

GENOME STRUCTURAL-FUNCTIONAL PECULIARITIES AFFECTING PLANT EPIGENETIC VARIABILITY AND EVOLUTION

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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 a 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.

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

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 (Schmalhausen, 1946; Russell, 1986). 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 (Stebbins, 1950; Matzke et al., 1999). 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 nucleus (Stegny, 1991) 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 (Levites, 2005; 2007) 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. Investigations of agamospermous sugar beet progenies became the base for this hypothesis. Thus, polymorphism and unusual ratios of phenotypic classes (Levites, 2005, 2007) were revealed in agamospermous 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 embryosac. Endoreduplication degree of different sites within one chromosome and homological sites of homological 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. A somatic cell entering 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 present copies. Preservation of each pair of chromatid site copies in a number of following embryogenetic divisions is determined by the thing that these two copies attach either to the nuclear membrane or to the nuclear matrix. 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 agamospermous progenies will be *1FF* : *1FS*. Such ratios were observed in our experiments (Levites et al., 1999; 2000).

The hypothesis is based on numerous facts on the effect of colchicine on phenotypic ratio in an agamospermous progeny (Levites, 2000), existence of diploid sugar beet plants with high DNA content in cell nuclei (Maletskaya, Maletskaya, 1999) capable of agamospermous reproduction and diploid *Allium tuberosum* plants with endoreduplicational meiosis (Kojima, Nagato, 1992), high DNA content in nuclei of cell tissues surrounding the embryosac, also in cells of embryosac proper of most plant species number (Ermakov et al.; Morozova, 2002), decrease of DNA content to 2C during the first embryonic divisions (Mericle, Mericle, 1970), differences in the endoreduplication degree of allelic chromosome sites (Cionini et al., 1982), attachment of eucaryotic chromosomes to the nuclear membrane (Mosolov, 1972).

The effect of colchicine (Hassan et al., 1991; Matzke et al., 1999), nutrition level and character on DNA content in a cell nucleus (Durrant, Timmis, 1973; Cullis, 1973; Oh, Cullis,

2003), mixoploidy of cell populations in a polyploid expressed in the presence of both polyploid cells and those of high endoreduplication level in plants (Carvalho, 2000), also the effect of colchicine on the segregation character in plant agamosperous progenies (Levites et al., 2000) allow us to consider differential endoreduplication as inherited information coding in the second dimension and as a way of registration of inherited information about acquired traits.

To check the hypothesis on multidimensionality of inherited information coding, the effect of detergent TX-100, that can detach chromosome from the nuclear membrane, on the expression and inheritance of different traits in wheat and sugar beet was investigated. Triton X-100 induces inherited changes of plant morphological traits (Makhmudova et al., 2009). Tissue differences in sugar beet structural organization of enzyme loci (Vinichenko et al., 2007), which may appear due to the thing that chromosome sites carrying enzyme loci are differently endoreduplicated in different tissues, can also be in favor of the suggested hypothesis.

Based on the concept on differential chromosome endoreduplication, also on the known facts about the thing that chromosomes contact with the nuclear membrane in an interphase nucleus, and gene expression depends on this contact, it is possible to suggest the following hypothesis about the mechanisms of saltatory 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. Gene functioning can lead to an increase of endoreduplication degree in chromosome sites carrying these genes and, respectively, to higher competition of these sites for their 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 saltatory change. If such processes affect cells of generative organs, then a transfer of saltatory changes to the next generation is possible. The Triton X-100-induced inheritance of different traits that we observed indicates the thing that changes in nuclear membrane-chromosome interaction and, obviously, states of membranes 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 supermolecular 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 interchromosome 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.

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