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DARWIN REVIEW

Genomic asymmetry in allopolyploid plants: wheat as a model

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Abstract

The evolvement of duplicated gene loci in allopolyploid plants has become the subject of intensive studies. Most duplicated genes remain active in neoallopolyploids contributing either to a favourable effect of an extra gene dosage or to the build-up of positive inter-genomic interactions when genes or regulation factors on homoeologous chromosomes are divergent. However, in a small number of loci (about 10%), genes of only one genome are active, while the homoeoalleles on the other genome(s) are either eliminated or partially or completely suppressed by genetic or epigenetic means. For several traits, the retention of controlling genes is not random, favouring one genome over the other(s). Such genomic asymmetry is manifested in allopolyploid wheat by the control of various morphological and agronomical traits, in the production of rRNA and storage proteins, and in interaction with pathogens. It is suggested that the process of cytological diploidization leading to exclusive intra-genomic meiotic pairing and, consequently, to complete avoidance of inter-genomic recombination, has two contrasting effects. Firstly, it provides a means for the fixation of positive heterotic inter-genomic interactions and also maintains genomic asymmetry resulting from loss or silencing of genes. The possible mechanisms and evolutionary advantages of genomic asymmetry are discussed.

Key words: Common (bread) wheat, cytological diploidization, durum wheat, genetic diploidization, intra-genomic (homologous) pairing, inter-genomic (homoeologous) pairing, Triticum aestivum, Triticum turgidum.

Introduction

Allopolyploidization is a biological process that has played a major role in plant speciation and evolution (Manton, 1950; Stebbins, 1950, 1971; Grant, 1971; Soltis and Soltis, 1993, 1995; Soltis *et al.*, 2009; Masterson, 1994: De Bodt *et al.*, 2005; Tang *et al.*, 2008), and has driven and shaped the evolution of vascular plants perhaps more than any other evolutionary process (Feldman and Levy, 2005, 2009). It constitutes a radical and rapid mode of speciation that produces a new species by means of inter-specific or inter-generic hybridization followed by chromosome doubling. Allopolyploidization forms a hybrid species bearing two or more different genomes enveloped within one nucleus. As a result, the newly formed allopolyploid species, particularly annual and predominantly self-pollinating, faces several immediate challenges (Levy and Feldman, 2002, 2004; Feldman and Levy, 2005, 2009). It must secure an exclusive intra-genomic pairing at meiosis that will lead to full fertility and disomic inheritance, i.e. undergo cytological diploidization. In addition, it must orchestrate inter-genomic gene expression, namely, adapt to the new interaction between regulatory factors of the different genomes, and DNA replication. For example, it must deal with redundant and sometimes conflicting patterns of gene expression by eliminating duplicated genes or suppressing their expression via genetic or epigenetic means (genetic diploidization). These challenges exert considerable genetic stress that triggers a variety of cardinal genetic and epigenetic changes, affecting genome structure and gene expression and resulting in cytological and genetic diploidization (Leitch and Bennett, 1997; Feldman *et al.*, 1997; Liu *et al.*, 1998a, b; Comai, 2000;

Soltis and Soltis, 2000; Ozkan *et al.*, 2001; Shaked *et al.*, 2001; Pikaard, 2001; Levy and Feldman, 2002, 2004; Ma *et al.*, 2004; Feldman and Levy, 2005, 2009; Ma and Gustafson, 2005, 2006; Eilam *et al.*, 2008, 2010).

Cytological diploidization in allopolyploid wheat results from the elimination of DNA sequences from one genome in allotetraploids and from two genomes in allohexaploids, augmenting the physical divergence between the homoeologous chromosomes (Feldman *et al.*, 1997). These sequences, which thereby become homologous-specific sequences, may contribute to homology recognition and the initiation of meiotic pairing. This leads to exclusive pairing and recombination at meiosis between homologues rather than between homoeologues (Feldman *et al.*, 1997). In allopolyploid wheat, unlike the closely related *Aegilops* allopolyploids, cytological diploidization is also sustained by the *Ph1* and *Ph2* gene systems (Sears, 1976), ensuring that chromosome pairing is restricted to homologous chromosomes. The *Ph* gene systems evolved at the polyploid level and reinforce the cytological diploidization determined by the physical divergence between homoeologous chromosomes.

Genetic diploidization is a regulatory process that brings redundant or unbalanced gene systems in polyploids toward a diploid-like mode of expression (Ohno, 1970). It results either from elimination, mutation or repression of genes that, in many cases, restrict the activity of sets of genes to only one genome (Liu *et al.*, 1998b; Wendel, 2000; Shaked *et al.*, 2001; Levy and Feldman, 2002, 2004; Feldman and Levy 2005, 2009; Comai, 2005; Chen, 2007). These genomic changes may affect the fitness of the newly formed allopolyploid and increase its competitiveness, leading to its successful establishment in nature. Hence, successful allopolyploidizations are those that successfully trigger an array of genomic changes that confer evolutionary advantages. If heightened fitness is not achieved rapidly enough, the nascent species will be out-competed by its parents and by other species.

Cytological diploidization-driven prevention of inter-genomic (homoeologous) pairing and meiotic recombination in allopolyploid wheat leads to full fertility and disomic inheritance. In other plant species, certain homoeologous recombination events can occur during and/or after diploidization of the evolving allopolyploid and contribute both to its further diploidization and adaptive radiation (Doyle *et al.*, 2008; Gaeta and Pires, 2010; Wang and Paterson, 2011). However, there is little evidence that this occurs in allopolyploid wheat, seemingly due to the scarcity of homoeologous recombination (Sears, 1976).

Cytological diploidization enables and sustains the occurrence of two contrasting and complementary phenomena, both of which contribute to the evolutionary success of allopolyploids: (i) build-up and maintenance of enduring and favourable inter-genomic genetic combinations, enabled by the absence of homoeologous pairing and recombination, and (ii) genomic asymmetry in the control of a variety of morphological, physiological, and molecular traits, i.e. complete or predominant control of certain traits by one of the constituent genomes. While the first phenomenon was taken for granted by plant geneticists, genomic asymmetry was mainly ascribed to ribosomal RNA genes (reviewed in Pikaard, 2000), and has only recently been documented for other traits (Peng *et al.*, 2003a, b; Fahima *et al.*, 2006; Rapp *et al.*, 2009; Feldman and Levy, 2009; Flagel *et al.*, 2009; Flagel and Wendel, 2010; Gegas *et al.*, 2010). In spite of the importance of this phenomenon, not much is known of its impact on the allopolyploid phenotype and its adaptive potential. This review describes and discusses various aspects of genomic asymmetry in the allopolyploid species of the wheat group (the genera *Aegilops* and *Triticum*), focusing on wild allotetraploid wheat, *Triticum turgidum* subsp. *dicoccoides* (wild emmer)—the wild progenitor of domesticated tetraploid wheat, and on domesticated allopolyploid wheat. Mechanisms underlying the establishment and maintenance of genomic asymmetry in the allopolyploid species and the evolutionary advantages of this phenomenon are discussed.

