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Research Article

Epigenetic Concepts and Relationships with Polyploidy

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Abstract

Polyploidy or whole genome duplication (WGD) has been an important genomic feature for all eukaryotes, especially many plants and some animals. It is produced by duplication of a single genome (autopolyploid) or a combination of two or more different genomes (allopolyploid). Available data from the study of synthetic (nascent or man-made) plant allopolyploids have documented dynamic and stochastic changes in genomic organization and gene expression, including sequence elimination, interchromosomal exchanges, cytosine methylation, gene repression, new activation. The co-occurrence of polyploidy demonstrated an evolutionary advantage to having more than one set of genetic material for adaptive evolution. Thus, new allopolyploids were required to establish a harmonious relationship between foreign cytoplasm and nuclei and between two different genomes, resulting in rapid changes in genome structure, gene expression and developmental traits such as fertility, inbreeding, apomixis, flowering time and hybrid vigor. Convincing evidence has been found that changes in DNA sequence, cis- and trans-acting effects, chromatin modifications, RNA-mediated pathways and regulatory networks modulate differential expression of homologous genes and phenotypic variation, which may facilitate adaptive evolution in polyploid plants and domestication in crops.

Keywords

Polyploidy, epigenetics, gene expression, genome duplication, evolution

Declaration of Conflicting Interest

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Login

Polyploidy has been observed in flowering plants of eukaryotes used in agriculture throughout the evolutionary process (1,2,3). Compared to plants, it has been encountered more rarely in animals (4,5).

Winkler coined the term polyploidy in 1916 (6), and then Winge (1917) drew attention to the importance of polyploidy in the evolution of angiosperms (7). In 1937, Blakeslee and Avery induced polyploidy in plants by using colchicine (an alkaloid extracted from autumn crocus, which is known as a chemical inhibitor of mitotic cell divisions. It prevents the formation of spindle fibers during the transition from metaphase to anaphase during mitosis). Thanks to this technique, the doubling of chromosomes in meristem cells of diploids and hybrids between species has been achieved. Autopolyploid is formed by the doubling of one diploid genome. An allopolyploid is formed by the combination of clusters of two or more genomes and also different types of genomes. Doubling of chromosomes in hybrids that were not used specifically resulted in the formation of allotetraploids. With this method, the gene se-

quencing of many plants was examined in the laboratory environment. Synthetic (either newly formed or man-made) polyploids have offered a very good opportunity to study and monitor gene expression and comparative analysis of genomic changes.

On the other hand, there are some plant and animal species that exist as interspecies and specific hybrids. Many plant species that have survived as diploids are poleopolyploids and have resulted from at least one whole genome duplication (WGD). Then, in this process called diploidization, serious gene loss and genomic restructuring occurred. Examples of poleopolyploid plants are maize *(Zea)*, rice *(Oryza)*, and *Arabidopsis*.

To briefly touch on the evolution of polyploids, many polyploid plant origins date back to ancient times and their ancestry is unknown. Re-synthesized polyploids with known progenitors can be used for examination and reciprocal analysis for genomic features and gene expression (11,12). Polyplods gave rise to new phenotypes in addition to the parental phenotypes, suggesting non-additive gene expression. At the same time, environmental conditions also had an effect on polyploids. For example, they were able to develop new forms by revealing results such as drought tolerance, resistance to parasites, and process changes in organ development. In this way, they became more resistant than their diploid ancestors. They supported their development by shortening the adaptation processes. Furthermore, polyploidy is a way of permanently stabilizing hybrid viability and dosage regulation, so that many crops *(wheat/Triticum, cotton/Gossypium, strawberry/Fragaria, maize/Zea)* are of polyploid origin (13, 14).

The concept of polyploid is seen in animals compared to plants; Hybrids can occur between species, but cannot reproduce (eg mules) due to genomic incompatibility. Polyploid cells seen in the human species can cause malignant cell proliferation (15).

Epigenetic Effects in Allopolyploid Plants

Allopolyploid plants are hybrid plants that have double copies of the genomes inherited from the parents. While allopolyploid plants grown and cultured under natural conditions did not have any problems in adaptation, artificially obtained ones had difficulty in adapting, showed changes in the number and distribution of chromosomal rearrangements and repetitive DNA sequences, as well as homeotic transformation and lethality. Increases in the size of some chromosomes have been observed and recorded in allopolyploid hybrids. The reason for these increases was the activation of dormant retrotransposons, as in marsupial hybrids. Synthetic allotetraploids of *Arabidopsis* exhibit rapid changes in gene regulation. These situations may be due to ploidy changes and/or incompatibilities between parental genomes. However, comparing auto- and allopolyploids, the main cause was intergenomic incompatibilities. They better expressed intergenomic incompatibilities in the fields of genetics and epigenetics. For example, in one model, activation of heterochromatic transposons (McClinktock's genomic shock) activated, creating a silencing effect between transposons and euchromatic genes, resulting in impaired gene expression. Qualitatively similar responses may occur in fewer, intraspecific hybrids. Thus, the subject of genome functions of allopolyploidy studies can be applied to hybrids of any species and has shown positive results such as those responsible for the continuation of hybrid organisms (16).

Gene Expression Mechanisms Between Allopolyploids and Their Parents

There may be some mechanisms that affect the development and progression of orthologous and homologous genes possessed by polyploids (figure 2). Many homologous genes are expressed together, some repetitive genes are lost, while others mutate or diverge (17). The half-life of these genes is thought to be 2-7 million years.

On the other hand, there are epigenetic changes that can reprogram gene expression and developmental patterns of new allopolyploids. Reactivation of transposons via chromatin modifications or RNA can cause chromosomal breakage and rearrangements (18).

Epigenetic Regulation of Orthologous Genes

Many silencing events of polyploids are epigenetically controlled. When attempting to assemble different genomes in a single cell, genes with similar or redundant functions as a result of duplication of genomes must respond to their duplicate copies. Increased gene or genome dosage can cause diseases and abnormal development (19). For these reasons, the expression of orthologous genes needs to be reprogrammed by epigenetic mechanisms (figure 2a) early in polyploidization. This situation is similar to the concept of genomic shock proposed by McClintock, which we briefly mentioned before (20). Potentially epigenetic changes are reversible. It enabled the polyploid cell to respond to genomic shock.

The gene editing mechanism associated with polyploidy has some peculiarities. First, epigenetic interactions are established between four alleles of two homologous loci in allotetraploids and two alleles of one locus in a diploid. Second, homologous genes from different parents may be up- and down-regulated in a different chromosomal domain from dosage compensation causing congruent or

unidirectional changes in gene expression (21). Third, more than one generation is needed for chromosome pairing in allopolyploids. Fourth, coupling has occurred between homologous chromosomes and between chromosomes, which can affect gene expression (fig. 1e). Finally, cis/trans effects on homologous genes in different biological pathways, due to differences in regulatory sequences between heterologous proteins produced in progenitors and allopolyploids, constitute a major mode of gene regulation in allopolyploids (22).

