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The evolutionary role of the dependence of recombination on environment

Two and three loci models

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Summary. The recombination frequency (rf) is known to be dependent not only on genetic background, but on the environment as well. In our numerical experiments we examine the role of the dependence of recombination on environment in the evolution of the genetic system. Variable rf-strategies, ensuring mean fitnesses greater than the optimum constant rf*-level, exist in both cyclical and stochastic environments. The conclusion that environment dependent recombination is evolutionary advantageous can be shown to be valid when variation in the frequency of recombination modifiers rather than mean fitness (which implies the concept of group selection) is used as a criterion for strategy comparisons. In this case, an evolutionary advantageous type of variable rf-strategies is the one ensuring restricted genetic variability dispersion in an optimal environment and an increase in released variation with the deterioration of environmental conditions. Another important result is that, taking into account the dependence of recombination on environment, it is possible to account for the maintenance of a higher level of population recombination than that predicted by models with the constant rf-level. On the whole, the data obtained indicate that the direct influence of external factors upon the rf-value could have been a significant factor in the evolution of the genetic system.

Key words: Evolution of recombination – Dependence of recombination on environment – Constant and variable rf-strategies – Mean fitness – Selection of *rec*-genes

Introduction

In recent years interest has increased in the problem of the role of recombination and linkage in gene-pool transformations of natural and artificial populations. This is due, firstly, to the ubiquity of recombination in nature and, secondly, to the significance of induced recombinogenesis in breeding programmes (especially in plants). The nature of response to selection and peculiarities of accelerated and correlated responses are determined to a considerable extent by linkage relationships of the respective polygenic systems (Dubinin 1948; Mather and Harrison 1949). Therefore, from the standpoint of practical application of genetics in breeding programmes, the induction of genetic recombination and the widening of the spectrum of recombinants can be regarded as one of the most important problems, whose solution would make available considerable, previously unemployed reserves of genetic variability (Mather and Harrison 1949).

Scant theoretical knowledge of the evolutionary role of the recombination process is one of the main reasons retarding the development of induced recombinogenesis. The first attempt to construct a model of interaction between selection and recombination was made by Fisher (1930). He suggested that under constant conditions selection will tighten the linkage between loci, epistatically affecting fitness, since recombination breaks down allelic combinations advantageous to the given environment. Further elaboration of arguments of this sort, questioning the very "evolutionary expedience" of recombination, resulted in raising the question of "Why does the genotype not congeal?" (Turner 1967).

It is currently believed that recombination leads to two opposite evolutionary effects (Darlington 1939; Mather 1943; Stebbins 1950; Grant 1958). On the one hand, it decreases the immediate population fitness by breaking down coadapted gene blocks. On the other hand, by incessantly generating new genotypes, recombination increases the probability of population survival in a varying environment. This contradiction between "the present" and "the future", between the requirements to maximize immediate fitness and to preserve species genetic plasticity is the motivating force of the genetic system evolution (Darlington 1958).

However, the characterization and detailed analysis of these general speculations entails serious difficulties. Over the past two decades a great number of theoretical works have been published studying the evolutionary role of recombination (see for review Maynard Smith 1978). One of the most important results of these studies is that under invariable conditions (i.e. with constant selection magnitude and direction as well as in the absence of gene flow) linkage tightening is provided (Lewontin 1974). As pointed out by Strobeck and coworkers (1976), it is not easy to construct a model in which selection would favour alleles increasing recombination between linked loci. It should be noted that, experimentally, the increase in recombination level under selection for adaptability has been observed only by two groups: Flexon and Rodell (1982); Zhuchenko et al. (1983). At present, several mechanisms have been suggested explaining how selection can maintain recombination (unpredictable environmental conditions, sib competition, hitch-hiking effect), but they do not provide a complete solution to the problem (Maynard Smith 1978).

