

A new look at the mechanisms of saltatory changes in living organisms

Abstract

There is an attempt to explain some evolutionary processes in plants such as saltatory changes on the base of multidimensionality of plant inherited information coding. According to the suggested hypothesis, inherited information is coded by not only a nucleotide sequence but also by chromosome differential endoreduplication. It is supposed that chromosomes compete among each other for the contact with the nuclear membrane, but a change in the endoreduplication degree of various chromosome sites can result in a change of competition ability for the contact with a nuclear membrane. A simultaneous increase of chromosome endoreduplication degree of many sites can lead to an increase of nuclear membrane surface and to a change in chromosome competitive interrelations and, respectively, to a change of activity of many genes. Phenotypically it may manifest itself as a saltatory change of many traits.

Keywords: multidimensionality of plant inherited information coding, endoreduplication, nuclear membrane, epigenetic variability, saltatory changes, agamospermy, isozymes

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Introduction

Presently most spread ideas about the evolutionary process as a gradual accumulation of mutations, their low frequency and negative influence of most mutations on the genotype do not allow us to give a clear explanation for the existing species diversity.^{1,2} Contributions which dwell upon the existence of big complex (saltatory) changes of traits that lead to evolutionary transformations are a big progress in the explanation of evolutionary processes. Here belong such a saltatory change as, e.g., polyploidy, which is the genomic (epigenomic) mutation characterized by a change of cell genome number and a wide spectrum of inherited morphological and physiological traits.^{3,4} These changes can be considered as epigenetic due to the absence of changes in DNA nucleotide sequences, their high frequency and inheritability. A change of chromosome spatial distribution in the cell nucleus⁵ also leads to saltatory changes. New forms that appear under saltatory changes differ from those of ancestors in a complex of traits. If a wide complex of changes appearing under polyploidisation can be explained by a change of all genes dose and the following dosage compensation processes (excessive gene doses inactivation), then these ideas turn to be insufficient to explain the rest cases of saltatory changes. The hypothesis of multidimensionality of plant inherited information coding^{6,7} can be one of the basic moments to explain saltatory changes. According to the suggested hypothesis, inherited information is coded by not only a nucleotide sequence but also by chromosome differential endoreduplication (differential polyteny). Investigations of agamosperous sugar beet progenies became the base for this hypothesis. Thus, polymorphism and unusual ratios of phenotypic classes^{8,9} were revealed in agamosperous sugar beet progenies that arose on the base of one parent genome from cells that did not undergo meiosis.

The hypothesis that explains this polymorphism consists in the following:

- Chromosomes are endoreduplicated in tissue cells surrounding this embryo sac. Endoreduplication degree of different sites within one chromosome and corresponding homologous sites of homologous chromosomes can be different. Due to this, alleles of heterozygous loci can be presented in a cell by a different copies number, i.e. at a different dose.
- It is supposed, that a somatic cell entering into embryogenesis by agamospermy can have only one copy of every allele. Therefore, excessive allelic copies are eliminated from the genome.
- Elimination of excessive chromatid sites copies proceeds together with the combinatorial process which consists in the choice of a random pair from a multitude of having copies.
- Preservation of pair of chromatid site copies in a number of following embryogenetic divisions is determined by the fact that these two copies attach to the nuclear membrane. Copies of alleles that remain in the cell entering into embryogenesis determine the genotype of the developing seed.
- If, for instance, one of the alleles of a marker locus is endoreduplicated and presented by three copies in the genome and the second one-by only one (*FFFS*), then the theoretical ratio of isozyme phenotypes in agamosperous progenies will be 1FF: 1FS. Such ratios were observed in our experiments.^{8,9} It should be noted that this hypothesis is applicable also in those cases when an unfertilized diploid ovum enters into embryogenesis.