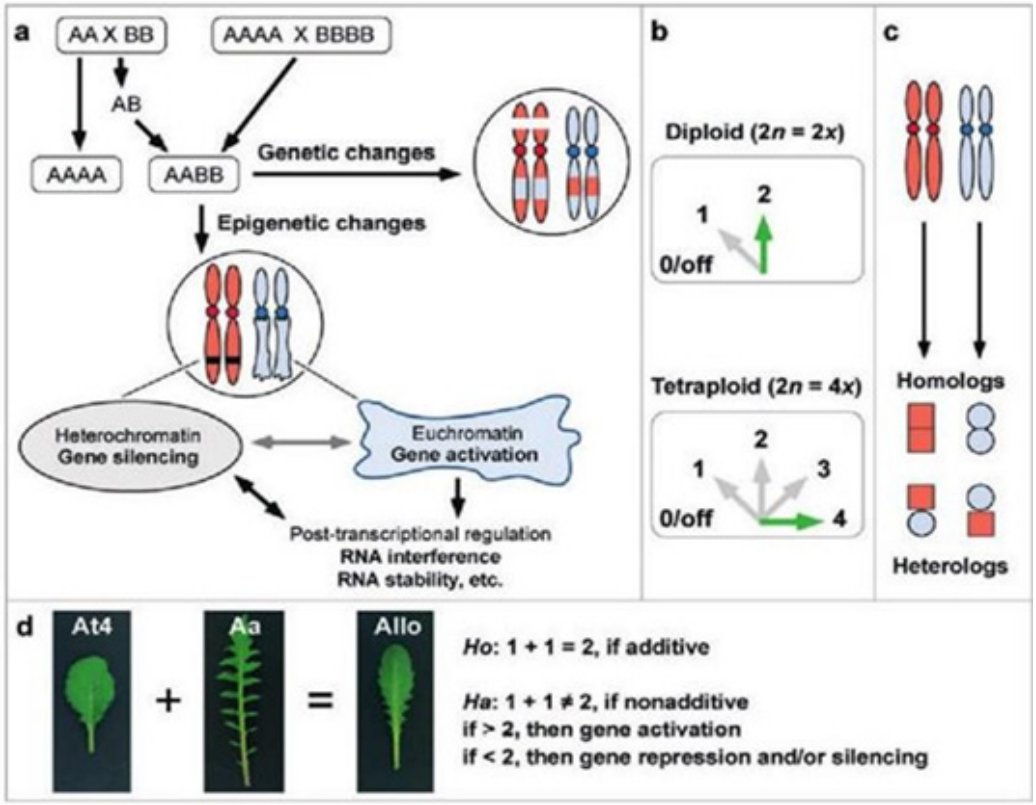


Figure 2.
Illustrations for hypotheses explaining changes in genome structure and function in polyploids are given. (a) Genetic and epigenetic changes in polyploid genomes. Genetic changes include sequence mutations and chromosomal imbalances (deletion / insertion, replacement, relocation, etc.). Epigenetic changes can occur at transcriptional and post-transcriptional levels. Transcriptional regulation is associated with the formation of heterochromatin (black segments on red chromosomes) and euchromatin (long blue chromosome arms of irregular shape), leading to silencing or activation of the gene. Chromatin modifications [through multiple mechanisms, including RNA interference (RNAi)] can transcriptionally silence or activate mobile elements, protein-coding genes, and rRNA genes responsible for novel variation in allopolyploids. Post-transcriptional editing includes RNAi, RNA processing and stability. AA: diploid genome; AAAA or BBBB: autotetraploid; AABB: allotetraploid. Blue segments on red chromosomes or red segments on blue chromosomes in an allotetraploid indicate non-opposite exchanges between homoeologous chromosomes. White segments on red chromosomes indicate a deletion. (b) A dose-dependent (12) or "rheostat" (102) model suggests additive effects of gene expression in a diploid (upper panel) and tetraploid (lower panel). Dual loci in tetraploid provide additional levels of control for gene expression. Levels of gene expression are indicated by "off" (0) and gray arrows (1, 2, and 3), and the maximum level (2 in diploid and 4 in tetraploid) is indicated by green arrows. This model may explain the dominant effects of hybrid energy, but not over-dominant performance or novel variation in allopolyploids. (c) A regulatory compatibility model suggests that regulatory factors (proteins) produced from orthologous genes produce mismatched heterologous products (heterodimers between red squares and blue circles). Alternatively, heterologous proteins may outperform homologs (homodimers between red squares or blue circles), which may explain over-dominant effects and hybrid viability. (d) Hypotheses to test additive and non-additive gene regulation in Arabidopsis allotetraploids. The null hypothesis (Ho) is that the gene expression levels in an allotetraploid (Allo) are equal to the sum of the two progenitors, A. thaliana autotetraploid (At4) and A. arenosa (Aa). Typical seedling leaves in At4, Aa and Allo are shown.

Genetic Changes

Extinction can occur in genome-specific sequences as polyploids form. Stochastic changes in dual genes may increase polyploid speciation in *Tragopogon, Brassica*, wheat studies (23). Observations supported the loss of major fragments and/or the formation of new fragments in resynthesized allopolyploids. The high amount (approximately 14%) of genome- or chromosome-specific DNA sequences could explain the rapid sequence elimination in newly synthesized allopolyploid wheat (24). This suggests that facilitating pairing in homologous chromosomes is achieved by removing different genome-specific sequences, but they are not homologous.

Some changes in DNA sequence may cause loss of double gene expression and functions (25). In fact, many isozyme loci, such as phosphoglucose isomerase loci in Clarkia and chlorophyll a and b binding protein genes in *Polystichum munitum*, were lost during polyploidization (26).

When an estimation is made with the data obtained, it has been shown that the loss of double isozyme loci can increase up to about 35-65% in fish such as Cyorinid (27). This situation suggested that the double genes lost their functions after the polyploidization event that occurred in the lineage 50 million years ago.

Activation of Transposons and Changes in DNA Methylation in Allopolyploids

The evolutionary combination of different genomes in allopolyploids is similar to genomic shock leading to the activation of quiescent transposons (28). Although transposable elements, which make up 40% of the human genome and 50-80% of plant genomes, are dormant in many genomes, they can become active in response to stress and genomic shock under certain conditions (29). Transposons containing DNA transposons and retrotransposons are reactivated in wheat and Arabidopsis allotetraploids (30). Neighboring genes are activated due to overproduction of sense reading transcripts or silenced by anti-sense reading transcripts, which can serve as a negative regulator through interference (31). The data obtained include that the activation of retrotransposons plays a role in the cis-trans regulation of neighboring genes in allopolyploids (32).

Silencing of transposons by DNA methylation has been thought to be a defense mechanism against genome rearrangement during allopolyploid evolution (33). In addition, the data found in wheat synthetic amphidiploids did not support the action of the replaceable elements. Instead, grain hardness may cause rearrangements of sequences at loci that control leaf rust resistance (34). Recombination between homologous chromosomes with or without transposon participation has been a general mechanism for the interchromosomal exchanges observed in allopolyploids.

Gene Editing Mechanisms in Allopolyploids

Increasing data, together with the results obtained from polyploidy studies, have led to detailed research on the causes of genetic variation and gene expression difference. These studies have recently focused attention on genetics, epigenetic regulation, genome evolution, and the morphological and physiological responses of polyploids (35).

Expression changes examined in synthetic allotetraploids and their progenitors include genetic dominance, gene suppression, new activation and sub-functionalization. Some of these changes may be due to changes in DNA sequences such as interchromosomal changes, sequence deletion and rearrangements (36). Other changes were observed at transcriptional and post-transcriptional levels. It should be possible to apply the knowledge of seen and learned chromatin modifications and transcriptional regulation from a diploid system to the expression of orthologous genes in an allopolyploid system. The key detail here is how orthologous genes are differentiated for expression changes in new allopolyploid cells containing two or more genomes. After establishing expression patterns, they are protected by chromatin modifications such as DNA methylation (37). Inhibition of DNA methylation by some chemical inhibitors or predominantly negative regulation of DNA methyltransferase genes resulted in activation of silenced genes.

Transcriptional Regulation in Allopolyploids

During evolution, selective modifications of the mechanisms controlling gene expression allow colonization of new ecological niches and are thought to respond to environmental cues and developmental programs (38).

The conditions determining species specificity have been interactions between external influences and internal programming of gene expression networks (39). To give an example of this situation, we can say the adaptive evolution of the polymerase I transcription mechanism of rDNA sequences characterized by species-specific factors. Consequently, human SL1 (a human-specific factor) is present in human rRNA genes. Along with this concept, the enhancer disequilibrium model suggested that in Xenopus interspecies hybrids, dominant rDNA clusters have stronger enhancers, which separates existing transcription factors so that rDNA clusters with weaker enhancers are inaccessible and not replicated by transcription activators (40). This model has been taken into account by including species-specific factors in plants. These factors may represent upstream regulators. If the regulatory factors (X and/or X') (figures 3A, A1-4) are compatible with both downstream genes, the downstream genes are activated via trans- acting effects on the cis regulatory elements of X and (X') (figure 3A). ,

A1). Thus, it may be the quantitative variation and competition for binding affinity between transcription factors and binding sites in the respective promoters that determines the expression levels and fitness of the corresponding paralog genes. Also, a single orthologous gene can be activated primarily through cis and trans-acting effects if only one factor is present, or if the X and X' factors are incompatible with one of the orthologous downstream genes (Figure 3A, A2-3). Silencing of both loci was expected if both factors were absent or if the factors were inhibitory to downstream genes (figures 3A,A4) (41). Effects produced by gene activation or silencing of transcription repressors can be brought about by recruiting the chromatin remodeling complex to a particular locus. Another method is that chromatin can be reconstructed in allotetraploids (figures 3A,A1-4). The reason is that the interactions between the two genomes may disrupt the innate chromatin structure. By using dominant-negative mutants and upstream regulators in chromatin proteins that can overcome genetic redundancy in allopolyploids, the detailed mode of action in this system can be elucidated (42). In fact, some silenced genes block DNA methylation associated with promoter demethylation in met1-RNAi lines or at these specific loci in A. suecica (a natural and specific self-sufficient allotetraploid native to northern Europe– Hylander 1957; Lind Hallden et al. 2002). was re-enabled. This model also suggested that some key regulators, such as transcription factors or chromatin remodeling factors, could control the expression of many downstream genes, including components of DNA methylation and histone modifications (43). More than 50% of the transcriptome has been split between D. melanogester and D. simulans within 2-3 million years since the common ancestor of evolution. Many of these genes have evolved to establish sex-based gene expression patterns that can cause hybrid male lethality or hybrid dysgenesis between the two species unless hybrid rescue mutants are used.

Chromatin modifications are overcome by progenitor-dependent cis regulation through transcription factors such as Myb (44). Likewise, some transcription factors and chromatin remodeling components were able to contribute to genome-wide non-additive gene regulation and/or species.

