii) 24 long-established laboratory strains from the Institute of Animal Genetics Edinburgh, not previously tested for either system. Group (i) was tested for *SF* sterility only and group (ii) for both *GD* and *SF* sterilities. For *GD* sterility, males and virgin females of the strain under test were mated respectively with females from a strong *M* strain (E) and with males from a strong

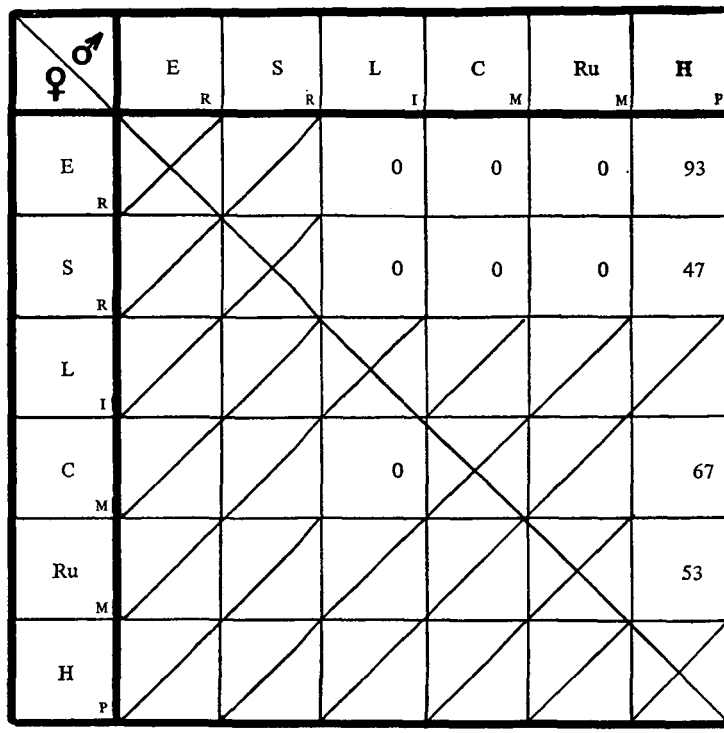

Fig. 5. Percent F_1 males producing no progeny from the indicated strain crosses. Fifteen males were tested per cross.

P strain (H). For *SF* sterility, males and virgin females of the strain under test were mated respectively with females from a strong *R* strain (E) and males from a strong *I* strain (L). The F_1 developmental regimes and procedures for each type of sterility test are given in the Materials and Methods. At least 100 eggs were tested for *SF* sterility and approximately 20 F_1 females were tested for *GD* sterility.

The results for group (i) and (ii) strains are given in Tables 1 and 2 respectively. They confirm that the majority of strains have the potential for both *P–M* and *I–R* types of interaction. In other words, a single strain may be classified as *P* or *M* and *I* or *R*. Furthermore, there are several examples demonstrating that a strain can carry both the maternal component (*M*) of the *P–M* interaction and the paternal component (*I*) of the *I–R* interaction. The patterns of distribution of strains within each individual system conform with those previously established for each system independently (Kidwell *et al.* 1977*b*; Picard *et al.* 1976, and

Table 1. *Frequencies of* SF *sterility* (% *unhatched eggs*) *and designations within the* I–R *system for five strains previously shown to be strongly interactive in the* P–M *system*

	P–M system		*I–R* system		
			% *SF* sterility		
Strain	Previous designation	Reference	× E♀	× L♂	Designation
al cl b c sp[2]	M	Kidwell & Kidwell (1975)	10·6	85·0	strong R
Cranston	P	Kidwell *et al.* (1977*a*)	99·0	11·8	strong I
H-41	M	Kidwell *et al* (1977*b*)	15·2	82·2	strong R
Basc	M	Kidwell *et al* (1977*a*)	7·1	15·6	weak R
C-scan	M	Unpublished results	4·7	1·9	N

Table 2. *Frequencies of* GD *and* SF *sterilities and dual designations within the* P–M *and* I–R *systems for* 30 *long-established laboratory strains*