The proposed hypothesis is based on numerous facts

The first of these facts is the effect of colchicine on the phenotypic ratio in an agamosperous progeny.^{9,10} This was manifested, for example, in the fact that the processing of sugar beet plants

with colchicine increased the proportion of plants producing agamosperous progeny with ratios of phenotypic classes that did not correspond to Mendelian proportions⁹ or led to a significant decrease in the proportion of heterozygous class in agamosperous progeny.¹⁰ This decrease in the share of the heterozygous class was easily explained on the basis of the assumption of the presence of polyteny of chromosomes in cells entering into embryogenesis without fertilization. The hypothesis is supported by the existence of a diploid sugar beet plant with high DNA content and capable of reproduction by agamospermy in contrast to a plant that has a low DNA content in the nucleus of the cell and was incapable of reproduction by agamospermy.¹¹ On the existence of polyteny of chromosomes in the cells of generative organs point many facts: the endoreduplicational meiosis in diploid *Allium tuberosum* plants,¹² high DNA content in the nuclei of the cells surrounding the embryo sac, also in cells of embryo sac proper in many plant species.^{13,14}

The assumed in this hypothesis the diminution of excess copies of the alleles of enzyme genes from cells entering into embryogenesis is based on known facts: decrease of DNA content to 2C during the first embryonic divisions in many plant species.^{13–15} Mentioned in the hypothesis probable differences in the endoreduplication degree of chromosome allelic sites were well shown on *Phaseolus coccineus*.¹⁶ This phenomenon logically stands alongside with such phenomenon as differences in the degree of polyteny of non-allelic regions of chromosomes. In a recent study, an almost twenty-fold increase in the copy number of *hobo*-transposons in the polytene chromosomes of the wild *Drosophila* lines, that acquired resistance to methotrexate after long-term selection and methotrexate treatment, was detected.¹⁷ In the cytological preparation given in this article, obtained with the use of the FISH method, the different intensity of the glow of the fluorescent label in the localization sites of *hobo*-transposons is shown, indicating the differences in their copy number.¹⁷ A differing level of amplification was found in different chromosome regions of cancer cells.¹⁸ The used research method allows these authors to associate the revealed amplification only with tandem repeats, although in fact, the polyteny among these repeats is also not excluded.

It was also shown that the level of resistance to methotrexate in the selected AT-3000 cell line of murine Sarcoma 180 is directly proportional to the level of activity of the dihydrofolate reductase enzyme, which in turn is due to the copy number of the gene controlling this enzyme.¹⁹ Moreover, a decrease in resistance when growing cells on a medium without methotrexate is associated with a corresponding decrease in the number of copies of the gene controlling the dihydrofolate reductase.¹⁹ It should be noted again that in both on *Drosophila* experiments and in experiments on AT-3000 cells, the increase in resistance to methotrexate did not arise in a moment, but during selection and with gradual exposure to methotrexate.¹⁹ However, there is evidence that in one of the cell lines, stable forms appeared spontaneously during development even in the absence of methotrexate.¹⁹ In the authors' opinion, methotrexate acts only as a selective agent and has no direct role in the resistance (gene multiplication) process, but it allows selection of the gene doubling.¹⁹ It can be assumed that a similar increase in a gene copy number can occur in natural conditions, if there are appropriate selection factors.

Attention is drawn to the fact that the increase in the gene copy number at resistance to methotrexate is accompanied by intensive staining of a specific region of chromosomes in the cell lines of the Chinese hamster lung,¹⁹ with the same chromosome changes found in the cells of the Chinese hamster ovary.¹⁹ In this regard, it can be added that in the cells of tissues of generative organs in animals and plants,

polyteny of chromosomes is observed quite often.²⁰ Thus, it can be assumed that the demand for increasing the activity of a gene caused by environmental conditions can be ensured by increasing gene copy number not only by tandem repeats, but also by polyteny. Attachment of eucaryotic chromosomes to the nuclear membrane was first shown by Mosolow A.N.,²¹ and now this is a well-known fact, which has long been included in textbooks.²² There are many specific binding sites for chromosomes with the nuclear membrane, and they provide the spatial organization of the interphase nucleus.^{22–24} It should also be added that eukaryotes also have a large number of replicating sites, which ensures rapid replication of the entire DNA of the genome.²⁵