Genomic asymmetry in the control of morphological traits in allopolyploid wheat species

On the basis of plant habitus, spike morphology, and cytogenetic data, Zohary and Feldman (1962) classified the allopolyploid species of the wheat group (the genera *Triticum* and *Aegilops*) into three natural clusters (Table 1). Genome analysis of the allopolyploids within each cluster showed that they share one unaltered genome (the pivotal genome) and a genome or genomes that is/are modified [the differential genome(s)]. Thus, all seven allopolyploids of the U-genome cluster share a genome homologous to that of diploid *Aegilops umbellulata* (Kihara, 1954), all the six allopolyploids of the D-genome cluster share a genome homologous to that of diploid *Ae. tauschii* (Kihara, 1954; Kihara *et al.*, 1959), and all four allopolyploid species of the A-genome

Table 1. The allopolyploid species clusters of the genera *Aegilops* and *Triticum* (after Zohary and Feldman, 1962)

Genome cluster	Genome[a]
The U genome cluster	
Ae. biuncialis	UM
Ae. geniculata (=Ae. ovata)	MU
Ae. neglecta (=Ae. triaristata 4x)	UM
Ae. recta (=Ae. triaristata 6x)	UMN
Ae. clumnaris	UM
Ae. triuncialis	UC
Ae. peregrina (=Ae. variabilis)	SU
Ae. kotschyi	SU
The D genome cluster	
Ae. cylindrica	DC
Ae. ventricosa	DN
Ae. crassa 4x	DM
Ae. crassa 6x	DDM
Ae. vavilovii	DMS
Ae. juvenalis	DMU
The A genome cluster	
T. turgidum	BBAA
T. timopheevii	GGAA
T. aestivum	BBAADD
T. zhukovski	$GGAA^{m}A^{m}$

[a] Genome designations according to Kimber and Tsunewaki (1988); underlined designation indicates a modified genome.

cluster, including all the wild and domesticated forms, share a genome homologous to that of diploid *Triticum urartu* (Dvorak, 1976; Chapman *et al.*, 1976). The allopolyploids of each cluster resemble the diploid donor of the shared genome and differ in features of the differential genome(s) in their basic morphology (stature, leaf shape, and spike and spikelet morphology) and in the structure of the seed dispersal unit. The differential genomes modified through intra-clustering, and to a lesser extent, also via inter-cluster hybridizations (Zohary and Feldman, 1962; Feldman, 1965a, b, c), are primarily responsible for the eco-geographical adaptation of the various allopolyploid species in each cluster.

Evidence accumulated over the last decade from molecular studies in allopolyploid wheat, indicates that genomic asymmetry, i.e. biased expression toward only one parental genome (Flagel *et al.*, 2009), is more prevalent in these species than previously thought. Korol and co-workers (Peng *et al.*, 2003a, b) have already reported genomic asymmetry in wild allotetraploid wheat *T. turgidum* ssp. *dicoccoides*. The contribution of the A and B genomes to various traits in wild allotetraploid wheat are presented in Table 2. The A genome controls morphological traits including inflorescence structure, grain shape, free caryopsis, glumes with keels, plant habitus, and growth habit. This genome also controls the autogamy of allotetraploid wheat (assuming that the donor of the B genome is allogamous, i.e. *Ae. speltoides*) and harbours many domestication genes, such as the genes for non-brittle spike on 3AS (Rong, 1999; Nalam *et al.*, 2006), free-threshing on 5AL (Sears, 1954), QTLs for kernel size predominantly on A genome (1A, 2A, 3A, 4A, 7A, 5B, and 7B) (Elias *et al.*, 1996), and a number of domestication-related QTLs (Peng *et al.*, 2003a, b). The *Q* gene, encoding an Apetala2-like transcription factor, has been shown to have a critical effect on wheat domestication (Simons *et al.*, 2006). The *Q/q* loci include orthologues and paralogues located on group 5. A recent study showed that a combination of mutations in *Q* genes contributed to the domestic spike phenotype, namely non-fragile, soft glumes and free threshing (Zhang *et al.*, 2011). The mutation with the most significant phenotypic effect is an amino acid substitution in the protein coded by the 5A locus. Mutations, such as pseudogenization, namely, truncated open reading frame, of the locus on 5B or subfunctionalization, namely, partition between the role of this gene in different tissues or conditions, of the locus on 5D also contributed to the domestication phenotype, but to a lesser extent (Zhang *et al.*, 2011). Remarkably, these mutations occurred after polyploidization (Zhang *et al.*, 2011). Hence, the A genome tends to preserve a complete set of vital genes (Peng *et al.*, 2003a, b), while the B genome regulates ecological adaptation and tolerance to biotic and abiotic stresses (Peng *et al.*, 2003a, b) and plays a leading role in population adaptation to environmental conditions (Fahima *et al.*, 2006). Similar genomic asymmetry was found in a recent study of grain size and grain form traits in six mapping populations representing a wide range of primitive wheat species and modern elite varieties (Gegas *et al.*, 2010). QTLs were identified in most of the homeologous groups, but those on chromosomes 1A, 3A, 4B, 5A, and 6A had the largest and most consistent (across different populations) effects on the studied traits. Sub-genome specialization in the control of various morphological and resistance traits was also found in other allopolyploids, including cotton (reviewed by Wendel and Cronn, 2003).

