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SIGNIFICANCE OF INTROGRESSION HYBRIDIZATION FOR EXTENSION OF GENETIC VARIABILITY IN RECIPIENT GENOME

Alien chromatin (introgressions) can be incorporated into the wheat genome either through recombination or through translocation. Lines of introgressive origin may not contain identified alien chromatin, although they appear to be changed relative to the original wheat sample by some characteristics that are registered at different levels of phenotype assessment. It has been shown numerous facts of the variability of the recipient genome of hybrid origin. They can be caused by irregular behavior of chromosomes in mitoses of somatic cells with hybrid genome, and DNA changes. Wide phenotypic variability was observed among the progeny of hybrid genomes up to appearance of phenotypic novelties. The study of DNA profiles using several methods revealed the presence of numerous genetic and epigenetic changes, including deletions, changes in gene expression, changes in the methylation pattern, and activation of retrotransposons in the recipient genome. When these changes were not directly related to alien fragments, they are considered as possible mechanisms of extension of genetic variability intra genome of hybrid origin. Transcriptomic analysis of lines of hybrid origin and parental plants using the RNA-seq analyses showed that the change of expression affected a different number of genes. The change in the expression of alien genes occurred in the direction of down-regulation, upregulation was typical for wheat genes. Phenotypic variability during introgressive hybridization can be accompanied by attenuation of the expression of an alien gene when it enters the recipient genome. That may be a consequence of the interaction between the alien gene and the genetic environment of the host genome. Today there is a lot of evidence that these mechanisms are epigenetic, which include DNA methylation, histone modification, the involvement of small RNAs in the regulation of gene expression, and the involvement of transposons. Moreover, none of these mechanisms act independently, but are a component of events, the results of which can be a change in gene expression and the appearance of a new phenotype that is not related to the expression of an alien gene.

Keywords: wheat, amphidiploids, hybrid genome, introgression, phenotypic novelty.

It is known that as a result of introgressive hybridization, alien chromatin can be incorporated into the wheat genome either through recombination (homologous or homoeologous), or through translocation, or through the replacement of an entire wheat chromosome with an alien one. Alien addition lines are not considered as introgression lines by all researchers. But in our opinion, this term can be applied to all lines that are descended from a distant hybrid. Our experience shows that lines of

introgressive origin may not contain identified alien chromatin, although they appear to be changed relative to the original wheat sample by some characteristics that are registered at different levels of phenotype assessment (morphological, physiological, electrophoretic spectra of proteins or DNA fragments).

It seems that lines of hybrid origin (distant crossings) should be called introgressive regardless of whether it was possible to prove the presence of

alien chromatin in their genome. We still do not know what the so-called cryptic introgressions are. The question is whether the inclusion of alien chromatin is so small that it is impossible to find a tool for its detection, or whether the changes affected the wheat chromatin, so that we can record them only by the changed phenotype. In both cases, the triggering mechanism of changes is a temporary presence of the wheat genome together with an alien chromatin, and the line of such origin is better to be called introgression lines. Such a name of the line in a certain way orients the researcher to understand the nature of those changes that have occurred in the genome, which we can see at the phenotypic level.

Facts of the variability of the recipient genome of hybrid origin

It has been shown (cited in [1]) that the behavior of chromosomes in mitoses of somatic cells is disturbed in the plants of wheat-rye monosomic addition lines with chromosome 1R. As a result, daughter cells are different from the original cell that underwent mitosis. The authors directly indicate the presence of a rye chromosome in the genome as a stress factor capable of changing the wheat karyotype. Wheat-rye chromosome addition lines were studied by IRAP and REMAP methods. Such spectrum components were found that were not present in the DNA spectrum of the samples used to create the lines. The authors believe that the changes that have already occurred in the genome of alien-addition lines are not directly related to alien chromatin, but are a manifestation of changes in nucleotide sequences due, most likely, to deletions, which are induced by hybridization of the original to create genome lines [2]. Even the structural rearrangements of chromosomes in wheat-rye disomic lines occur on a larger scale compared to those in triticale [2].