Possibly, an important factor relaxing the contradiction between the requirements of individual fitness maximization and of population genetic plasticity maintenance is the dependence of recombination frequency on environment (Zhuchenko and Korol 1983, 1985). Environmental conditions can affect recombination frequency (rf) in two ways. First, indirectly, when the dynamics of alleles in selectively neutral loci acting as recombination modifiers is determined by changes in selected loci. Second, directly, when the organism responds to environment by changes – in genetically determined ways – in the rf-value (i.e. when the norm of reaction for the rf-level rather than the recombination frequency is inherited). That environmental conditions directly influence recombination levels has long been known in genetics (Plough 1917), it has been established in a great number of organisms. Various ecological factors – temperature, UV radiation, chemical mutagens, sodium, potassium, and calcium ion concentration changes, etc. – have been shown to possess recombinogenic activity. Available data indicate the existence of a genotypically determined norm of reaction for the recombination value. However, in the analysis of the evolutionary role of recombination, the direct effect of external factors on the rf-value has not been taken into account in any of the works (except in Zhuchenko 1980; Zhuchenko and Korol 1983; Zhuchenko et al. 1984).

The possible evolutionary significance of the dependence of recombination on environment is considered in this article. To this end, the dynamics of an infinite panmictic population with two selected (major) diallel loci were analysed. Two types of models are considered. In the first group of models recombination frequency is assumed to be genotype-independent (i.e. the same for all population members). In models of the second type, recombination is under genetic control, i.e. the rf-value between major loci is determined by a third locus – a selectively neutral modifier of recombination (rec-locus).

Numerical experiments carried out by us have shown that when environment affects the rf-value directly, the population mean fitness may increase (examined were cases of a cyclically varying environment, and an environment that follows a Markovian chain). The conclusion of the advantage of a recombination strategy under which the level of rf depends on environment holds when considerations are in terms of modifier gene frequency changes: selection favours modifier alleles providing direct responce for rf to environment. On the whole, the results obtained indicate that when analysing the problem of the evolution of recombination it is necessary to take into account the dependence of rf-values on external factors.

Two-locus model: problem and simulation results

The simplest model to be used in studies of the interaction between selection and ecologically determined recombination level is a two-locus model (Kimura 1956; Lewontin and Kojima 1960). Let us consider a panmictic diploid population with two diallele loci A/a and B/b. Let the frequencies of gametes AB, Ab, aB and ab be denoted by p_1, p_2, p_3, and p_4, respectively $\left(\sum_{i=1}^{4} p_i = 1,\ p_i \geqq 0 \text{ for } 1 \leqq i \leqq 4\right)$; the genotype fitness matrix – by $(w_{ij})_{i,j=1}^{4}$; and the value of recombination between the loci – R. For non-overlapping generations the dynamics equations relating gamete frequencies p_i in a given generation to gamete frequencies p_i' in the next one are (Li 1976):

$$w p_1' = w_1 p_1 - w_{14} R D$$
$$w p_2' = w_2 p_2 + w_{23} R D$$
$$w p_3' = w_3 p_3 + w_{23} R D$$
$$w p_4' = w_4 p_4 - w_{14} R D\,,$$

where $w_i = \sum_{j=1}^{4} w_{ij} p_j$, $w = \sum_{i=1}^{4} w_i p_i$, $D = p_1 p_4 - p_2 p_3$.

Normalizing multiplier w is known as the population mean fitness. It is mean fitness (averaged over generations, or equilibrium – in constant environment) that is most often used as a criterion in estimating the effect of recombination on the population evolution. It has been shown (Lewontin 1971) that under constant external conditions (w_{ij} remains constant over generations) maximum mean fitness is achieved when there is no recombination between the selected loci (rf = 0).

Linkage disequilibrium coefficient, D, measuring the correlation between alleles of different loci, is very informative in analysing recombination-selection interaction in varying environment. Thus, it has been shown in numerical experiments that if environmental variation is accompanied by a switch in the sign of the equilibrium D-value, then a non-zero level of recombination turns out to be optimal (Charlesworth 1976).