Table 2. Genome asymmetry in the control of various traits in the wild allotetraploid wheat, *T. turgidum* subsp. *dicoccoides* (genome BBAA)

Traits under the control of Genome A	Traits under the control of Genome B
Inflorescence morphology	Regulation of ecological adaptation
Free caryopsis	Double the number of disease-resistance genes
Glumes with keels	Contains more stress-related genes?
The shape of the edge of the glumes (beaked glumes)	Higher polymorphism of molecular markers
Hairs at the base of every spikeket	Higher polymorphism of HMW glutenin genes
Plant habitus	Larger amount of repetitive sequences
Growth habit	Activity on nucleolar organizers
Autogamy	Larger number of rRNA genes
Many domestication genes	

Molecular manifestation of genomic asymmetry in the allopolyploid wheat sub-genomes

Allotetraploid wheat was formed about 0.5 million years ago (Huang *et al.*, 2002) and allohexaploid wheat about 10 000 years ago (Feldman *et al.*, 1995). Such young allopolyploid species, originating presumably from a small number of inter-specific or inter-generic hybridizations, are expected to exhibit low phenotypic and molecular variation, due to the genetic bottleneck of the founder effect (Haudry *et al.*, 2007). Yet, over the last several decades, studies have shown that the allopolyploid wheat species harbour considerable genetic diversity whose levels differ between the two or three genomes of the allotetraploid and allohexaploid species, respectively. The B genome exhibits a higher marker polymorphism than the A genome in allohexaploid wheat (Chao *et al.*, 1989; Liu and Tsunewaki, 1991; Devos *et al.*, 1992; Siedler *et al.*, 1994), in wild and domesticated allotetraploid wheat (Liu and Tsunewaki, 1991; Huang *et al.*, 1999; Rong *et al.*, 1999; Li *et al.*, 2000), as well as between wild and domesticated allotetraploid wheats (Peng *et al.*, 2000; Peleg *et al.*, 2008). Such differences were most pronounced for loci revealed by gDNA rather than cDNA probes (Huang *et al.*, 1999; Rong *et al.*, 1999). Similarly, higher polymorphism in the B compared with the A genome were seen in microsatellites (Röder *et al.*, 1998; Li *et al.*, 2000). B-genome chromosomes are characterized by more c-banding than chromosomes of A and D genomes (Gill, 1987) and therefore, a higher quantity of repetitive DNA sequences. Similarly, more retrotransposons and variations within them have been observed in the B genome, when compared with the A and D genomes (K Kashkush, personal communication).

Shaked *et al.* (2001) reported immediate sequence loss in the F_1 and in the newly formed allotetraploids *Aegilops longissima–Ae. umbellulata* and *Ae. sharonensis–Triticum monococcum*, mainly

affecting one of the parental genomes. A high level of sequence elimination occurring immediately after hybridization or after chromosome doubling, was registered in Triticale (wheat–rye allopolyploid). Interestingly, the rye parental genome of Triticale underwent more changes than that of the wheat genome, with cytoplasmic–nuclear interaction playing a key role in the direction, amount, timing, and rate of sequence changes (reviewed by Ma and Gustafson, 2008). Similarly, the B genome in *Brassica juncea* and *B. napus* showed fewer changes than the A or C genomes in the allotetraploid background (Liu and Wang 2006).

In addition to sequence elimination, Shaked *et al.* (2001) reported alterations in cytosine methylation in 13% of the loci of the allotetraploid *Aegilops sharonensis–Triticun monococcum*, affecting both repetitive DNA sequences and low-copy DNA in approximately equal proportions. Cytosine methylation was also asymmetric; twice as many sequences were affected in *T. monococcum*, when compared with those of *Ae. sharonensis*.

Genome-wide transcriptome analyses in synthetic *Arabidopsis* allotetraploids showed that expression patterns from one genome could be dominant over the other genome (Wang *et al.* 2006a, b). Pumphery *et al.* (2009) found that approximately 16% of the 825 genes analysed displayed non-additive expression in the first generation of synthetic hexaploid wheat: 2.9% showed overdominance while the remaining 13.1% were similar to one of the parents. Similarly, Chague *et al.* (2010) analysed 55 052 transcripts in two lines of synthetic allohexaploid wheat and found that 7% of the genes displayed non-additive expression, approximately half of which showed asymmetry. Further compounding evidence was provided by Akhunova *et al.* (2010), who measured homoeologue-specific expression in synthetic allohexaploid wheat. They found that about 19% of the studied genes showed homoeologue-specific non-additive up- or down-regulation of expression. In *Tragopogon miscellus* (Asteraceae), a non-crop young (40 generations-old) allotetraploid plant species, frequent tissue- and sub-genome-specific silencing (partition) in natural allopolyploids was noted among the 144 genes analysed, globally activated by hybridization (Buggs *et al.*, 2011). Comparison with the parental diploids led the authors to conclude that tissue-specific silencing of one of the homoeoalleles occurs within the first 40 generations of allopolyploidy of many genes. Coate and Doyle (2010) compared natural allopolyploid *Glycine dolichocarpa* and its diploid progenitors and found that the number of genes expressed in the leaves (the size of leaf transcriptome) of the allopolyploid was only 70% of the sum of the progenitor transcriptomes, while the reduction in the genome size was much smaller (allopolyploid genome size was 94.3% of the sum of the progenitor genomes). Thus, 'transcriptome downsizing' is greater than genome downsizing. Their analysis of a few thousand genes showed massive partial dosage compensation. But, in 11.5% of the examined accompanied pairs, one of two copies was silent; in cases of complete silencing strong up-regulation of the homoelogous gene was found.

In a survey-sequencing study recently conducted by Wicker *et al.* (2011), 6–10 000 gene sequences were sampled per chromosome, in all six arms of the group 1 chromosomes of hexaploid wheat. These gene sequences were compared with their closest homologues in the Triticeae group 1 syntenic region in the *Brachypodium*, rice, and sorghum model genomes. Although the number of syntenic genes was similar between the homoeologous chromosomes, the number of non-syntenic genes was found to be highly diverse between wheat subgenomes. For example, the long arms of wheat group 1 chromosomes contain between 577 (1DL) and 1035 (1BL) gene homologues that are specific to their respective chromosome arm only. Interestingly, deviations from synteny on the short arms of group 1 were more extreme. The most extreme events were reported along the wheat 1BS chromosome arm, where 2251 putative non-syntenic genes were identified, more than five times the number of syntenic genes (Wicker *et al.*, 2011). These findings suggest that genomic regions are differentially affected by this homoeologue diversification—a phenomenon that may enable the establishment of asymmetry. Many of these non-syntenic genes represent pseudogenes that arose from transposable element (TE) activity and double-strand break repair (Wicker *et al.*, 2011). Wicker *et al.* (2011) propose that this accumulation of genic sequences is driven by TE activity, and that these findings indicate that homoeologous wheat chromosomes can exhibit different evolutionary dynamics. The authors conclude that it is still unclear if this process has contributed to functional diversity or to the evolution of agriculturally important genes or if it mostly represents genomic noise. However, the accumulated data reviewed in the current report supports that such evolutionary dynamics may have contributed to genomic asymmetry in allopolyploid wheat.