In an earlier research by the same authors [3], the appearance of new components not typical of any of the parental genomes was indicated in the IRAP and REMAP spectra. This also indicates that the new properties of the genome (in this case, nucleotide sequences) may not be a direct consequence of the inclusion of alien chromatin into the resident genome, especially since no changes were observed at the cytological level [3,4]. Chromosomes 2R and 5R of wheat-rye monosomic addition lines were studied [1]. AFLP and MSAP (methylation) methods were used. A large-scale genetic/epigenetic variability was found both in the genomes of these lines and in the genomes of selfed progeny that had no rye chromosome. It shows that

the presence of rye chromatin is not mandatory for the occurrence of such variability [1]. Evaluating the results of this work and the conclusion of the authors, it is not possible to be sure of the absence of alien chromatin. After all, neither a certain set of molecular markers nor molecular cytological methods can provide a hundred percent guarantee of the absence of cryptic introgressions. However, according to the authors, the results of the study provide direct evidence that significant genotypic and epigenetic variability is induced in the genome of the monosomic alien addition line. Direct evidence of the occurrence of genetic and epigenetic variability based on the presence in the genome of the introgression line of rye chromosomes differing in number and homoeologous affiliation is provided later [5].

Wide phenotypic variability was induced among the progeny of asymmetric vegetative hybridization of common wheat and *Thinopyrum ponticum* [6]. How exactly such variability arose remains unclear. Six lines were isolated that did not differ from common wheat by karyotype, but GISH analysis indicated the presence of short segments of DNA introgressed from *Elitrigia* in their genomes. The study of DNA profiles using several methods revealed the presence of numerous genetic and epigenetic changes, including deletions, changes in gene expression, changes in the methylation pattern, and activation of retrotransposons. But these changes were not directly related to alien fragments. The authors believe that the phenotypic variability arose from changes in the repetitive sequences of the resident genome together with epigenetic changes in the regulation of gene expression and/or transposon movement. The genetic and epigenetic variability that was reported in wheat plant cells maintained in cell culture was much weaker compared to introgression cell lines in culture. The authors consider somatic hybridization as an inducer of genetic and epigenetic changes and consider such material to be useful for studying molecular mechanisms leading to changes in the genome due to its introgressive origin [6].

Changes in the electrophoretic spectrum of glutenins among F_2 hybrids from the crossing of tetraploid wheat plants with *Ae. sharonensis* were observed compared to F_1 hybrids and parental genotypes: mutations of single nucleotides, insertions, and deletions in open reading frames [7]. According to [8], the evolution of nucleotide sequences takes place in only four ways: substitution of single nucleotides, deletion (insertion) of repeating units, changes in individual repeats, deletion (insertion) of repeats' blocks. All these

ways of genetic changes are considered as possible mechanisms of genomic asymmetry of wheat allopolyploids [9] and indeed, the presence of all these changes is shown in modern studies of hybrid genomes. Deletions of sequences in the HMW loci of F_2 plants from this crossing may be the result of genomic asymmetry that occurs for the chromosomes of *Ae. sharonensis* and wheat chromosomes.

Glutenins as a model for studying genetic changes in wide hybrids were also used in the analysis of wheat-rye hybrids [10] and hybrids between hexaploid and tetraploid wheats [11]. In both studies, the authors point to the appearance of new glutenin genes, for high molecular weight glutenins in the first paper and low molecular weight glutenins in the second one. They consider introgression (wide) hybridization as a factor in *de novo* DNA variation.

Almost exactly the same results were described for an asymmetric somatic hybrid between cauliflower (*Brassica oleracea* var. *botrytis*, $2n = 18$, CC gene) and mustard (*Brassica nigra*, $2n = 16$, BB gene) [12]. The mechanisms of changes have not been determined. However, 28 introgression lines were identified, which were characterized by certain morphological traits that distinguished them from the parent variety of cauliflower. The multi-color FISH method showed that the lines contain 18 cauliflower chromosomes. By molecular markers (65 SSR and 77 ALFP) the presence of DNA fragments of the mustard genome in the genome of the lines was identified, on average it was 7.5 % of the genome of the lines. The study of DNA profiles obtained by various methods revealed numerous genetic and epigenetic differences between introgression lines, including changes in the composition of sequences, deletions, and changes in the methylation pattern. The frequency of fragment loss (5.1 %) was higher than the appearance of new components (1.4 %). The authors believe that asymmetric somatic hybridization is an inducer of genetic and epigenetic changes, therefore, it is an important source of new variability, which, theoretically, can be useful for expanding the genetic pool of cultivated species [12].

