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Polyploidy and genome evolution in plants

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Genome doubling (polyploidy) has been and continues to be a pervasive force in plant evolution. Modern plant genomes harbor evidence of multiple rounds of past polyploidization events, often followed by massive silencing and elimination of duplicated genes. Recent studies have refined our inferences of the number and timing of polyploidy events and the impact of these events on genome structure. Many polyploids experience extensive and rapid genomic alterations, some arising with the onset of polyploidy. Survivorship of duplicated genes are differential across gene classes, with some duplicate genes more prone to retention than others. Recent theory is now supported by evidence showing that genes that are retained in duplicate typically diversify in function or undergo subfunctionalization. Polyploidy has extensive effects on gene expression, with gene silencing accompanying polyploid formation and continuing over evolutionary time.

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Introduction

Among the more illuminating realizations to emerge from the genomics era has been the extent to which genome doubling (polyploidy) has been a pervasive force in plant evolution. Analyses of whole-genome sequences, extensive expressed sequence tag (EST) sets, and duplicated genomic regions have led to the realization that genome doubling has occurred repeatedly during plant evolution and that even plants with relatively small genomes, such as *Arabidopsis thaliana*, have been impacted by polyploidy [1,2]. Recent studies convincingly demonstrate that polyploidy entails far more than the mere merger of two genomes who passively acquiesce to their sudden collaboration, but instead involves a whole spectrum of molecular and physiological adjustments. Extensive genomic rearrangements, including exchanges between genomes and gene loss, often arise with the onset of polyploidization [3•]. Genome doubling also significantly effects gene expression, resulting in epigenetically induced gene silencing [4,5]. Novel phenotypes are known to emerge from this genomic amalgam, including some with high visibility to natural selection, such as organ size and flowering time. Thus, polyploidy is a prominent and significant force in plant evolution, at temporal scales ranging from ancient to contemporary, and with profound effects at scales ranging from molecular to ecological.

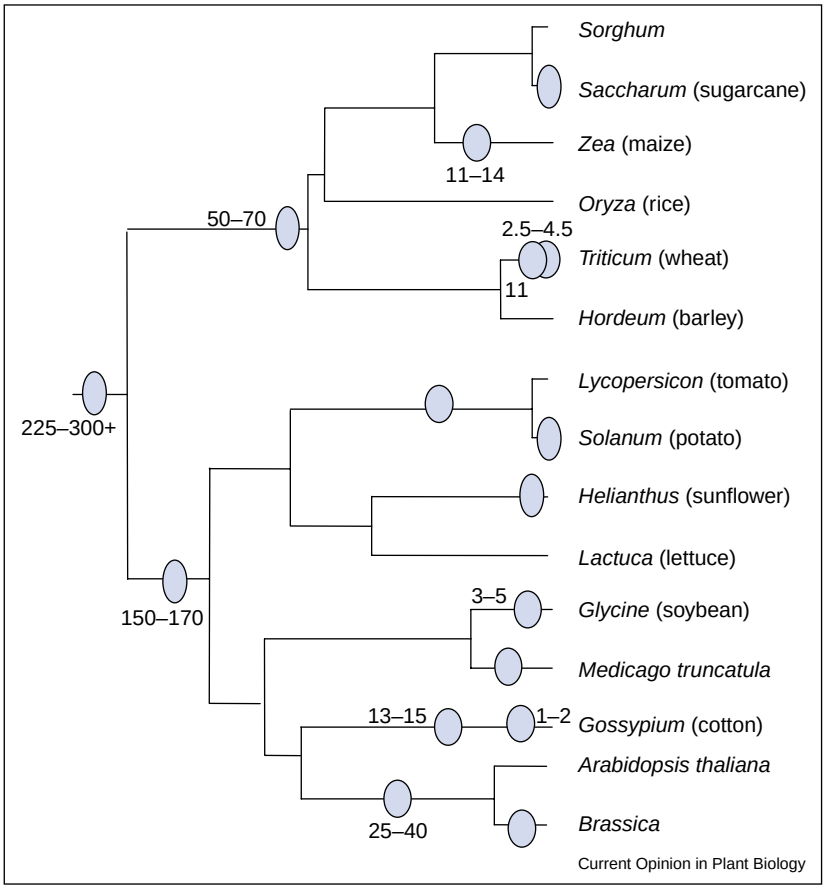
In this review, we draw attention to some of the more surprising and important recent advances in our understanding of polyploidy that have arisen from numerous studies, providing a gateway to the recent literature in the process.

