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Genome evolution in allopolyploid wheat—a revolutionary reprogramming followed by gradual changes

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Abstract

Allopolyploidy accelerates genome evolution in wheat in two ways: 1) allopolyploidization triggers rapid genome alterations (revolutionary changes) through the instantaneous generation of a variety of cardinal genetic and epigenetic changes, and 2) the allopolyploid condition facilitates sporadic genomic changes during the life of the species (evolutionary changes) that are not attainable at the diploid level. The revolutionary alterations, occurring during the formation of the allopolyploid and leading to rapid cytological and genetic diploidization, facilitate the successful establishment of the newly formed allopolyploid in nature. On the other hand, the evolutionary changes, occurring during the life of the allopolyploids, increase the intra-specific genetic diversity, and consequently, increased fitness, adaptability and competitiveness. These phenomena, emphasizing the dynamic plasticity of the allopolyploid wheat genome with regards to both structure and function, are described and discussed in this review.

Keywords: allopolyploidization; cytological diploidization; epigenetics; genetic diploidization; *Triticum*; wheat

Introduction

Tetraploid and hexaploid wheat were originated *via* allopolyploidization, i.e., by inter-generic hybridization followed by chromosome doubling (Feldman et al., 2005). Allopolyploidy, being a revolutionary rather than an evolutionary mode of speciation, is a major way through which a new species is formed in one step. Since an allopolyploid species is a hybrid containing two or more different genomes, enveloped within one nucleus, allopolyploidization exerts a considerable stress on the newly formed species. Consequently, the nascent allopolyploid faces several challenges such as the immediate need to secure an exclusive intra-genomic pairing at meiosis, to orchestrate inter-genomic gene expression and DNA replication, and to reduce the cost of large genomes (Levy and Feldman, 2002, 2004; Feldman and Levy, 2005). To meet these challenges and ensure increased fitness and consequently, successful establishment in nature, the newly formed allopolyploid genome must undergo immediate changes. For example, differentiation of the homoeologous chromosomes (cytological diploidization) should be established rapidly so that they will not be able to pair and recombine at meiosis. There is also a need to orchestrate gene expression (genetic diploidization) to enable harmonic inter-genomic coexistence. The above changes can be achieved through alterations in the DNA or in chromatin structure. In wheat, cytological diploidization involves elimination of DNA sequences. These elimination events may generate random polymorphisms causing further physical divergence between homoeologues. Another possibility is that the eliminated sequences are implicated in homology recognition and initiation of pairing at meiosis.

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Elimination of these sequences from one pair of homoeologous chromosomes in tetraploids and from two pairs in hexaploids further augments the differentiation between homoeologues and thus, leads to diploid-like meiotic behavior. Genetic diploidization of duplicate genes involves both gene silencing or gene elimination (Levy and Feldman, 2002, 2004; Feldman and Levy, 2005).

During the last twenty years methods and materials have been developed to facilitate the studies on genomic alterations that occur during allopolyploidization and lead to cytological and genetic diploidization in allopolyploid wheat. Also they provide the means for studying sporadic genomic changes that occur during the life of the allopolyploids and result in increased intra-specific diversity. This review will describe and discuss some of these genomic alterations.

The effect of allopolyploidization on genome alterations

Allopolyploid species can tolerate genomic changes that are either unattainable or unfavorable at the diploid level. These changes were divided into two types: revolutionary and evolutionary (Table 1). Revolutionary changes, triggered by the genetic shock exerted in the process of allopolyploidization, generate, during F_1 and/or soon after chromosome doubling, a wide range of genetic and epigenetic genomic alterations that are species specific. They might play an important role to ensure diploid-like meiotic behavior, restore full fertility, and improve the harmonic functioning of the two or more diverged genomes that are included in one nucleus. Evolutionary changes on the other hand, are mostly genetic changes, occurring sporadically at random over a long time period during the life of the allopolyploid and therefore, they characterize population(s) or biotype(s). The evolutionary changes promote genetic diversity, flexibility and adaptability.

Revolutionary changes

Recent molecular studies have shown that the allopolyploidization process induces a variety of cardinal, non-Mendelian, genomic changes that are not attainable at the diploid level (Table 2). Some of these changes are crucial for the construction of an efficient genetic system facilitating the establishment in nature of the newly formed allopolyploids and for the rapid build up of a wealth of genetic variability. The revolutionary changes are expressed in two levels: structural (cytological diploidization) and functional (genetic diploidization).

Table 1
Genomic alterations triggered and/or facilitated by allopolyploidy in wheat

Type of Change	Features
Revolutionary	
Triggered immediately upon hybridization and/or genome doubling	• Genetic and epigenetic • Species-specific • Leads to cytological diploidization • Rewiring of gene expression between regulator components of parental genomes • Heterotic and/or incompatibility (e.g., necrosis, loss of disease resistance) features • Stabilize the nascent allopolyploid and facilitate its establishment as new species in nature
Evolutionary	
Occurring on an evolutionary scale and facilitated by allopolyploidy	• Accelerated evolution promoting genetic diversity • Sub- and neo-functionalization • Introgressions • Population- or biotype-specific • Flexibility and adaptability

Table 2
Revolutionary changes induced by allopolyploidization in wheat

Level	Genetic	Epigenetic
Genome	• Elimination of low-copy DNA sequences • Elimination, reduction or amplification of high-copy sequences • Inter-genomic invasion of DNA sequences • Elimination of rRNA and 5S RNA genes	• Chromatin remodeling • Chromatin modifications • Heterochromatinization • DNA methylation • Small RNAs activation or repression
Gene	• Gene loss • Rewiring of gene expression through novel inter-genomic interactions • New dosage response (positive, negative, dosage compensation) • Gene suppression or activation	• Methylation (leading to silencing) • Demethylation (leading to gene activation)
Transposons	• Transcriptional activation (that may affect nearby genes in cis) • New transpositions	• Release from silencing • Silencing

Structural changes (cytological diploidization)

Allopolyploidization causes immediate elimination of non-coding, low copy and high copy DNA sequences, that are present in all the diploid species of *Aegilops* and *Triti-*