Nowadays research in this area is conducted through the study of transcriptomes of lines of hybrid origin (introgressive) and parental plants using the RNA-seq analyses [13]. It was shown that the presence of barley telosomes 7HL in the wheat genome changes the transcription of 3 % of wheat genes (960 genes out of 35,301 genes) [14]. In the disomic substitution line Chinese Spring/*Aegilops longissimi* 3Sl#2(3B) and the disomic addition line 6Sl, 5.37 % and 4.30 % of genes, respectively, were

expressed differently compared to the Chinese Spring genotype [15]. The same results were shown in wheat lines with fragments 7EL chromosome from *Th. elongatum* [16]. Transcriptomic analysis of six disomic substitution lines of *Triticum aestivum*/*Thinopyrum elongatum* in comparison with parental genotypes showed that the change of expression affected 57.43–69.22 % of *Thinopyrum* genes and only 2.19–8.97 % of wheat genes. The change in the expression of alien genes occurred in the direction of down-regulation (39.69–48.21 %). Upregulation was typical for wheat genes with altered expression [17].

On the other hand, mRNAseq analysis of six introgression lines of *Triticum aestivum*/*Amblyopyrum muticum* showed that the expression of *Amblyopyrum muticum* genes introduced into the wheat genome is reduced compared to wheat orthologs without corresponding compensation of the expression of homoeologous wheat genes [18]. This directly indicates the possibility of mutual epigenetic influences between alien chromatin and chromatin of the resident genome and can serve as an explanation for all the phenomena described above.

For the first time, conclusions about the effect of chromatin introgression as an inducer of recipient genome variability were formulated gradually in a series of experimental studies on introgressive hybridization between rice (*Oryza sativa* L.) and wild rice (*Zizania latifolia* Griseb.) [19–23]. The F1 hybrid was backcrossed once with rice. Numerous genetic and epigenetic changes were observed in introgression lines obtained from the hybrid [21,23]. Changes in the lines continued to occur several generations after the backcross. Mobilization of mobile genetic elements has been reported [20,24,25]. Later, it was found that one of the introgression lines derived from this crossing was less tolerant of salt stress than both parental samples. In this way, a new phenotype was observed, which was not present in any of the components of the crossing. Studies have shown that the expression of four genes affecting the removal of sodium ions from root cells is characterized by reduced regulation. These changes in gene transcription are considered by the authors to be responsible for the appearance of a new phenotype. The reason for the change in transcription is the introgression nature of the studied line [26]. The results described in [20,22,24,25,27] gave the authors a reason to assume that the phenotypic variability of introgression lines is not the result of direct incorporation of alien chromatin from *Zizania* into the genome. It appears that the changes arise from

secondary genomic modifications that are started up by introgression of *Zizania* DNA and do not come to a stop in subsequent generations. These changes are not simply the incorporation of alien chromatin into the recipient genome. Moreover, it was shown earlier in animal cell culture that random integration of alien DNA (it was a viral genome) triggers numerous epigenetic changes in the host genome [28–30].

Though, in more modern research with the same material, the introgression of a small segment of *Zizania* DNA into the rice genome is indicated as the cause of intense variability in the number of repeats in microsatellite loci in introgression lines. So, the presence of introgression is not rejected. This variability occurs immediately after introgression [31]. Mostly the repeats located in the non-coding sequences were mutated, the microsatellites from the coding regions showed greater stability. Microsatellite variability in the coding genes sequences can lead to the formation of premature stop codons, a shift in the reading frame (in a case of dinucleotide repeat), a break in functional motifs [31], so it can be subject to negative selection. Microsatellite variability was found even in chloroplast and mitochondrial DNA of introgression lines, including genes coding regions. Such variability is indicated to occur in F1 somatic primordial cells prior to their differentiation into gametes and is therefore inherited across generations. In most cases variability is related to the number of repeats. Nucleotide substitutions were observed much less frequently. Nucleotide substitutions, deletions and insertions were detected in the flanking areas of microsatellite loci. The authors studied 13 and 10 genes that contain microsatellite sequences in the promoter region and introns, respectively. And only for three genes, Os02g15594 (encodes phosphatase), Os05g35200 (encodes glycosyltransferase) and Os07g46750 (encodes translation elongation factor), the relationship between their expression and microsatellite variability was shown. Thus, this variability is essential for genes involved in signaling and translation processes, and therefore new phenotypes may appear [31].