The effect of colchicine^{22,26} and also of nutrition level and its character on DNA content in a cell nucleus,^{27–29} on mixoploidy of cell populations in a polyploid expressed in the presence of both polyploidy cells and those of high endoreduplication level in plants,³⁰ and also the effect of colchicine on the segregation character in plant agamosperous progenies^{9,10} allow us to consider the dose of DNA in the genome as a coding of hereditary information in the second dimension and as a way of recording of inherited information about acquired traits. To check the hypothesis on multidimensionality of inherited information coding, the effect of detergent Triton X-100 that can detach chromosome from the nuclear membrane on the expression and inheritance of different traits in wheat was investigated. Triton X-100 induces inherited changes of morphological traits in wheat.³¹ At present, the mechanism leading to inherited changes in wheat is unclear; however, such signs as the shape of the ear, the number of grains in the ear, persisted for 6 generations after Triton X-100 treatment.^{31,32}

We observed differences in the PCR profiles of enzyme genes obtained for different tissues of the same sugar beet plant.³³ This coincides with the known data that different tissues of the same plant may differ in the level of the polyteny of the chromosomes. This fact, in our opinion, also speaks in favor of our hypothesis. Moreover, in haploid plants enzyme phenotypes similar to heterozygous ones^{34,35} were discovered. Since the concept of heterozygosity is applicable only to organisms having a diploid or higher level of ploidy, we have designated this phenomenon as heteroallelicity.³⁵ Heteroallelic phenotype in a haploid plant could arise only as a result of the polytene structure of chromosomes, which supports the hypothesis proposed. Based on the concept on differential chromosome endoreduplication, also on the known facts about the fact that chromosomes contact with the nuclear membrane in an interphase nucleus, and gene expression depends on this contact,^{21,22} it is possible to suggest the following hypothesis about the mechanisms of salutatory changes.

Chromosomes are competitive for their contact with the nuclear membrane whose surface is limited and tends to minimum according to the laws of physics. The need to increase the activity of some genes combined with natural selection caused by external conditions can lead to an increase copy number of these genes and degree of polyteny in the chromosome regions carrying these genes and, accordingly, to a higher competition of these sites for contact with the nuclear membrane. An increase of endoreduplication degree in a small number of loci may not affect a genome size and that of nuclear membrane surface. If the number of endoreduplicated regions exceeds some critical value, then it may lead to an increase of the nuclear surface and, as a consequence, to a new activity ratio of different loci expressed as a salutatory change. If such processes affect cells of generative organs, then a transfer of salutatory changes to the next generation is possible.

The Triton X-100-induced inheritance of different traits that we observed^{31,32} indicates the fact that changes in nuclear membrane-chromosome interaction are inherited. We referred Triton X-100-induced changes to those of epigenetic. The suggested hypothesis well accords with the ideas about a huge role of dosage effects in genome functioning. Dosage effects can be considered as an evolutionarily established, at the super molecular level, an action of chemical law according to which the rate of chemical reaction is determined by the concentration of agents entering into it. Gene dosages, in this case, are analogous to agent concentrations in elementary chemical reactions. Comparing the two reasons for saltatory changes-increase of genome dosage and a change of chromosome spatial distribution-it is possible to hypothesize that the change of chromosome spatial distribution is also determined by dosage effect, as there may be competition between and among chromosome sites having a different endoreduplication degree for the contact with the nuclear membrane. A change of chromosome spatial distribution and gene expression may arise as a result of changes of inters chromosome competitive abilities for the contact with the nuclear membrane. The suggested hypothesis is based on the fact that dosage relations play a huge role in genome reorganization; they, due to their dependence on environmental conditions, are an effective way of epigenetic changes and a powerful acceleration mechanism of evolutionary process in response to changing environmental conditions.

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Conflict of interest

The author declares that there is no conflict of interest.

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