RNA Mediated Gene Regulation in Allopolyploids

RNA interference (RNAi) is an evolutionarily conserved mechanism for modulating gene expression. Short anti-sense RNAs were produced by cleavage of dsRNA precursors to target the corresponding RNAs for degradation (45). In conclusion, short interfering RNAs (siRNAs) and microRNAs (miRNAs) are negative regulators of target transcript accumulation. Although they also share similar biogenesis pathways involving different sets of RNA processing, siRNAs and miRNAs have different origins and mechanism of action. siRNAs were generated from transposons, heterochromatic repeats, and viral sequences. They also acted as negative regulators and chromatin modulators (46). MiRNAs encoded in intergenic regions regulate other loci important for animal and plant development. In addition to functioning as translational repressors like animal miRNAs, plant miRNAs acted as siRNAs exerting negative cis- and trans-acting effects on cleavage of targeted loci via defective pairings. RNAi, on the other hand, has worked at the genome scale. This could directly affect gene silencing and DNA elimination. Therefore, RNAi pathways are sensitively modulated in all species, including progenitors of polyploids (47).

Evidence for the involvement of RNA-mediated gene regulation was obtained in a study of wheat in synthetic allotetraploids (31). Transcript analysis showed that Arabidopsis contains a large amount of anti-sense and transcript of unknown function. These transcripts were involved in the regulation of target genes. Overexpression of double-stranded RNAs effectively reduced the expression of endogenous target genes in A. suecica. In addition, transgene expression in Arabidopsis autopolyploids was regulated by ploidy levels, and the transgene silenced in diploids was reactivated in triploids (31).

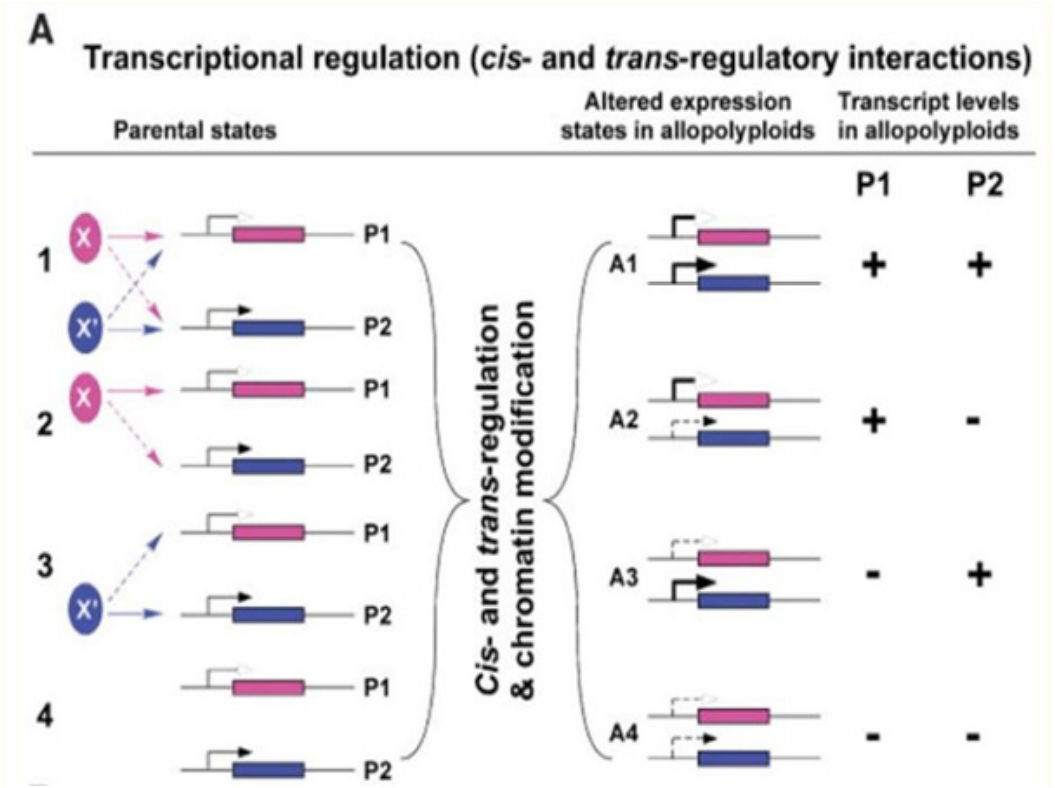
Expression levels of endogenous genes varied in response to single and double dosage in maize. The data suggested that, in addition to RNAi, chromosome pairing and paramutation- like interactions are responsible for gene regulation in polyploids (48). On a genome-wide scale, innate RNAi pathways from progenitors can be disrupted in specific hybrids or allopolyploids due to incompatibilities between two different species (49).

The degradation state can alter and modify the efficiency of RNA biogenesis machinery, the accumulation and specificity of siRNAs and miRNAs. Another possibility is differential accumulation of siRNA and miRNAs in allopolyploids (figure 3B,A5-8), which led to downregulation of target loci (49). If small miRNAs with mixed RNA targets have high fidelity of their targets, only one of the autologous or homologous targets was suppressed (Figure 3B,A6-7). On the other hand, targeted specificity was achieved by the cis or trans movement capacity of siRNAs and miRNAs. As a result, target loci were downregulated from one progenitor (Figures 3B, A6-7), two progenitors (Figures 3B, A5), or neither (Figures 3B-A8).

We do not yet know whether and how siRNAs and miRNAs of different origins are differentially expressed in allopolyploids. For miRNAs encoded by precursors in the intergene regions, it is speculated that differential accumulation is likely to be controlled by the transcript levels of the precursors produced through any of the transcriptional regulatory mechanisms discussed above (figure 3A). Alter-

natively, each siRNA species and heterochromatin transcripts may be mediated differently by the RNA polymerase IV machinery (50).

There is no reason to exclude other post-transcriptional regulatory mechanisms such as RNA stability, alternative splicing, RNA processing, editing, and RNA caching that may be involved in differential accumulation of transcript levels in allopolyploids (50). For example, the stability of species-varying mRNAs and the half-life of mRNAs produced from progenitors have been directly related to differential accumulation of transcripts in allopolyploids.



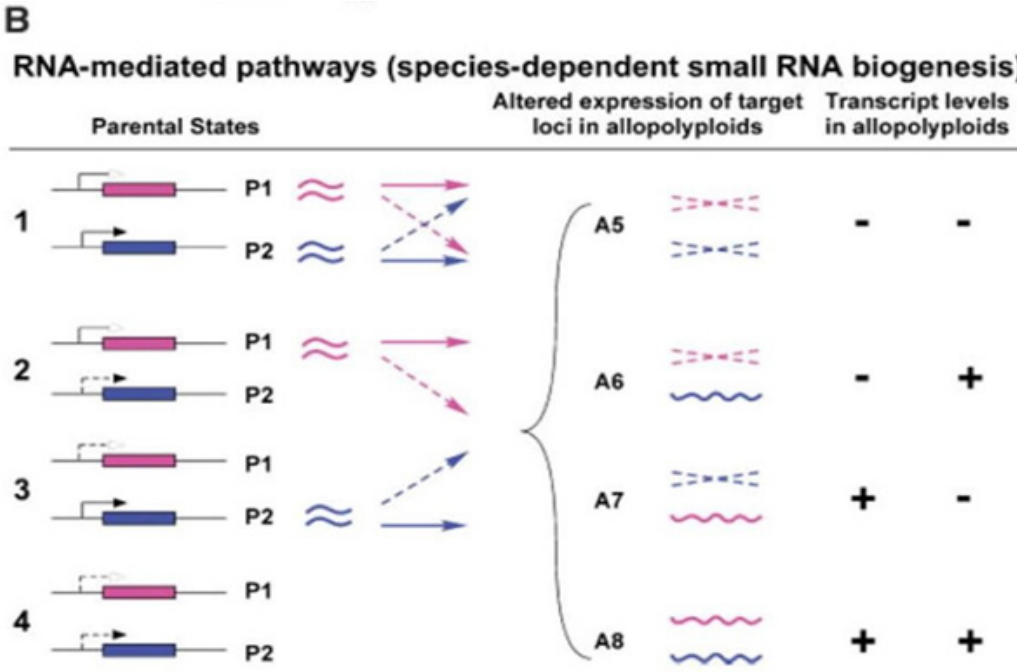


Figure 3
Two models for gene expression changes observed in allopolyploids. A: The transcriptional regulation model proposes the interactive roles of sequence evolution, transcriptional regulation, and chromatin modification in modulating the expression of orthologous genes in allopolyploids. Transcriptional regulators (X, P1 and X' , P2) are compatible with orthologous loci leading to expression of both in allotetraploids (A1). Only one regulator (X or X') is present or is compatible with one of the loci leading to expression of a single locus (A2 or A3). Absence of upstream regulators or incompatibility between two loci results in silencing of both loci (A4). The B:RNA-mediated pathway model shows differential accumulation of small RNAs that can act as negative regulators for target genes. Production of small RNAs (siRNA and miRNA) from orthologous genes is associated with downregulation of both genes ("crossover" symbols) in allotetraploids (A5). Production of small RNAs from one species results in silencing of a locus (A6 or 7). The absence of small RNAs promotes transcript accumulation at both orthologous loci (A8). Blue and red colors represent protein regulators (ovals), loci (boxes), small RNAs (short wavy lines), and RNA transcripts (long wavy lines) from parent 1 (P1) and parent 2 (P2), respectively. Blue and red arrows indicate possible cis (solid lines) or trans (dashed lines) interactions, whereas arrows at each locus indicate transcription (open head, P1 and solid head, P2, all solid lines) and low transcription levels (dashed lines). "+" and "-" indicate accumulation and downregulation of transcripts in allotetraploids, respectively. Bold arrows indicate up-editing.