However, in a later work performed with the same material [32] it is stated with absolute certainty that the introgression lines originated from the incongruent crossing of two types of rice arose exclusively under the influence of pollen that did not incorporate DNA into the genome of the lines. In this study, the activation of transposons was confirmed. A total of 33 *de novo* mobilization events involving 13 TEs were reported, namely MITE

mPing, Pong and 11 LTR retrotransposons. Transposition was established using locus-specific PCR and Southern hybridization. Gene expression analysis confirmed that at least some of the mobilized TEs caused heritable changes in the expression of nearby genes, including QTLs affecting grain weight and size. According to the authors, the obtained results indicate that the pollination of a related species, although incompatible for crossing, causes the mobilization of endogenous transposons, which can cause inherited changes in gene expression, therefore, the appearance of new variations of traits.

To understand exactly what genetic changes occur in lines that have an introgressive origin since they arose as “hybrid” offspring from the already described crossing of *Oryza sativa* ssp. *Japonica* cv. *Matsumae* with *Zizania latifolia* Griseb., the genome sequence of the specified rice variety and the introgression line Z35 was performed [22]. We put the word hybrid in quotation marks because the authors of the study point to the unusual, non-canonical hybrid nature of this line and those similar to it. The line was obtained by the method of “repeated-pollination” [19]. According to this method, emasculated *Matsumae* panicle flowers were treated with pollen of *Z. latifolia* species. In 40–50 hours, the panicle was pollinated again with the pollen of the variety. The authors indicate that all introgression lines were derived from a single “F1” plant ([19] authors’ quotes) through subsequent strict self-pollination. Researchers believe that the effect of foreign pollen on the newly formed organism can be compared to the effect of the genome of pathogens, when it interacts with the genome of the host, not through the inclusion of its segments into the genome of the host, but through the initiation of some genetic and epigenetic rearrangements [33,34]. And still, the authors call their lines introgression. Moreover, in several studies involving this material, it was shown that the chromatin content of *Z. latifolia* in the lines is less than 0.1 % of the host genome and the lines are characterized by the appearance of certain new features that were not present in the parental components of the “crossing” [19,21,22,24,25,31,35]. How these two statements are reconciled: there was no “true” (*bona fide*) hybridization, on the one side, and there is alien chromatin in the lines, on the other side – we have not been able to understand. However, the quoted series of research confirms our understanding of the term introgression line: the one that originated from a distant crossing, even if alien chromatin is not detected in it. However, the authors [35] insist that it is foreign pollen that causes genetic

and epigenetic instability of the recipient plant genome. According to whole-genome sequencing data, relative to the Matsumae genome, the RZ35 line has 41,724 homozygous single-nucleotide polymorphisms (SNPs) and 17,839 homozygous indels. 3797 SNPs were non-synonymous mutations. Intensive mobilization of transposons was detected in the genome of the RZ35 line. In the course of a comprehensive study of the line, it was found that it acquired enhanced resistance to the rice-blast disease, which was not characteristic of the Matsumae variety. One non-synonymous mutation was found within a known resistance gene for this disease, *Pid3/Pi25*, and real-time PCR reported increased expression of the mutant gene. According to the authors' conclusions, the factor of intensive genetic changes in lines is introgressive hybridization. If we take into account the nature of these lines and the authors' conviction that the role of foreign pollen consists only in a certain destabilization of the recipient genome, which is accompanied by genetic changes, then this series of research provides convincing evidence that the process of contacting different genomes through the products of their expression, even if it is not accompanied by their combination and the creation of a *bona fide* hybrid, it triggers the mechanism of genetic changes in the resident genome and can be a factor in the appearance of the newest variants of traits among the descendants [35].