Polyploidy is an ancient and recurrent process leading to differential gene loss

Several studies have revealed that multiple rounds of polyploidy have occurred during angiosperm evolution. Empirical observations come from diverse sources, including analysis of complete genomes, comparative genome mapping, micro-colinearity studies, and analyses of EST collections. Illustrative of these approaches are the many studies that have inferred polyploidy events at different times in the evolutionary history of *Arabidopsis* [6–8,9•10•,11–13]. Inferences of the number and timing of polyploidy events vary from study to study, probably as a result of methodological differences, but there is strong evidence for one round of genome doubling after the eudicot divergence and a second polyploidization event sometime following the divergence of *Arabidopsis* and *Brassica* from their common ancestor with the Malvaceae, represented by cotton (Figure 1). These studies are especially compelling in that *Arabidopsis* is widely thought to represent a 'streamlined' or minimum angiosperm genome, yet even this relatively small genome has undergone cyclical genome doubling.

Not surprisingly, evidence of polyploidy abounds in most other plant genomes that have been investigated in detail (Figure 1). Prominent examples include an ancient genome-doubling event in the common ancestor of the modern grasses [14•], as well as a more recent polyploidy in the maize lineage [15,16•,17]. Other more recent polyploidization events occurred in the ancestor of the solanaceous crops tomato and potato [17,18••], in the legumes *Glycine* (soybean) and *Medicago truncatula* [17,18••], and in a common ancestor of the cotton (*Gossypium*) genus [18••,19].

