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# Polyploidy: recurrent formation and genome evolution

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Polyploidy is an important evolutionary force. Recent estimates suggest that 70% of all angiosperms have experienced one or more episodes of polyploidization<sup>1</sup>. The frequency of polyploidy in pteridophytes could be as high as 95% (Ref. 2). Recent evidence suggests that polyploidy has also played an important role in the evolution of other eukaryotes. Two episodes of polyploidy are hypothesized for the vertebrates<sup>3,4</sup>, and the entire genome of yeast was duplicated anciently<sup>5</sup>. Thus, elucidating the causes and consequences of polyploid evolution is central to understanding not only the diversification of angiosperms and pteridophytes, but other eukaryotic lineages as well. During the past few years, the study of polyploidy has experienced a renaissance owing, in part, to genetic studies, both at the population and genome levels, prompting a dramatic reformulation of several crucial aspects of polyploidy. There has also been renewed interest in the mechanisms and rates of polyploid formation<sup>6</sup> and polyploidy and plant–insect interactions<sup>7</sup>.

## Origins of species

An important recent discovery is that most taxonomically recognized polyploid species are of multiple origin<sup>8,9</sup>. This realization has shattered earlier perceptions of polyploids as genetically depauperate species, perhaps representing evolutionary dead-ends<sup>10</sup>. Recurrent origins of polyploid species are the rule, not the exception. Soltis and Soltis<sup>8</sup> reviewed over 30 examples of polyploid species of recurrent origin, most of which are angiosperms and ferns, with a few bryophytes. During the past five years, molecular investigations have continued to reveal that multiple origins typify polyploid plant species, with over 15 additional

**Polyploidy has played a major role in the evolution of many eukaryotes. Recent studies have dramatically reshaped views of polyploid evolution, demonstrating that most polyploid species examined, both plant and animal, have formed recurrently from different populations of their progenitors. Populations of independent origin can subsequently come into contact and hybridize, generating new genotypes. Because of the frequency of polyploidy in plants, many recognized species are probably polyphyletic. Extensive and rapid genome restructuring can occur after polyploidization. Such changes can be mediated by transposons. Polyploidization could represent a period of transience, during which genomic changes occur, potentially producing new gene complexes and facilitating rapid evolution.**

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examples (list available from authors). Lineages of independent origin can also differ morphologically<sup>11–13</sup>. Several studies also suggest that polyploid animal species have arisen recurrently, including ostracodes<sup>14,15</sup> and the treefrog *Hyla versicolor*<sup>16</sup>. In complete contrast to traditional views (Fig. 1), there are few examples of well studied polyploid taxa for which only a single origin appears likely; possible examples include the peanut *Arachis hypogaea*<sup>17</sup> and the salt marsh grass *Spartina anglica*<sup>18</sup>. Polyploids constitute a significant proportion of both angiosperm and fern species. The fact that recurrent origins typify those taxa investigated has important implications. For diploids, we think in terms of the origin of species, but for many, perhaps most, land plants it appears more appropriate to refer to the origins of recognized species. If we consider

monophyly as a necessary criterion for recognizing species, most taxonomically recognized polyploid species should be divided into a number of cryptic phylogenetic species. The application of a phylogenetic species concept to polyploids of recurrent origin deserves additional attention, but is beyond the scope of this article.

## Extent of multiple origins

For most examples of recurrent polyploidization, few populations have been studied. Hence, the actual extent of multiple origins for most polyploids is unknown, but is likely to have been underestimated. For polyploids studied extensively, the number of multiple polyploidizations is often high. Three origins of autotetraploid *Heuchera grossularifolia* were suggested originally, but more thorough population sampling and the use of additional markers raised that number to five<sup>19</sup>. *Draba norvegica* (Brassicaceae) has formed at least 13 times

in a small area of Scandinavia<sup>9,20</sup>. *Tragopogon miscellus* and *T. mirus*, two allopolyploid species of goatsbeard, may have formed as many as 20 and 12 times, respectively, in eastern Washington and adjacent Idaho (USA) in only the past 60–70 years; multiple polyploidizations have even occurred within single small towns<sup>13,21</sup>. Studies of recent allopolyploidy in *Tragopogon* indicate that multiple origins can occur frequently over a short timespan and in a small area.