Cis-Trans Effects on Transcriptional Regulation in Allopolyploids

Stable allopolyploids have provided a very good system for testing cis and trans effects. This is due to the fact that the same tetraploid cells contain a common set of protein factors. After splicing different genomes, differences in cis and trans regulation contributed to changes in the expression of orthologs that became homologous pairs in the allopolyploid or interspecific nucleus (51). Cis regulatory aberration may result in asymmetric accumulation of homologous transcripts in allopolyploids, as well as directly acting on localized chromatin areas such as single genes, promoters or enhancers.

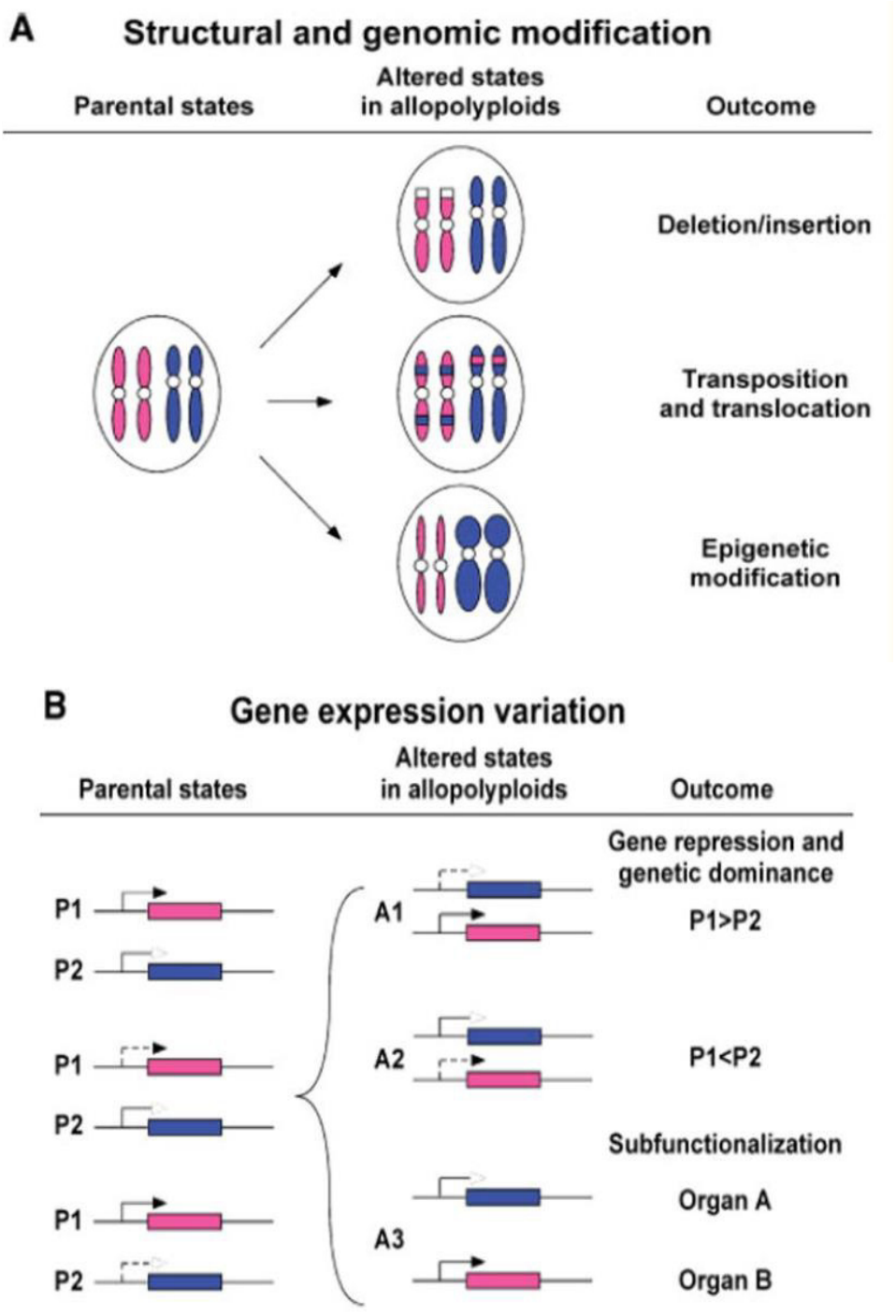
Evidence for cis and trans effects has been found in studies on orthologous or homologous genes in allopolyploids and interspecies hybrids. Differential expression of genes of progenitors in Drosophila interspecies *hybrids, Arabidopsis* allopolyploids and interspecies hybrids, and maize diploid hybrids 52 was mainly due to cis-regulatory changes. Progenitor- specific differences occurred in the same cells, most likely allelic or epigenetic differences. In contrast, expression differentiation resulting from changes in regulatory hierarchies had to result in two types of expression changes. The first consisted of a difference in the sum of homologous mRNAs compared with either parent's median or non-additive gene expression. In fact, divergently expressed orthologs accounted for approximately 68% of non-additively expressed genes in the two allotetraploids (52), which included trans-acting effects. Second, it is a change in the ratio of homologously encoded mRNAs in an allopolyploid compared to the ratio of two orthologs in a 1:1 mixture of parent mRNAs. Such a difference indicated a regulatory interaction between parental genomes (53, figure 4C).

A model of regulatory hierarchy showed that trans-regulatory differences predominate in allopolyploids. The species-specific expression patterns observed in *Arabidopsis* allotetraploids(54) may have resulted from sequence differences in regulatory elements over the approximately 6 million years that separated the parent species. Cis- and trans-acting regulation and epigenetic modifications of homologous genes were able to alter regulatory interactions in the biological process (fig. 5A). They found this in a subset of a gene that controls flowering time variation. A. arenosa and A. *thaliana* (Ler) have differentiated flowering habits due to their selective adaptation to cold and hot climates. The natural variation of flowering time was largely controlled by two epistatically acting loci, namely FRIGIDA (FRI) and FLOWERING LOCUS C (FLC). FRI, A. thaliana has a dysfunctional AtFRI, whereas A. arenosa FRI (AaFRI) is functional (51).

Compared to *A. Thaliana* (AtFLC), the *A. arenosa* FLC (AaFLC) loci have deletions in the promoter and in the first intron that are important for cis regulation of FLC expression. In resynthesized allotetraploids, AaFRI complements the non-functional AtFRI and interacts with AtFLC in trance to overwinter synthetic allotetraploids in a dose-dependent manner. Aa FRI acts on AtFLC in trans and AaFLC in cis because *A. thaliana* FRI is non-functional. The differential effects of AaFRI on the AtFLC and AaFLC loci were most likely due to sequence variation in their cis-regulatory elements. AtFLC and AaFLC upregulation was mediated by H3-K9 acetylation and H3K4 methylation, suggesting locus-specific chromatin modifications of the FRI (51).

Although it simplifies the flowering pathway with more than 80 genes in the model (fig. 5a), it did provide some insight into the functioning of orthologous genes involved in biological pathways during allopolyploidization and how they would proceed (55). Many orthologous genes may be differentiated into strong or weak, dominant or recessive alleles, cis-regulatory elements that provide tissue-specific expression and/or developmentally regulation. Regulatory networks could be reset by cis and trans effects via chromatin modification immediately after allopolyploidization. Genetic and epigenetic change over generations has been subject to selection and adaptation, and additional genes (eg MAF, an FLC-

MAF family member of MADS-box genes) can be activated for allopolyploids to invade a cell. A similar mechanism may be responsible for the functional diversification of orthologous genes in the developmental regulation of gene expression; this phenomenon has been known as the subfunctionalization of dual genes (56). Flowering time in plants directly affected reproduction and adaptation. Thus, sequence evolution and epigenetic regulation have played an interactive and pervasive role in mediating regulatory mismatches between divergent genomes that lead to natural variation and selective adaptation during allopolyploid evolution.



