Commentary

The dynamic nature of polyploid genomes

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It is well known that polyploidy is a major force in evolution, particularly in plants. Perhaps 50% of all angiosperms are of polyploid origin; estimates for the ferns and fern allies range from 44 to 95% (1, 2). Because of the significant role that it has played in plant evolution, polyploidy has been the focus of great interest and controversy for >50 years. Diverse aspects of polyploidy have been reviewed, including types of polyploids (3–8), ecological and evolutionary attributes of polyploids (8–10), genetic consequences of polyploid evolution (10–17), and mode of polyploid formation (4, 18, 19). The application of molecular techniques has dramatically increased our understanding of polyploid evolution and has fundamentally reshaped traditional views. The paper by Song et al. (20) in this journal further elucidates the process of polyploid evolution and represents a key breakthrough in our understanding of the evolution of polyploid genomes. To appreciate the great significance of the paper by Song et al. (20), it is important to consider briefly some of the traditional tenets of polyploid evolution.

Polyploidy: Traditional Tenets

Although polyploidy has long been considered a major force in plant evolution (1, 5, 7, 8, 21), polyploids traditionally have been viewed as possessing fundamentally different genetic characteristics than diploids. Because polyploidization events were considered rare, each polyploid species typically was thought to have had a single origin, initially resulting in genetic uniformity across all individuals of the species. Furthermore, because of the proposed "buffering" effect of multiple genomes, mutation and recombination were considered less effective at constructing new adaptive complexes in polyploids than in diploids (21). This hypothesis is based, of course, on the logical but untested assumption that diploid and polyploid genomes have approximately equal mutation rates. Reflecting this traditional line of thinking, Stebbins (21) suggested that the primary mechanism by which polyploids enlarge their gene pools was via acquisition of genetic diversity from related diploid species through hybridization. The presumed genetic uniformity of polyploids, coupled with their hypothesized reduced capacity for molding new

genotypes, led to the extreme view of polyploid species as evolutionary dead ends (22). Another traditional tenet of polyploid evolution involved the prevalence of the two categories of polyploids generally recognized (allopolyploid and autopolyploid). Of these, only alloploidy was considered a major force in evolution; in contrast, autopolyploid evolution was viewed as maladaptive and extremely rare in natural populations (8, 21).

Molecular Data and Polyploid Evolution

During only the past decade molecular approaches have provided a wealth of data that have dramatically reshaped views of polyploid evolution, providing a much more dynamic picture than traditionally espoused. In particular, molecular data (i) demonstrate that both autopolyploids and allopolyploids exhibit a high frequency of recurrent formation (multiple origin), (ii) reveal that multiple polyploidization events within species have significant genetic and evolutionary implications, and (iii) contradict the traditional view of autoploidy as being rare and maladaptive (17). Perhaps one of the most important contributions of molecular data to the study of polyploid evolution is the documentation that a single polyploid species may have separate, independent origins from the same diploid progenitor species. Multiple origins of polyploids have now been documented in bryophytes (23) and in >40 species of ferns (e.g., refs. 24 and 25) and angiosperms (e.g., refs. 26–29). In fact, molecular data indicate that multiple origins of polyploids are the rule and not the exception (17). In several species studied in detail with molecular markers, recurrent polyploidization was shown to occur with great frequency during short time spans and in small geographic areas (26, 28). For example, *Tragopogon mirus* and *Tragopogon miscellus* may have formed as many as 9 and 21 times, respectively, in a small region of eastern Washington and adjacent Idaho during just the past 50 years (26).

