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Epigenetic perspectives on the evolution and domestication of polyploid plant and crops

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Polyploidy or whole genome duplication (WGD) is a prominent feature for genome evolution of some animals and all flowering plants, including many important crops such as wheat, cotton, and canola. In autopolyploids, genome duplication often perturbs dosage regulation on biological networks. In allopolyploids, interspecific hybridization could induce genetic and epigenetic changes, the effects of which could be amplified by genome doubling (ploidy changes). Albeit the importance of genetic changes, some epigenetic changes can be stabilized and transmitted as epialleles into the progeny, which are subject to natural selection, adaptation, and domestication. Here we review recent advances for general and specific roles of epigenetic changes in the evolution of flowering plants and domestication of agricultural crops.

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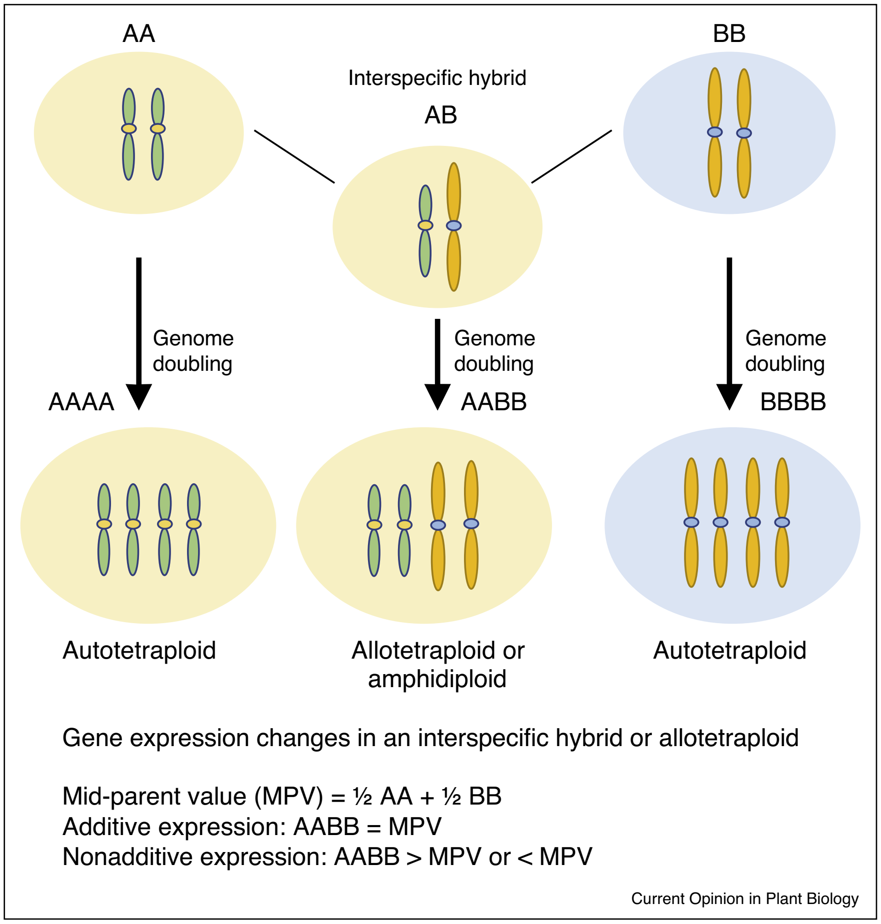
Introduction

Polyploidy results from whole genome duplication (WGD), generating an organism or cell that has more than two sets of chromosomes. While polyploidy is rare in animals compared to plants, polyploid incidences occur frequently in amphibians, reptiles, fishes, and insects [1], in addition to the presence of two rounds of genome duplication in vertebrates relative to invertebrates [2]. The view about the evolutionary fate of polyploidy has been changed from the 'dead-end' [3] or occasional incidences [4] to contemporary innovation [5–7]. This is partly because the number of plant and animal species being sequenced has been increased dramatically. Estimates indicate that before the divergence of extant seed plants and angiosperms, two rounds of ancestral WGDs occurred, allowing selection and evolution of genes and pathways important to seed and flower development and eventually the dominance of angiosperms on the earth [6,8]. Counting against WGD, polyploids often undergo a diploidization process, including genome fractionation, reshuffling, gene loss, pseudogenization, and neofunctionalization [9,10]. Many of these polyploids are called paleopolyploids, and their chromosomes pair normally as diploids.