Shitsukawa *et al.* (2007) reported both genetic and epigenetic alterations in the homoeologues of a wheat class E MADS-box gene. Two class E genes are identified in wheat, *WSEP* (*wheat SEPALLATA*) and *WLHS1* (*wheat Leafy Hull Sterile 1*). The three wheat homoeologues of *WSEP* showed similar genomic structures and expression profiles. By contrast, the three homoeologues of *WLHS1* showed genetic and epigenetic alterations. The A genome *WLHS1* homoeologue (*WLHS1-A*) had a structural alteration that contained a large novel sequence in place of the K domain sequence. Both a yeast two-hybrid analysis and a transgenic experiment indicated that the WLHS1-A protein had no apparent function. The B and D genome homoeologues, *WLHS1-B* and *WLHS1-D*, respectively, had an intact MADS-box gene structure, but *WLHS1-B* was predominantly silenced by cytosine methylation. Consequently, of the three *WLHS1* homoeologues, only *WLHS1-D* functions in hexaploid wheat. This represents a situation where three homoeologues are differentially regulated by genetic and epigenetic mechanisms.

Genomic asymmetry in nucleolar formation and ribosomal RNA gene activity

Nucleolar dominance, i.e. inter-genomic suppression of the formation of a nucleolus or nucleoli of one species by the presence of nucleolar organizer(s) of another species, is characteristic of many inter-specific and inter-generic plant hybrids (Navashin, 1928, 1934; Pikaard, 2000) and is a general phenomenon in the allopolyploid species of the genera *Aegilops* and *Triticum*.

The diploid species of wheat *T. monococcum* and *T. urartu* contain two nucleolar organizer regions (NORs), one on chromosome arm 1AS and the second on 5AS (Gerlach *et al.*, 1980; Miller *et al.*, 1983). In the allopolyploid wheat species, the NOR

of 1AS is inactive, while that of 5AS was lost (Miller *et al.*, 1983; Jiang and Gill, 1994). Thus, allohexaploid wheat (genome BBAADD) possesses four pairs of NORs on the short arm of chromosomes 1A, 1B, 6B, and 5D (Crosby, 1957; Crosby-Longwell and Svihla, 1960; Bhowal, 1972; Darvey and Driscoll, 1972). In this species, the nucleolar organizers of the B genome suppress the nucleolar organizers of the A and D genomes (Crosby, 1957; Crosby-Longwell and Svihla, 1960; Darvey and Driscoll, 1972; Flavell and O'Dell, 1979). Similarly, the nucleolar organizers of the B genome suppress those of the A genome in allotetraploid wheat, *T. turgidum* (genome BBAA) (Frankel *et al.*, 1987) and those of the R genome in 6x and 8x triticale (genome BBAARR and BBAADDRR, respectively) (Darvey and Driscoll, 1972; Cermeño *et al.*, 1984a; Martini and Flavell, 1985; Appels *et al.*, 1986).

Nucleolar dominance was observed in all allopolyploid species of *Aegilops* (Cermeño and Lacadena, 1984; Cermeño *et al.*, 1984b). In these species, the U genome from *Aegilops umbellulata* completely suppresses the NOR activity of the M genome of *Ae. geniculata*, the S genome of *Ae. peregrina*, the D genome of *Ae. juvenalis*, and the C genome of *Ae. triuncialis* and that of one pair of the nucleolar organizer chromosomes of the M genome of *Ae. columnaris*, *Ae. biuncialis*, *Ae. juvenalis*, *Ae. recta*. The nucleolar activity of the D genome is completely suppressed by the U genome in *Ae. juvenalis*, the C genome in *Ae. cylindrica*, and the M genome in *Ae. ventricosa* (Cermeño *et al.*, 1984b). The nucleolar organizers of the U genome also suppress the activity of those of the rye R genome in hybrids between allopolyploid species of the U genome-bearing *Aegilops* and *Secale cereale* or *S. vavilovii* (Cermeño and Lacadena, 1985).

Every genome possesses one or more NORs that contain clusters of the 45S ribosomal RNA (rRNA)-encoding genes that are active inside the nucleolus; the extent of their activity is proportional to the size of the nucleolus (Birnstiel *et al.*, 1971; Appels *et al.*, 1980). Consequently, nucleolus formation is considered evidence for rRNA gene expression and the lack thereof, indicates the absence of rRNA gene transcription (Flavell *et al.*, 1986). Moreover, the relative size of nucleoli within the same nucleus has been taken as a measure of the differential activity between one NOR and another (Flavell *et al.*, 1986).

The number of rRNA-encoding genes in each of the four NOR sites of allohexaploid wheat was determined by Flavell and coworkers. In the standard laboratory Chinese Spring cultivar, chromosomes 1A and 5D contain a very small proportion of the rRNA-encoding genes (10%), while chromosomes 1B and 6B possess 30% and 60% of these genes, respectively (2700 and 5500 copies, respectively) (Mohan and Flavell, 1974; Flavell and O'Dell, 1976). Similar patterns were found for allotetraploid wheat (Frankel *et al.*, 1987). Chromosomes 1A and 5D produced very small nucleoli or none at all in the Chinese Spring variety (Crosby, 1957; Crosby-Longwell and Svihla, 1960). These findings stand in line with chromosomes 1A and 5D having a small proportion of the total rRNA gene complement.

Nucleolar dominance in the allopolyploid species of the wheat group is achieved either by elimination of rRNA-encoding genes, as is the case of 5AS, or by suppression of their activity. Gustafson and Flavell (1996) and Houchins *et al.* (1997) found that inactivation of the rRNA-encoding genes is associated with increased cytosine methylation at their CCGG sites. Similarly, Chen and Pikaard (1997) found that the silenced rRNA-encoding genes in *Brassica* allotetraploids are maintained by DNA methylation and histone deacetlyation. Further evidence suggesting that nucleolar suppression is triggered by cytosine methylation came from the fact that the suppression of the NORs of genome R was reversed in wheat×rye hybrids and triticale (a synthetic allopolyploid between tetraploid wheat and rye, *Secale cereale*) by treatment with the demethylating agent 5-aza-cytosine (Vieira *et al.*, 1990; Neves *et al.*, 1995; Amado *et al.*, 1997).