Of course, in our opinion, the appearance of the most recent variants of the trait in relation to the parental phenotypes, at least new components in the electrophoretic spectrum of the introgression line, is not at a proof of the fact that the formation of this component is not connected with the presence of introgression somewhere in the same chromosome to which molecular markers were specifically selected. Such uncertainty in the interpretation of the results only indicates the limited informativeness of DNA electrophoretic spectra obtained by a certain technology. The results should be obtained by different methods and then compared, because the molecular processes that occur in genomes of hybrid origin are still far from being fully understood [36].

Attenuation of alien gene expression

Phenotypic variability during introgressive hybridization has another aspect – attenuation of the expression of an alien gene when it enters the recipient genome. The question has been studied for a long time on many models, and this line of observation of the phenotypic variability generated by the genome with introgression was

the first, starting with the well-known phenomenon of transgene silencing.

Numerous studies on the expression of alien genes against the background of the resident genome have shown that a change in the expression of such a gene is quite common and is a consequence of the interaction between the alien gene and the genetic environment of the host genome [32,37–40]. For wheat, the attenuation of resistance was repeatedly shown when a resistance gene was transferred from an alien species to the background of the wheat genome [9,40–43,45]. In particular, the *Sr6* resistance gene changes its expression due to interaction with the *sr6* allele of a sensitive crossing partner [46], as the author suggests, through the action of a transposon or through a paramutation-like mechanism. It is quite possible to assume that similar mechanisms of changes in the expression of the resident gene can be included in introgressive hybridization. The polyploid state of the wheat genome affects the expression of genes, including those of alien origin. For example, when a stem rust resistance gene was transferred from *T. monococcum* L. to durum and common wheat, a progressive loss of resistance was observed together with an increase in the ploidy of the recipient genome [47]. Suppression of resistance can be caused by a negative interaction between homoeologous and non-homoeologous loci of different subgenomes of the polyploid, as was shown for the *Lr34* gene, which suppressed the effect of the inhibitor of wheat stem rust resistance genes located on chromosome 7DL [48], as well as for the *Pm3* gene, which suppressed the *Pm8* gene in some lines with 1BL.1RS translocation [40,43]. At the same time, it was shown that this loss of resistance is not related to gene loss, mutation, or gene silencing [49]. It was found that the protein products of both genes are formed, create a heteromeric complex, and it becomes ineffective for participating in the signaling cascade, which should provide a protective reaction [50]. The authors hypothesized that the simultaneous expression of several NB-LRR resistance genes leads to a dominant-negative interaction through a post-translational mechanism involving LRR domains. Research on F_1 – F_4 hybrids of transgenic lines pyramided with different combinations of alleles of the *Pm3* gene revealed the fact of genetic suppression between different alleles [50]. By performing infection tests using *Blumeria graminis tritici* Em. Marchal (*Bgt*) isolates avirulent to certain alleles of the *Pm3* gene, it was found that *Pm3a*- and *Pm3f*-mediated resistance was suppressed to varying degrees in the *Pm3b/Pm3a* and *Pm3b/Pm3f* transgenic lines. In transgenic lines with combinations

of alleles *Pm3a/Pm3c*, *Pm3a/Pm3d*, *Pm3b/Pm3d*, no suppression of resistance to different races of *Bgt* was observed [51].

However, the reason for the attenuation of the expression of the alien resistance gene may be different, if the resistance was controlled by several genes, and one was transferred, for which, let's say, a marker was found that made it possible to track it. In addition, immune self-incompatibility is currently recognized as a significant force that can influence gene expression in hybrid offspring [52,53].

