npg

NEWS AND COMMENTARY

Plant hybridization and transposable elements
....

An eruption of mobile elements in genomes of hybrid sunflowers

P Michalak

....

Successful hybridization between distinct species de facto results in the creation of a new genome, providing a fascinating experimental model for evolutionary genomics. Merging two divergent genomes necessitates extensive chromatin reconfigurations and is often accompanied by genome duplications and chromosomal rearrangements. These dramatic genomic modifications trigger cascades of novel expression patterns and regulatory interactions.

One of the most intriguing consequences of hybridization as a 'genome shock' is the mobilization and transposition of mobile (transposable) elements (TEs), a phenomenon first predicted by the discoverer of transposition herself, Barbara McClintock, and then observed in a number of case studies (reviewed by Michalak, 2009). TEs can be classified as DNA transposons and retrotransposons. The former move within genomes as DNA fragments through a 'cut-and-paste' mechanism, whereas the latter duplicate through reverse-transcribed RNA intermediates (a 'copy-and-paste' mechanism). Retrotransposons can be divided into long terminal repeat (LTR)- and non-LTR retrotransposons based on the presence or absence of LTRs, a structural feature that they share with retroviruses. Given that mobile elements account for a large fraction of eukaryotic genomes (not uncommonly exceeding 50% of their content), their dynamics in hybrid genomes is by no means of trivial significance to our understanding of genome evolution.

Massive TE derepression due to hybridization occurs in three species of sunflowers: Helianthus anomalus, H. deserticola and H. paradoxus (Ungerer et al., 2006). All three originated as hybrids between two ancestral species, H. annuus and H. petiolaris (Rieseberg, 1991). It is common that hybridization leading to the origin of new plant species is associated with genome duplications (allopolyploidization). However, this is not the case in the sunflower species, as all five species are diploids

with the same chromosome number ($n = 17$), despite the fact that the three hybrid derivatives have genomes at least 50% larger than their parental species. Ungerer et al. (2006) showed that the genome size increase can be partially explained by proliferation of Ty3/gypsy-like LTR retrotransposon sequences in hybrids.

In their report, Ungerer and colleagues (Kawakami et al., 2010, this issue) take on another major superfamily of LTR retrotransposons, the Ty1/copia-like group, and their relative abundance in sunflower hybrid species. Ty3/gypsy-like and Ty1/copia-like superfamilies are mainly distinguished by the order of protein domains within the pol region containing genes required for cDNA synthesis and integration of cDNA into host chromosomes (Kumar and Bennetzen, 1999). Lo and behold! Ty1/copia-like retrotransposons underwent a similar burst of transposition in genomes of hybrid sunflower species, although a less extensive one compared to Ty3/gypsy-like TEs. In contrast to Ty3/gypsy-like TEs, the eruption of Ty1/copia-like TEs varied between hybrid species, and was most pronounced in H. paradoxus, a species occurring in saline environments (H. anomalus and H. deserticola are found in desert-like habitats). Although external stress factors may contribute to derepression of TEs (Grandbastien, 1998), the authors admit that this habitat–TE frequency association may be purely coincidental.

It is unclear when the hybrid species underwent the TE burst. To get a sense of the timing, Kawakami et al. sequenced a pool of PCR amplicons representing Ty1/copia-like sequences from the hybrid and parental species. Sequences from the five taxa were also found in other plant species, indicating that these Ty1/copia-like lineages are ancient and predate the origin of the sunflower group. However, the majority (70%) of sequences underlying the TE burst were derived from a single lineage of elements and this implicates a recent proliferation event.

This study poses a number of essential questions to pursue in future experiments. For example, are these retroelements also derepressed in newly created synthetic hybrids between H. annuus and H. petiolaris? Does hybridization unleash other types of mobile elements as well? What is the molecular mechanism of derepression in each case? DNA methylation is deployed as a part of the genomic 'immune' system against mobile elements and therefore comparing genome-wide methylation patterns between ancestral and hybrid Helianthus species could provide useful insights. Hybridization is known to alter DNA methylation in synthetic Arabidopsis thaliana × A arenosa allotetraploids (Madlung et al., 2002), Solanum tuberosum × S kurtzianum diploids (Marfil et al., 2006) and synthetic hybrids of wheat (Triticum aestivum) (Ozkan et al., 2001) among others.

The high density of TEs and their activity as 'genomic parasites' raise the question of what role they have had in the origin of new species. Assuming that mobilization and proliferation of mobile elements due to hybridization is widespread in plants, it is tempting to speculate that subsequent hybrid genome duplications (allopolyploidization) occurring in many plant taxa serve as a defense response to deleterious effects of TE mobilization and proliferation. Perhaps larger genomes with 'spare' gene duplicates are more robust to reactivation of mobile elements.

Conflict of interest

The author declares no conflict of interest.

Dr P Michalak is at the Department of Biology, The University of Texas in Arlington, Box 19498, Arlington, TX 76019-0498, USA

e-mail: Michalak@uta.edu

Grandbastien MA (1998). Activation of plant retrotransposons under stress conditions. Trends Plant Sci 3: 181–187.

Kawakami T, Strakosh SC, Zhen Y, Ungerer MC (2010). Different scales of Ty1/copia-like retrotransposon proliferation in the genomes of three diploid hybrid sunflower species. Heredity 104: 341–350.

Kumar A, Bennetzen JL (1999). Plant retrotransposons. Annu Rev Genet 33: 479–532.

Madlung A, Masuelli RW, Watson B, Reynolds SH, Davison J, Comai L (2002). Remodeling of DNA methylation and phenotypic and transcriptional changes in synthetic Arabidopsis allotetraploids. Plant Physiol 129: 733–746.

Marfil CF, Masuelli RW, Davison J, Comai L (2006). Genomic instability in Solanum tuberosum × Solanum kurtzianum interspecific hybrids. Genome 49: 104–113.

Michalak P (2009). Epigenetic, transposon, and small RNA determinants of hybrid dysfunctions. Heredity 102: 45–50.

Ozkan H, Levy AA, Feldman M (2001). Allopoly-ploidy-induced rapid genome evolution in the wheat (*Aegilops-Triticum*) group. *Plant Cell* **13**: 1735–1747.

Rieseberg LH (1991). Homoploid reticulate evolution in *Helianthus* (Asteraceae): evidence from ribosomal genes. *Am J Bot* **78**: 1218–1237.

Ungerer MC, Strakosh SC, Zhen Y (2006). Genome expansion in three hybrid sunflower species is associated with retrotransposon proliferation. *Curr Biol* **16**: R872–R873.

Editor's suggested reading

Bernasconi G, Antonovics J, Biere A, Charlesworth D, Delph LF, Filatov D *et al.* (2009). Silene as a model system in ecology and evolution. *Heredity* **103**: 5–14.

Buggs RJA, Doust AN, Tate JA, Koh J, Soltis K, Feltus FA *et al.* (2009). Gene loss and silencing in *Tragopogon miscellus* (Asteraceae): comparison of natural and synthetic allotetraploids. *Heredity* **103**: 73–81.

Gregory TR, Johnston JS (2008). Genome size diversity in the family Drosophilidae. *Heredity* **101**: 228–238.