*Close encounters*

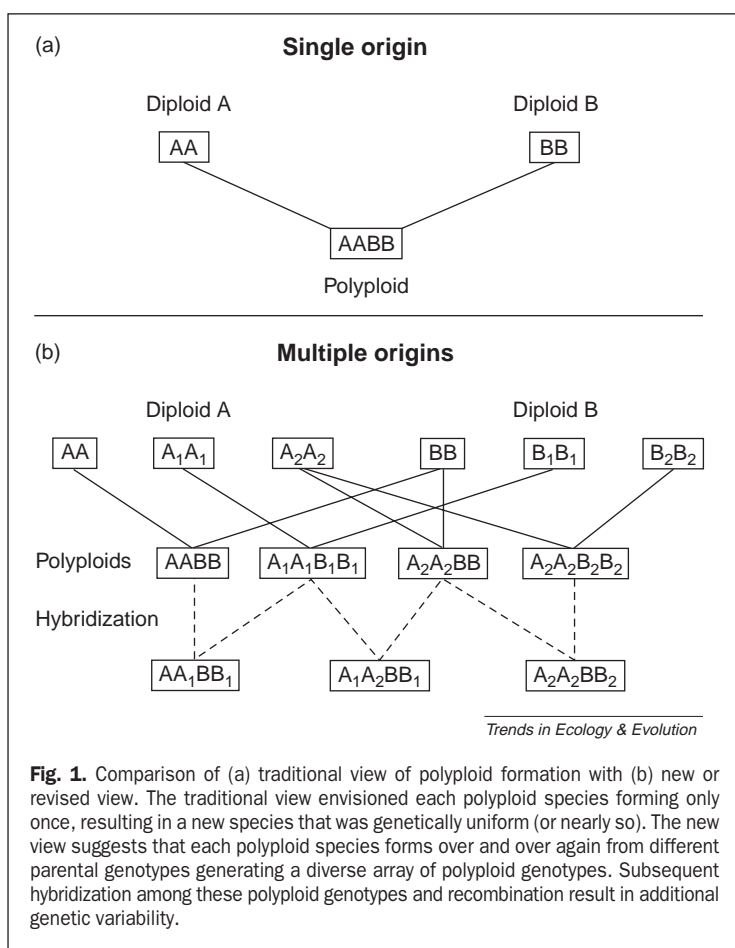
Recurrent polyploidization involving genetically different diploids can create a series of genetically distinct polyploid populations. Gene flow between polyploid populations of independent origin might permit recombination and the production of additional genotypes (Fig. 1). Recent studies suggest that this occurs in nature. In species of *Draba*, distinct genotypes of separate polyploid origins co-occur in the same populations, along with putative recombinants<sup>20</sup>. Autopolyploid populations of *H. grossulariifolia* often comprise a mosaic of genotypes representing separate origins<sup>19</sup>. Application of RAPD (random amplified polymorphic DNA) markers to the allopolyploid *Tragopogon* species indicates that populations of separate origin come into contact<sup>21</sup>. The short time since the origin of *Tragopogon* allotetraploids indicates the rapidity with which polyploid genotypes can come into contact after their formation.

