

ON THE SELECTIVE CONSEQUENCES OF
EAST'S (1927) THEORY OF HETEROSTYLISM
IN *LYTHRUM*.

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I. INTRODUCTION.

EAST (1927) put forward a genetic theory of trimorphism in *Lythrum salicaria* in explanation of his own experimental results and of those previously obtained by Barlow. In a second paper (East, 1932) the theory was withdrawn, but was not replaced by any alternative capable of explaining the results previously discussed. The principal reason for withdrawal appears to have been that in the intervening period one plant had been found which behaved as though homozygous for the factor causing styles of the mid-length, and that on crossing with long a large progeny was obtained all of which had mid-styles, with one exception, possibly ascribable to error. The failure in previous work to discover any such apparently homozygous plant had led East first to postulate that mid-stylism was caused by either or both of two lethal factors, linked in their inheritance, and such a hypothesis is at present the only one proposed for the many progenies which have been grown, showing a minority of about 5 per cent. long-styled plants. Since this hypothesis is not contradicted by the observation that in some cases the proportion of long plants is much less than 5 per cent., it would seem that its abandonment may have been premature. It cannot, however, be regarded as yet certainly established, since a number of consequences independent of those which led to its being put forward are available for verification and have not yet been unequivocally verified. The exact working of the genetic mechanism proposed in 1927 seems, moreover, not to have been fully recognised, and contains points which seem to the author very well worthy of a more detailed consideration.

The system put forward by East involves the action of three factors; of these, two, both of which are lethal when homozygous, have, when heterozygous, the effect of changing long to mid-length styles. The mid-styled plants may thus contain either or both of these two lethals, always, however, in the heterozygous condition. Further, the two lethals are linked, so that the doubly heterozygous mid-styled plants are of two kinds, according as the lethals are carried in the same chromosome (coupling) or in opposite chromosomes (repulsion).

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The four mid-styled genotypes may thus be represented by the symbols

$$M_1, M_2, M_1M_2, M_1/M_2,$$

standing for plants having respectively the first lethal only, the second only, both in coupling, and both in repulsion. Long-styled plants will conformably be represented by +.

The third factor *A* changes long or mid-style to short. There are therefore five short-styled genotypes:

$$A, AM_1, AM_2, AM_1M_2, AM_1/M_2,$$

according as, apart from *A*, the plants contain neither lethal, one, or the other, or both, in coupling, or in repulsion.

II. THE CALCULATION OF FREQUENCIES IN SUCCESSIVE GENERATIONS.

In order to study the effects of the genetic system of heterostylism proposed by East, apart from any effects of such differential fertility or viability as may really exist between the different forms, we shall take as basis for further calculation the assumption that plants of the different genotypes set on the average an equal number of equally viable seeds. The pollen available for the fertilisation of these seeds will be supposed to come from the different genotypes of neighbouring plants in the proportion in which these genotypes occur. Owing to the lethal factors some of this pollen has a definite chance of failing, through the formation of lethal zygotic combinations, to give rise to viable seed. It will be supposed that the formation of such inviable zygotes does not diminish the mother plants' yield of good seed; but that the seeds failing are replaced by viable seeds arising from pollen of the same character as that producing other viable seeds on that type of plant.

It is evident that we have here chosen one of three simple hypotheses as to the selective effects of the lethal factors. It might have been assumed:

(a) That there is no replacement of seeds failing owing to the inviability of the zygotes, in which case mid-styled plants, and others carrying the lethal factors, would be less fertile as seed bearers than long-styled plants.

(b) The assumption we have chosen is that the inviability of some zygotes does not affect maternal fertility, which is regarded as dependent on the nutritional condition of the seed-bearing parents, and further that the additional seeds produced have the same genotypic distribution as the other viable seeds borne by the same type of mother plant.

(c) It might, in the third place, have been assumed that while maternal fertility is completely unaffected, the lethal seeds are replaced by others of the same paternal parentage as those which perish, *i.e.* by seeds derived from other pollen from the same plant, seeing that we know that pollen from this plant has in fact been brought to this particular seed bearer.

In the author's opinion it is quite unimportant which of these hypotheses, or what blend of them, is used for calculation, so long as it is used with consistent exactitude. It is, however, necessary to grasp plainly exactly what has been assumed, in order that no inconsistent assumption shall be thought applicable to later stages of the argument.