In addition to paleopolyploids, autopolyploids and allopolyploids are commonly formed (Figure 1). Autopolyploids result from WGD within a population of the same species, while allopolyploids are formed by hybridization between species followed by chromosome doubling or through fusion of unreduced gametes from different species [11,12]. Allopolyploid plants are generally more common than autopolyploids, which are related to disrupted chromosome segregation during meiosis, leading to a reduced fertility in autopolyploids. The low fertility problem also exists in newly formed allopolyploids, but it can be overcome over time, producing progeny and populations with competitive growth and reproductive advantages [11,13–15], in a condition known as amphidiploid or disomic diploid [12]. Compared with diploid plants, polyploid plants usually increase their cell size, consequently developing large organs, such as roots, leaves, flowers, and seeds [16]. This suggests an advantage for polyploids to develop complex agronomic traits that are selected and domesticated in polyploid crops [13], which may explain the common occurrence of polyploidy in crops, including wheat (*Triticum aestivum* L.) [17], cotton (*Gossypium hirsutum* L.) [18], oilseed rape or canola (*Brassica napus* L.) [19], banana (*Musa acuminata* L.) [20], and potato (*Solanum tuberosum* L.) [21], whose genomes are sequenced.

The genomic consequences and underlying mechanisms for generating evolutionary novelty and morphological diversity have been the focus of many recent studies (see reviews in [5,7,11,15,22–25]). Some changes are largely dependent on genetic and sequence variation, as observed in polyploids of *Brassica* [26,27•], *Tragopogon* [28,29], and wheat [30,31], while many others have an epigenetic basis, as seen in polyploids of *Arabidopsis* [32–34], cotton [35,36••,37•], and wheat [38,39].

Figure 1



Formation of polyploid plants and nonadditive gene expression in allopolyploids. An autotetraploid (AAAA or BBBB) is formed by genome doubling from respective parents (AA or BB), while an allotetraploid (AABB) is produced by interspecific hybridization followed by genome doubling. Gene expression changes in an interspecific hybrid or allotetraploid can be additive or nonadditive (deviated from mid-parent value, MPV), suggesting an epigenetic cause. For simplicity, only one pair of chromosomes is used for each species.

In addition to the genetic changes, polyploidy is known to induce a multitude of epigenetic modifications [31], which include DNA methylation, histone modifications, and chromatin remodeling [12,22,40,41]. A partial list of chromatin modifications relevant to gene expression changes in polyploids and hybrids is shown in Table 1. DNA methylation is heritable epigenetic modifications for gene expression variation in plants and animals [42,43]. In plants, DNA methylation can occur in CG, CHG (H = A, T or C), and CHH sites [43]. DNA methylation in the coding regions is associated with the genes that are expressed at medium to high levels and enriched for housekeeping functions [44–46], while the methylation in the promoter regions is generally associated with gene repression or silencing. Moreover, CG methylation maintains centromere and chromatin stability [47], while CHG and CHH methylation that occurs in transposons and transposable element (TE) fragments associated with genes, resulting in silencing of genes and TEs or heterochromatin formation [48]. An exception is the positive association of small interfering RNA (siRNA)-directed DNA methylation (RdDM) [49] in the promoter regions with activation of the genes that are involved in developmental regulation, as observed in maize [50], cotton [51], and soybean [52]. Like DNA methylation, histone modifications mediate epigenetic regulation of gene expression, growth and development in plants and animals [40,42,53]. Some histone modifications, such as acetylation of histones H3 and H4 and trimethylation of H3 lysine 4 (H3K4me3), are known as euchromatic marks and often associated with active transcription, whereas other modifications, such as methylation of H3K9 and H3K27, are known as heterochromatic marks and related to gene repression [53,54].

Like genetic variation, some epigenetic changes could form epialleles, which are defined as genes associated with stable DNA methylation or histone methylation