The frequent recurrence of polyploidization also has major evolutionary implications, suggesting that polyploids are much more genetically dynamic than formerly envisioned. Multiple polyploidization events from genetically distinct parents would certainly enrich the total gene

pool of a polyploid species, particularly given the high frequency with which these polyploid events have been shown to occur within at least some species. Furthermore, molecular data also provide evidence for significant gene flow across ploidal levels through semifertile hybrids between diploids and polyploids (30–32). Once variation is introduced into a polyploid species, molecular evidence also indicates that dynamic evolutionary processes continue to act at the polyploid level. In several polyploid species, individuals with multilocus genotypes indicative of separate origins have been shown to co-occur as a result of migration after their initial formation (26, 28). That different genotypes resulting from independent polyploidizations come into contact obviously affords the opportunity for subsequent recombination and the production of new genotypes, further contributing to the dynamic nature of polyploid gene pools (17). With these various processes acting in concert, the amount of genetic diversity present in polyploids as revealed by molecular investigations is remarkably high (e.g., refs. 17 and 25–29). Genetic evidence, therefore, provides a new view of polyploidy that is in striking contrast to the traditional notion of polyploids as genetically uniform.

Molecular data also provide compelling genetic evidence to contradict longstanding views of autopolyploidy as maladaptive (refs. 8 and 21, but see ref. 10). Stebbins (21) stated, for example, that chromosome doubling ". . . is not a help but a hindrance to the evolutionary success of higher plants." Molecular data, however, have revealed three important genetic attributes of autoploids compared to their diploid progenitors: (i) enzyme multiplicity, (ii) increased heterozygosity, and (iii) increased allelic diversity (15, 17). These attributes are the direct result of polysomic inheritance and provide strong genetic arguments for the potential success of autoploids in nature.

The Evolution of Polyploid Genomes

Although molecular data have recently provided critical insights into the parentage, formation, and immediate genetic consequences of polyploidy, less is known about the subsequent evolution of polyploid genomes after their formation. Thus, the findings of Song et al. (20) are

particularly exciting and noteworthy in that they provide convincing evidence for extensive and rapid genome change in polyploids.

The work of Song et al. (20) relies on a model allopolyploid system based on three diploid species of the genus *Brassica: B. rapa* (A genome), *B. oleracea* (C genome), and *B. nigra* (B genome) (33). Two pairs of synthetic polyploids were produced [AB and BA; AC and CA (34)]; each synthetic polyploid was completely homozygous. Hence, after self-fertilization of these raw polyploids, no nuclear genome changes were expected in the progeny. At this point it is important to stress again the traditional view that polyploidy provides a genetic buffering against the effects of individual alleles; hence, new alleles should contribute less to the evolution of polyploids than to diploids. This hypothesis assumes, of course, that diploids and polyploids have roughly equal mutation rates. Song et al. (20) asked, however, if genome change is, in fact, greatly accelerated in new polyploids, perhaps due to greater instability resulting from the interaction of diverse genomes.

Significantly, Song et al. (20) detected extensive changes in the nuclear genome of each synthetic polyploid during each of just five generations. In contrast, there was no evidence of change in the chloroplast and mitochondrial genomes of these synthetic polyploids. Song et al. (20) also demonstrated that the frequency of genome change was different between the two pairs of synthetic polyploids—that is, twice as many genome changes were detected in the AB and BA polyploids as in the AC and CA polyploids. Given that previous studies (35–37) had shown that *B. rapa* (contributor of the A genome) is much more closely related to *B. oleracea* (C genome) than to *B. nigra* (B genome), the data suggest that the higher the degree of divergence between the parental diploid genomes, the greater the frequency of nuclear genomic change in the resulting polyploid (20). Song et al. (20) also provide evidence for what they term "directional genome changes" that are possibly influenced by cytoplasmic–nuclear interactions. In the AB polyploid (which contains the A cytoplasm) the paternally donated nuclear genome (B) changed significantly, whereas the maternally donated nuclear genome (A) did not exhibit modification. Lastly, based on preliminary data, Song et al. (20) also suggest that chromosome rearrangements involving intergenomic (homoeologous) recombination could be a major factor contributing to the extensive genome change seen in these synthetic *Brassica* polyploids.