Unlike traditional models, it is assumed in our work that not only fitness coefficients, but recombination value as well can vary from generation to generation. The general pattern of investigation is as follows. First, an "optimal" constant rf-strategy is determined, i.e. such a value of rf for which mean fitness ($\bar{w}$) averaged over a certain period of time reaches its highest magnitude. The next step is to find out whether there exists in a set of variable (i.e. dependent on environment) rf-strategies the one which is more "advantageous" for the population, i.e. providing the level of averaged mean fitness higher than $\bar{w}^* = \bar{w}(rf^*)$. We considered three different types of varying environment:

1) cyclical environment with four states;
2) cyclical environment with two states;
3) environment following the Markovian chain with two states.

Case 1

Let us consider a cyclically varying environment with four states. Let selection in each state be determined by a symmetrical matrix characterized by the parameters $\alpha, \beta, \gamma, \delta$:

$$\begin{array}{cc} & \begin{array}{ccc} AA & Aa & aa \end{array} \\ \begin{array}{c} BB \\ Bb \\ bb \end{array} & \begin{pmatrix} 1-\alpha & 1-\beta & 1-\delta \\ 1-\gamma & 1 & 1-\gamma \\ 1-\delta & 1-\beta & 1-\alpha \end{pmatrix}. \end{array}$$

The corresponding numerical values used are as follows: in state 1 – $\alpha = 0.3$; $\beta = 0.25$; $\gamma = 0.1$; $\delta = 1.0$; in state 3 – $\alpha = 1.0$; $\beta = 0.25$; $\gamma = 0.1$; $\delta = 0.3$.

It is assumed in states 2 and 4 that $\alpha = \beta = \gamma = \delta = 1.0$, which suggests the absence of selective elimination; the environment possessing such a feature will be referred to as "selection-free".

Fitness parameters were chosen in such a way that equilibrium values of D in the environment states 1 and 3 are opposite in sign (Charlesworth 1976). In a selection-free environment, D approaches zero with a rate increasing with the level of recombination (Geiringer 1944). Recombination evolution in a varying environment is highly correlated with the dynamics of D. Therefore, it is possible, given the gamete disequilibrium dynamics, to try to predict how the population mean fitness will be affected by recombination decrease (increase) in each of the environment states. Clearly, a high crossing-over rate in states 1 and 3 reduces mean fitness by preventing the formation of coadapted gene blocks (AB and ab in state 1, Ab and aB in state 3). At the same time, the higher the rf-value, the easier the break-down of linkage disequilibrium produced in the previous state. Therefore, the variable rf-strategy (rf depends on environment), under which recombination in a selection-free environment increases, can be expected to have evolutionary advantage over the constant rf-strategy (rf is independent of environment).

Table 1. Comparison of rf-strategies on the fitness criterion (four-state cyclical environment)

Type of environmental change (N_1–N_2–N_3–N_4)	rf-strategies: either R, or (R_1, R_2)	Averaged mean fitness ($\bar{w}$)
8–4–8–4	0.00	0.7518
	0.23[a]	0.8443[a]
	0.50	0.8403
	(0.10; 0.20)	0.8447
	(0.25; 0.50)	0.8463
	(0.00; 0.50)[b]	0.8555[b]
28–8–3–8	0.00[a]	0.8694[a]
	(0.00; 0.50)[b]	0.8778[b]
	(0.04; 0.30)	0.8709

[a] The best constant strategy; [b] The best variable strategy
N_i = number of generations in state i for a single period
R_1 = rf in states 1, 3 (selection environment); R_2 = rf in states 2, 4 (selection-free environment)

In our numerical experiments the gamete frequency dynamics, starting with a certain period, repeats (with the given accuracy) the previous one. Let us consider the mean fitness averaged (as a geometric mean) over the whole of such a quasistationary period as a population characteristic. A constant strategy is defined by the single value $rf = R$, a variable one – by pair of values $rf = (R_1, R_2)$, where R_1 is recombination in a selection environment (i.e. in states 1 and 3) and R_2 – in a selection-free environment. Table 1 lists the results of comparing various strategies for some environment variants. As expected, there exist variable strategies providing higher population fitnesses than an optimal constant level of rf^* does.

