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Ecological Aspects of the Recombination Problem

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Summary. Some consequences of the effect of environmental factors on the recombination system are dealt with in this paper. There are two components involved – the system of individual adaptation (F-system) and the genetic system of population adaptation (R-system). Their interaction offers an optimum interrelation of immediate adaptivity and genetic flexibility within the population. Familiar data on the evolution of recombination control systems are considered in connection with the problems of induced broadening of genotypic variation spectrum with a view to selection.

A notion of combined recombination rate and spectrum control is introduced here: disturbance control – due to direct influence of environmental factors on R-system (including meiotic processes), negative feedback control – due to dominance-recessiveness relationship between *rec*-loci alleles of the "fine" control system, and to the dependence of the R-system on the F-system norms of reaction to environment variation. The problem of dependence of the recombination spectrum on environmental factors has been considered and the hypothesis of a possible mechanism of such a dependence suggested.

Key words: Components of the genetic system – Recombination spectrum – Coadapted gene blocks – Environmental control

Introduction

The studies of mechanisms and gene regulation of recombination are of great importance in genetics. Significant attention in the synthetic theory of evolution is given to the role of linkage and recombination in processes of population gene-pool transformation. Over the last few decades the interest in these problems has increased, and the number of theoretical works has enlarged. The result was the replacement of the earlier notion of gene as a unit of selection by the conception of the integrity of genetic material; a whole chromosome or even genome came to be considered a unit of selection (Franklin and Lewontin 1970; Lewontin 1974). Previously, the evolutionary integration of hereditary systems and its role in adaptation of organisms was studied experimentally (Dubinin 1948). The recombination level was shown to be capable of determining not only the dynamics of population changes, but the nature of stationary states as well (Lewontin 1974). However, except for Huxley's (1942) book, none of the generalizing works on evolution and population genetics take into account the influence of environment on recombination processes as a factor of microevolutionary changes, and the underlying work of Plough (1917) is usually not even mentioned. The aim of this publication is to draw attention to the problem of the dependence of recombination level and spectrum on environmental factors, and to show its biological significance.

Two Components of the Genetic System

The combining of reproductive functions of genetic organization with those generating new variation within meiosis-fertilization processes is characteristic of higher organisms. A set of mechanisms ensuring the optimum balance between the hereditary stability and variation and determining the dynamic, qualitative and quantitative features of this variation is referred to as the genetic system (Darlington 1939; Mather 1943; Schmalhausen 1949; Stebbins 1950; Grant 1958). This notion covers control of the life-cycle duration, mutation rate, duration of meiosis and its separate phases, frequency and distribution of crossover exchanges, fertility level, ploidy, and factors determining the peculiarities of the reproductive system. According to Darlington, the primary function of the genetic system consists in

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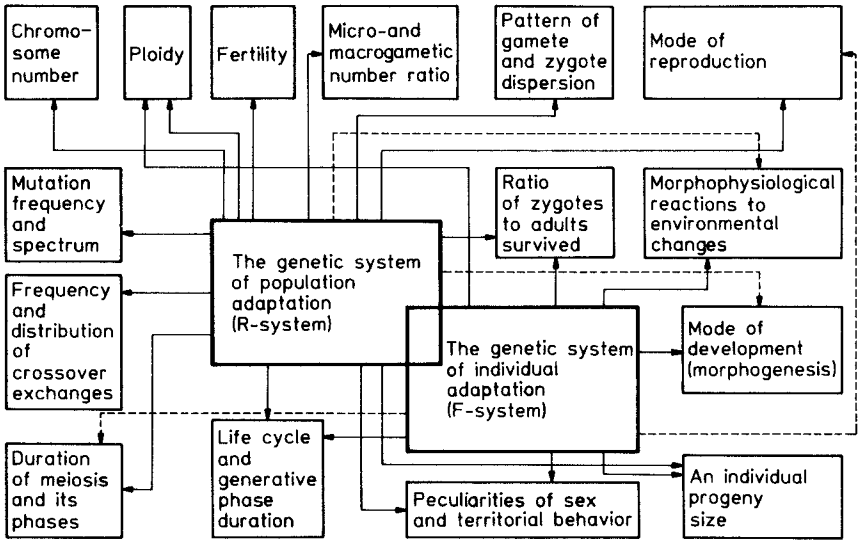