Newly synthesized allopolyploids exhibit genetic and epigenetic changes in their rRNA-encoding genes similar to those occurring in natural allopolyploids, indicating that these changes are generated during allopolyploid formation (Baum and Feldman, 2010). Shcherban *et al.* (2008b) detected rapid elimination of the *Aegilops sharonensis* rRNA-encoding genes in the synthetic allopolyploid *Aegilops sharonensis–Ae. umbellulata*, which stands in agreement with the pattern in the natural allopolyploid having the same genomic combination, i.e. *Ae. peregrina* and *Ae. kotschyi*. Similarly, Brettell *et al.* (1986) reported that, in hybrids between wheat and rye, the rRNA-encoding genes from one of the rye chromosomal sites were deleted immediately after hybridization. Silencing of rRNA-encoding genes has also been found to be a rapid response of Brassicaceae genomes to allopolyploidization (Chen and Pikaard, 1997).

Wheat 5S DNA also undergoes immediate changes in response to allopolyploidization, followed by the elimination of unit classes of 5S DNA (Baum and Feldman, 2010). This elimination was reproducible, i.e. the same unit classes were eliminated in natural and synthetic allopolyploids having the same genomic combinations, indicating that no further elimination occurred in the unit classes of the 5S DNA during the life of the allopolyploids.

Genomic asymmetry in the control of storage proteins in allopolyploid wheat

Genetic control of high molecular weight (HMW) glutenin subunits, important components of wheat seed-storage proteins, was studied in allohexaploid wheat (Brown *et al.*, 1979; Payne *et al.*, 1981, 1982; Galili and Feldman, 1983a) and in domesticated and wild allotetraploid wheat (Galili and Feldman, 1983b; Nevo and Payne, 1987; Levy and Feldman, 1988; Levy *et al.*, 1988; Felsenburg *et al.*, 1991). These subunits, constituting about 10% of total wheat-endosperm proteins, are resolved in sodium dodecyl sulphate (SDS) and are easily discernible in polyacrylamide gel electrophoresis (PAGE). The HMW glutenin subunits are encoded by the *Glu-A1* and *Glu-B1* gene clusters in allotetraploid wheat, and by the *Glu-A1*, *Glu-B1*, *and Glu-D1* gene clusters in allohexaploid wheat (Payne *et al.*, 1982; Galili and Feldman, 1983a), located on the long arm of homoeologous-group-1 chromosomes (Payne *et al.*, 1982; Galili and Feldman 1983a, and reference therein). In allohexaploid wheat, each of these gene clusters is composed of two multi-allelic gene loci: *Glu-A1-1* and *Glu-A1-2* on chromosome 1A, *Glu-B1-1* and *Glu-B1-2* on chromosome 1B, and *Glu-D1-1* and *Glu-D1-2* on chromosome 1D. The products of *Glu-A1-1*, *Glu B1-1*, and *Glu-D1-1* comprise the

slow migrating subunits (x) while those of *Glu-A1-2*, *Glu-B1-2*, and *Glu-D1-2* comprise the fast-migrating subunits (y).

Most lines of allohexaploid wheat have two HMW glutenin subunits controlled by chromosome 1B, two bands controlled by 1D and 0–2 bands controlled by 1A (Lawrence and Shepherd, 1981; Payne *et al.*, 1984a, b; Galili and Feldman, 1983b). Galili and Feldman (1983b) analysed 109 different lines of allohexaploid wheat, representing a wide spectrum of genetic backgrounds, and found that 22 lines (20.2%) had no HMW glutenin subunits controlled by chromosome 1A, 44 lines (40.4%) had only one such band and 43 lines (39.4%) had two bands. Moreover, in all lines having one subunit controlled by 1A, only the slow migrating subunit, the x subunit, was involved, i.e. only *Glu-1A-1* was active. Hence, in 60% of the studied hexaploid lines, *Glu-A1-2* was inactive, although this gene is regularly active in diploid wheat (Waines and Payne, 1987).

Levy *et al.* (1988) studied the HMW glutenin subunits in 456 accessions of the wild allotetraploid wheat *Triticum turgidum* subsp. *dicoccoides*, originating from 21 different populations in Israel. In 82% of the accessions, the fast-migrating subunit of the A genome, the y subunit, was absent, and in 17% of the accessions, the slow-migrating subunit of this genome, the x subunit, was also absent. Namely, only the *Glu-B1* genes of the B genome were active. The fast-migrating subunit of the A genome was absent in all of the 11 studied lines of the primitive domesticated allotetraploid wheat, *T. turgidum* subsp. *dicoccum*, i.e. *Glu-A1-2* was inactive. *Glu-A1-1* was also inactive, while only *Glu-B1-1* and *Glu-B1-2* were active in all of the 19 evaluated lines of modern allotetraploid wheat, *T. turgidum* subsp. *durum* (Feldman *et al.*, 1986). Moreover, the HMW glutenin loci of the B genome were much more polymorphic than those of the A genome (Felsenburg *et al.*, 1991). The reduced polymorphism of the A genome loci were suggested to reflect the non-random inactivation of HMW glutenin genes mainly affecting the A genome genes in allopolyploid wheat (Galili and Feldman, 1983b; Levy *et al.*, 1988).

Thus, in both allotetraploid and allohexaploid wheat, inactivation of HMW glutenin genes is massive and non-random and occurs in the *Glu* genes of the A genome (Galili and Feldman, 1983a, b; Feldman *et al.*, 1986; Levy *et al.*, 1988, and reference therein). This tendency has also been found in hexaploid wheat for HMW gliadin genes (Galili and Feldman 1983a, b). The order of inactivation was also non-random, starting with the rapidly migrating subunits and continuing with the slowly migrating ones.

Evidence showing that the *Glu-A1-2* gene exists in the Chinese Spring cultivar of allohexaploid wheat, that lacks the fast-migrating HMW glutenin band coded by this gene (Thompson *et al.*, 1983), supports the assumption of inactivation rather than elimination of this gene. This is in accord with the finding that the inactivation of *Glu-A1-2* in allohexaploid wheat is caused by the presence of a terminating sequence inside the transcribed portion of the gene (Forde *et al.*, 1985).