According to [26], a common practice in plant breeding is to use some unspecified small introgression in the genome to induce the newest variants of the traits observed by the breeder. At the same time, not only a change in the level of expression, but also its attenuation can be observed at the level of expression of host and alien genes. For example, [54] showed that introgression changes many phenotypic traits of *Helianthus annuus* that have an adaptive response to biotic and abiotic stresses. As was shown above, it is now clear that introgression causes the appearance of new traits not only due to the expected incorporation of alien chromatin into the host genome and its interaction with the resident genome, but also can generate new genetic and epigenetic variability in this genome [55–59].

Although almost any article devoted to the study of the consequences of introgressive hybridization ends with the statement that the nature of the physiological and molecular mechanisms of the phenotypic changes in the products of introgressive hybridization that are observed remains unclear, today there is a lot of evidence that these mechanisms are epigenetic, which include DNA methylation, histone modification, the involvement of small RNAs in the regulation of gene expression, and the involvement of transposons. Moreover, none of these mechanisms act independently, but are a component of events, the results of which can be a change in gene expression and the appearance of a new phenotype that is not related to the expression of an alien gene [60,61].

Epigenetic mechanisms of expansion of the variability of introgression genotypes

A large amount of research has described the change in the methylation pattern of DNA cytosines in distant hybrids and amphidiploids. Very little is known about changes in DNA methylation in the genome of introgression lines, most likely due to the fact that creating introgression lines is much more difficult than hybrids and amphidiploids. For now,

we are aware of only a few papers on this topic. Researchers worked with three wheat-rye translocation lines, which were characterized by the formation of novel heritable morphological characteristics in comparison with the parental lines. Neither genome *in situ* hybridization nor the AFLP method revealed a difference in the genomic structure of the translocated lines, while the methylation-sensitive amplified polymorphism (MSAP) analyzes showed the following: an increase in the number of fully methylated sites and a decrease in the number of half-methylated sites in comparison with the wheat component of crossing. Sequencing of 44 fragments with a changed methylation pattern showed that the changes affected both coding genes and mobile genetic elements [62].

Six introgression lines of *Triticum aestivum*/*Thinopyrum ponticum* obtained from somatic hybridization were studied. They were similar by karyotype to wheat, but GISH showed the presence of numerous short wheat segments. DNA analysis revealed genetic and epigenetic differences compared to the wheat genotype, including a change in the methylation pattern and reactivation of transposons [6].

Two introgression lines of *Oryza sativa* L./*O. rufipogon* were studied for changes in DNA methylation using the methylation sensitive amplification polymorphism method. In one line, the level of total methylation in comparison with the recipient genotype increased (30.94 %), in the second it decreased (24.17 %). Demethylation is shown for 109 loci and 56 loci of two lines, hypermethylation – for 28 and 30 loci. Analysis of 17 sequences characterized by changes in methylation showed that 9 of them are similar to coding genes, and the rest are similar to transposons. RT-qPCR proved that the demethylation process increases the level of expression, so it is part of the regulation of this process [59].

The two historically first works on the study of the phenomenon of DNA methylation in introgression lines refer to the *Oryza sativa*/*Zizania latifolia* introgression lines described in detail above. Two introgression lines were studied for DNA methylation and expression of several selected sequences, including cellular genes and transposons. 21 sequences out of 30 showed changes in methylation and/or transcription compared to rice, and the changes were stable when examining 5 separate samples from each introgression line. Similar changes were registered in the same introgression lines of somatic origin. In both cases, they affected both coding genes and transposon

sequences. The authors concluded that the presence of introgressions in the plant genome is a trigger for changing the methylation pattern, therefore, it is a source of variability at the epigenetic level. In 2004, such a conclusion was made for the first time [21]. In a subsequent work [23], three introgression lines were studied with the same material using the methylation-sensitive amplified polymorphism (MSAP) method in relation to 2700 genomic loci. 15.9 % of these loci were fully or partially methylated in the original rice genotype, and 19.2, 18.6, and 19.6 % in introgression lines. Sequencing of the fragments with a changed methylation pattern showed that they belong to different of the 12 pairs of rice chromosomes and represent both coding genes and transposons. The authors insist on the presence of introgression in the genome as a promoter of changes in the methylation pattern. However, we remember that in later works with the same material, the authors deny the presence of introgressions in the rice genome and consider as an inducer of variability only the fact of an attempt to obtain a hybrid (irritation of the receptacle with foreign pollen) without combining the genomes of different species.