Fig. 1. Function of the two components of the species genetic system; solid arrows – primary function; dashed arrows – secondary function

the creating, protecting, and recombining of hereditary changes within a species, and, therefore, in ensuring the possibility of their effective usage by natural selection. The genetic system continuously generates and organizes variation and thus prepares the species for unforeseen situations. This represents its "property of foresight" (Darlington 1958).

However, the genetic system has another, no less important, function; it controls the organism's development in a particular environment (Grant 1958) determining its entire set of characters and adaptive reactions associated with survival. Darwinian selection of the fittest acts primarily on the basis of "estimation" by the environment of these very results of the functioning genetic complex. Therefore, it seems reasonable to regard two components of the hereditary constitution of organisms as relatively independent systems (Fig. 1) – the genetic system proper determining all the peculiarities of gene recombinations within a species (the system of population adaptation – R-system), and the control system of "vegetative" development and physiological response of an individual organism to environmental changes (the system of individual adaptation – F-system) (Zhuchenko and Korol 1981).

The expedience of such a division, conventional as it seems, is quite evident. The above mentioned statements of Darlington characterize the first component of the genetic system rather precisely, but they would simply be incorrect when applied to the genetic complex as a whole. Between the singled out components of the genetic system there are numerous relations which depend on the environmental conditions (Fig. 2). So, the mode of hereditary changes in the F-system, and particularly the combining of these changes, are determined by the R-system due to which the action of selection passes from the level of elementary chemical changes (individual gene mutations) to the biological adaptation level (Darlington 1939; Chaikovsky 1978).

The hierarchy of genetic regulation systems from gene to population level is explored from a cybernetic point of view in Ratner's (1966) monograph. The lowest levels of regulation are analysed in this book in most particular detail. Close to our division of the genetic complex into overlapping sets F and R, Layzer (1980) singles out two classes of genes (α and β) with similar functions. His division is based on the principle of evolution of hierarchic constructions directed by the genetic system β. Some of the results in this stimulating paper represent a new formulation of the ideas first stated by Darlington (1939).

The contradiction between the requirements of maximum individual adaptation at present and maintenance of a species capacity for variation in the future (Darlington 1939; Mather 1943) is resolved by the genetic system of population adaptation (R). This contradiction may be considered to be the motive force of R-system evolution, since natural selection may bring about its change only indirectly through the changes in the F-system generated by successful variants of the population adaptation system (R). As mentioned above, the most important element of the R-system is the system of recombination control (system of *rec*-genes).

About the Evolution of Recombination

The achieved level of population adaptation is continuously threatened due to mutation and recombination pressures. Stabilizing and canalizing selection are known to be factors of organization maintenance

(Schmalhausen 1949; Waddington 1957). Taking into account the data about high polymorphism and heterozygosity of natural populations (Dubinin et al. 1937; Lewontin 1974), it should be admitted that the greatest deleterious effect could be brought about by recombination itself. The phenomenon of sharp decrease in adaptation of the first segregating generations of distant hybrids caused by recombination was given a special name – "hybrid breakdown" (Dobzhansky 1970; Grant 1977). In more particular detail, the effect of recombination on fitness distribution in the progeny was studied within the framework of the problem of "synthetic lethals" (Dobzhansky 1946; Wallace et al. 1953; Batten and Thoday 1969). It is obvious that mechanisms of recombination restriction must possess a high selective advantage. This is probably one of the basic causes underlying the universality of the species phenomenon in life organization (Dobzhansky 1958; Mayr 1970; Grant 1977). The origination of species differentiation of organisms as a means for gene-pool isolation may be regarded as an important adaptation for the optimization of the recombination rates and spectrum within the system of sexual reproduction with its great combinatorial potential which provides the opportunity for high adaptive radiation.