Choosing, then, hypothesis (b) as probably nearest the truth, let us designate the proportionate frequency of long-styled plants by v , the frequencies of the four mid-styled plants by w, x, y, z , while v', w', x', y', z' stand for the corresponding types of short-styled plants.

Let also

$$\begin{aligned}v &= P, \\w + x + y + z &= Q, \\v' + w' + x' + y' + z' &= R, \\P + Q + R &= 1,\end{aligned}$$

so that P, Q and R stand for the frequencies of long-, mid- and short-styled plants.

Consider now the pollen available for fertilising the ovules on the long-styled plants; this must be derived from mid- or short-styled plants, of which the total frequency is $Q + R$. Consequently in the next generation the frequency of seed borne by long-styled plants, pollinated by each of the nine types of mid- and short-styled plants, is found by multiplying the frequency of these types ($w, x, \dots, v', w', \dots$) by $v/(Q + R)$. Exactly the same considerations apply to the seed borne by short-styled plants without the lethal, using the factor $v'/(P + Q)$.

In the case of a genotype carrying a lethal such as mid-styled M_1 , a modification is necessary, for of the pollen from short-styled AM_1 , one-quarter will fail, and the same will be true of pollen from AM_1M_2 and AM_1/M_2 . Instead of the denominator $P + R$ we shall then have

$$P + R - \frac{1}{4}(w' + y' + z'),$$

and the number of seeds formed by M_1 plants to long-styled pollen parents will be

$$\frac{w}{P + R - \frac{1}{4}(w' + y' + z')} v,$$

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of which half evidently will be long-styled and half M_1 , while the number borne to pollen parents AM_1 will be

$$\frac{w}{P + R - \frac{1}{4}(w' + y' + z')} w',$$

of which $\frac{1}{8}$ will be long, $\frac{1}{8}$ short of type A , $\frac{1}{4}$ mid of type M_1 , $\frac{1}{4}$ short of type AM_1 , while $\frac{1}{4}$ are inviable and perish. A necessary preliminary to calculating the genotypes of the next generation is therefore to evaluate the denominator appropriate to each seed parent. We shall use capital letters corresponding to those used for frequencies to designate the reciprocals of these denominators. Thus:

$$\begin{aligned} 1/V &= Q + R, \\ 1/W &= P + R - \frac{1}{4}(w' + y' + z'), \\ 1/X &= P + R - \frac{1}{4}(x' + y' + z'), \\ 1/Y &= P + R - \frac{1}{4}(w' + x') - \frac{1}{2}(1 - \frac{1}{2}q^2)y' - \frac{1}{2}(1 - \frac{1}{2}pq)z', \\ 1/Z &= P + R - \frac{1}{4}(w' + x') - \frac{1}{2}(1 - \frac{1}{2}pq)y' - \frac{1}{2}(1 - \frac{1}{2}p^2)z', \\ 1/V' &= P + Q, \\ 1/W' &= P + Q - \frac{1}{4}(w + y + z), \\ 1/X' &= P + Q - \frac{1}{4}(x + y + z), \\ 1/Y' &= P + Q - \frac{1}{4}(w + x) - \frac{1}{2}(1 - \frac{1}{2}q^2)y - \frac{1}{2}(1 - \frac{1}{2}pq)z, \\ 1/Z' &= P + Q - \frac{1}{4}(w + x) - \frac{1}{2}(1 - \frac{1}{2}pq)y - \frac{1}{2}(1 - \frac{1}{2}p^2)z, \end{aligned}$$

in which p stands for the recombination fraction between the two lethal factors, and q for $1-p$.

Then the frequency of offspring from any compatible pair of genotypes, such as those having parental frequencies y and w' , will be easily written as

$$yw' (Y + W'),$$

and the distribution of these offspring among the different phenotypes in the next generation will be found by multiplying this frequency by the theoretical expectation from this mating, *i.e.* in this case all ten genotypes in the proportions

	+	M_1	M_2	M_1M_2	M_1/M_2
+	$\frac{1}{8}q$	$\frac{1}{8}$	$\frac{1}{8}p$	$\frac{1}{8}q$	$\frac{1}{8}p$
A	$\frac{1}{8}q$	$\frac{1}{8}$	$\frac{1}{8}p$	$\frac{1}{8}q$	$\frac{1}{8}p$

These proportions do not add up to unity but to $\frac{3}{4}$ owing to the $\frac{1}{4}$ lethal combinations eliminated.