Galili and Feldman (1984) showed that inactivation of endosperm-protein genes is also brought about by an inter-genomic suppression. Extracted allotetraploid wheat, lacking the D-genome and possessing the A and B genomes of its allohexaploid progenitor (Kerber, 1964), facilitates the study of inter-genomic relationships between genes of the D genome and those of the other two genomes. SDS-PAGE analysis of such extracted tetraploid lines exhibited several bands with increased staining intensity, as well as some new bands. The latter seemed to result from novel activity of genes located on the A or B genomes, as the repression exerted by the D genome was removed. Addition of the D genome resumed the suppression of these genes. Galili and Feldman (1984) suggested that these endosperm-protein genes were repressed immediately following the formation of allohexaploid wheat, about 10 000 years ago, but have retained their potential for activity. Likewise, microarray analyses have pointed to a group of genes, located on chromosomes of the A and B genomes, that are strictly regulated by the presence of the D genome; they are not expressed in allohexaploid wheat, expressed in an extracted allotetraploid (genome BBAA), and are silenced again upon supplementation the D genome to the extracted tetraploid plants (B Liu, personal communication). Similarly, Kerber and Green (1980) described an inter-genomic suppression of a rust resistance gene, located in the D-genome, by gene(s) of the A or B genomes.

Genomic asymmetry in the control of agronomic traits in domesticated allopolyploid wheat

Wheat genome-driven control of various agronomic traits and of disease and pest resistance in domesticated allopolyploid is categorized in Tables 3 and 4, respectively. The B and D genomes control the most important genes associated with reduced plant height (*Rht*) and gibberelic acid insensitivity (*Ga*), yielding dwarf and semi-dwarf wheat, the main types of modern wheat varieties. Dwarf and semi-dwarf wheat varieties are characterized by an improved harvest index and, consequently, are high-yielding varieties. These varieties have replaced the traditional tall, low-yield varieties in many parts of the world during the 'green revolution' and thus, increased global wheat production.

The B and D genomes control grain protein content (Law *et al.*, 1978; Joppa and Cantrell, 1990) and grain hardness (Morris *et al.*, 1999; Chantret *et al.*, 2005). These genomes also control wax production (Tsunewaki and Ebona, 1999), an important trait that affects drought tolerance. The B and D genomes are responsible for tolerance to abiotic stresses. The B genome contains genes associated with boron tolerance (Paull *et al.*, 1991), low cadmium uptake (Penner *et al.*, 1995), and tolerance to iron deficiency (Maystrenko, 1992), while the D genome contains gene(s) conferring aluminium tolerance (Riede and Anderson, 1996) and response to salinity (Dubcovsky *et al.*, 1996). Most genes for herbicide resistance are located in the B genome (Snape *et al.*, 1987), and those responsive to photoperiod and most of those responsive to vernalization are located on the B and D genomes (Table 3). The A genome controls plant and spike morphology and the main traits of the 'domestication syndrome', e.g. non-brittle rachis (Nalam *et al.*, 2006) and free threshing (Sears, 1954).

The B genome harbours double the number of disease-resistance genes and resistance-gene analogue (RGA)

Table 3. Genome asymmetry in the control of agronomic traits in domesticated durum (genome BBAA) and bread wheat (genome BBAADD) [Data from the 2008 wheat Gene Catalogue (http://wheat.pw.usda.gov/GG2/index.shtml)]

Traits	Traits under control of		
	Genome A	**Genome B**	**Genome D**
Elongated glumes	*Eg P1* on 7AL	*Eg P2* on 7BL (?)	
Branched spikes	*Bh* on 2AS		
Non-brittle rachis	*br A1* on 3AS	*br B1* on 3BS	
	br A2 on 2A		
Free-threshing	*Q* on 5AL		
Non-tenacious glume (lax glume)		*tg2* on 2BS	*tg1* on 2DS
Reduce plant height	*Rht7* on 2A	*Rht B1* on 4BS	*Rht D1* on 4DS
	Rht12 on 5AL	*Rh4* on 2Bl	*Rht8* on 2DL
		Rht5 on 3BS	
		Rht9 on 7BS	
		Rht13 on 7BS	
Grain protein content		*Gpc B1* on 6BS	*Pro1* on 5DL
			Pro2 on 5Ds
Grain hardness			*Ha* on 5DS
Puroindolines and grain softness protein			*Pin D1* on 5DS
Gibberellic acid response		*Ga1, Ga3* on 4BS	*Ga2* on 4DS
Waxiness		*W1* on 2BS	*W2* on 2DS (?)
Epistatic inhibitors of waxiness		*W1*^{I} on 2BS	*W2I* on 2DS
		W3^{I} on 1BL	
Male sterility	*Ms3* on 5AS	*ms1* on 4BS	*Ms2* 0n 4DS
	ms5 on 3A		*Ms4* on 4DS
Pairing homoeologous		*Ph1* on 5BL	*Ph2* on 3DS
Hybrid necrosis		*Ne1* on 5BL	
		Ne2 on 2B	
Hybrid chlorosis	*Ch1* on 2A		*Ch2* on 3DL
Aluminium tolerance			*Alt2* on 4DL
Boron tolerance		*Bo1* on 7BL	
Low cadmium uptake		*Cdu1* on 5BL	
Iron deficiency		*Fe2* on 7BS	*Fe1* on 7DL
Difenzoquat insensitivity		*Dfg 1* on 2BL	
Chlortoluron insensitivity		*Su1* on 6BS	
Imidazolinone resistance	*Imi3* on 6AL	*Imi2* on 6BL	*Imi1* on 6DL
Response to photoperiod		*Ppd-B1* on 2BS	*Ppd-D1* on 2DS
Response to vernalization	*Vrn-A1* on 5AL	*Vrn-B1* on 5BL	*Vrn-D1* on 5DL
		Vrn-B3 on 7BS	Vern-D4 on 5DL
			Vern-D5 on 5DL
Response to salinity			*Kna1* on 4DL
Frost resistance	*Fr1* on 5AL		*Fr2* on 5DL

loci than the A and D genomes (Peng *et al.*, 2003b; Fahima *et al.*, 2006). It is noteworthy that upon screening the GrainGenes web site (http://wheat.pw.usda.gov/), we found that of 184 mapped wheat disease resistance genes, 88 were in the B genome, demonstrating significant (P <0.008) deviation from equal distribution among the three genomes (Table 4). Most genes conferring resistance to stem rust, stripe rust, and leaf rust, the most common wheat diseases that cause significant global yield loss each year, are located in the B genome.