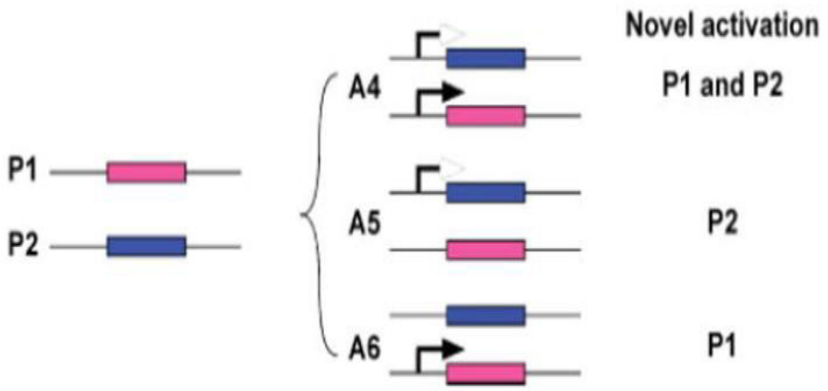


Figure 4

Types of genomic and gene expression changes documented in polyploids. A: Genomic modification includes deletion, translocation, and interstitial homoeologous changes (transposition), and epigenetic modification (eg, changes in DNA methylation). Blue and red colors represent two genomes or chromosomes from P1 and P2, respectively. B: Gene expression changes include genetic dominance, gene silencing, downstream functionalization, and new activation. In all cases, loci showing expression changes in allotetraploids (A1 – A6) may be from one or both parents compared to expression levels in the original parent (P1, red or P2, blue). For simplicity, only one of the two alleles at each parent locus is shown. Arrows at each locus indicate transcription (open head, P1 and full head, P2, all solid lines), low transcription levels (dashed lines), and no transcription (no arrows). Bold arrows indicate new gene activation.

DNA Loss in Allopolyploids

Allopolyploid genomes have copies (homologs) of each gene immediately following WGD (whole genome duplication) (Figure 1). This redundancy means that homeologists can disappear from the genome without losing the function they encoded. Homeologous loss occurs as part of the diploidization process—the tendency of the polyploid genome to revert to a diploid-like state (57).

Some of the earliest insights into loss of homologs in allopolyploids came from the use of anonymous genetic markers. Enhanced fragment length polymorphism (AFLP) and restriction fragment length polymorphism (RFLP) profiles in various synthetic allopolyploids yielded a wide range of predictions about the frequency of gene loss. For example, losses of AFLP bands in Gossypium tetra' and hexaploids ranged from only 0.0–0.7%, whereas individuals representing four different lines of fifth-generation (S 5) synthetic Brassica allopolyploids lost 4.7–13.0% (58). , 59). Synthetic allopolyploids of *Nicotiana attenuata×N. obtusifolia* in the fifth generation lost 51% (30% from N. attenuata and 71.5% from N. obtusifolia) of their parent markers using universally prepared PCR-derived sequence (UP) and It obtained new markers of 1.5%. ' PCR profiles. These data were compared with an apparent loss of 88% of RAPD bands and 83% of AFLP bands in the autotetraploid *Paspalum notatum* (60).

Following the use of AFLPs and RFLPs in the polyploidy study, the targeted "one at a time" gene approach soon followed. In order to identify possible target genes in detailed research, gene sequences from the study organism are de novo sequenced (61). This was accomplished by cloning and sequencing ESTs in the study organism, or by designing PCR primers for a gene sequence from another species, amplifying that gene in the study organism, and sequencing the product (61). When a gene is sequenced successfully in the study organism, special PCR primers are designed and the gene is sequenced in both parental diploid strains of the polyploid. The parental sequences are then aligned and single nucleotide polymorphisms (SNPs) are identified. These SNPs can then be tested in natural populations of allopolyploid using restriction enzymes that cut only one homolog (an approach called split amplified polymorphic sequence [CAPS] analysis) or PCR primers that amplify only one homolog.

Application of this approach gave initial information about both gene losses. *Tragopogon Mirus and T. miscellus* are two allotetraploids that have been formed continuously over the past 80 years. (Fig. 2, 62). *Tragopogon* constitutes an excellent evolutionary model for the study of novel and recurrent natural allopolyploidy, but until recently it had insufficient resources as a genetic model, thus limiting the types of questions that can be addressed in this polyploid system. In both polyploids, the loss of homologs was extensive, with losses observed in at least one individual for most of the loci examined (61). Moreover, most of the homologous losses involved the same diploid parent (*T. dubius*) in multiple populations of both polyploid species; the same genes were kept consistently replicated, and a few were lost in more than one population.

Despite the new insights and insights into genome evolution in polyploids provided by these

methods, these approaches have shortcomings. Studies based on some unknown sources have shown band loss due to methylation changes rather than true loss of homologs (63). Loss of AFLP and RFLP bands may be the result of processes other than true homolog loss, as any mutation that changes the length of a band causes it to move its position in a gel profile. These limitations are discussed by (Gaeta, R. T., and J. C. Pires. 2010), who refer to these methods as "bandology" and recommend the use of genome-wide markers mapped to homeologous genomes along with physical analysis of karyotypes. Additionally, one-at-a-time gene survey approaches are slow and labor-intensive. For example, studies with *Tragopogon polyploids* required 4 years to characterize and examine only 29 genes (64).

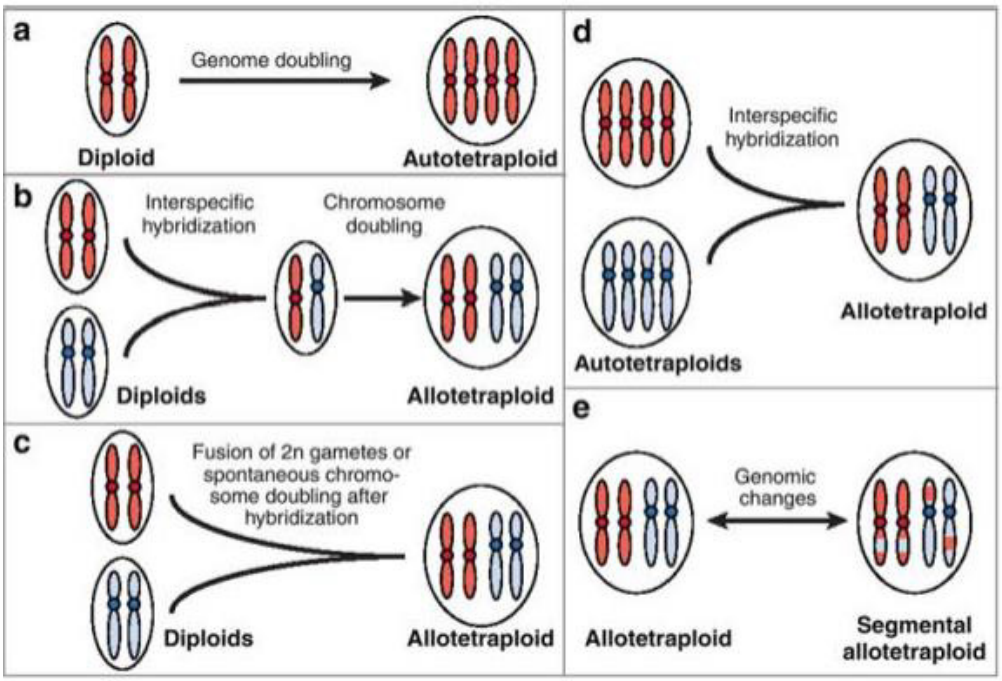


Figure 1

Representation of auto- and allopolyploids. For simplicity, only one pair of homologous chromosomes (red or blue) is shown in the diploid. (a) Formation of an autotetraploid by doubling a basic set of chromosomes. A triploid (not shown) can be formed by hybridization between a diploid and an autotetraploid. (b) Formation of an allotetraploid by interspecific hybridization followed by chromosome doubling. (c) Formation of an allopolyploid by the fusion of unreduced gametes in two diploid species. (d) Formation of an allotetraploid by interspecific hybridization between two autotetraploid species. (e) An allotetraploid (left) may become a segmental allotetraploid (right) if homoeologous chromosomes contain some homologous chromosomal segments.

Allopolyploidy and Heterosis

The genome-wide non-additive gene regulation seen in allotetraploids is associated with variation in expression between parents. Therefore, hybrids derived from distantly related species can cause high levels of gene expression changes in a non-additive manner, providing the molecular basis of hybrid viability (65) and phenotypic variation in the allotetraploid progeny. Hybrid viability refers to the higher performance of an F1 hybrid than the MPV or the best parent. The genetic basis for heterosis is predicted to be related to dominant complementation (dominance model) of mildly deleterious recessives or over-dominant gene action (over-dominance model), in which genes have greater expression in heterozygous conditions (66). According to the dominance model, peak performance should be observed when all dominant positive genes from both parents are in homozygous conditions. The extreme dominance model suggested that heterosis should peak at levels of maximum heterozygosity and dissipate as homozygosity approaches. Moreover, extreme dominance is accompanied by non-allelic or epistatic interactions, and epistasis is involved in most QTLs associated with inbreeding depression and heterosis in maize and rice. Comparison of genome-wide gene expression data with phenotypic traits (QTLs) can provide new insights into the role of gene expression changes in various biological pathways leading to hybrid viability.