The offspring to be expected from each of the twenty-nine types of legitimate mating may be calculated in the same way. The frequency of the ten types in the next generation may be calculated from that of the prevailing generation by adding the contribution to any one type from

all the types of mating that could give rise to it. All types of mating, for example, produce long-styled plants, and we may list the contribution to the longs of the next generation.

(a) From long \times mid and reciprocal:

$$\begin{aligned}vw (V + W) &\times \frac{1}{2}, \\vx (V + X) &\times \frac{1}{2}, \\vy (V + Y) &\times \frac{1}{2}q, \\vz (V + Z) &\times \frac{1}{2}p.\end{aligned}$$

(b) From long \times short and reciprocal:

$$\begin{aligned}vv' (V + V') &\times \frac{1}{2}, \\vw' (V + W') &\times \frac{1}{4}, \\vx' (V + X') &\times \frac{1}{4}, \\vy' (V + Y') &\times \frac{1}{4}q, \\vz' (V + Z') &\times \frac{1}{4}p.\end{aligned}$$

(c) From mid \times short and reciprocal:

$$\begin{aligned}v'w (V' + W) &\times \frac{1}{4}, & x'w (X' + W) &\times \frac{1}{8}, \\v'x (V' + X) &\times \frac{1}{4}, & x'x (X' + X) &\times \frac{1}{8}, \\v'y (V' + Y) &\times \frac{1}{4}q, & x'y (X' + Y) &\times \frac{1}{8}q, \\v'z (V' + Z) &\times \frac{1}{4}p; & x'z (X' + Z) &\times \frac{1}{8}p; \\w'w (W' + W) &\times \frac{1}{8}, & z'w (Z' + W) &\times \frac{1}{8}p, \\w'x (W' + X) &\times \frac{1}{8}, & z'x (Z' + X) &\times \frac{1}{8}p, \\w'y (W' + Y) &\times \frac{1}{8}q, & z'y (Z' + Y) &\times \frac{1}{8}pq, \\w'z (W' + Z) &\times \frac{1}{8}p; & z'z (Z' + Z) &\times \frac{1}{8}p^2, \\y'w (Y' + W) &\times \frac{1}{8}q, & & \\y'x (Y' + X) &\times \frac{1}{8}q, & & \\y'y (Y' + Y) &\times \frac{1}{8}q^2, & & \\y'z (Y' + Z) &\times \frac{1}{8}pq; & & \end{aligned}$$

III. THE FREQUENCIES IN EQUILIBRIUM.

The complexity of the algebraic expressions has doubtless hitherto precluded an investigation of the system. We would emphasise, however, that an algebraic investigation is not necessary, and that a merely arithmetical approach possesses considerable advantages. Adopting East's estimate of 10 per cent. for p , and choosing any appropriate system of frequencies for $v, w, x, y, z; v', w', x', y', z'$, we may calculate the frequencies in the next generation. It is then open to us either to calculate again the frequencies in the third generation, so following the course by which a natural population will approach its equilibrium

condition, or, if our chosen frequencies seem to be not far from the equilibrium, by making a set of systematic calculations based on trial frequencies, to reduce the problem to one of solving a number of linear equations.

By this process we arrive at the frequencies which in Table I are given in per mille to five decimal places, or in hundred-millionths of the population. It will appear that accuracy of this order is not redundant for the purpose for which it is required.

TABLE I.

*Frequencies of the ten genotypes in equilibrium,
for 10 per cent. recombination.*

	+	M_1, M_2	M_1M_2	M_1/M_2	Total
+	381.63200	135.02316	5.80705	6.30552	282.15889 mid
A	221.50872	53.01029	2.37429	6.30552	336.20911 short

In examining these frequencies, we notice at once the equal frequency of AM_1/M_2 and M_1/M_2 . This arises from the circumstance that M_1/M_2 plants only occur when both parents carry either M_1 or M_2 . Both must therefore be either mid- or short-styled, and therefore for a legitimate mating one must be of each kind. But all matings of short-styled parents bear half short offspring of each viable type, hence AM_1/M_2 and M_1/M_2 are always produced in equal numbers.