In the context of our genome asymmetry concept, it is interesting to note that the predominant location of R-gene clusters and clusters of R-gene analogues in the B genome of wheat coincides with certain asymmetry of recombination. Namely, earlier a striking difference was found between A and B genomes in recombination distribution, reflected in high marker clustering in the B but not in the A genome (Peng *et al.*, 2000).

Evidence of genome asymmetry in the context of domestication was obtained in other plants as well. In both species of independently domesticated cotton, *Gossypium hirsutum* and *G. barbadense*, transcription of genes related to fibre development, the major target of selection in domesticated *Gossypium*, was found to be preferentially enhanced in the D genome when compared with the A genome (Hovav *et al.*, 2008), despite the fact that D-genome diploids do not produce spinnable fibres. This bias in favour of the D genome coincides with a predominant occurrence of fibre-related QTL (~70%) on the D genome (Paterson,

Table 4. Genome asymmetry in the control of reaction to diseases or pests in the domesticated durum wheat (genome BBAA) and bread wheat (genome BBAADD) [data from the 2008 wheat Gene Catalogue (http://wheat.pw.usda.gov/GG2/index.shtml) in the control of reaction to diseases or pests]

Disease/pest	Number of functional genes		
	Genome A	Genome B	Genome D
Barley yellow dwarf virus			3
Powdery mildew	9	11	8
Russian wheat aphid		1	7
Cochlibolus root rot		1	
Fusarium head scab		3	1
Cereal cyst nematode		2	1
Magnaporthe grisea	1	1	1
Hessian fly	10	*2*	6
Septoria tritici	4	6	3
Septoria nodorum	2		1
Root lesion nematode	1		
Stem rust	5	13	7
Stripe rust	4	21	7
Leaf rust	6	19	3
Tan spot	1	3	1
Wheat midge		1	
Greenbug	1		2
Eyespot	1		1
Karnal bunt		4	1
Wheat yellow mosaic virus			1
Total	45	88	51

2002). These findings were further supported by Xu *et al.* (2010) who compared the distribution of the fibre development genes and transcription factors in the cotton A and D genomes, using genetic and physical mapping techniques. More transcription factors were from D than from A, while opposite trends were found for fibre development genes. These results, combined with previous publications on the prevailing abundance of fibre QTLs in the D-genome, were explained as hypothesis detailed below (Hovav *et al.*, 2008). After merging of the two diploid *Gossypium* genomes, the A genome of the allotetraploid continued to function in a similar manner as its fibre-producing A-genome ancestor, while the D genome, coming from the non-fibre-producing ancestor, provided more transcription factors regulating the expression of the fibre genes than the A genome did.

Another example of genome asymmetry in allopolyploid cotton *Gossypium hirsutum* was recently found in the accumulation of seed storage proteins (Hu *et al.*, 2011). A higher degree of proteomic similarity was found between the allopolyploid and its D-genome donor than between its A-genome donor. Hu *et al.* (2011) concluded that unequal expression of proteins from diploid parental genomes occurs in allopolyploids.

Discussion

Evolvement of multiple gene loci in allopolyploids

The reviewed evidence can be best explained by assuming that the genetic and epigenetic changes in the newly formed allopolyploid wheat species led to the construction of two contrasting genetic systems: (i) retention of expression of all homoeoalleles of those duplicated or triplicated gene loci whose extra gene dosage has a positive effect by itself or may facilitate the build-up of positive inter-genomic interactions between divergent regulation factors, and (ii) elimination or suppression of genes from one genome in allotetraploids and from two genomes in allohexaploids in those gene loci whose extra dosage or new inter-genomic interactions are deleterious, thus bringing about genome asymmetry for various traits. The latter process may be tissue-specific (Buggs *et al.*, 2011).

In wheat allopolyploids, as discussed above, different gene types show a differential propensity for homoeologous change or retention. Genes encoding functional proteins (enzymes) constitute one category of genes that shows a high degree of retention of homoeoalleles (Mitra and Bhatia, 1971; Hart, 1983a, b, 1987). Such retention enables inter-genomic interactions at both the transcriptional level and between gene products, giving rise to 'hybrid' functional proteins in multimeric enzymes consisting of subunits encoded by different genomes. These new heteromeric proteins may have new and desirable properties. Similarly, protein complexes, such as gluten, may also be 'hybrid'. These inter-genomic protein interactions seem also to have had direct relevance to wheat cultivation. For example, the baking quality of allohexaploid wheat (bread wheat) is due to the unique properties of its gluten, a product derived from the combined contribution of multiple subunits encoded by the three genomes of hexaploid wheat.

The retention of genes corresponding to *trans*-acting factors, such as transcription factors, suppressors, and microRNAs, may enable the generation of novel *trans* interactions that may lead to new expression patterns absent in the diploid parents, as seen in yeast (Tirosh *et al.*, 2009).

For other categories of genes, a lack of retention of parental genes or the expression patterns is frequent and non-random. This includes the genes that encode for ribosomal RNA, for structural proteins, such as histones and subunits of tubulins, and for storage proteins, such as subunits of glutenins and gliadins. In these cases, expression of all homoeoalleles may be redundant, resulting in over-production and even deleterious dosage effects. In addition, activity of all homoeoalleles may produce intermediate phenotypes in several traits that decrease the viability of the plants (e.g. hybrid incompatibility genes). Hence, for some traits, control by genes from only one genome (genome asymmetry) may have a higher adaptive value than additive expression, preventing a genomic clash or avoiding deleterious dosage effects. Non-random elimination of DNA sequences, as reported in wheat (Levy and Feldman, 2004; Feldman and Levy, 2005), may contribute to genome asymmetry in alloploy ploids.

The new evidence presented by Wicker *et al.* (2011), obtained by next generation sequencing of individual wheat group 1-sorted chromosome arms, indicates that very different levels of amplifications of gene sequences occurred between the three wheat genomes. This kind of gene amplification seems also to have played an important role in homoeologous genome divergence and may also contribute to genomic asymmetry.