		P–M system			*I–R* system		
		% *GD* sterility*			% *SF* sterility†		
Strain	Previous history	× E♀	× H♂	Desig-nation	× E♀	× L♂	Desig-nation
Cy°/BlL[2]	I.A.G.‡	0	50	M	9·8	20·4	R
M–5	I.A.G.	0	48	M	3·5	17·4	R
Oregon–K	I.A.G.	0	100	M	0·6	21·3	R
st	Gruningen Univ.	0	100	M	1·8	12·1	R
h	I.A.G.	0	37·5	M	1·4	1·8	N
v	I.A.G.	0	96	M	2·5	3·6	N
se	I.A.G.	0	56	M	2·3	13·7	R
cn	I.A.G.	0	96	M	2·3	86·9	R
wm	I.A.G.	0	96	M	9·3	5·8	N
vg	I.A.G.	0	72	M	100	8·4	I
Pacific	1960's U.S.A.	0	100	M	95·2	37·5	I
bw st	I.A.G.	0	77	M	0	3·3	N
GlSb/LVM	I.A.G.	0	92	M	4·7	8·5	N
dp b cn bw	I.A.G.	0	100	M	17·4	14·3	N
bw	I.A.G.	0	96	M	0	9·3	R
B	I.A.G.	0	100	M	88·1	25·3	I
bw[75]st	I.A.G.	0	40	M	8·4	29·1	R
y a	I.A.G.	0	100	M	0·9	13·6	R
so	I.A.G.	0	80	M	2·6	22·1	R
SMS	Spain	0	100	M	81·1	17·5	I
fB/yf:=	I.A.G.	0	95	M	0	50·7	R
AL35–4	I.A.G.	0	100	M	11·3	53·2	R
AL34–3	I.A.G.	0	90	M	12·5	39·3	R
dp;e	Sussex Univ.	0	100	M	13·3	35·6	R

* % Females laying no eggs. † Unhatched eggs (%).
‡ Institute of Animal Genetics, Edinburgh

unpublished results). Within the *P–M* system all long-established laboratory stocks are unambiguously *M* strains and those collected recently from the wild in North America are *P* strains. In the *I–R* system, established laboratory stocks are of all three categories, *R*, *I* and *N*, and recently collected strains are *I* strains. This similarity of patterns to those previously described provides further reassurance that the results are being correctly interpreted.

DISCUSSION

The qualitative differences in the nature of associated dysgenic traits, described in the introduction, had suggested that the *I–R* and *P–M* systems of hybrid dysgenesis might be independent. The results of crosses among *P*, *M*, *I* and *R* strains, reported here, do seem to provide evidence for some independence of the two systems. The results of this study indicate that a given cross may exhibit both *SF* and *GD* sterilities, *SF* sterility alone, *GD* sterility alone or neither type of sterility, according to the dual designation of the parent strains.

It now seems appropriate and informative to allocate a dual designation to all tested strains. For example, following the terminology used previously, e_{st} = *RM*, seF_8 = *RM*, Luminy = *IQ*, Canton-S = *IM*; *rucuca* = *IM* and Harwich = *IP*. These results, in general, conform well with the patterns of distribution of *I* and *R* strains on the one hand and *P* and *M* strains on the other which have already been established. The importance for *Drosophila* research of widespread testing for interaction potential within both the *P–M* and *I–R* systems has been stressed by Picard *et al.* (1978).

It has been demonstrated that *M* strains can be either *I* or *R* within the *SF* system. This means that a single strain may carry the maternal component for the *P–M* system of hybrid dysgenesis and also the paternal component for the *I–R* system. So far, all *P* strains tested have also been classified as *I* strains. Distributional similarity does not, however, necessarily imply causal dependence. The observation that all *P* strains are also *I* strains might alternatively be explained in terms of a model of evolution which assumes that all populations at an earlier time were of the *RM* type. It is further postulated that the *I* type appeared first (by some type of 'mutational' event) and spread rapidly by means of migration and chromosomal contamination throughout populations in the wild. Later, and perhaps very recently, it is suggested that in a similar way the *P* type appeared and spread in natural populations. Such an ordering of events could provide an explanation for the rarity or possible complete absence of *RP* strains and also for the observed distribution of the various types in 'isolated' laboratory populations. Further details and some evidence to support this model of evolution of hybrid dysgenesis will be described elsewhere (M. G. Kidwell, in preparation).

The selection of *P*, *M*, *I* and *R* strains of known strong activity for use in this experiment was made in order to avoid the possibility of qualitatively ambiguous results arising from the low frequencies of sterility expected with the use of weak activity strains. Using various combinations of strong and weak *I* and *R* strains,

Bucheton *et al.* (1976) have shown that the *SF* sterility, characteristic of the *I–R* system is manifested in all interacting combinations but that the frequency of such sterility is strongly influenced by the reactivity level of the maternal strain. A similar relationship between the frequency of *GD* sterility and the activity level of both parental strains seems to exist in the *P–M* system (M. G. Kidwell, unpublished results). Thus we recognize not only qualitative variability manifested in the differences *between GD* and *SF* sterility but also considerable quantitative variability *within* each system dependent on parental activity levels. Bearing in mind this distinction between two types of variability, it is claimed that selection of the test strains on the basis of activity level does not in any way invalidate the results of a qualitative nature which are those of interest in the present study.