Figure 1

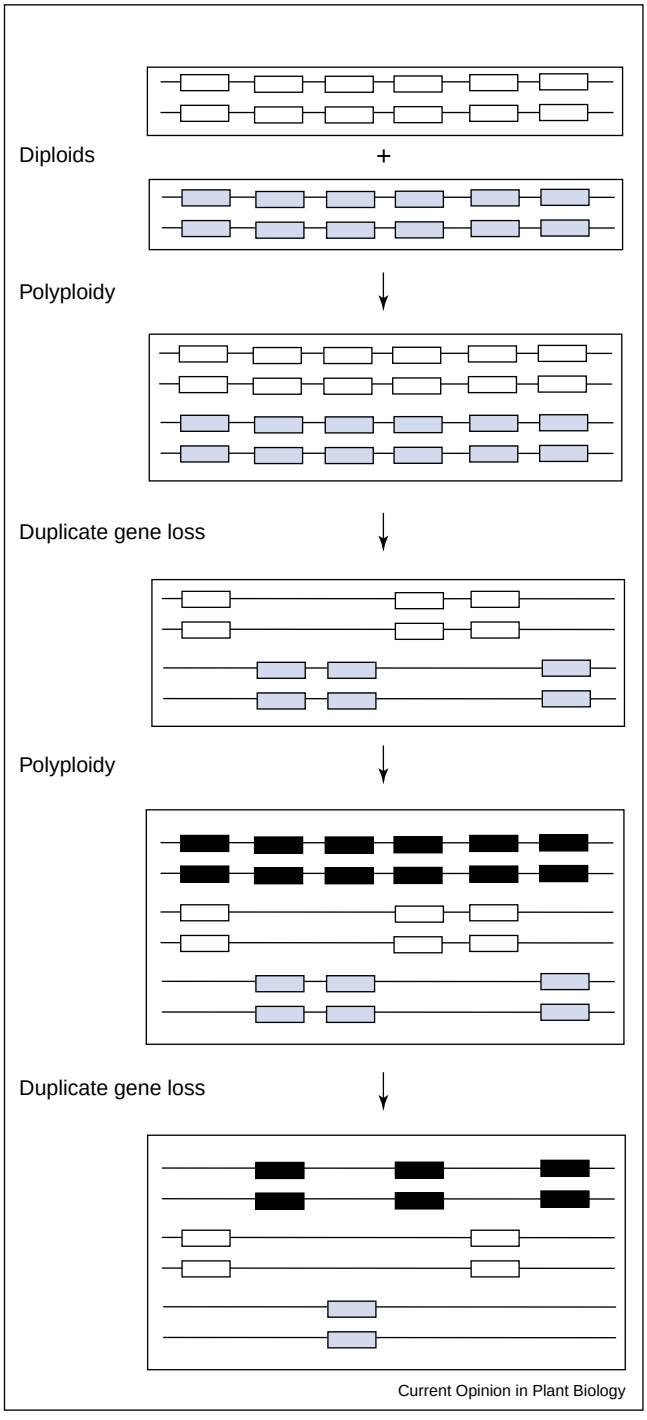


Inferred polyploidy events during the evolution of angiosperms. The figure shows species that were analyzed by Blanc and Wolfe [18••] and by Paterson *et al*. [14•]. Blue shaded ovals indicate suspected large-scale duplication events. Branch lengths are not to scale. Numbers indicate roughly estimated dates (in millions of years) since the duplication event. Figure modified from [18••].

Given the widespread occurrence of successive episodes of genome doubling, how is it that the evolutionary process has forged modern genomes as small as those of *Arabidopsis*, or with gene numbers that are far less than that expected by the doubling process *per se*? The answer appears to be that polyploidy is followed by a genome-wide removal of some but not all of the redundant genomic material. Differential gene loss (i.e. loss of some duplicates but not others) following polyploidy (Figure 2) is responsible for much of the deviation in co-linearity among relatively closely related plants, such as the cereals [20]; when differential gene loss is considered, colinearity of genes on orthologous chromosomes among cereal (and other) genomes is higher than previously recognized. Particularly illustrative of the process of gene removal following genome duplication are recent studies from maize [15,16•,21] that demonstrate that about half of all duplicated genes have been lost in the approximately 11 million years since the polyploidy event that gave rise to the progenitor of maize. On a longer evolutionary timescale, the cumulative effects of these twin processes of genome doubling and gene loss have created modern angiosperm genomes that exhibit clustered, hierarchical networks of synteny with only partial gene membership of any single linkage group [20,21], as well as the differential survivorship of duplicated genes. This phenomenon extends beyond angiosperms, as elegantly shown by a comparative analysis of genome sequences in common baker's yeast, *Saccharomyces cereviseae* [22•], and its close relative *Kluyveromyces waltii*; sequence data unambiguously demonstrate a *2*:1 relationship of linkage groups for these two lineages, with the duplicated chromosomes in yeast having mostly decayed into collective single-copy status.

One of the more intriguing aspects of the differential retention of duplicated genes concerns the question of whether or not gene loss is random or subject to natural selection. Which duplicated genes are lost and which are retained following polyploidy? Insights into this problem are beginning to emerge from model systems. Analysis of the most recent genome duplication event in *Arabidopsis*

Figure 2



A model of cyclical polyploidy and stochastic survivorship of genes. Small boxes indicate genes arranged along homoeologous chromosomes (lines) and shading indicates a new set of genes provided by each polyploidy event. Large boxes indicate genes in a polyploid nucleus. Differential gene survivorship leads to deviations from co-linearity in homoeologous regions.

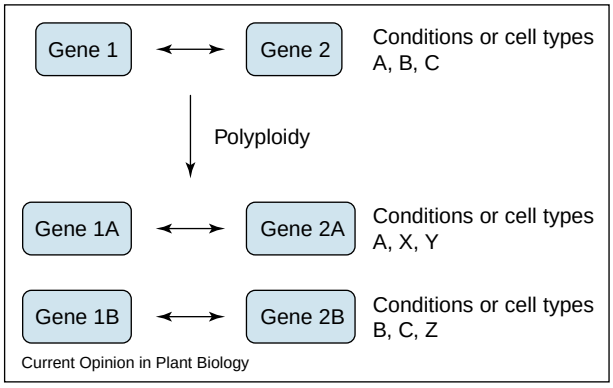
revealed that some classes of genes, such as those involved in transcription and signal transduction, have been preferentially retained, whereas other classes, including those involved in DNA repair and those for organellar proteins, have been preferentially lost [23••]. A striking recent observation, from analyses of the three hypothesized polyploidy events in the evolutionary history of *Arabidopsis*, is that duplicated genes that are retained in a genome after one round of polyploidy are more likely to be retained in duplicate after a subsequent duplication [24•], further supporting the idea that the loss of duplicate genes is not a random process.