Genome-wide transcriptome dominance in *Arabidopsis* allotetraploids and gene expression changes observed in maize diploid hybrids supported both dominance and overdomination models. Many genes in energy, metabolism, cellular biogenesis, and plant hormonal regulation are up-regulated in allotetraploids, which may contribute to the hybrid vigor observed in allotetraploids (54). While the underlying mechanisms are not yet known, one possibility is modulation of several key regulators in allotetraploids that can control downstream genes in various biological pathways (51, 54), such as photosynthesis and metabolism (Z. Ni & Z.J. Chen, unpublished).

If we consider the other alternative, cis- and trans-acting effects (53, Figure 2a) involving regulatory sequence changes, chromatin modifications, and RNA-mediated pathways may explain dominance, overdomination, and epistasis. Interactions between diverging orthologous protein products can determine suppression or activation of progenitors' genes in allopolyploids of interspecies hybrids of Arabidopsis (54), cotton, Senecio and wheat (Figure 2c). In Drosophila, intraspecific diploid hybrids in maize (65) and sex-linked gene regulation in Drosophila. These mechanisms are not mutually exclusive and different protein-protein and protein-DNA interactions in allopolyploids may result in suppression of protein-coding genes and rDNA loci derived from a progenitor (e.g. A. thaliana) through chromatin modifications (51, 54, 68) or new expression patterns leading to hybrid viability. (Figure 2c).

Species Interactions and Plant Polyploidy

The myriad ways in which plants interact with other organisms have resulted in extraordinary species radiations. For example, evolutionary differentiation in flower form due to interactions with expert pollinators may have promoted speciation in angiosperms (Bradshaw and Schemske, 2003; Crepet and Niklas, 2009; Van der Niet et al., 2014). Coevolutionary arms races between plants and herbivorous insects have also been suggested as another potential diversification mechanism (Ehrlich and Raven, 1964; Wiens et al., 2015), and specialization in these herbivores may have triggered the later speciation of natural enemies during the third trophic period (Abrahamson and Blair). , 2008). The diverse interactions of plants with pollinators, herbivores, parasitoids, seed dispersers, microbes and other organisms create rich opportunities for trait differentiation, which will be driven in part by the plant's underlying genetic architecture (De Bodt et al., 2005). An important change in the genetic architecture is polyploidy, a phenomenon commonly seen in plant lineages. The many phenotypic and genotypic effects of whole genome duplication make polyploidy an important force that can shape species interactions, and similarly, interactions with other species are expected to play a role in shaping polyploid lineages.

Despite the importance of both species interactions and polyploidy in plant evolution, there are new efforts to grasp how these factors together contribute to diversity. Part of the challenge in unraveling these links is identifying changes that are directly caused by polyploidy, changes that develop following whole genome duplication. Each of these pathways is likely to have opposite effects on whether there are predictable effects on species interactions. For example, polyploidy itself can cause predictable phenotypic changes that directly affect interactions with other organisms, such as increases in flower size leading to withdrawal of different pollinator species. However, polyploidy also has indirect effects that can alter species interactions. For example, the formation of an immediate, reproductively isolated polyploid lineage opens an opportunity for selection, variation in traits and species interactions. In this example, the bias caused by the local selective environment will likely be erratic. Consequently, the primary goal of ecological research on polyploidy is to distinguish between direct and indirect effects of polyploidy on species interactions.

Paramutation Effects in Polyploids

The term paramutation is the result of heritable changes in gene expression that occur through interaction between alleles. This concept was first discovered in plants and later found in many other organisms, including mammals (mouse and human) (69, 70). The paramutagenic allele causes a change in the expression status of the paramutagenic allele. A paramutation-like phenomenon has also been discovered in tetraploid plants containing active and inactive transgene alleles of hygromycin phosphotransferase (HPT) (71). Active alleles that are trans-inactivated by their silent counterparts are observed in tetraploid but not diploid plants, and this has occurred only in progeny resulting from self-pollination of plants heterozygous for the active and inactive HPT allele. The occurrence of transgene paramutation only in tetraploid plants indicated that active and inactive alleles undergo meiosis together. This has led to the pairing-based trans-inactivation hypothesis. Estimates in the results obtained are consistent with observations in the tetraploid tomato, where the frequency of paramutation of a specific paramutagenic allele at the sulfur locus differs between diploid, triploid, and tetraploid plants and depends on the ratio of paramutagenic and paramutable alleles. This suggests a counting mechanism similar to X chromosome inactivation for paramutation due to polyploidy (70).

A paramutation-like phenomenon has occurred as a result of genetic crosses between heterozygotes and wild-type mice, regardless of sex combination (70). This phenomenon is presumed to be associated with abnormal RNAs originating from the paramutagenic allele that is packaged

in sperm and causes paramutation when passed on to the next generation. In fact, the paramutation depends on an RNA polymerase that is RNA dependent; The rdr101 mutation prevents paramutation in maize. However, the paramutation in Arabidopsis tetraploids is most likely not RNA-related because trans activation does not occur in the F1 generation. Moreover, drop crosses with a paramutable tetraploid in the DNA methylation (ddm1) mutant do not change the paramutation phenotypes in F1 or F2 but in the F3 family, which is consistent with the gradual loss of DNA methylation by ddm1. Data suggest that methylation occurs later and occurs during meiosis and during physical contact of epialleles after silencing has been established (71). Alternatively, separating the pairing between homologous and homoeologous chromosomes in polyploids may require several more rounds of meiosis.

Many paramutation phenomena have been associated with repeated sequences (69). Multi-duplicate genes or repetitive intergene regions are an important trigger for the formation of silenced chromatin. Repeated sequences, whether reverse or sequential, can lead to dsRNA production, which is an important trigger for RNA silencing and heterochromatin formation (73). In addition, repetitive sequences can physically associate with their homologs in nonmiotic cells (74). It is conceivable that different repeat sequences originating from progenitors may trigger aberrant siRNA production and heterochromation generatioN, which is responsible for paramutation-like or other epigenetic events in allopolyploids.

Model for the Study of Polyploidy

New ancestral species often formed gradually due to geographical and ecological differences (75). However, it is believed that new species emerge abruptly through polyploidization in plants and some animals, including vertebrates such as amphibians and lizards (75, 76). For example, Arabidopsis suecica (2n = 4x = 26) is a natural allotetraploid that formed between 12,000 and 1.5 Mya. Two progenitor species, A. thaliana and Arabidopsis arenosa (77), split ~6 Mya, similar to the distance between humans and chimpanzees (~6.3 million years). Despite this distance, A. thaliana autotetraploid (2n = 4x = 20) and A. arenosa tetraploid (2n = 4x = 32) can hybridize to produce A. suecica-like plants (2n = 4x = 26) (Fig. 5a, b, c). A. arenosa is thought to be an autotetraploid, but sequencing analysis has shown that it is not a pure autotetraploid (L. Tian, J. Wang & Z.J. Chen). Re-synthesized allotetraploids are meiotically stable and contain five pairs of A. thaliana chromosomes and eight pairs of A. arenosa chromosomes (54, Figure 5c). Compared with resynthesized Brassica and wheat allopolyploids, which undergo rapid changes in chromosomal DNA sequences, the frequency of aneuploidies and chromosomal aberrations in Arabidopsis resynthesized allotetraploids is low (78).

The newly formed allotetraploids (F1 individuals) were genetically identical (Fig. 5a) and showed subtle phenotypic variation. Some variations among F1 individuals may result from heterozygosity of the crossing tetraploid A. arenosa parent, while other variations may result from interactions between different genotypes of A. arenosa and A. thaliana used in interspecies hybridizations. The degree of variation depends on the parental genotypes used in interspecies hybridization. For example, seed set was higher in nascent allotetraploids (F1) between A. arenosa and A. thaliana C24 or Ler ecotype than between A. arenosa and A. thaliana Columbia (79), indicating genotypic effects on interspecies hybridization. Hybridization was successful only in crosses using A. thaliana as the maternal parent and A. arenosa as the pollen donor (J. Wang, L. Tian & ZJ Chen). Most of the F1 individuals in recent generations and the self-fertile lineage are similar to the A. arenosa parent and A. suecica (54, 79, Figure 5c), although different phenotypes are observed in segregated populations (F2-F3) (Figure 5b). Therefore, A. arenosa appears to be phenotypically dominant over A. thaliana in allotetraploids (54).