On three introgression lines of *Gossypium hirsutum*/*Gossypium bickii*, 2000 genetic and 800 epigenetic sites were studied by the method of amplified fragment length polymorphism (AFLP) and methylation-sensitive amplified polymorphism (MSAP). The first method showed that the lines contain on average 0.5 % alien DNA segments from *Gossypium bickii*, which proves their true introgressive nature. The overall level of methylation was similar to that of the recipient father (an average of 22.6 %), but cases of both hypo- and hypermethylation were recorded [63].

Information on the dynamics of miRNA composition in introgression lines is still very limited. In three introgression lines of rice *O. sativa*/*O. longistaminata*, which differed from the recipient rice variety in terms of plant height, gene and miRNA expression profiles were studied using high-throughput RNA sequencing technology. It was established that compared to the rice variety, high lines are characterized by a decrease in the expression of genes, some of which are related to the formation of the cell wall and the synthesis of hormones, and such a decrease is associated with an increase in the expression of miRNAs, for which the mentioned genes are the target [64,65]. Introgression lines of the same origin were investigated by the same method for lncRNAs. Of the 1254 lncRNAs identified, the difference in their expression in lines and in parental genotypes was significantly less

between lines and *O. sativa* than between lines and *O. longistaminata* [66]. In our opinion, this fully corresponds to the nature of the studied plant material, because the genome of introgression lines contains only a small part of alien chromatin.

Currently, a huge amount of evidence has been accumulated regarding the participation of transposons in numerous molecular processes that occur when the stability of the genome is disturbed: during hybridization and polyploidization, which constantly accompany the evolution of plants [61,67–70]. The activity of transposons induces structural changes in the genome, causes deletions and duplications, and affects gene expression [67–69]. They can contribute to changes in epigenetic patterns [71,72]. Transposons can generate new genes [61,70], affect their exon-intron structure and, because of this, their expression [73]. All this makes transposons a promoter for all those processes that underlie what is now called genome instability. Even though the role of transposons in these processes was studied on hybrids and polyploids, in introgression lines they also participate in all those genetic and epigenetic changes that are registered when studying their genomes. Introgression lines did not participate in such studies so often, however, when examining their genomes for the purpose of detecting the activity of transposons, such activity was always recorded [6,20,21,23–25,32,59,62]. As for now, it has been proven that the activation of transposons as a result of “genomic shock” in the form of elimination, proliferation and movement of TEs will contribute to changes in the recipient genome even if no alien chromatin is included in its composition [74,75].

In a study with wheat-rye monosomic addition line [1], the authors consider the activity of transposons as an inducer of genetic variability. According to their opinion, the inducer of variability in the offspring of alien addition lines that lost the alien chromosome was the activation of retrotransposon activity, which was induced in the introgression genome of the parents of such offspring. Using AFLP and MSAP methods, the authors concluded that Gypsy-like retrotransposons are responsible for the genetic variability of the offspring, and Copia-like and Gypsy-like retrotransposons are equally responsible for epigenetic variability. It is noted that the sequences in which changes occur, induced in monosomic alien addition lines, differ from the sequences that change by induction by allopolyploidization. The authors claim that wheat-rye monosomic addition lines can be used as an effective method of expanding the genetic diversity of common wheat [1]. In

addition, it is suggested that the smaller the amount of alien chromatin involved in the composition of the genome formed after the act of combining two different genomes, the greater the probability of chromosomal breaks, elimination of chromosomes, structural rearrangements, including the elimination of specific sequences, translocations, TE movement [1]. A new term “reshuffling” of nucleotide sequences in the genome of lines of such origin has appeared. Referring to the well-known instability of wheat-rye addition lines [76], the authors consider the temporary presence of alien chromatin in the genome (added rye chromosome) as a permanent cause of genome rearrangement processes, which does not attenuate for a long time in lines of introgressive origin, although the alien chromosome in their genomes are gone. At the same time, they refer to the old works of Gustafson [79], where the presence of rearrangements in subtelomeric regions of rye chromosomes was shown only in F3 from crossing triticale with wheat, and they were not registered in previous generations.

