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NEWS AND COMMENTARY

Allopolyploid genomes

The complex nature of allopolyploid plant genomes

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Polyploidy is a major creative force in plant evolution, from ferns to flowering plants. Estimates suggest that ∼70% of flowering plants have undergone at least one whole-genome duplication event during their evolutionary history (Levin, 2002), and that 2–4% of all speciation events involve polyploidisation (Otto and Whitton, 2000). The majority of polyploid plants arise through the combined effects of interspecific hybridisation and polyploidy (allopolyploidy), and much attention has focused on understanding what happens when divergent genomes are brought together by these processes. A recent study by Buggs *et al.* (2009) has shown that at a genomic level the possible outcomes of allopolyploidy are not always as predictable as we might expect. As it is known that many polyploid genomes eventually return to a diploid-like state through loss or divergence of duplicated genes, Buggs *et al.* (2009) set out to determine the timing of these events in the allotetraploid hybrid *Tragopogon miscellus*. This hybrid is an excellent system to examine the timing of genomic changes associated with allopolyploidy, as it is known to have arisen within the last 80 years, unlike many other natural hybrids that have formed many thousands or even millions of years ago, such as wheat (Peterson *et al.*, 2006) or cotton (Adams *et al.*, 2003). By assaying the detectability of cleaved amplified polymorphic sequence markers on both genomic DNA and cDNA, Buggs *et al.* (2009) were able to determine whether parental gene copies for 10 loci were being lost or silenced in 57 hybrids from five natural populations. They were also able to compare these hybrids to a resynthesised allotetraploid created under glasshouse conditions. They found that, across 10 homoeologous gene pairs in the 57 natural hybrids, 3.2% of loci had been rendered undetectable in the genomic DNA, suggesting loss of one parental gene copy. In addition, analysis of seven of these homoeologue pairs using cDNA as a template showed that expression of one parental gene copy had been lost in 6.8% of loci. In none of these cases, silencing or allele loss was detected in the resynthesised allopolyploid.

These findings demonstrate that silencing and/or elimination of parental gene copies in *Tragopogon* allopolyploids is not an immediate consequence of interspecific hybridisation or genome duplication, but rather an ongoing process that varies in frequency among different hybrid populations. As the authors note, this is in stark contrast to the evidence from some other allopolyploid systems, for example, allohexaploid bread wheat (*Triticum aestivum*), where some gene loss occurs immediately upon interspecific hybridisation and again after polyploidisation (Ozkan *et al.*, 2001; Shaked *et al.*, 2001). Nevertheless, other allopolyploids are also known to be subjected to an ongoing process of recombination between homoeologous chromosomes (Figure 1), for example *Brassica*, which shows gradual loss of certain parental DNA fragments (Song *et al.*, 1995; Gaeta *et al.*, 2007). The timing of parental gene silencing in the *Tragopogon* hybrids also differs from that observed in other systems. Immediate changes to gene expression occur upon interspecific hybridisation in cotton (Flagel *et al.*, 2008) in a manner that can be both temporally or spatially dependent, even within a single cell (Adams *et al.*, 2003; Hovav *et al.*, 2008). Immediate changes to gene expression have also been observed in other hybrids, notably *Arabidopsis suecica* allotetraploids (Wang *et al.*, 2006), and in *Senecio* allopolyploids (Hegarty *et al.*, 2005) where distinct changes to gene expression are associated with both interspecific hybridisation and genome duplication (Hegarty *et al.*, 2006). Such changes in gene expression are not simply the 'additive' product of the progenitor species because ∼24% of the affected genes display non-additive expression in both cotton (Flagel *et al.*, 2008) and *Senecio* (Hegarty *et al.*, 2008), with the percentage of microarray features displaying non-additive expression in *Senecio* being similar to that seen in *A. suecica* at 3 and 5%, respectively (Wang *et al.*, 2006; Hegarty *et al.*, 2008). In *Senecio*, 42% of genes showing non-additive changes in expression also showed 'trangressive' patterns of gene expression—that is, expression change significantly higher or lower than that observed in either parent (Hegarty *et al.*, 2008). Buggs *et al.* (2009) suggest that the contrast between findings in *Tragopogon* and the other systems may be due to their methodology, which detects only the presence or absence of gene expression, and is not capable of distinguishing changes to expression level in cases where complete silencing does not occur. Nonetheless, they raise the important point that allopolyploidy may vary in its effects between species. This is certainly true at the level of chromosomal organisation in the case of allotetraploid cotton, which shows none of the large-scale genetic rearrangements typically observed in plant hybrids (Liu *et al.*,

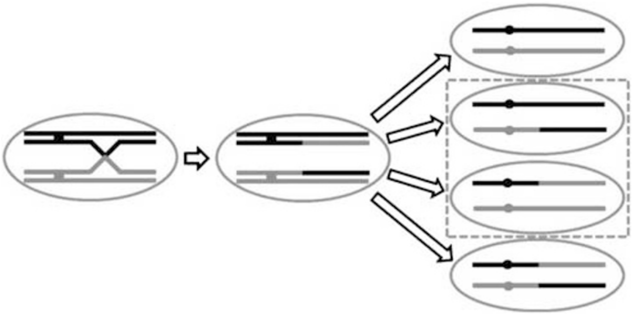

Figure 1 Loss of parental DNA due to recombination between homoeologous chromosomes. This figure shows a simplified representation of recombination between homoeologues in an allopolyploid, leading to loss of DNA from one parent. A reciprocal exchange between homoeologues is followed by segregation of the recombinants such that certain gametes (boxed) may not possess either the original parental chromatid type or both recombinants, resulting in loss of one homoeologous fragment in offspring derived from these gametes (Figure adapted from Nicolas *et al.*, 2008).

2001), nor does it seem to undergo any widespread changes in the pattern of DNA methylation seen in systems such as *Spartina* (Liu *et al*., 2001; Salmon *et al*., 2005). As Buggs *et al*. (2009) note, the level of divergence between the progenitors of a given hybrid is likely to be a factor in differences between hybrid systems, and, therefore, must be taken into account when making predictions as to the likely genetic and epigenetic consequences of genome mergers and duplication events.

The processes by which two genomes adapt to coexistence within the same nucleus are complex and can differ markedly between species. Ongoing studies of natural hybrid systems, such as *Tragopogon* and *Senecio*—where hybridisation and polyploidy have arisen relatively recently from an evolutionary perspective—are therefore crucial to identifying these processes and the factors that drive them. Given the recent resurgence of interest in recreating allopolyploid crop species to improve genetic diversity, the more data we can gather on the consequences of allopolyploidisation, the better.

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