*The arctic flora*

On a broad geographical scale, recurrent polyploidization and subsequent interbreeding of genotypes are best seen in the arctic flora, where diploids and polyploid derivatives exhibit overlapping circumboreal distributions. Traditionally, each polyploid was thought to have formed once; subsequent migration was considered responsible for establishing a broad geographical distribution. Genetic data suggest, instead, that diploid progenitors co-occur repeatedly on a circumboreal scale; polyploid species of *Draba* and *Saxifraga* have formed repeatedly from their diploid progenitors<sup>20,22</sup>. Multiple polyploid events from genetically and morphologically differentiated diploid populations yield a complex of different genotypes and morphotypes at the polyploid level. These genotypes ultimately come into contact and hybridize; subsequent segregation and recombination generate even more genetic and morphological complexity. This scenario, repeated in numerous lineages, would explain the well known taxonomic uncertainty surrounding polyploid complexes in the arctic.

**Genome restructuring**

Another important recent discovery is the extent and rapidity of genome reorganization in polyploids (Fig. 2). Modification of parental diploid genomes, once in a common polyploid nucleus, has until recently been considered minimal. However, chromosome painting, genetic mapping, and comparative genetics provide evidence for both intra- and intergenomic reorganization of polyploid genomes; this reorganization can be extensive and occur rapidly. Chromosome painting (i.e. using chromosome-specific fluorescent markers) has identified intergenomic chromosomal rearrangements in polyploids relative to their diploid progenitors: nine such intergenomic translocations have been detected in allotetraploid tobacco (*Nicotiana*), five intergenomic translocations in allotetraploid oats *Avena maroccana*, and ~18 in allohexaploid *Avena sativa*<sup>23</sup>. Furthermore, intergenomic translocations have been detected in F<sub>1</sub> hybrids, demonstrating the rapidity with which such changes can occur when divergent genomes are placed in a common nucleus<sup>23</sup>.

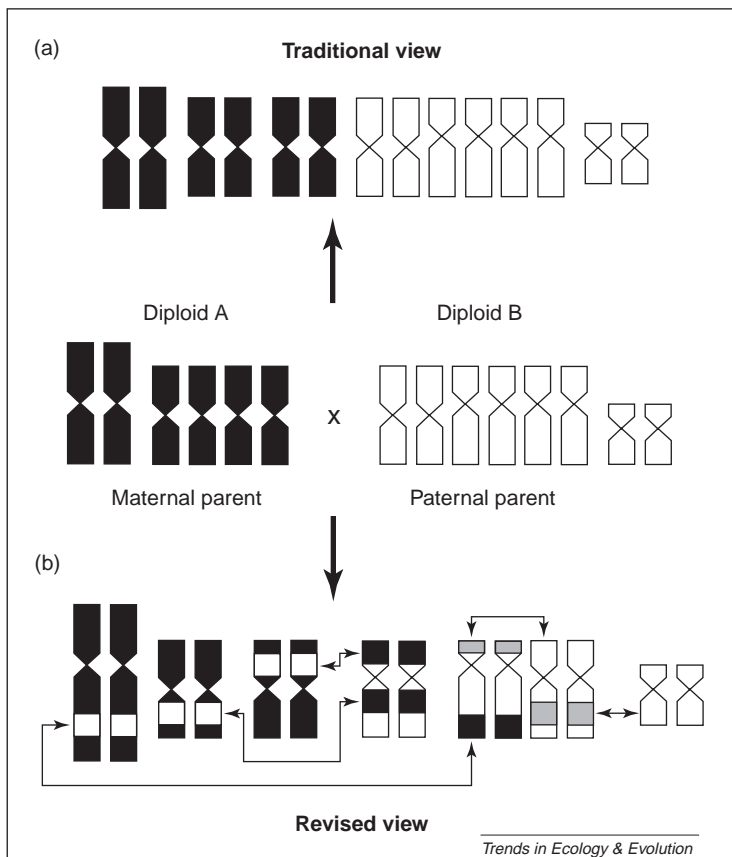


**Fig. 1.** Comparison of (a) traditional view of polyploid formation with (b) new or revised view. The traditional view envisioned each polyploid species forming only once, resulting in a new species that was genetically uniform (or nearly so). The new view suggests that each polyploid species forms over and over again from different parental genotypes generating a diverse array of polyploid genotypes. Subsequent hybridization among these polyploid genotypes and recombination result in additional genetic variability.