According to Fisher's (1930) hypothesis, the selection for increase in the population adaptation may result in reduction of crossing-over rate. It is difficult to say how often it really occurs in the course of microevolutionary changes. In the experiments with *Drosophila,* the absence of any directedness in crossing-over frequency (rf) changes between four isoenzyme markers was shown for 20 successive generations, though the initial state of the population was characterized by maximum possible linkage disequilibrium (Clegg et al. 1979). According to the known results in population genetics and model experiments, the selection directed to linkage equilibrium restoration had to result in change of recombination level, providing there was high enough epistatic interaction between the loci and genetic variation for rf (Hill and Robertson 1966; Kidwell 1972a; Karlin and McGregor 1974; Maynard Smith 1978). The presence of such variation, available to selection, is shown experimentally both for plants and for animals. Thus, the direct selection for crossing-over frequency change is usually effective in one direction, at least (Allard 1963; Chinnici 1971; Kidwell 1972b). Crossing-over rates may also change as a result of correlated response to selection for other quantitative characters (Mochi et al. 1978).

As is known, a significant decrease in crossing-over frequency per DNA physical length unit is observed in passing from lower to higher organisms (Catcheside 1977). The reasons for this are essentially clear. Increasing complexity and coordinatedness during the ontogenesis of the higher organism ensured new adaptation possibilities in comparison with the lower forms (Schmalhausen 1942). Microorganisms achieve population adaptation through the great abundancy of members and due to mutations (and partly recombinations) of relatively independent genes, while with higher forms the value of each individual for the population is greater, and adaptation to the environment depends to a considerable extent on the individual adaptivity (Dobzhansky, 1959; Schmalhausen 1968; Zavadsky 1968). The rising complexity of functional organization enhances the danger of balance disturbance of the system as a whole. So it has to be accompanied by replacement of relatively free recombination with various adjustments for protecting the most adaptively significant genome regions (concentrated regions of coadapted gene systems) from destruction through pairing restriction, chiasmata localization, chromosome rearrangements, systems of balanced lethals, etc. In other words, along with the decrease in total crossing over amount, an increase in heterogeneity of genetic material with respect to recombination occurs in the course of evolutionary integration of hereditary systems, which ensures the narrowing of variation spectrum up to a "reasonable" level. This process is related to sexual reproduction, which is proved by a known fact that the genetic maps constructed on the basis of mitotic recombination are more colinear with physical (cytological) maps than those of meiotic recombination.

Data on the recombination heterogeneity of genetic material have a direct bearing on the problem of efficiency of the synthetic breeding methods. The possibilities of using the gene-bank adaptive potential of wild relatives of cultivated plants are determined by frequency and distribution peculiarities of crossover exchanges in the chromosomes of respective hybrids. As mentioned above, there exist numerous mechanisms protecting the integrity of significant gene complexes, thereby narrowing the spectrum of the progeny genotypic variation available for selection. They are especially effective in distant crosses. So, the development of methods for inducing recombination, and primarily for increasing the spectrum of exchanges at the expense of coadapted gene-block breaks and manipulation with entire blocks, must be considered to be one of the most important tasks of applied genetics (Zhuchenko 1980). Its solution should allow us to reveal significant and previously unemployed resources of genetic variation (Mather and Harrison 1949). The results evidencing the potency of this line of studies were obtained in a series of works (Sears 1956; Maistrenko and Palchikova 1966; Rajan 1968; Zhuchenko 1973, 1980; Savov 1975; Zhuchenko et al. 1980a).