An obvious and critical question regarding the work of Song et al. (20) is as follows: can results from synthetic alloploids be extended to natural populations? The synthetic polyploids produced and analyzed by Song et al. are completely homozygous, whereas natural polyploids likely arise through fusion of unreduced gametes and are therefore heterozygous (17, 19). Despite these differences, the data for synthetic polyploids complement earlier data on natural *Brassica* polyploids. DNA-based genomic maps for these same diploid *Brassica* species and both synthetic and natural polyploids provide evidence for considerable plasticity of the nuclear genome within these polyploid *Brassica* species (38). For example, in a comparison of natural and synthetic *Brassica napus*, convincing evidence was provided for considerable intragenomic rearrangement (38, 39); intergenomic recombination has also occurred in *B. napus* (38). In addition, Song et al. (35) earlier obtained and compared nuclear restriction fragment length polymorphism data for naturally occurring *Brassica* polyploids and their diploid progenitors. On the basis of these comparisons, Song et al. (35) suggested that the cytoplasmic genomes in *Brassica* alloploids had important roles in the subsequent evolution of the nuclear genomes of these polyploids—that is, their analysis revealed that the nuclear DNA composition of each natural *Brassica* allopolyploid is more closely related to the diploid parent that contributed the cytoplasm to that tetraploid. Thus, the work of Song et al. (20) on naturally occurring *Brassica* diploids and polyploids complements their recent paper on synthetic polyploids. Taken together, the data for both natural and synthetic alloploids in *Brassica* suggest a coevolution of the nuclear and cytoplasmic genomes. Both studies suggest that the cytoplasmic donor plays an important role in the formation of a new polyploid. During polyploidization, the native cytoplasm may provide a selection pressure on portions of the foreign nuclear genome, stabilizing the newly produced polyploid by establishing a "harmonious relationship between cytoplasmic and nuclear genomes."

In addition to *Brassica*, other possible examples of genome evolution and chromosomal repatterning have also been provided as a result of comparative genome mapping (40, 41). The use of a genomic *in situ* hybridization method has similarly provided evidence for intergenomic transfer of DNA in the alloploid *Milium montianum* (42). More recently, use of this "chromosome painting" approach has also provided evidence for chromosomal repatterning in both the allotetraploid *Nicotiana tabacum* (tobacco) (43, 44) and in artificial *Nicotiana* hybrids (45). Such studies indicate clearly that genome reorganization not only occurs in polyploids as well as hybrids but that this reorganization can occur quickly.

In addition to the evidence provided for genome diversification and subsequent chromosomal repatterning in polyploids, compelling, but more limited, genetic evidence has also been obtained in molecular analyses of polyploid species, suggesting that two other processes are also occurring in polyploid genomes. These are as follows: (*i*) gene silencing, eventually leading to extensively diploidized polyploid genomes; and (*ii*) gene diversification, resulting in regulatory or functional divergence of duplicate genes (for review, see ref. 17).

The occurrence of all three of the above-noted processes in polyploid genomes indicates that polyploid genomes are plastic and susceptible to evolutionary change. All available evidence clearly suggests that polyploids and polyploid genomes are much more dynamic than formerly envisioned. The view of polyploidy actually acting to "retard . . . evolutionary progress at the gene level" (21), as well as the more extreme concept of polyploids as evolutionary dead ends (22), certainly are contradicted by the evidence provided by Song et al. (20), as well as by other molecular studies of polyploids (17). Thus, molecular data have prompted a dramatic rethinking of polyploid evolution and polyploid genome evolution. Using *Brassica* as a model system, Song et al. (20) have added an important new component to our view of polyploids. Their work, in concert with other recent studies on genome evolution in polyploids, suggests not only that polyploid genomes can undergo substantial intra- and intergenomic changes but that these processes can occur rapidly. Polyploidization and the subsequent evolution of polyploid genomes are extremely dynamic processes.

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