Dramatic evidence for genome restructuring in polyploids comes from comparative genetics<sup>24,25</sup>. Although gene order is generally conserved over millions of years within plant families, genome restructuring also occurs, and this is more rapid and extensive in polyploids than in diploids<sup>24</sup>.

Evidence for extensive and rapid genomic change is available for *Brassica* via the analysis of naturally occurring and synthetic polyploids. Chromosome mapping suggests that the naturally occurring allopolyploid genomes exhibit extensive reorganization compared with their diploid progenitors<sup>24,26,27</sup>. Extensive genomic change was detected in only a few generations in synthetic allopolyploid *Brassica* lines that were initially completely homozygous<sup>28</sup>. Furthermore, the degree of change in the diploid genomes present in the synthetic allopolyploids agrees with mapping and genetic data for the naturally occurring polyploids. Therefore, *Brassica* provides two important suggestions regarding genomic change after polyploidization: (1) the more divergent the parents, the greater the subsequent genomic change in the polyploid; and (2) the nuclear genome of maternal origin experiences less change than the paternal contribution. Results for cereals similarly indicate that rapid genomic changes can occur in newly synthesized allopolyploids<sup>29</sup>, and that the extent of genomic change in a polyploid can be influenced by cytoplasmic–nuclear interactions<sup>23,25,30</sup>. In a new allopolyploid, there are adverse interactions between the nuclear genome contributed by the male parental diploid and both the nuclear and cytoplasmic genomes contributed by the maternal diploid (in most angiosperms, cytoplasmic organelles are maternally inherited); genome adjustments must occur to restore nuclear–cytoplasmic compatibility<sup>30</sup>.

Genomic maps are presently available for several grasses, including wheat (*Triticum*), barley (*Hordeum*), rye



**Fig. 2.** Comparison of (a) traditional view of genomic evolution subsequent to polyploid formation with (b) new or revised view. The classic view of genome evolution suggested that interactions between the parental genomes of an allopolyploid were minimal. Recently, it has become apparent that both intra- as well as intergenomic rearrangements occur. (b) In this example, arrows indicate genomic rearrangements – intragenomic rearrangements are represented by hatched areas on chromosomes from ‘diploid B’; intergenomic rearrangements are represented by translocation of ‘black’ or ‘white’ chromosomal segments between the genomes of ‘diploid A’ and ‘diploid B’. The degree of genomic change can also be influenced by cytoplasmic–nuclear interactions. In a newly formed allopolyploid, there are adverse interactions between the nuclear genome contributed by the male parental diploid and both the nuclear and cytoplasmic genomes of the female parental diploid; genome adjustments must occur to restore nuclear–cytoplasmic compatibility. Available data suggest that the nuclear genome of maternal origin experiences less change than does the paternal nuclear genome. Other evidence implicates transposable elements in the genome reorganization that has been detected in polyploids.

*Trends in Ecology & Evolution*

(*Secale*), oats (*Avena*) and maize (*Zea*). Whereas the overall ‘big picture’ is one of genome colinearity, chromosome rearrangements have occurred<sup>24</sup>. In hexaploid wheat, several intergenomic rearrangements have occurred following polyploidization<sup>31,32</sup>, but genome restructuring is not as extensive as in *Brassica*. Genome mapping of soybean, *Glycine max*, an ancient tetraploid, suggests significant intra-chromosomal rearrangement, whereas interchromosomal recombination has had a minor role<sup>33</sup>.