It is somewhat unexpected that an increase in $\bar{w}$ is promoted not only by "fringing" strategies with recombination in a selection-free environment (R_2) higher, and in a selection environment (R_1) lower, than rf^*, but also by strategies with both R_1 and R_2 values higher or lower than rf^* (understandably, $R_1 < R_2$). This result is especially interesting when rf^* is close to zero, since it indicates a possibility of selection for increasing recombination.

The advantage of a variable rf-strategy is revealed not only with alternating selection and a selection-free environment, but also in the somewhat less artificial situations considered below.

Case 2

Suppose the environment is cyclic but can have only two states: in the first state selection produces a positive linkage disequilibrium, and in the second state a negative one of equal value. Let, then, the population spend more time in one of the states than in the other one (for convenience, the first state will be referred to as typical, and the second one as atypical). By a variable rf-strategy we understand, in this case, a pair of values: $rf = (R_1, R_2)$, where R_1 denotes the level of recombination in a typical environment, and R_2 – in an atypical one. A question arises whether in such asymmetric case there are variable rf-strategies more advantageous for the population than any of the constant strategies.

The same fitness matrices as those for states 1 and 3 in the previous model were used in these computations. It has been established, that the conclusion of the evolutionary advantage of variable rf-strategies holds for this case as well (Table 2).

As would be expected, the presence of such an effect and the degree of its expression depend on the period length $N_1 + N_2$ and the environment asymmetry coefficient N_1/N_2. If the population stays in an atypical environment for only $1-2$ generations, then a zero level of recombination appears to be an optimal one, and none of the possible types of the reaction norm provides a greater mean fitness (Table 3).

Table 2. Comparison of rf-strategies on the mean fitness criterion (two-state cyclic environment)

Period length	Type of environmental change (N_1-N_2)	rf^*	$\bar{w}^* = \bar{w}(rf^*)$	$rf = (R_1, R_2)$	$\bar{w} = \bar{w}(rf)$
15	14 – 1	0.00	0.8205	(0.00; 0.50)[b]	0.7921
	12 – 3	0.01	0.7816	(0.00; 0.50)[b]	0.7765
	10 – 5	0.32	0.7667	(0.10; 0.50)[b]	0.7709
				(0.35; 0.50)	0.7675
	8 – 7	0.35	0.7666	(0.20; 0.50)[b]	0.7673
				(0.10; 0.50)	0.7671
25	20 – 5	0.04	0.7816	(0.00; 0.50)[b]	0.7931
				(0.05; 0.50)	0.7903
				(0.10; 0.50)	0.7865
				(0.00; 0.40)	0.7908
				(0.50; 0.00)	0.7670

[b] The best variable strategy

Table 3. The existence of an evolutionary superior variable rf-strategy depending on the environment characteristics

Period length $N_1 + N_2$	Asymmetry coefficient $N_1 : N_2$			
	1 : 1	2 : 1	4 : 1	14 : 1
15	–	+	–	–
30	–	+	+	–
60	–	+	+	+

+ denotes that at least one rf-strategy has been found which enhances mean fitness (as compared with the optimal constant level rf*); – denotes no such strategy has been found

In the previous model with a four-states environment (case 1), the best strategies were variable strategies of the "full linkage – free recombination" type whereas in the situation now under consideration more realistic reaction norms are optimal. As in case 1, mean fitness is increased not only by "fringing" strategies ($R_1 < rf^* < R_2$), but "non-fringing" ones ($R_1, R_2 < rf^*$, or $R_1, R_2 > rf^*$) as well. For example, for $N_1 = 20$, $N_2 = 5$ the optimal level of recombination is $rf^* = 0.04$ ($\bar{w}^* = 0.7816$). For the "non-fringing" strategy of $rf = (0.1; 0.5)$ the mean fitness is $\bar{w} = 0.7865$. Moreover, situations have been found in which the dependence of recombination on environment enhances mean fitness, with "non-fringing" strategies being the most advantageous ones in this respect among variable rf-strategies. Thus, for $N_1 = 9$, $N_2 = 3$, the best in the class of constant strategies is the strategy with $rf^* = 0.01$ ($\bar{w}^* = 0.7657$). The "fringing" strategy with $rf = (0.0; 0.5)$ increases fitness up to $\bar{w} = 0.7667$. But the most advantageous in this case is the "non-fringing" strategy with $rf = (0.1; 0.5)$ ($\bar{w} = 0.7679$). This result is particularly interesting in view of the problem of "Why does the genome not congeal?", since the "non-fringing" strategies provide even in typical conditions a higher level of recombination than rf*.