It must be taken into account that the crossover distribution changes at meiosis do not necessarily account for the extension of genotype spectrum in progeny. It is common knowledge that natural selection acts on all stages of life cycle, being often opposite in direction to artificial selection. Consequently, recombinants valuable for breeding may simply not reach the identification stage (due to the effects of hybrid breakdown, synthetic lethality, etc.). A similar situation is observed under natural conditions in genetic material exchange between individuals on population and species level: before being included in the gene complex of related species, the gene must pass through powerful selective filters (Levin 1975). So, the prerequisite for recombinogenesis efficiency is the development and use of "gametic" and "zygotic" selection methods allowing reduction in the elimination of new crossover gene combinations at all stages of the life cycle (Zhuchenko 1980). That this task could really be solved has been proved experimentally (Zhuchenko et al. 1979).

Feedback and Disturbance-Compensating Control in the System of Recombination Regulation

The system of *rec*-genes and the factors controlling the mode of reproduction are basic among the components which determine the strategy of species adaptation to varying environments. Particular mechanisms of the adaptive interactions between these systems and the environment must have evolved. It is assumed that, for the maintenance of a population's (species) genetic plasticity, a low recombination level is sufficient and, therefore, a low crossing-over frequency is commonly preferable, especially for the most important regions of the chromosome (Darlington and Mather 1949; Dobzhansky 1959).

Since environmental changes in time and space are usually unpredictable, the genetic system of population adaptation must ensure the possibility of releasing variation (albeit at comparatively low levels) even under conditions of an ecological optimum. There are different ways to realize this principle. Thus, self-pollinated species are characterized by a relatively high chiasma frequency and release of significant amounts of variation as a result of rare cross-pollinations, while cross-pollinated ones usually have a lower chiasma frequency, and variation is being released in small portions, but regularly, from generation to generation (Grant 1958).

On the other hand, constant "scattering" of stored variation exhausts the gene-pool and diminishes evolutionary guarantees for survival (Rees and Jones 1977). Therefore, it is natural to assume the existence of mechanisms limiting such scattering in conditions that are optimum for the species, and, on the contrary, increasing variation with disturbance of the conditions. It is our belief, that one such mechanisms is the dominance-recessivity relationship of alleles in loci of the fine control system of crossing-over frequency. The alleles of this system increasing recombination frequency are usually known to be recessive, and those reducing it are generally dominant (Kidwell 1972; Pandey 1972), though the reverse, or even heterosis, is sometimes possible (Rees and Thompson 1956; Catcheside 1977; Srivastava 1980). Unfortunately, this question has not been studied with respect to such an important index of recombinational variation as the spectrum of recombinants. But, it is the spectrum, and not the frequency, of recombinants that determines in the first place the species capacity for adaptation to new environments (Zhuchenko 1980).

Impaired conditions for an existing population must result in lowering its numbers, increasing the degree of inbreeding, and in *rec*-loci homozygosity. This will mostly bring about a rise in the level (and possibly the spectrum) of genetic variation and, therefore, in selection efficiency. As soon as the population reaches a new balanced state and restores its optimum size, the recombination level will decrease again, though not necessarily down to the original value (negative feedback). If the decrease in number, or the elimination, of some or other gene combinations is accompanied by selectivity in the homozygosity of *rec*-system elements, this also ensures a certain nonrandomness in the spectrum of released variation.

However, the higher the individual plasticity of genotypes, the lower the selectivity of elimination. Consequently, high modificative variation may serve as a kind of protection of potential genetic variation from excessive scattering (Zhuchenko 1980).

The dependence of recombination frequency (rf) on the environment is, in our opinion, an equally important mechanism for reducing the contradiction between the requirements for maximum adaptation and maintenance of genetic plasticity.

The estimation of the influence of external factors on recombination frequency takes a significant place in genetic studies beginning with the pioneering works of Plough (1917, 1921). Recombinogenic effects of temperature, X- and γ-radiation, ultraviolet radiation, chemical mutagens, inhibitors of DNA and protein synthesis, variations in ion concentrations of sodium, potassium, calcium, magnesium, manganese, and selenium have been studied in different organisms (for reviews see, Wilson 1959; Bodmer and Parsons 1962; Kushev 1971; Zhuchenko 1973, 1980; Mock 1973). Seasonal fluctuations of recombination values have been shown as well (Allard 1963; King and Hayman 1978; Zhuchenko et al. 1979).