Conclusion

From the very beginning, introgressive hybridization was considered as a method of genetic improvement of cultivated plants by introducing appropriate genes from wild relatives into their genetic pool. With introgression lines created by various methods, a large amount of work has to be done to bring a useful gene to its practical use in commercial varieties, getting rid of the bad influence

of alien inclusions on agronomically important properties. In addition, the unfortunate fact of rapid loss of resistance to pathogens acquired through introgression is already widely known. Finally, today methods of direct genetic transformation of plants have already been developed, which make it possible to introduce only the target gene into the genome without accompanying unnecessary chromatin [78,79]. And yet the idea remains that introgressive hybridization leaves behind an important place in plant breeding technology. This is confirmed by the intensification of research in this area in the last couple of decades after a certain decline of interest in this direction at the end of the last century [80,81]. There are papers that consider the role of hybridization in evolution as a provider of new variability that is not available to populations in the absence of hybridization [12,82]. And thereby indicating its role as a supplier of new variability, which was previously recognized only by mutations. Indeed, in our view, given the definition of mutation as any change in the nucleotide sequence, introgressive hybridization should be considered a mutagenic factor rather than an alternative primary source of variability. For a change in gene expression that is inherited, in modern genetics there is a term epimutation [83]. And yet, we would like to think that this revival of interest in introgressive hybridization is not least related to the accumulation of evidence that introgressive hybridization itself is a factor of enhancing genetic plasticity in the offspring of distant hybridization compared to parental genotypes.

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РОЛЬ ІНТРОГРЕСИВНОЇ ГІБРИДИЗАЦІЇ В РОЗШИРЕННІ ГЕНЕТИЧНОЇ МІНЛИВОСТІ РЕЦИПІЄНТНОГО ГЕНОМУ

У статті розглянуто питання, пов'язані з розширенням генотипної та фенотипної мінливості в нащадків рослин з геномом гібридного походження. Інтрогресивними завжди вважались лінії, геном яких містить чужинний хроматин унаслідок рекомбінаційних чи транслокаційних подій після віддаленого схрещування. Не завжди в таких лініях можна детектувати чужинний хроматин, хоча лінії в поколіннях демонструють ознаки, що відрізняють їх від нативних рослин з реципієнтним геномом. Така фенотипна мінливість може бути спричинена як порушеннями в поведінці хромосом у гібридному геномі, так і змінами у ДНК. Широта фенотипної мінливості може виявлятися в появі ознак, які є новітніми щодо фенотипних характеристик компонентів ініціального схрещування. Вивчення ДНК-профілів свідчить про наявність у геномах гібридного походження як генетичних, так і епігенетичних змін, включно з делецією/інсерцією, змінами в експресії генів, картинах ДНК-метилування, активацією ретротранспозонів у реципієнтному геномі. Транскрипційний аналіз показав, що зміна експресії стосується різної кількості генів. Водночас експресії чужинних генів зазвичай властиво зниження активності, тоді як пшеничних – здебільшого підвищення транскрипційної активності. У разі інтрогресивної гібридизації характерним є затухання експресії чужинного гена в поколіннях. Це може бути наслідком взаємодії між чужинним геном і генетичним оточенням хазяйського геному. Накопичено багато доказів того, що зміни в експресії гена, зокрема його затухання, контролюються на епігенетичному рівні. Інтрогресивну гібридизацію з часу її виникнення розглядали як засіб генетичного поліпшення генетичного пулу рослин, що культивуються. Таке поліпшення вважали результатом перенесення чужинного гена(ів) до реципієнтного геному. На сьогодні стає зрозуміло, що роль інтрогресивної гібридизації, можливо, головна, полягає в тому, що вона є промотором генетичних та/або епігенетичних змін у реципієнтному геномі, продукті інтрогресивної гібридизації. Можливо, саме з цим пов'язане відновлення інтересу до інтрогресивної гібридизації та її впливу на геном рослин, який спостерігається останніми роками.

Ключові слова: пшениця, амфідиплоїди, гібридний геном, інтрогресія, фенотипна новітність.

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