It should be noted that the $\bar{w}$ value is enhanced by only those strategies under which the level of recombination in a typical environment is lower than that in an atypical one. This can be accounted for by considering that the relationship between the rf, D, and $\bar{w}$ values are similar to those applied to the explanation of the case 1 situation.

Three-locus model

As already mentioned, there are at present two essentially different types of models of the evolution of recombination: models based on mean population fitness and those based on systems with modifier rec-loci. Inclusion of recombination modifiers allows the vague and misty question of whether or not recombination is "advantageous" to the population to be replaced by a more rigorous question: "What are the dynamics of allelic frequencies at the rec-locus; when will the allele for increased recombination be fixed in the population, and when will it be eliminated?"

The relationship between these types of models (to be more exact, between the population mean fitness behaviour and the dynamics of the selectively neutral modifier locus) is established by the heuristic principle of mean fitness (Karlin and McGregor 1974). The essence of this principle is as follows. In a constant environment, the rate of a neutral modifier gene under panmixia is decided by the population mean fitness: there is selection for modifier locus alleles increasing mean fitness. This principle, however, does not always hold. For example, such factors as limitations on panmixia, migration, meiotic drive, etc., are known to be the cause of Karlin–McGregor principle violations.

Thereby a question arises: will the conclusion of the advantage of a variable rf-strategy still hold if one thinks not in terms of mean fitness, but of selection of alleles at a modifier locus?

We performed a numerical simulation of the dynamics of an infinite panmictic diploid population with three loci: selected loci A/a and B/b, and a selectively neutral locus M/m determining the level of recombination between the first two (see Feldman 1976 for gamete frequency dynamics equations). Unlike a traditional rec-locus model, in our case alleles M and m determine not two different levels of constant rf, but a variable and a constant rf-strategies. In view of the available evidence on the existence of the reaction norm for rf such formalization seems to be quite reasonable.

The procedure of numerical experiments and results obtained being virtually the same for a cyclic environment with two and with four states, these results are discussed together.

1 Cyclically varying environment

Let allele m determine the constant strategy $rf = rf^*$, and allele M – some variable strategy $rf = (R_1, R_2)$. For a four-state model R_1 is the rf-value in the selection environment, R_2 – being recombination in the selection-free environment. For a two-state situation, R_1 defines the level of recombination in the first, (typical) and R_2 in the second (atypical) state. Various situations were considered: a modifier linked ($R_{AM} = 0.05$) and non-linked ($R_{AM} = 0.5$) to the selected system, dominant and recessive M-allele. For comparisons with an optimum constant strategy those variable strategies were used which were more advantageous in terms of mean fitness.

The analysis of the three-locus model showed that the conclusion of the variable rf-strategy superiority also holds if the problem is regarded in terms of modifier locus behaviour: in the majority of cases the allele for variable strategy increases in frequency, whereas an alternative allele for optimum constant strategy is removed from the population (Tables 4 and 5). A stable polymorphism for the modifier locus is observed in several situations. The final frequency of the variable rf-strategy allele in some cases depends on its initial frequency. On the whole, as indicated by the calculations performed, there is generally selection at the modifier locus of alleles for increased mean fitness. This direction of selection on rec-locus is observed not only when one of the alleles determines a constant and the other a variable rf-strategy, but also when both alleles determine strategies of the same type.