It was established in these studies that changes of recombination level depend on type and duration of treatment, the stage of meiosis at the moment of treatment, sex, age, physiological state of the organism, its genotype, the chromosome and segment studied. A well known example of segmental specificity is the effect of "proximal increasing and compensatory distal decreasing" of crossing-over frequency in *Drosophila* (Kikkawa 1934).

External influences may be the cause of changes not only in intrachromosomal and intragenic recombination, but in mutual behavior of nonhomologous chromosome-pairs as well – the induced change of quasi-linkage (Zhuchenko et al. 1977).

In a large number of cases a significant heterogeneity of the data obtained is observed; the sources of this heterogeneity may be as follows: unaccounted for genetical and ecological differences; nonsynchronized states of cell populations subjected to treatment; the effects of differential elimination in post-meiotic stages (also dependent on environment and genotype); artefacts caused by insufficient resolving capacity of cytological methods; inconsistency of the method with the object and aim of investigation; and inadequacy of the statistical models used.

Different parameters characterizing recombination frequency, similar to those dealt with in the problem of genetic control of recombination, were used in the induces recombinogenesis. However, for estimation of the evolutionary significance of the recombination dependence on environment and of the prospects for practical application it is necessary to supplement these parameters with the system of indices which could afford an objective estimation of recombinant spectrum changes. Such supplementation could probably be made by means of protein electrophoresis, and the combined analysis of marker and quantitative characters with multivariate statistical methods (Shevchenko et al. 1979; Zhuchenko et al. 1980b; Zhivotovskii and Altukhov 1980).

In Plough's experiments, rf-value was minimum at optimal temperature, and it rose with the increase of temperature deviations from optimum. Such a U-shaped dependence ensures the lowest genetic variation in ecological optimum having minimum requirements for variation, and its increase in extreme environments. This leads to a certain "expediency" of population reaction, but with one generation delay, at least: the influence of environment on the recombination brings about a change in genetic content of the next generation. Such a mechanism may be of real value only with high enough positive autocorrelation of environmental changes in time and space. It should be noted, that strengthening of the mutation process occurs with the deviation of the environment from optimum, as well (Zujtin 1937).

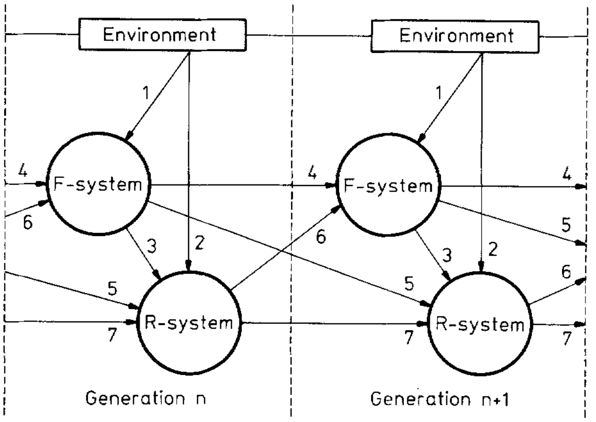

Fig. 2. Possible ways of the environment influence on recombination and genotypic structure of population. The changing of population content for the genetic system of individual adaptation (F) due to: natural selection for F-system (1–4), direct response of the R-system to the environment (2–6), reaction of the R-system to general metabolic changes (1–3–6). For similar changes in population content in the R-system, the ways 1–5, 2–7, and 1–3–7 are used respectively