Next we may notice that although the short-styled form occupies approximately one-third of the population, the other two forms are very unequal. This is a consequence of the elimination of lethals, which is constantly in progress, and which falls especially heavily on the mid-styled form. Our hypothesis has excluded differential viability or fertility among the ten viable genotypes, consequently the only way in which the lethality of the progeny of the mid-styled plants can be compensated is by their existing in smaller numbers, and therefore acting as pollen parent more frequently (per plant) than the short-, and especially than the long-styled forms. The actual proportions in which the forms exist in Nature seem never to have been established by substantial counts, and it would be a matter of interest to know whether the calculated excess of longs and deficiency of mid-styled forms really exists. In any case the comparison of the actual with the calculated frequencies would serve as an interesting measure of such differences as may exist in Nature between the viabilities and fertilities of the three forms.

An effect of the frequency equilibrium being a balance between an advantage affecting all mid-styled plants alike, and a disadvantage of the

lethals which increases with their frequency, is that in equilibrium the two lethal genes must occur in equal numbers; consequently the pair of mid-styled genotypes M_1 and M_2 , as well as the pair of short-styled genotypes AM_1 and AM_2 , will each have the frequency assigned in the table.

Moreover, since gametes of the constitution M_1M_2 are lethal with both M_1 and M_2 , they must be exposed to the heaviest counter-selection. We infer consequently that their numbers must be maintained by crossing-over, and that they must in fact be less frequent than the "repulsion" type of double heterozygote M_1/M_2 .

These qualitative considerations serve to make the main features of the table intelligible. They also suggest a slight amendment to East's form of presentation of his theory. East was evidently led to the hypothesis of two linked lethal factors determining the mid-styled condition, by analogy with Muller's brilliant demonstration of balanced lethals, and he speaks of these two lethals as though they were balanced lethals. The frequencies in the table show, however, that only in about twelve plants per mille are the two lethals carried in opposite chromosomes, and that little more than one mating in ten thousand is between two such plants. The amount of shelter which the lethals receive from selective elimination by reason of their linkage is therefore trifling. The elimination of the two lethal genes is not balanced *inter se*, but against a general selective advantage, enjoyed by the mid-styled plants, either as a seed bearer, or as in our hypothesis as pollen parent. It need hardly be said that the system developed by East (1927) loses none of its interest on this account.

IV. CONTRIBUTION OF DIFFERENT GENOTYPES TO THE ANCESTRY OF FUTURE GENERATIONS.

An important characteristic of the polymorphic equilibrium under consideration lies in the inequality of the different genotypes in respect of parentage. If we apply the calculations of Section II to the frequencies given in Section III, we may not only verify that the correct frequencies for equilibrium have been obtained, but also obtain the frequencies with which each genotype becomes the parent of every other genotype, so illustrating the explanatory remarks of Section III. Since each offspring must have two parents, we shall enumerate all the offspring of a given genotype and divide by two to show the contribution it makes to each genotype in the next generation.

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In Table II to avoid the accumulation of errors seven places have been retained. No precision can be attached to the last two places, since only five were used in the parental frequencies. The imperfect checking of the total which is harmless in the seventh place, would, however, have been unfortunate if only five places had been retained.

The full meaning of the differences in parental frequency shown in Table II is only brought out when we consider that, in consequence of the differential parentage, the different genotypes must make different

TABLE II.
Number and distribution of offspring of each type of parent.

Type of offspring	Type of parent				
	+	M_1	M_2	M_1M_2	M_1/M_2
+	162.7581062	52.9007256	52.9007256	2.0684318	0.2496496
M_1	50.0628626	54.4066081	1.5058826	0.2887038	2.2539534
M_2	50.0628626	1.5058826	54.4066081	0.2887038	2.2539534
M_1M_2	2.1531504	0.0727460	0.0727460	2.0712754	0.2499928
M_1/M_2	—	1.5058826	1.5058826	0.0130840	0.1279130
A	82.6964671	13.7280976	13.7280976	0.5368968	0.0648014
AM_1	9.0564296	15.2339802	1.5058826	0.1185332	0.5903190
AM_2	9.0564296	1.5058826	15.2339802	0.1185332	0.5903190
AM_1M_2	0.4367672	0.0727460	0.0727460	0.5397404	0.0651446
AM_1/M_2	—	1.5058826	1.5058826	0.0130840	0.1279130
Total	366.2830753	142.4384339	142.4384339	6.0569864	6.5739592