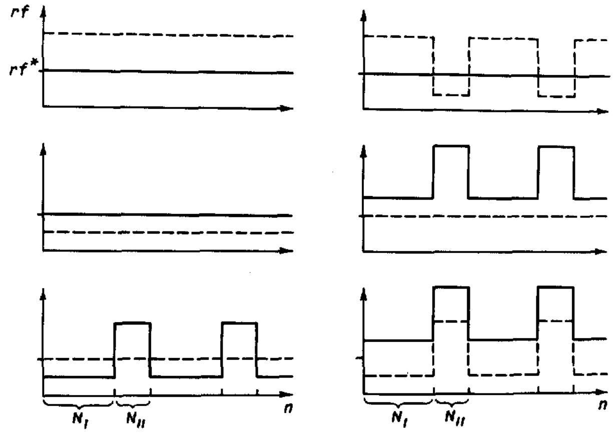

Fig. 1. Comparison of various rf-strategy types ($N_1 = 9$, $N_2 = 3$). The evolutionary advantageous rf-strategy is shown by an unbroken line, and the alternative one by a broken line

Let us consider in somewhat more detail an example of a two-state environment in which $N_1 = 9$, $N_2 = 3$ (Fig. 1). The conclusion of the $rf^* = \text{const} = 0.01$ being optimal in the class of constant strategies, previously obtained on the basis of mean fitness criterion, is also confirmed for a model with rec-modifier: allele m ($rf_m = rf^*$) replaces allele M responsible for any alternative constant strategy ($rf_M \neq rf^*$). On the other hand, if allele M determines such a variable strategy that recombination in a rare environment increases, then it can have an advantage even when the level of recombination in both environments exceeds rf^*. Thus, for $rf_M = (0.1; 0.5)$, and $rf_m = rf^* = 0.01$ the frequency of allele M increases. Moreover, allele m is eliminated from the population even if it determines a variable but "fringing" strategy, e.g. $rf_m = (0.0; 0.5)$. The results obtained indicate that the neglect of the dependence of recombination on environment conditions can lead to a wrong conclusion about the direction of selection on rf (for tight linkage).

2 Environment following a Markovian chain

Let the environment be represented by a Markovian chain with two states, whose transition matrix, P, is:

$$P = \begin{pmatrix} 1-c & c \\ d & 1-d \end{pmatrix}, \quad 0 < c, \ d < 1 .$$

Table 4. Frequency (PM) of a variable rf-strategy allele M in quasi-stationary cycle (for a four-state environment)

Environment change type $N_1-N_2-N_3-N_4$	rf = (R_1, R_2)	Initial PM	Modifier characteristic			
			Dominant linked	Recessive linked	Dominant unlinked	Recessive unlinked
28−8−4−8 rf* = 0.01	(0.05; 0.20)	0.1	0.527(156)	0.922(176)	0.186(125)	0.524(316)
	(0.02; 0.20)	0.1	0.951(254)	0.999(82)	0.794(642)	0.981(392)
	(0.00; 0.50)	0.1	0.944(294)	0.999(42)	0.888(571)	0.992(227)
8−4−8−4 rf* = 0.23	(0.10; 0.20)	0.9	0.394(947) 0.385(1000)	0.956(178) 0.997(1,000)	0.912(70) 0.972(1,000)	0.956(178) 1.000(1,000)
		0.1	0.120(433) 0.355(1,000)	0.956(814)	0.912(502)	0.994(471)
	(0.25; 0.50)	0.9	0.892(8) 0.943(1,000)	0.994(102) 1.000(1,000)	0.896(3) 0.881(1,000)	0.900(29) 0.973(1,000)
		0.1	0.856(676)	0.994(341)	0.518(894)	0.104(3) 0.681(1,000)
	(0.00; 0.50)	0.1	0.969(189) 0.995(1,000)	0.999(117)	0.959(261) 0.990(1,000)	0.998(181)

m determines a constant rf-strategy; M – a variable strategy rf = (R_1, R_2)
Number of periods to reach quasi-stationary state is given in brackets with accuracy to eps = 0.00005; in some case the value of PM after 1,000 periods is given as well

Table 5. Frequency (PM) of a variable rf-strategy allele M after 1,000 periods (a two-state cyclical environment)