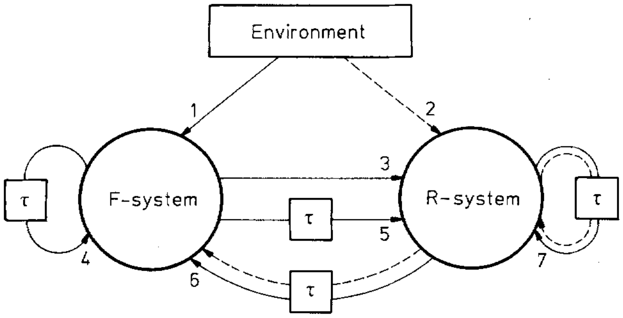

Fig. 3. The graph of reaction of gene-pool to the environment influence (1 and 2); solid arrows – circuits of control for feedback; dashed arrows – disturbance control; τ-duration of one generation life-cycle (see text for explanation)

If the recessiveness of alleles increasing the recombination rate provides the possibility for the control of variation on the basis of feedback, then the dependence of the frequency and distribution of crossover exchanges on the environment may be viewed as realization of the combined control principle (Besekersky and Popov 1968). With this, the regulation for disturbance is achieved due to direct influence of the environment on crossing-over, and for feedback – due to dependence of rf on fitness. The changing of *rec*-allele frequencies provides the regulation of recombination due to the genetic system of population adaptation (R) through selection for the individual adaptation system (F) elements; the direct influence of external conditions on recombination is the expression of the R-system reaction norm to the environmental change, the dependence of rf on the fitness being the expression of the

F-system reaction norm influence on the genetic system of population adaptation (Figs. 2 and 3).

In view of what is said above, the existence of a similar ecological dependence for the reproductive system has pertinence. Organisms with primarily an asexual reproduction pass to a sexual one under extreme conditions, and different forms of inbreeding are replaced by cross-fertilization (Huxley 1942; Grant 1975). We suggest that the functioning of two main components of the R-system, which determine the mode of reproduction and the recombination level, ensures minimum scattering of genetic variation in optimum environment but an increase under adverse conditions. However, examples of inverse relations are also known for each of these components (Wilson 1959; Kannenberg and Allard 1967). According to Grant (1958), different elements of the whole system of recombination regulation may act in opposite directions providing over-all balance on the level of a more open recombination system for one type of species, and on the level of a more closed system for another one (Carson 1957). Evidently, the reactions of the elements themselves and their relations to environmental changes may be quite complex, and the total result (overall balance change) can be estimated only on the basis of whole system analysis.

Therefore, in our model, unlike the classical evolutionary scheme, environment plays the role of a factor which not only "assorts" variation by means of natural selection for the most fitted, but determines, to a great extent, the level and, probably, the spectrum of this variation.

The formulation of ecological dependence of recombination may be restated in terms of the rf dependence on fitness: an increase in rf with the deviation of environment from the optimum for a given genotype is analogous to an rf increase with the lowering of genotype adaptivity in the given environment. Negative correlation between crossing-over frequency and some fitness components has been established in *Drosophila melanogaster* (Marinkovič et al. 1980; Tucič et al. 1981). But one of the abilities of a genotype having high adaptiveness is its capacity to provide the formation of normal phenotypes in a sufficiently wide range of conditions. Consequently, high adaptiveness protects genetic variation from rapid scattering both by means of relaxed selective elimination (protection of free variation), and by lowering the recombination level (protection of potential variation) (Zhuchenko 1980).

Possible Non-Randomness in Induction of Recombinational Variation

External factors may bring about recombination changes as a result of direct influence on molecular mechanisms of meiosis, or indirectly due to the effects caused by metabolic changes in the whole organism. In the first case, the efficiency of the treatment depends significantly on the stage of development. For example, one and the same factor is known to decrease crossingover frequency when treatment is given during interphase, to cause its increase when treated in prophase, and to have no influence during the other phases (Lawrence 1967). It may be suggested that, in the case of indirect influence on recombination (through total metabolic changes) of great significance are the conditions of environment during the whole ontogenesis – the organism seems to be "estimating" the normality of the environment, integrating deviations from the optimum and "remembering" them in the form of metabolic changes (Zhuchenko 1980). But how does it bring about changes in recombination level and, all the more, in the extension of their spectrum? At present, we can hardly give a satisfactory answer to this question. However, the existing theoretical presentations allow the suggestion of some models, one of which is considered below (Zhuchenko and Korol 1981). We would like to mention that there also exist some experimental data which directly or indirectly agree with the above-stated suggestion (Thompson 1964; McNelly-Ingle et al. 1966; Lamb 1969; Zhuchenko et al. 1980b).