Type of offspring	Type of parent					Total
	A	AM_1	AM_2	AM_1M_2	AM_1/M_2	
+	88.4039756	10.8824696	10.8824696	0.4519466	0.1334992	381.6319994
M_1	11.4676908	12.2960317	1.4135621	0.1090016	1.2188584	135.0231551
M_2	11.4676908	1.4135621	12.2960317	0.1090016	1.2188584	135.0231551
M_1M_2	0.4801699	0.0591708	0.0591708	0.4544065	0.1342259	5.8070545
M_1/M_2	—	1.4135621	1.4135621	0.0130634	0.3125746	6.3055244
A	88.4039756	10.8824696	10.8824696	0.4519466	0.1334992	221.5687211
AM_1	11.4676908	12.2960317	1.4135621	0.1090016	1.2188584	53.0102892
AM_2	11.4676908	1.4135621	12.2960317	0.1090016	1.2188584	53.0102892
AM_1M_2	0.4801699	0.0591708	0.0591708	0.4544065	0.1342259	2.3742881
AM_1/M_2	—	1.4135621	1.4135621	0.0130634	0.3125746	6.3055244
Total	223.6390542	52.1295926	52.1295926	2.2748394	6.0360330	1000.0000005

contributions to the ancestry of future generations. Thus the 382 long-styled plants are shown by the table to leave only the equivalent of 366 progeny; whence we may infer that long-styled plants supply less than a proportional share of this ancestry. The true proportion cannot, however, be inferred merely from the ratio 366 : 382, for the 366 offspring, although not all long-styled but distributed among eight types out of ten, are yet largely long-styled, and not distributed among all genotypes in their proportion in the general population. A second or a third generation

would, then, doubtless give a different figure for the value of a genotype as a contributor to the future generation.

The true values may, however, be obtained directly by the construction of a set of linear algebraic equations. For if, taking the value of the long-styled plants as unity (a convention which we shall later discard), we suppose the other seven types to have values l, u, v for the mid-styled genotypes, and s', t', u', v' for the short-styled genotypes, then equating the value of the parent to the aggregate value of the offspring we have an equation from each column of Table II. The equation from the second column, for example, is approximately

$$53 + 56l + 0.073(u + u') + 1.51(v + v') + 14s' + 17t' = 135l,$$

the left-hand side standing for the value of the offspring, and the right-hand side for that of the parents. For the seven unknowns we thus have seven independent equations; solving these we have the values of all other genotypes on the convention that the value of the long-styled plants is unity. A more natural unit of value is that which makes the total value of a population in its equilibrium proportions equal to the number of plants. With this convention the values of 1000 of each genotype, and the contributions of each genotype to the ancestry of future generations, are as follows:

TABLE III.

Values of each type of plant and the contribution of each to the total value of the population.

		Per 1000 plants	Per 1000 population	
			Frequency	Value
Long-styled	+	957.61461	381.63200	365.45638
Mid-styled	M_1 and M_2	1064.04320	270.04631	287.34094
Mid-styled	M_1M_2	1046.01889	5.80705	6.07429
Mid-styled	M_1/M_2	1087.48899	6.30552	6.85719
Short-styled	A	997.14446	221.50872	220.87619
Short-styled	AM_1 and AM_2	989.85241	106.02058	104.94473
Short-styled	AM_1M_2	955.02553	2.37429	2.26751
Short-styled	AM_1/M_2	980.53357	6.30552	6.18278

V. SELECTIVE EFFECT ON LINKAGE INTENSITY.

The phenomenon to which Table III calls attention, namely that the different genotypes make on the average unequal contributions to the ancestry of future generations, shows at a glance the stability mechanism of the lethal factors. For it is apparent that the two types homozygous for the absence of M_1 and M_2 have both values below the average. The

stability of both M_1 and M_2 is in fact determined by the superiority of the survival value of the heterozygote over both the homozygotes, a type of stability mechanism, the evolutionary consequences of which the author has discussed elsewhere in relation to polymorphic mimetic butterflies (1927), polymorphic grouse locusts and polymorphic snails (1930, 1931). Although this general factor is common to the trimorphic heterostyled plants and other cases of polymorphism, the present case is of exceptional interest in the relation of linkage between the two lethal factors.