The relationship between the *I–R* and *P–M* systems may be analogous to that between the different systems of controlling elements in maize (see review of Fincham & Sastry, 1974). The various types of controlling element systems have many common features but are considered to have arisen independently and to act independently. It is interesting to note that the effect of temperature may be reversed for different mutable genes in maize (Peterson, 1958; Rhoades, 1941). In a similar way, the *P–M* and *I–R* systems may be two variations on the common theme of hybrid dysgenesis with, possibly, other systems still to be described.

The question has been raised as to why these seemingly widespread interaction systems have not been detected prior to the present decade. One part of the answer may lie in the conditional nature of the various manifestations of interstrain interactions. The dependence of high sterility on rather precise temperature and ageing treatments, often outside normal husbandry conditions, could result in the masking of interactions and in the observation of quasi-normal fertility in dysgenic crosses. In addition, there appears to be quantatitive variation in the strength of interaction exhibited in both the *I–R* and *P–M* systems (Bucheton *et al.* 1976; Kidwell *et al.* 1977*b*). Strains with the potential for the strongest interactions have usually been selected for the experiments reported in the literature, but interactions between strains of average strength are expected to be weaker but, nevertheless, qualitatively of the same type. A third part of the answer to the question may lie in the possibility of a recent evolution of hybrid dysgenesis discussed briefly above. In any case, it now seems important to determine the designation of single strains within both the *I–R* and *P–M* systems in order to predict their potential for interaction in interstrain crosses. The dual classification of strains from a wide variety of sources is currently being undertaken in this laboratory. The possibility of the existence of additional systems of hybrid dysgenesis should also not be overlooked.

As stated earlier, the determination of sterility in $M \times P$ crosses has in our earlier work been carried out on the basis of complete absence of adult progeny production (Kidwell & Kidwell, 1975; Kidwell & Kidwell, 1976; Kidwell, Kidwell & Ives, 1977*a*). In the results presented here it has been concluded that absence of progeny may result from extreme *SF* sterility in addition to *GD* sterility. The

question is raised, therefore, as to the validity of the distribution patterns previously described for the *P–M* system (Kidwell, Kidwell & Sved, 1977*b*). There are three lines of evidence that our previous classification is essentially correct:

(i) The dual *I–R* and *P–M* designations for the reference strains previously used to define the *P–M* system within the U.S. are as follows: Canton-S = *IM*, Harwich = *IP*, *rucuca* = *IM*, *Basc* = *RM* (very weak *R*), Cranston = *IP*. None of these are strong *R* strains; therefore, in no combination of the five can a significant *I–R* interaction occur.

(ii) The presence of male recombination as well as sterility has been used as an indicator of *P–M* interaction, and there is now a serious doubt that male recombination is associated with the *I–R* system (Picard *et al.* 1978). It may well be diagnostic of only the *P–M* system.

(iii) The results reported above for the distribution of *P* and *M* strains within laboratory stocks is identical with that reported earlier based on lack of progeny production (Kidwell *et al*, 1977*b*). Thus it is claimed that, by and large, the distribution patterns of *P* and *M* strains previously described, within the U.S., are still valid.

It remains an outstanding question of some interest how the sterility and male recombination interaction systems reported from other laboratories may fit into the dual classification system proposed here. It seems fairly likely that the hybrid sterility recently reported by Kearsey *et al.* (1977) is associated with the *I–R* system. Clearly, the sterility and other dysgenic traits studied by Engels (1979) and Engles & Preston (1979) are manifestations of the *P–M* system. The results of Yannopoulos (1978) also strongly suggest interactions of the *P–M* type. However, hybrids from the strain Hunter Valley studied by Sved (1976) in Australia have some properties of both the *I–R* and the *P–M* systems. This may be a reflexion of the presence of both types of interaction but further clarification is needed. No high frequencies of dysgenic traits in hybrid males, including male recombination, have yet been reported in associtaion with the *I–R* system (Bregliano, personal communication). On the other hand, the association of male recombination with *GD* male and female sterility at restrictive temperatures is well established (Kidwell & Novy, 1979). Thus it seems a reasonable inference that the numerous examples of male recombination recently reported in the literature (for review see Thompson & Woodruff, 1978) are associated with the *P–M* rather than the *I–R* system. However, tests involving direct crosses with reference strains are necessary before we can be certain of their classification within both the *I–R* and *P–M* systems.

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