Environment change type N_1-N_2	rf = (R_1, R_2)	Initial PM	Modifier characteristic			
			Dominant linked	Recessive linked	Dominant unlinked	Recessive unlinked
20−5 rf* = 0.04	(0.00; 0.50)	0.1	0.994	1.000	0.990	1.000
	(0.05; 0.50)	0.1	0.991	1.000	0.980	1.000
	(0.10; 0.50)	0.1	0.953	0.017	0.884	1.000
		0.5	1.000	1.000	0.887	1.000
	(0.10; 0.10)	0.5	0.000	0.020	0.050	0.350
	(0.50; 0.50)	0.5	0.000	0.003	0.000	0.090
	(0.50; 0.00)	0.9	0.000	0.003	0.000	0.005
20−10 rf* = 0.13	(0.00; 0.50)	0.1	0.990	1.000	0.987	1.000

Analogs to N_1 and N_2 values (see the case of a cyclical environment with two states) in a Markovian situation are ratios 1/c and 1/d, characterizing, respectively, the mean time of first attaining state 2 from state 1, and vice versa. Clearly, the more the d/c ratio departs from a unit value, the more asymmetric the environment is, i.e. the more typical the first state is and the more rare the second one.

Let c = 0.1, d = 0.2. In a model without a rec-locus, an optimum constant rf-strategy is rf* = 0.04. Suppose the modifier locus is linked to the selected system ($R_{AM} = 0.05$), allele M determines a variable strategy $rf_M = (0.00;\ 0.50)$; allele m – the constant level rf* = 0.04. The dynamics of M-allele frequency is given in Fig. 2. The presented diagrams show that that the frequency of allele M increases, i.e. in the case of the Markovian environment the allele determining a variable rf-strategy is of evolutionary advantage as well.

Discussion

The question "Why does the genome not congeal?", understood in a narrow sense (i.e. why is there no com-

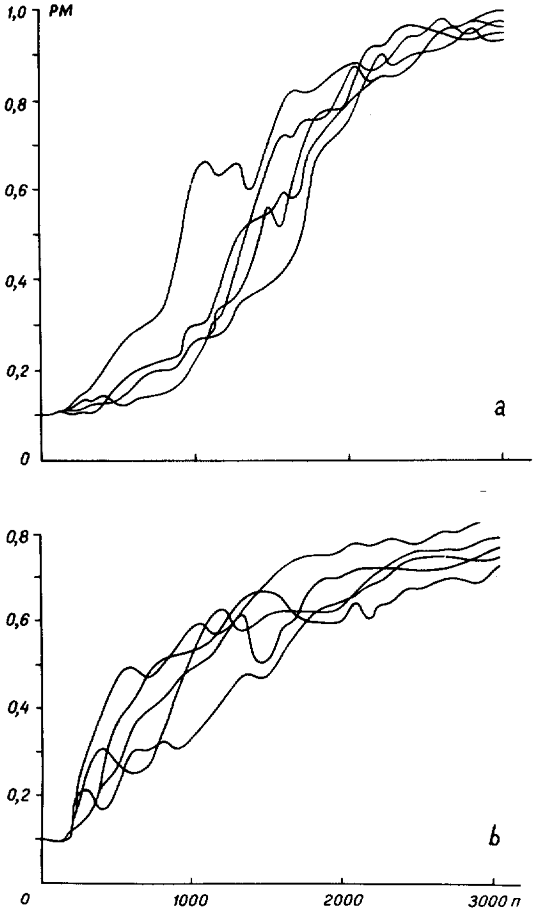

Fig. 2a, b. The dynamics of the variable rf-strategy allele M in an environment following the Markovian chain (c = 0.1; d = 0.2). **a** Allele M is recessive; **b** Allele M is dominant

plete crossing-over suppression in a population), is only part of the general problem of the evolution of recombination. An adequate theory of recombination evolution should not only explain the very existence of recombination, but also provide, in particular, an answer to the question of what factors are responsible for the maintenance of the observed level of recombination in natural populations (Maynard Smith 1978).

As indicated by our numerical experiments, the so-far neglected fact of direct effect of environment on the rf-value is of evolutionary importance.

The recombination system, providing such a dependence of rf on environment eases the contradiction between the requirement for maximum individual fitness and the necessity to maintain the ability of the population to adapt itself to future environmental changes (Zhuchenko and Korol 1983). Variable rf-strategies providing more flexible control over the process of releasing genetical variability, have an advantage at both inter- and intrapopulation levels.