If the intensity of linkage were modified in a plant of either of the doubly heterozygous kinds M_1M_2 and M_1/M_2 , whether mid-styled or short-styled, the proportions of the different genotypes produced would be altered, and in matings between two such double heterozygotes the proportion of eliminated lethal zygotes will also be affected. This last is an obviously selective action by which the linkage intensity might be expected to be modified, but once we recognise that the different genotypes have a different value in contributing to future generations it is apparent that the first effect of linkage also exerts a selective effect, since the genotypes produced by cross-over gametes will not have the same mean value as those produced by the non-cross-over gametes. Actually this effect on the kind of zygote produced is in the opposite direction to the effect of the elimination of lethals, and of greater numerical importance. It is this circumstance that has required the fundamental arithmetic to be carried out with somewhat high precision, and consistency in the basic hypothesis, since we have to examine and evaluate the balance of two opposing agencies.

Of the twenty-nine types of mating, by which each generation is produced by the last, eighteen involve one or both of the double heterozygotes, and so are affected by linkage. They may, however, be divided into groups for purposes of calculation. A simple group is the pair of matings of long-styled (+) plants with doubly heterozygous mid-styled plants M_1M_2 and M_1/M_2 . These matings yield the four types +, M_1 , M_2 , M_1M_2 in proportions which depend on the linkage. In the mating $+ \times M_1M_2$ a decrease in the recombination percentage will lead to equal increases in the offspring of types + and M_1M_2 and equal decreases in the offspring of types M_1 and M_2 . In the mating $+ \times M_1/M_2$ exactly the reverse effect will be realised. From our evaluation figures (Table III) it appears that the difference in value between an M_1 plant and an M_2 plant on the one hand, and a + plant and an M_1M_2 plant on the other, is

$$2(1.06404320) - 0.95761461 - 1.04601889 = 0.12445290.$$

Of 1000 offspring plants the mating $+ \times M_1M_2$ contributes (for 10 per cent. recombination) the numbers

$$3.06307 (+), \quad 0.34034 (M_1, M_2), \quad 3.06307 (M_1M_2),$$

so that the effect of *unit* change in the recombination fraction is to transfer 3.40341 plants from each of the larger to each of the smaller classes. The other mating, $+ \times M_1/M_2$, transfers 3.69696 in the opposite direction. This latter is the larger amount (due to the fact that "repulsion" heterozygotes M_1/M_2 are somewhat more frequent than the "coupling" type M_1M_2), so that the net effect in this group of matings per *unit* decrease in recombination fraction is $0.1244529 \times 0.2935542$ or 0.0365337 per mille.

It will be more convenient to reckon the change per unit decrease in the recombination percentage, or 0.01 decrease in the recombination fraction. The pair of matings under consideration thus exert a selective intensity in favour of closer linkage of magnitude 0.3653 per million for a 1 per cent. change in the recombination fraction.

An important group of four matings

$$(+ \times AM_1M_2, + \times AM_1/M_2, A \times M_1M_2, \text{ and } A \times M_1/M_2)$$

produce the same four genotypes as the first group together with an equal number of the genotypes A , AM_1 , AM_2 and AM_1M_2 . An increase of one in each of the four single lethal genotypes, and a decrease of one in the two doubly lethal and the two non-lethal, is now worth 0.15198773 in the contribution to the ancestry of future generations. For a 1 per cent. decrease in the recombination fraction this must be multiplied by the following factors for the four types of mating:

$+ \times AM_1M_2$	- 7.492719
$+ \times AM_1/M_2$	+ 19.918967
$A \times M_1M_2$	- 9.521260
$A \times M_1/M_2$	+ 10.342644
Total	+ 13.247632

Multiplying the total by the change in value, we have from this group an increase of 2.0135 per million.

The next group of eight types of mating, which fall into four identical pairs, is that between the singly heterozygous types M_1 or M_2 and the doubly heterozygous AM_1M_2 and AM_1/M_2 ; also between (AM_1 and AM_2) and (M_1M_2 and M_1/M_2). In these cases the effect of a change of linkage intensity is to increase equally the frequencies of M_1/M_2 , AM_1/M_2 and M_2 , AM_2 (or M_1 , AM_1) and to decrease equally the frequencies of $+$, A , M_1M_2 and AM_1M_2 , or *vice versa*. The change in value for unit increase or decrease of the eight genotypes concerned is (from Table III)

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0.16611468, but the matings are somewhat less important, owing to the lower frequencies of the parents. Using the same units, the factors are

$M_1 \times AM_1M_2$	- 1.247935
$M_2 \times AM_1M_2$	- 1.247935
$M_1 \times AM_1/M_2$	3.317773
$M_2 \times AM_1/M_2$	3.317773
$AM_1 \times M_1M_2$	- 1.173297
$AM_2 \times M_1M_2$	- 1.173297
$AM_1 \times M_1/M_2$	1.274500
$AM_2 \times M_1/M_2$	1.274500
Total	4.342080

Multiplied by the change in value this gives a contribution of +0.7213 part per million.