Unequal retention of genes is not unique to allopolyploid wheat; it has also been reported in allotetraploid soybean

(Coate *et al.*, 2011). Tate *et al.* (2006, 2009), Buggs *et al.* (2009, 2010a), and Koh *et al.* (2010) demonstrated, via cDNA–AFLPs followed by genomic and cDNA cleaved amplified polymorphic sequence (CAPS) analyses, that one parental gene copy was lost in several homoeologous loci of natural allotetraploid *Tragopogon miscellus* and in allotetraploid *T. mirus*. Moreover, expression of only one parental gene copy was detected in several other homoeologous loci. On the other hand, allele loss or silencing was not detected in synthetic *T. miscellus* (Buggs *et al.*, 2009, 2010a), indicating that these changes occur during the life history of the allotetraploid. By contrast, immediate gene elimination occurred upon allopolyploidization in allotetraploid *Triticum turgidum* and allohexaploid *T. aestivum* (Liu *et al.*, 1998b; Shaked *et al.*, 2001) and in allohexaploid and allooctoploid Triticale (a wheat–rye allopolyploid) (Ma and Gustafson, 2008). Similarly, immediate gene silencing was observed in allotetraploid *Arabidopsis suecica* (Wang *et al.*, 2006a, b), allohexaploid *Senecio cambrensis* (Hegarty *et al.*, 2005, 2006), allotetraploid cotton (Adams *et al.*, 2004; Flagel *et al.*, 2008) and allopolyploid wheat (Shaked *et al.*, 2001; Kashkusk *et al.*, 2002).

Genetic diploidization is not a random process, distinctly affecting specific gene categories and their corresponding traits and forming a clear-cut division of tasks between the constituent genomes of allopolyploid wheat. The A-genome preferentially controls morphological traits, while the B-genome in allotetraploid wheat and the B and D genomes in allohexaploid wheat preferentially control the reaction to biotic and abiotic factors. The process of genetic diploidization is also non-random in rRNA-encoding genes and storage protein genes, affecting mostly genes of genome A. Genetic diploidization may occur during or immediately after allopolyploidization (revolutionary changes), e.g. in rRNA-encoding genes, or through the life history of the species (evolutionary changes), for example, in HMW glutenin genes.

The stage of allopolyploid formation will dictate if genetic diploidization results from homoeologous recombination, illegitimate recombination, or gene conversion. Some of these processes may contribute to the reconstruction of the homoeologous chromosomes through the course of cytological and genetic diplodization. There is evidence that considerable genetic changes in artificially resynthesized *Brassica napus* resulted from homoeologous recombination (Gaeta and Pires, 2010, and references therein). After genome merging, a portion of genes can undergo directed genetic or epigenetic changes, resulting in gene loss or silencing. Obviously, diploidization yielding suppression of homoeologous recombination does not necessarily lead to universal exclusion of gene conversion, especially in the large orthologous blocks of retained genes, such as rice chromosomes 11 and 12 and their sorghum orthologues 5 and 8 (Wang and Paterson, 2011).

Mechanisms responsible to genomic asymmetry

Genome asymmetry may be brought about by either transcriptional dominance of one of the parental genomes (Wang *et al.*, 2006b; Flagel *et al.*, 2009; Rapp *et al.*, 2009; Flagel and Wendel, 2010) or inter-genomic suppression of gene activity (Galili and Feldman, 1984), due to incompatibility of regulatory elements (He *et al.*, 2003; Tirosh *et al.*, 2009), chromatin modification (Wang *et al.*, 2006b) or suppression of genes adjacent to transposable elements (Kashkush *et al.*, 2003). Differential elimination or inactivation of coding sequences from one of the parental genomes in allotetraploids and from two of the parental genomes in allohexaploids contributes to the asymmetrical control of the constituent genomes (Feldman and Levy, 2009; Tate *et al.*, 2006; Buggs *et al.*, 2009, 2010a, b; Koh *et al.*, 2010). Some major transcriptional suppressors, or small non-coding RNAs, such as microRNAs (Ha *et al.*, 2009), may also have genome-wide effects on asymmetry through the suppression of several targets that, in turn, can affect a cascade of genes, thus leading to asymmetry.

Significance of genomic asymmetry in the evolution of allopolyploids

The ability of one genome to suppress the activity of genes of another genome and thus, fully to control a set of traits in allopolyploids, may prevent conflicting gene expression that could potentially lead to defective organ shapes. This protective mechanism ensures the development of viable plants. Diploid species that lack this adaptive ability might fail to produce viable allopolyploids. There are two diploid wheat species and 11 diploid *Aegilops* species [including *Amblyopyrom muticum* (=*Ae. mutica*)] (Eig, 1929; van Slageren, 1994), most of which have geographical contact with one another (Kimber and Feldman, 1987; van Slageren, 1994). Many more allopolyploid species, apart from the currently existing ones, may have been generated over the 2–4 million years of the existence of the diploid species (Huang *et al.*, 2002). Allopolyploids involving the AD, AC, AM, AN, AU, AT, UD, UT, DS, and DT genomic combinations can be produced under artificial conditions, but have not been found in nature. We speculate that such hybrids and/or allopolyploids have reduced fitness, due to desirable genomic asymmetry manifested by some degree of inter-genomic incompatibilities overcome through silencing of incompatible loci from one of the parents.

Cytological diploidization of allopolyploids, during or soon after their production, provides the physical basis for their strict intra-genomic pairing of fully homologous chromosomes. Restriction of meiotic pairing and recombination to fully homologous chromosomes, coupled with a pre-dominant, self-pollination system, sustains the co-existence and maintenance of two contrasting systems in allopolyploid plants, namely, fixation of heterozygosity between homoeoalleles and genomic asymmetry. Inter-genomic pairing would have led to disruption of the linkage of the homoeoalleles that contribute to positive inter-genomic interactions and to the segregation of genes that participate in the asymmetrical genomic control of certain desirable traits. In conclusion, these two contrasting systems, related to the fate of duplicated or triplicated genes in allopolyploids, are especially important for the evolutionary success of these plants. Indeed, allopolyploids of the genera *Aegilops* and *Triticum* are very evolutionarily successful; they are aggressive, efficient colonizers, compete well with their diploid progenitors, are distributed over a larger geographical area, occupy more versatile habitats, and exhibit wider ranges of morphological,

biochemical, and molecular variations than their parental diploid species (Zohary and Feldmam, 1962; Feldman, 1965; Zohary, 1965; Kimber and Feldman, 1987).

Rapid progress of structural and functional Triticeae genomics will enable further insight into the mechanisms and functional importance of genomic asymmetry in wheat allopolyploids and other allopolyploids of this tribe.

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