From the results obtained it also follows that not all types of reaction norms for rf are evolutionary advantageous: environmental effects bring about not arbitrary, but, in a sense, directional changes in the amount of recombination. In view of this, let us analyse simulation data for various types of environment.

In models with the first type of environment a "favourable" rf-strategy is characterized by increasing recombination with the transition into a "selection-free" environment. To be able to provide a possible interpretation for such behaviour of the recombination system, let us consider the biological significance of the "selection-free" environment concept introduced above.

Let loci A/a and B/b, interacting epistatically, determine a certain, relatively independently evolving character. One can assume that periods of strong selection on this character alternate with periods of "evolutionary stasis". Such an assumption is quite legitimate, since at any moment of time there is a relatively limited number of characters that are adaptively significant. In addition, the loci selected in one environment can be neutral in another. High recombination frequency between neutral loci enables the population to build up a kind of "mobilizing variability reserve" and that without lowering the population fitness at the given moment. The importance of the phenomenon of powerful release of genetic variation during relaxed selection (reduced selection pressure) is pointed out, for example, by Carson (1975).

Another explanation of the selection-free environment concept is possible. There are situations when all members of a population, irrespective of their genotypes, are exposed to the same environmental effects. As a rule, such non-selective elimination occurs in the form of mass dying (Schmalhausen 1949; Shwarts 1980). In this case cyclic elimination is of great importance. In models dealing with gamete frequencies only and not involving population-size dynamics, the phenomenon of mass elimination can be described by the very concept of a selection-free environment. The considered pattern of environmental variation can thus be interpreted as an alternation of periods of genotype differential selection under relatively normal population conditions with periods of catastrophical population size decline characterized by nonselective elimination. Our calculations showed that the highest fitness is provided by those reaction norms under which the value of rf is higher in a selection-free environment. Strategies of this type are actually observed in nature; extreme environmental conditions act as a recombinogenic factor (Zhuchenko 1980; Zhuchenko and Korol 1985).

Biologically informative interpretation of the simulation results is also possible in the case of a two-state environment. A typical example for a given population environment is the one that the population most frequently encounters in the course of evolution and thus is better adapted to than to an alternative state (i.e. the environment that has become a sort of a norm). Typical external conditions, thus understood, may therefore be regarded as optimal for this population. Prediction of a lower rf-value in a typical environment for evolutionary favourable strategies, based on our model calculations, is in good agreement, in this interpretation, with a variety of experimental evidence. As early as 1917 Plough in his experiments on *Drosophila* pointed out the U-shaped dependence of the rf-value on temperature: recombination was minimal at an optimal temperature and it increased with the temperature deviating from the optimum (Plough 1917). A similar relation between regular meiosis conditions and conditions under which recombination frequency is minimal was observed with other organisms as well (Towe and Stadler 1964; McNelly-Ingle et al. 1966; Lamb 1969). The genetic system of a species, being a "memory bank" of specific environmental conditions built-up in the course of evolution, seems to be a sort of environment "typicality" estimator, responding to deviations from an optimum by corresponding metabolic changes and, as a result of these, a change in the level and, possibly, spectrum of recombination (Zhuchenko 1980). It is not known so far how this effect of external conditions on the rec-system occurs (a possible mechanism is suggested by Zhuchenko and Korol 1983, 1985). However, the numerical experiments conducted provide an explanation as to how mechanism, restricting the genetic variability dispersal in an optimal environment and increasing free variability with the deterioration of conditions, could become fixed in the course of the genetic system evolution.

Another no less interesting conclusion is that taking into account the dependence of recombination on environment makes it possible to explain the maintenance in the population of a higher recombination level than predicted by traditional models with the constant rf-level. Namely, it has been found that variable rf-strategies under which recombination even in optimal (and the more so in extreme) conditions is higher than rf* can be evolutionary more favourable. Therefore, the direct effect of environment on rf should be taken into account, when discussing the problem of recombination evolution, as one of the important factors determining a relatively high rf-level characteristic for natural populations.

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