Whitehouse, on the basis of studies made by him together with Hastings, suggested the operator model of recombinations in which the coincidence of recombination and transcription operators was postulated (Whitehouse 1966). He believes that the study of *rec*-genes could provide information concerning the regulatory mechanisms of genic activity and of recombination simultaneously. Thuriaux (1977) argues along the same line, trying to explain sharp decrease in intergenic recombination frequency per unit of DNA physical length in transition from lower organisms to higher ones with constancy of structural gene recombination lengths.

The frequency of mutation damages during the formation of chromosome aberrations is considered to be much lower for structural genes than for regulatory ones (Soyfer and Akifjev 1976). This, probably, reflects a certain separation of functions of structural genes and regulatory genes (unique and repeated DNA sequences) in determining the position of points for crossover and aberration breaks, respectively.

The above-mentioned models have a direct bearing on the problem under consideration. They may serve as a basis for suggesting positive dependence of the mode of variation released due to induced recombinogenesis on the nature of the acting external factor. Two questions must be distinguished here: is it possible to increase the recombination level due to the factor's influence on the vegetative stages of development, and does the spectrum of recombinants depend on the type of treatment? It should be noted that the second question also applies to the case of direct influence on meiosis.

If the aforesaid considerations of Whitehouse (1966) and Thuriaux (1977) are correct, then a sharp change of the environment resulting in selective increase of matrix activity in a certain part of the genome (e.g. derepression of structural genes which code for enzymes determining the resistance to given environment) may be at the same time the cause of increase in recombination frequency in that part. This provides an increase in diversity in the progeny for adaptivity to the new environment; negative variants, though they might be prevailing among the recombinants, undergo the eliminating action of selection, and positive ones increase the probability of population survival in the new environment. The suggested model is quite similar to those considered in connection with the problem of increasing locus specificity in induced mutagenesis (Swaminathan 1969; Auerbach 1976; Salganik et al. 1977).

The postulated mechanisms may, at first sight, resemble the so called "adequate change of heredity" in response to the environmental change. In reality, the manner of recombinational transformations of genetic information under the environmental changes is determined by meiotic mechanisms formed in the course of evolution, by peculiarities of the reproductive system and chromosome organization of higher organisms (the formation of coadapted gene blocks, functional integration of block systems, etc.). These systems and mechanisms may be regarded as a peculiar "memory" of ecological situations in the past which determined the qualitative specificity of the given phyletic group (Zhuchenko 1980). The possibility for population reconstruction with the changing of environment is known to be provided thanks to genetic variation (free and potential) stored in its gene-pool due to mutations and influx of new alleles from the outside. A certain non-randomness in recombination spectrum may be achieved, according to our suggestion, by means of "attaching" the exchange point distributions in the chromosome to the non-random process of gene transcription within the respective blocks which "adequately" reacts to the environmental changes.

Therefore, highly specific distribution of the coadapted genes within the functional blocks and their non-random relative position in the genome impose fundamental restrictions on the recombination variability spectrum comparable in their significance with reproductive isolation of species. So, notwithstanding the randomness (i.e. the absence of dependence on environment) of the primary process of origination of new hereditary changes (mutations), a definite "adequacy" in the shift of the crossover exchange distribution pattern is possible in response to environmental changes. It is not unlikely that this ensures a certain directedness in releasing genetic variation stored in the population gene-pool by means of known mechanisms. In all these processes, the organizing role belongs to the genetic system of population adaptation and to selection.

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