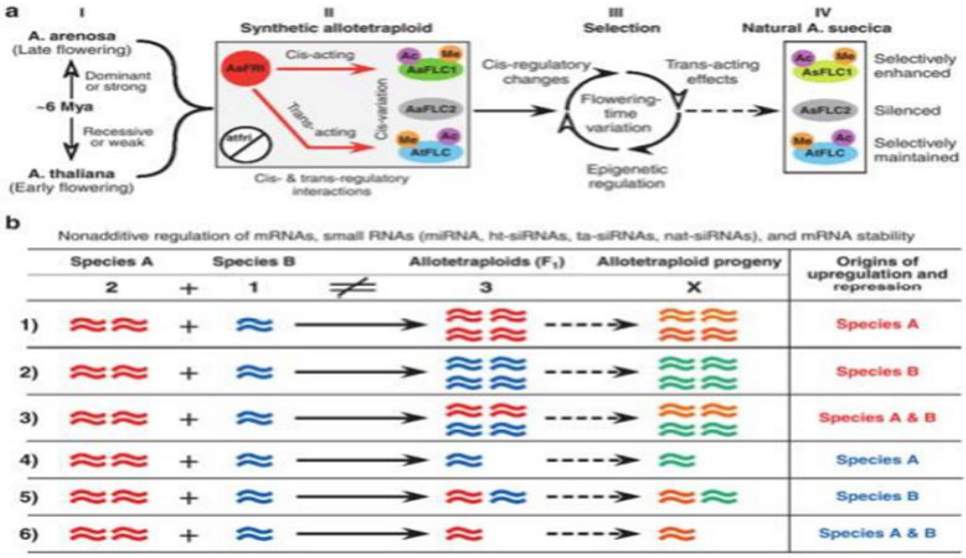


Figure 5

Models for transcriptional and post-transcriptional regulation of non-additive gene expression in allopolyploids. (a) Cis and transactive effects on transcriptional regulation of non-additive gene expression in allotetraploids. I. During evolution, changes in cis-regulatory elements can yield "strong/dominant" and "weak/recessive" loci. II. Combination of these loci in the same allotetraploid cells induces cis- and trans-acting effects. Because A. thaliana FRI (AtFRI) is non-functional, A. arenosa FRI (AaFRI) trans-activates A. thaliana FLC (AtFLC) and upregulates one of the cis - A. arenosa FLC (AaFLC1) loci for either excessive dominance or too late reinstatement. flowering in synthesized allotetraploids. Cis-regulation and trans-activation are maintained by histone acetylation (Ac in a small purple circle) and methylation (Me in a small orange circle). Functional AaFRI is in a large red circle and non-functional A. thaliana FRI (atflc) is in a small white circle with a slash. Straight and curved red arrows indicate cis- and trans-acting effects by AaFRI, respectively. FLC loci are in oval circles. Blue and green indicate active AtFLC1 and AaFLC1, respectively, and gray indicates silenced AaFLC2. Differences in expression of the three FLC loci may reflect cis-regulatory variation. III. Cis- and trans-effective interactions and epigenetic regulation of the FRI and FLC loci may facilitate selection for flowering time variation in resynthesized allotetraploids (indicated by a circular wheel). IV. In A. suecica, additional selection forces can increase the expression of related genes such as AaFLC1 (color change from dark green in II to yellow green in IV) and MAFs, which facilitate cold climate adaptation. This simple model can be generalized to explain a mechanism for regulatory interactions between divergent loci in other pathways in allotetraploids (see text for details). (b) Non-additive accumulation of mRNAs and small RNAs in allotetraploids. There is evidence that 15-40% of genes are differentially expressed between two closely related Arabidopsis species and that a subset of these genes undergo non-additive expression in allotetraploids. Up- or down-regulation of mRNAs can result from activation of genes originating from parent A, B, or both. We exclude the case where expression of a locus is compensated by the corresponding homoeologous locus. The spliced transcripts are small, such as microRNAs (miRNAs), heterochromatic and transposon-related siRNAs (htsiRNAs), trans-acting siRNAs (ta-siRNAs), and native antisense (natsiRNAs). RNAs, on the other hand, typically negatively regulate the expression of their target genes. Red and blue wave lines indicate RNA transcripts or small RNAs produced in species A and B, respectively. We hypothetically assign two RNA molecules for A-types and one RNA molecule for B-types. Note that the number of RNA in the newly formed allotetraploids (F 1) is not equal to 3 (2 + 1), suppression if greater than 3 or less than 3). Possible changes in RNA composition and accumulation (column X) (dashed arrows) may occur in the self-pollinating lineage indicated by the orange and green wave lines, respectively. According to the hypothetical result, the origins of small RNA upregulation (red at 1-3) and repression (blue at 4-6) are shown in the last column.

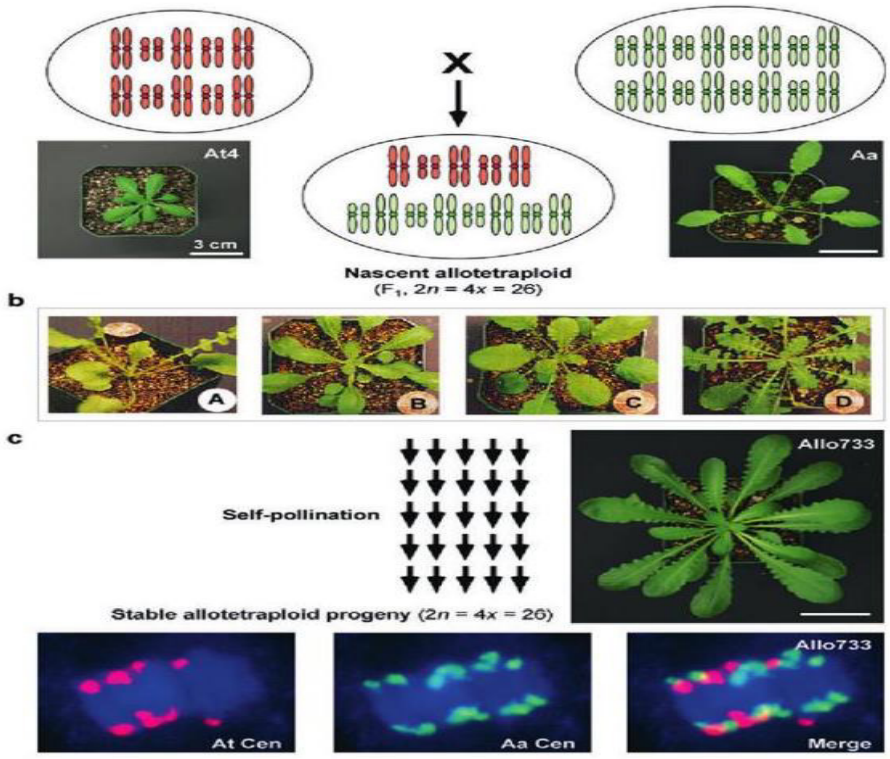


Figure 5
Production of Arabidopsis allotetraploids. (a) Schematic karyotypes of F1 nascent allotetraploids and their progenitors. Seedlings of two progenitors, A. thaliana autotetraploid (At4) and A. arenosa tetraploid (Aa), are shown. (b) Phenotypic variation was observed infrequently in F 1 allotetraploids, but very common in segregated populations (F 2) (A–D). A and D: A. arenosa-like, B: A. thaliana-like, and C: medium. (c) Independent progeny of allotetraploids are produced by self-production of multiple F 1 lines. Allopolyploids are self-pollinating (or can be manually self-pollinated), and progressive inbreeding occurs in subsequent generations. Karyotypes in a meiotic cell of a resynthesized allotetraploid (Allo733 in the fifth generation), 5 pairs of A. thaliana centromeres (At Cen, red) and 8 pairs of A. arenosa centromeres (Aa Cen, green). The seedlings of Allo733 are shown. All plants were photographed when they were 4-5 weeks old. Size bars indicate 3 cm.

Allotetraploids obtained by self-crossing F1s show stable karyotypes in the fifth generation (Figure 5c), but exhibit a wide variety of variants (Figure 6a), some of which are absent from both parents (transgression). Moreover, allotetraploids exhibit hybrid vigor: larger rosettes, more leaves, longer and wider leaves, and plants taller than the parents. The fertility rate of plants in the self-pollinated generation varies from one lineage to another (78, 79). The overall fertility level improves after each generation is self-born, suggesting that genome mismatch and ancestral gene expression difference are gradually being overcome (80).

Flower colors ranged from pink (as A. arenosa) in the early generation (F1) to a mixture of pink and white flowers in the intermediate (S2–4) and white in the late generation (S5). During selfing (S3), there is a low frequency of mixed white and pink flowers, transient and mosaic (derived from the same zygote) on the same flower branch (Fig. 6b). The emergence of variation within the same flower branch suggested rapid changes in the expression of genes involved in anthocyanin synthesis pathways, possibly through epigenetic regulation.