**Diploidization**

In addition to genome restructuring, gene-level changes, including concerted evolution and gene silencing, also occur in polyploids<sup>8,9,23,25</sup>. In some polyploids, chromosomal reorganization and gene silencing (‘diploidization’) are so extensive that the genome is no longer structured as an allopolyploid. Paradoxically, the more extensive this process of diploidization, the more difficult it is to discern. There was longstanding debate, for example, as to whether *Zea mays* was a diploid or an ancient allopolyploid. Genetic mapping has provided compelling evidence that maize is

an allopolyploid, having undergone extensive chromosomal rearrangement. The maize genome is so extensively rearranged that it is no longer structured as a clear allopolyploid; gene silencing has also occurred<sup>34,35</sup>. The pattern of sequence divergence among duplicated genes suggests that the maize genome is the product of a segmental allotetraploid that formed ~11.4 million years ago<sup>34</sup>. Hence, maize is an excellent example of a partially ‘diploidized’ polyploid.

Although many polyploids, such as maize, have been referred to as diploidized, detailed genomic studies have been conducted for few such taxa. However, maize is just one of a growing number of well documented diploidized or ‘degenerate’ polyploids. Available data, including genomic comparisons with rice, suggest that the genome of sorghum (*Sorghum bicolor*) is also extensively reorganized and represents a partially diploidized polyploid<sup>36</sup>. Genomic comparisons also suggest that diploidization has occurred in polyploid species of sugarcane<sup>37</sup> (*Saccharum* spp.).

Comparative genetic data indicate that ‘diploid’ *Brassica* species ( $n = 9$ ) are themselves ancient polyploids, with genomes so extensively reorganized that their polyploid nature was not obvious. Ancient polyploidy was determined by crossmapping of the genes of the model organism *Arabidopsis* on to the diploid *Brassica* genomes. These studies revealed that ‘diploid’ *Brassica* genomes consist of three complete, but rearranged, copies of an ancestral *Arabidopsis*-like genome<sup>24,38</sup> (but see Ref. 39). The data not only suggest that ‘diploid’ brassicas are diploidized polyploids, perhaps representing ancient hexaploids, but also indicate that *Brassica* genomes have evolved through chromosomal fusions and frequent rearrangements. Furthermore, chromosomal fusion events might facilitate further chromosomal rearrangement because the former telomeres (now internal) are chromosomal weak points.

**Polyploidy and transposable elements**

Transposable elements (TEs) might facilitate rapid genome restructuring after polyploidization. Matzke and Matzke<sup>40</sup> argue that polyploidy permits extensive gene modification by TEs because, by nature, polyploid genomes contain duplicate copies of all genes; hence, they are well buffered from the deleterious consequences of transposition. Transposable elements will tend to multiply and be maintained in polyploids because the additional copies of genes they maintain will compensate for the loss of altered expression of genes that might result from TE insertion. The end result could be higher genomic restructuring in polyploids compared with their diploid progenitors.

Recent studies suggest the spread of DNA repeat families from one parental diploid genome to the other in allopolyploid cotton, *Gossypium*. In cotton, most dispersed repeat families are restricted to A-genome diploids and are absent from D-genome diploids. However, in the allotetraploids (which combine the A and D genomes), the A-genome repeats have spread to the D genome, perhaps by replicative transposition<sup>41</sup>.

Transposable elements might also have been the driving force in the evolution of gene silencing mechanisms, such as methylation and heterochromatin formation, throughout eukaryotes in general<sup>42</sup>. These ‘global repression’ mechanisms might have evolved as adaptive responses to the selfish drive of TEs to expand in number in a host genome<sup>42</sup>. Matzke and Matzke<sup>40</sup> argue that if TEs are indeed the primary targets of methylation and other global repression mechanisms and that polyploids tolerate transposition because of their duplicate genes, then it follows that polyploid genomes will not only contain more



TEs than diploid genomes, but will also be more highly methylated. Matzke and Matzke<sup>40</sup> suggest that a rough correlation exists. Widespread ('global') methylation is found in vertebrate genomes, which represent several rounds of polyploidization, as well as in polyploid plant genomes, which contain a high number of TEs. In contrast, 'fractional' (partial), rather than global, methylation occurs in invertebrates and true diploid plants. For example, *Arabidopsis*, which is diploid and has a small genome, also has a small number of TEs, whereas >50% of the maize genome (an ancient polyploid) is composed of interspersed repetitive DNAs, primarily nested retrotransposons that insert between genes<sup>43</sup>. These retrotransposons are much less abundant, however, in diploid grasses, such as rice<sup>43</sup>. The hypotheses of Matzke and Matzke are provocative; we need more data.