Divergence and functional diversification following genome duplication

The foregoing discussion encapsulates the important observations that although much of the genetic redundancy created by ancient polyploidy vanishes through gene loss, some duplicated gene pairs are retained over millions of years. This observation constitutes *prima facie* evidence for a functional role of duplicated genes, and suggests that polyploidy provides fodder for evolutionary adaptation via divergence following duplication [25]. Additional support for this notion stems from the fact that the retention of duplicate genes is non-random [22•,23••,24•], and from a large body of theory showing that duplicate gene preservation is unlikely except where one member of a duplicated gene pair has acquired a new function (neofunctionalization) or when the gene pair has partitioned aggregate ancestral function (subfunctionalization) [26–28]. However, both copies can retain their original function, and perhaps this outcome is expected in cases in which gene-product dosage is evolutionarily constrained and dosage is transcriptionally regulated, or for genes that encode subunits of protein complexes, mutation of which could lead to a nonfunctional complex.

A thorough analysis of the functional divergence of genes that have been duplicated by polyploidy during the evolutionary history of *Arabidopsis* was recently reported by Blanc and Wolfe [23••]. They showed that more than half of the gene pairs formed by the most recent polyploidy have significantly different expression patterns. These authors also provide evidence, from expression divergence and asymmetrical sequence divergence, that 62% (316) of recently duplicated gene pairs have undergone functional diversification, which is consistent with the hypothesis (cited above) that duplicated genes are more likely to survive mutational pseudogenization only when they acquire something new and useful to do. Interestingly, Blanc and Wolfe [23••] found that some duplicated gene pairs have diverged *in concert*, forming two parallel networks that are expressed in different cell types or under different environmental conditions, a process they termed 'concerted divergence' (Figure 3). This fascinating observation has important implications for divergence in metabolic pathways, expansion of the

Figure 3



Schematic diagram illustrating the concept of concerted divergence. Double-headed arrows indicate interacting gene products. Genes 1 and 2 are unrelated in sequence. Notice that multiple sets of duplicated genes can diverge in function. For example, A copies of genes 1 and 2 differ in expression patterns and/or function from their homoeologous B copies of the same genes. Figure modified from [23••].

overall physiological repertoire in polyploids and, hence, evolutionary diversification.

Genome evolution in recently formed polyploids

The foregoing discussion has centered on paleopolyploid events (i.e. polyploid events that occurred many millions of years ago) and their consequences, but polyploidy is an active and ongoing process in many plant genera. Several allopolyploids that formed within the past five million years or so, including wheat, cotton, *Brassica napus*, *Arabidopsis suecica*, soybean, and tobacco, have become experimental systems for addressing questions in younger allopolyploids. Even more recent are allopolyploids in *Tragopogon*, *Spartina* and *Senecio* that were formed within the past 200 years [29,30•,31,32•]. These situations provide a rich opportunity to observe the earliest changes in polyploid genome structure using natural populations and in an ecological context. In *Tragopogon*, new polyploid populations are still being formed, offering a replicated natural experiment of genome merger. Molecular investigations of these 'nascent' polyploids in the aforementioned genera are providing evidence of gene silencing, alterations in cytosine methylation, and other manifestations of parental 'non-additivity'.

One of the lessons of the past decade is that recurrent formation of allopolyploids is the rule rather than the exception (reviewed in [33]). This is the case, for example, in *Tragopogon* and *Glycine* [32•,34•,35] where different populations of diploid progenitors experience hybridization and polyploid formation leading to genomically similar allopolyploidy products. A consequence of this mode of formation is that reciprocal loss or silencing of duplicated genes ('divergent resolution') in independently formed and geographically isolated populations can lead to hybrids that lack both copies of a duplicated gene pair, resulting in hybrid inviability, reproductive isolation, and speciation [32•,36–38]. Even loss of one duplicated gene copy might result in speciation by divergent resolution if the gene product from one copy is insufficient for normal function, particularly if subfunctionalization has occurred between the two duplicates [36]. The implications of recurrent origin and reciprocal gene loss/silencing are even more profound given the recent demonstration that, at least in some polyploid groups, recombination between homoeologous chromosomes might suddenly create lineages that are reciprocally distinguished not just for single genes but for whole chromosome arms or chromosome segments [39]. These considerations document the creative aspects of polyploidy at an ecological level, where speciation and biodiversity are promoted by the interplay between population-level phenomena and genic- or genomic-level mechanisms.