There remain the four types of mating in which both parents are doubly heterozygous. In the groups considered hitherto it has always been advantageous to lower the recombination percentage, or to make the linkage closer, for the reason that the gametes of types + and M_1M_2 are together worth less in respect of ancestry of future generations than the gametes of types M_1 and M_2 , and that the "repulsion" double heterozygotes of type M_1/M_2 are more frequent than the "coupling" double heterozygotes of types M_1M_2 . These reasons are operative also in the last group of matings, but in these the elimination due to lethality also is influenced by linkage, so that we must take account not only of the alteration in quality (genotype) but in quantity of the offspring.

Let us take for detailed consideration the mating $M_1M_2 \times AM_1M_2$ in which both parents are double heterozygotes in the coupling phase. The offspring will be of all the possible genotypes in the proportions shown in the table, where p is the recombination percentage and $q = 1 - p$.

TABLE IV.

Frequencies of different genotypes in the progeny from $M_1M_2 \times AM_1M_2$ in terms of the recombination percentage.

	+	M_1 or M_2	M_1M_2	M_1/M_2
+	$\frac{1}{2}q^2$	pq	q^2	p^2
A	$\frac{1}{2}q^2$	pq	q^2	p^2

If we differentiate these frequencies with respect to q , we shall have the change in number ($\times 100$) for a decrease in 1 per cent. of recombination. The differential coefficients are given in Table IV A.

TABLE IV A.

Increase or decrease in the frequencies of genotypes from the mating $M_1M_2 \times AM_1M_2$ for unit change in the recombination fraction.

	+	M_1 or M_2	M_1M_2	M_1/M_2
+	q	$-(q-p)$	$2q$	$-2p$
A	q	$-(q-p)$	$2q$	$-2p$

If these are multiplied by the respective values (Table III) of the genotypes produced, we shall have the total effect on the contribution to the ancestry of future generations of a change in linkage. The contribution of the first column will be that due to the increase or decrease in the actual number of the progeny, while the contribution of the remainder is due only to change from one set of genotypes to another of different value.

Exactly similar calculations can be followed out with the other three types of mating between double heterozygotes. Table V shows the contributions of the two parts, and the frequency factor for each type of mating.

TABLE V.

	Quantity	Quality	Total	Factor	Effect
$M_1 M_2 \times A M_1 M_2$	+1.75928	-0.09796	+1.66132	0.108398	+0.1801
$M_1 M_2 \times A M_1 / M_2$	-0.78190	+0.03098	-0.75092	0.238186	-0.2164
$M_1 / M_2 \times A M_1 M_2$	-0.78190	+0.03098	-0.75092	0.117746	-0.0884
$M_1 / M_2 \times A M_1 / M_2$	-0.19548	+0.03600	-0.15948	0.313040	-0.0499
					0.1746

On these four matings together, therefore, there is a loss on quantity of 0.18789 and a gain on quality of 0.01323 part per million; the net gain on these and the other types of mating is shown in Table VI.

The net selective advantage shown in Table VI is in favour of closer linkage, or of a lower recombination percentage. The magnitude of the selective intensity, about 3 per million, is of interest possibly as indicating the ordinary level of selective intensities to be found unbalanced in Nature. It may of course happen to be an exceptionally small value, or,

TABLE VI.

Matings of double heterozygotes with	Selective intensity per million
Non-lethal	{ 0.3653
	{ 2.0135
Single heterozygote	0.7213
Double heterozygote: Quality	0.0132
Number	-0.1879
Total	2.9254

on the other hand, it may in reality be partly or wholly counterbalanced by other selective influences. In the absence of these, however, we have in the type of selection found a simple explanation of the close linkage believed to exist in *Lythrum*, and an indication that this linkage will in the future become closer very gradually until complete linkage is established.

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