### Evolutionary implications

The genetic and evolutionary implications of recurrent polyploidization and genome reshuffling are obvious in that both processes represent important sources of genetic variation. Population-level genetic studies of polyploid plants and animals indicate that polyploidization should no longer be viewed as a rare event producing a polyploid species of unique origin and uniform genotype. Instead, polyploid species can maintain high levels of segregating genetic variation through the incorporation of genetic diversity from multiple populations of their diploid progenitors<sup>8,13,19,21,22</sup>. Polyploid genotypes ultimately come into contact via migration and hybridize – with subsequent segregation and recombination generating even more genetic complexity. Concomitantly, the genome reshuffling of polyploid genomes is an important additional source of genetic diversity in polyploid species.

### Polyploidy as transience

Templeton<sup>44</sup> suggested that diploid speciation involves transience, a period during which the genome is more amenable to or tolerant of change, such as recombination. Growing evidence suggests that polyploidy should also be viewed as transience. The extensive genomic change detected in only five generations in synthetic allopolyploid *Brassica*<sup>28</sup>, as well as the chromosomal rearrangements detected in hybrid *Nicotiana*<sup>23</sup>, support this view. The presence of the same chromosomal changes throughout the populations of a polyploid species suggests that genome reorganization accompanied speciation, or occurred shortly thereafter. Species-wide intergenomic translocations have been detected in several angiosperms, including tetraploid wheat and tobacco<sup>23</sup>. Other chromosomal changes detected in tobacco and wheat are not present in all populations analysed and apparently represent subsequent chromosomal divergence that occurred in different populations after speciation.

The chromosomal and gene-level changes reviewed above are made possible by polyploidization; that is, polyploidy could represent a source of novel evolutionary processes. Rather than being stable, non-interacting entities, two or more divergent genomes in a common 'polyploid' nucleus could facilitate intergenomic interactions, ultimately resulting in new chromosomal and gene arrangements. Polyploidization might be a source of genomic stress that facilitates rapid evolution<sup>45</sup>.

### Future directions

The discoveries of the past few years set the stage for a new series of questions surrounding the genetic and genomic aspects of polyploid evolution. One set of questions

involves the evolutionary and ecological consequences of multiple origins of polyploid species. What is the extent of gene flow among polyploid lineages of separate origins? Are different genomic rearrangements detected in populations of separate origins? What are the genetic, as well as morphological and physiological, consequences of multiple origins? What are the genetic, morphological and physiological consequences of reciprocal maternal parentage in populations of separate origin?

A second suite of questions involves genome organization. How common is chromosomal and/or genome restructuring in naturally occurring polyploids? How rapidly does genome restructuring occur? Is it prevalent in recently formed polyploids? What is the role of TEs in genome restructuring and gene silencing? Do autopolyploids and allopolyploids differ in the extent and frequency of genome restructuring?

Progress in the area of comparative genome organization will be facilitated greatly by large-scale genomic projects already under way for model organisms such as maize, wheat, *Arabidopsis* and members of Solanaceae. These studies will provide fine-scale genomic maps for polyploid plants including maize, the polyploid brassicas, potato and tobacco. Such data will provide additional insights into genome evolution in polyploids. It is important, however, that comparative genetics be applied not only to crops and close relatives, but also to diploids and their polyploid derivatives in natural populations.

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