Polyploidy and Bioinformatics

Bioinformatics has many applications in a variety of sciences, including agriculture, pharmaceuticals, clinical and biomedical sciences. The major application of bioinformatics is the computer-assisted drug discovery process in the pharmaceutical sciences. Tasks include molecular modeling; molecular dynamics simulation; molecular docking; virtual scan; pharmacophore modeling; absorption, distribution, metabolism, excretion and toxicity (ADMET) properties etc. He has been involved in structure-based and ligand-based drug/inhibitor design processes. Bioinformatics has also been used in the development and analysis of genetically modified plants and animals. It can be used in determining the position of genes to be modified, calculating various possible gene modifications, computational analysis of the structure and functions of modified genes, etc. has been helpful. Bioinformatics tools are used in clinical and biomedical sciences especially computational research of genetic disorders, gene therapy, personalized medicine, etc., in addition to computer-aided drug design. used (81).

On the other hand, the use of microorganisms for the improvement of farm animals and the production of bread, cheese and wine is one of the oldest biotechnology methods. Today, modern biotechnology methods are used. Modern biotechnology uses genetic engineering as a tool. For example, while obtaining a living thing by transferring a gene to a living thing is the field of genetic engineering; Obtaining a purposeful product from this living thing is the field of biotechnology. With modern biotechnology, cheaper, easier and more efficient products are obtained. If we list the modern biotechnology methods;

It is aimed to obtain high quality and more yielding species.

- **Crossbreeding:** Breeds that only exchange genes among themselves for a long time are considered genetically weak. Because this situation causes harmful recessive genes to appear in the phenotype with homozygous conditions. Crossing between individuals homozygous in terms of different characters is made to obtain hybrid individuals with superior characteristics. For example, large and sweet plums were produced by crossing small and sweet plums with large and tasteless plums.

-**Artificial Fertilization:** Sperm taken from animals with superior characteristics are stored in sperm banks and used to fertilize the egg cell at the appropriate time.

-**Polyploidy:** It is the condition where the number of chromosome pairs in the cells is 3n or more. Polyploidy individuals are more common in plants than animals. Polyploid plants are commercially valuable because the fruits of polyploid plants are larger than the fruits of diploid plants. The polyploidy condition is usually; Potatoes, bananas, seedless watermelons and apples are also common.

Today, with the joint work of biotechnology, fields of study such as bioinformatics, genomics and proteomics have emerged.

Figure 6

(a) Phenotypic variation of plants after five generations of spontaneous. The plants contain two parents, A. thaliana autotetraploid (At4) and A. arenosa (Aa), six allotetraploids (S-1 to S-6), and a natural allotetraploid, A. suecica (As). Allotetraploids have the same chromosome number (Figure 3c and data not shown) but show phenotypic and flowering time variation. Some plants (S5–5 and S5–6) are similar to A. suecica, while others (S5–1 to S5–4) show novel phenotypes. Differential expression of parental genes may contribute to the phenotypic variation of Arabidopsis allotetraploids. (b) Evidence for epigenetic silencing in resynthesized allopolyploids. A. suecica (As, white flower) is a naturally occurring allotetraploid derived from A. thaliana (not shown) and A. arenosa (Aa) with white and pink flowers, respectively. Flower colors in the third generation resynthesized allotetraploids (S3–1, 2, and 3) range from completely white (S3–1) to completely pink (S3–3). Variegated flower colors in the same flowering branch (S3-2) show epigenetic regulation of genes controlling flower color pathways. Same size bars are (a) 50 mm excluding At4 and (b) 5 mm excluding Ace.

The Evolutionary Origin of Plant Polyploidization

Polyploidy is widely distributed in the plant universe. Genomic comparisons based on sequenced genomes show that all plant species evolved from one or more polyploidization events; therefore, all plants are paleo-polyploids (Figure 7) (Wendel, 2015). In addition, about 30% of cultivated crops (Yang et al., 2016) are neo-polyploids whose genomes consist of multiple sets of chromosomes (Salman-Minkov et al., 2016). Many researchers aimed to elucidate the polyploidization events of plant polyploids. So far, about 50 polyploidization events have been accurately identified in plant phylogenetic trees through genome sequencing and comparative genomic analysis (Vanneste et al, 2014; Cheng et al, 2018; Ren et al, 2018). Kagale (2014) analyzed the transcriptome data of multiple Brassicaceae species, inferring polyploidization events and the corresponding origin of cruciferous species. Ancient α and ß whole-genome duplications (WGDs) occurred approximately 47 and 124 million years ago (MY), respectively, before the diversification of the Brassicaceae family, while an extra whole-genome triplet (WGT) emerged much more recently (< 23 Myo).) belongs to the Brassiceae tribe (Wang et al., 2011). Polyploidization events have also been reported in gymnosperms, although the occurrence of polyploidization has been uncertain for a long time. According to Li et al. (2015), three independent events of ancient polyploidization were identified using a phylogenetic framework constructed by comparing transcriptome data from 24 gymnosperms. This indicated that conifer polyploidizations occurred about 200-342 Ma, demonstrating their significant contribution to the diversity of conifer species.

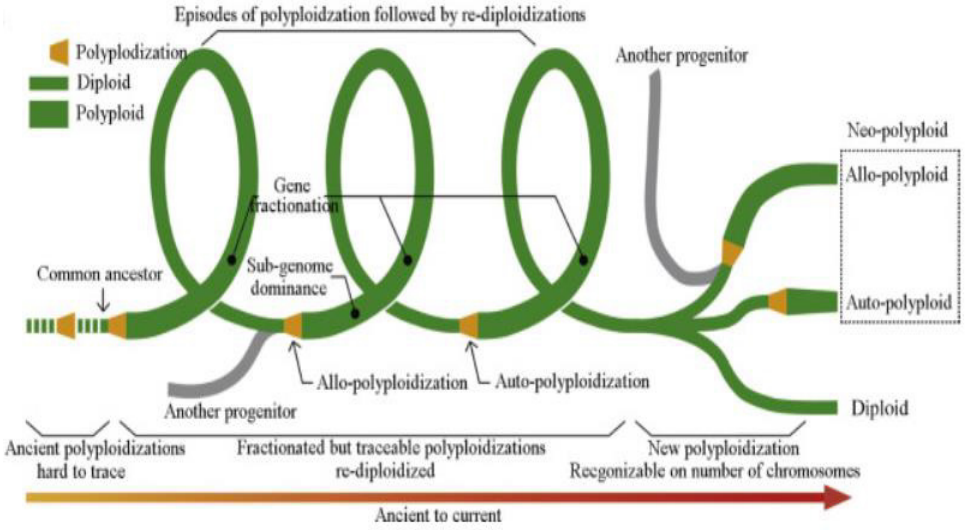


Figure 7
Life cycles of plants that experience repeated polyploidization and re-diploidization events

The origin of plant paleo-polyploidy can be associated with important historical events. The researchers compared the times of occurrence of all known polyploidization events in plant species (van de Peer et al., 2017). They discovered that many ancient polyploidization events centered around specific historical periods, such as the Cretaceous-Paleogene boundary, when a meteor hit the earth and resulted in a mass extinction. It was predicted that polyploid plants show higher adaptation to extreme environments than their diploid parents and therefore survive these disasters and climatic events, replacing their diploid ancestors' ecological niches. However, Freeling (2017) provided another interesting perspective to explain this phenomenon, considering polyploids as byproducts or gussets of adaptive selection during prolonged asexual reproduction, a strategy that plants use to protect themselves from the damage of extreme environments. In general, asexual reproduction underground or underwater helped plants survive extreme weather conditions caused by meteorites, which damaged the ozone layer, resulting in intense ionizing radiation. Thus, asexual reproduction facilitated the formation of polyploids. A promising explanation is that meiotic-related genes in species that rarely exhibit sexual reproduction are subject to relaxed selection, and accumulated mutations in these genes can promote non-reduced gamete formation (2n) and also promote events of polyploidization. The resulting polyploids are re-diploidized and reproduced sexually during or after the disaster, as sexual reproduction is more preferable for long-term adaptation. The advantages inherent in these polyploids made the polyploids more adaptable than their diploid relatives, which may have also survived mass extinction by asexual reproduction. This hypothesis is supported by flow cytometry experiments evaluating male 2n gamete production in 60 populations from 24 Brassicaceae species (Kreiner et al., 2017). They found that 2n gamete production was significantly higher in predominantly asexual species than in mixed mating, crossing and self-reproducing types.

Result

Allopolyploidy has provided a unique system for the study of mechanisms for reconstructing functional biological pathways through evolutionarily diverse genomes, orthologous genes, their products, and genetic and epigenetic interactions between different regulatory networks. The changes observed in polyploids could be mediated by genetic (sequence-dependent), epigenetic (sequence-independent) mechanisms, or both. Genetic alterations have included translocation and transposition, sequence deletion and insertion, non-homologous chromosome pairing, and additive gene editing, while epigenetic phenomena have included non-additive gene editing, transposon activation, silencing of homologous genes, and subfunctionality. Thus, studies continue in many fields, including today, both genetically and epigenetically of polyploidy.

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