In addition to naturally occurring polyploids, many insights have emerged from recent explorations using laboratory generated or synthetic polyploids. Study of these experimental polyploids has revealed extensive and rapid genomic changes in some groups, including sequence rearrangements, homoeologous recombination, sequence elimination, and changes in DNA methylation [3•,4,5,40,41,42•]. Some genomic changes have arisen immediately with the onset of polyploidy, whereas others have occurred within a few generations. The above spectrum of phenomena illustrates the immediate impact of polyploidy on genome structure, and its profound implications for evolution. For example, some of the observed genomic changes are known to effect phenotypes in ways that are highly visible to natural selection. A case in point concerns genomic rearrangements that affect a flowering-time locus in a newly synthesized *Brassica* polyploid. These rearrangements are associated with flowering-time divergence [42•].

Polyploidy can lead to immediate and extensive changes in gene expression

Genes that are duplicated by polyploidy could be expressed at equal levels, or there could be unequal expression or silencing of one copy. An interesting recent revelation is that the silencing of some duplicated genes often accompanies the onset of allopolyploidy, as shown by studies of newly created synthetic polyploids [43•,44,45,46••,47•], indicating that gene silencing is a common response to polyploidy. Silencing can occur as early as the first generation following polyploidy, although some genes are not silenced until later generations [43•]. Surprisingly, some duplicated genes are silenced immediately upon allopolyploidy in some organs of the plant but remain expressed in other organs at varying levels [47•]. Even more unexpected was the

finding in cotton polyploids that some genes have been reciprocally silenced (i.e. one copy has been silenced in some organs and the other copy has been silenced in other organs) [46••], providing an evolutionarily recent example of subfunctionalization. Reciprocal silencing of genes in different tissues or organs can be a rapid response to allopolyploidy or even hybridization alone. An interspecific cotton F_1 hybrid displays reciprocal silencing of parental alleles in different floral organs (KL Adams, JF Wendel, unpublished). Such instantaneous subfunctionalization has profound implications for speciation by divergent resolution in hybrid populations, as discussed above.

What causes gene silencing in polyploids? Silencing arising immediately upon polyploid formation, in the absence of gene deletion, is probably epigenetically induced (*sensu lato*) because there is insufficient time for point mutations to accumulate. Changes in cytosine methylation, histone modifications (such as deacetylation and methylation), and positional effects from higher-order changes in chromatin structure can play a role in silencing [4,5]. Such positional effects might include poorly understood architectural requirements that are made necessary by the packaging of a suddenly doubled complement of chromosomes into a single nucleus. Mechanisms of silencing almost certainly vary by gene. It is possible that epigenetic gene silencing might persist over evolutionary time. However, duplicate gene silencing in polyploids need not necessarily be an epigenetic phenomenon. Models for homoeologous gene silencing, involving repeats and long terminal repeats (LTRs) of retroelements, have been proposed [48]. In synthetic wheat, polyploid antisense transcripts generated by read-out transcription of a retrotransposon caused silencing of an adjacent gene [49••]. Small RNAs and RNA interference (RNAi) could also play a role in gene silencing in polyploids. Superimposed on these immediate and short-term responses to genome doubling are those that arise over a longer evolutionary timescale in natural allopolyploids, such as mutations in promoter regions or other *cis*-regulatory elements.

An important functional question is whether gene silencing is a directed or a stochastic process. Are some duplicated genes more prone to silencing than others? Recent studies have shown parallel silencing of the same duplicate gene in multiple polyploid genotypes or lines [43•,45,46••,47•], suggesting that the silencing of some genes is a directed process that could be caused by aspects of chromosomal context or by dosage requirements. However, other genes displayed a more random pattern of silencing and biased expression across genotypes, lines, and generations [42•,43•,47•,50], indicating a stochastic process. Overall, it appears that the silencing of duplicated genes in polyploids is directed for some genes and stochastic for others, but the evolutionary rules that govern these outcomes remain to be elucidated.

Why are duplicated genes silenced in polyploids? Possible explanations are many and varied, but include preservation of appropriate gene dosage and the requirements imposed by interacting and diverged regulatory hierarchies [4,51]. Also, if duplicated genes from each parent have different amino-acid sequences, one gene copy might interact better with other proteins in multi-subunit complexes or in enzyme–substrate interactions [52]. For example, all of the maternal genes whose sequences have co-adapted to each other might be expressed and the paternal copies silenced. These cases are likely to be visible to natural selection and are predicted to be evolutionarily stabilized in natural polyploids. Alternatively, silencing of some genes might be a side effect of other mechanistic processes occurring in the cell and thus functionally neutral. We think it probable that all of the above causes are operating and that they vary by gene. Overall, the scale of the phenomenon of duplicate gene silencing suggests that this is a significant aspect of polyploid evolution.

Conclusions and perspectives

Insights into polyploidy at the molecular level have experienced a quantum leap forward during the past few years, concomitant with the exponential increase in sequence information, the availability of bioinformatic tools, and new approaches to study gene expression. These advances have increased our awareness of the frequency and timing of polyploidy, as well as of phenomena such as duplicate gene retention and loss, gene silencing, functional diversification, and subfunctionalization. In conjunction with advances in theory, these empirical realizations have enabled the first tentative steps toward bridging the gulf between our ecological and systematic awareness of the prevalence of polyploidy and a mechanistic understanding of how genome merger generates functional diversity, and thereby contributes to evolutionary diversification and speciation.

Future studies will refine our phylogenetic perspective on the number, phylogenetic distribution, and timing of polyploidy events during angiosperm evolution, and will generate precise data on modern systems in nature in which polyploidy is an ongoing, often recurrent process. As more information accumulates from various plant model systems and multiple synthetic polyploids, we will better understand the spectrum of genic and genomic effects of polyploidy and gain additional insight into gene expression alterations on a genome-wide level following polyploidy. One would hope that these multiple, comparative analyses will ultimately facilitate an inference of the rules and principles that control the fate of duplicated genes, and will lead to an enhanced appreciation of the effects of polyploidy on the evolution of morphology, reproductive characteristics, metabolic pathways and other features that are significant to adaptation and speciation.

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- •• of outstanding interest

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Many of the early surprises about polyploid genomes come from allotetraploid and allohexaploid wheat, mostly in the laboratories of these authors. In this review, a synopsis is provided of the major findings, including the non-additivity of parental genomes in new hybrids, epigenetic changes that lead to gene silencing, and the activation of retroelements. See also Kashkush *et al*. [44].

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One of the key principles of polyploidy is its episodic and recurring nature over long evolutionary time-spans. Yet genomes do not just grow; they also contract via deletion of redundant genetic material. In this paper, the authors show how this process has occurred in the modern maize genome, which traces its ancestry to an allopolyploidy event but whose genome contains only residual gene duplications tracing to this event. See also [14•].

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In this elegant and compelling paper, the genome of brewer's yeast is compared to a newly sequenced genome from a close relative, revealing a clear pattern of whole-genome duplication in the ancestry of *Saccharomyces* followed by massive gene loss. Moreover, the authors present evidence of the accelerated sequence evolution of a high percentage of retained duplicates in one member. These retained duplicates are also inferred to have diverged in expression pattern.

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This seminal study documents the non-random retention of duplicated genes following ancient polyploidy in the ancestry of *Arabidopsis thaliana*. Genes that are preferentially retained and lost are shown to be biased with respect to functional category. In addition, many of these genes are demonstrated to have undergone functional differentiation. A particularly intriguing inference in this study is the suggestion of divergence in entire pathways encoded by multiple pairs of retained duplicated genes. See also [24•].

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These authors examined the fate of duplicated genes resulting from ancient genome duplications that occurred in the evolutionary history of *Arabidopsis*. Their analysis reveals non-random survivorship, with a bias toward the retention of genes that are involved in the regulation of transcription. In addition, the authors show that genes that were retained in duplicate after one polyploidy event are also more likely than other genes to be retained after a subsequent polyploidy event. See also [23••].

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The genus *Tragopogon* offers the best-known classic example of the recent origin of plant species, in this case two different allopolyploid species generated from combinations among three parental diploids. In this review, the authors summarize the recurrent formation of these allopolyploids and present data on gene expression changes and concerted evolution in the polyploids. See also the paper by Ainouche *et al*. [30•] who describe another polyploid species of very recent origin.

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