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Malika Ainouche, Eric Jenczewski

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Commentary

Focus on polyploidy

Polyploidy (whole-genome duplication) has played a pervasive role in the evolution of fungi and animals, and is particularly prominent in plants (Wendel & Doyle, 2005; Cui *et al.*, 2006; Otto, 2007; Wood *et al.*, 2009). This important evolutionary phenomenon has attracted renewed and growing interest from the scientific community in the last decade since it was discovered that even the smallest plant genomes considered to be 'diploid' (e.g. *Arabidopsis thaliana*, reviewed in Henry *et al.*, 2006) have incurred at least one round of whole-genome duplication, possibly predating the origins of the angiosperms (Soltis *et al.*, 2009). Polyploidy is an important speciation mechanism for all eukaryotes and has profound impacts on biodiversity dynamics and ecosystem functioning. Newly formed polyploids, and particularly those of hybrid origin (allopolyploids), frequently exhibit rapid range expansion (Ainouche *et al.*, 2009), and over long periods of evolutionary time, polyploidy has increased morphological complexity and probably reduced the risk of species extinction (Fawcett *et al.*, 2009). Last, but not least, genome duplication has often provided the raw material for plant domestication (e.g. wheat, Dubkovsky & Dvorak, 2007) and thus has had a major impact on human societies and the development of an agrarian lifestyle.

'... there are reasons to ask whether genome multiplication represents an evolutionary advantage per se.'

Why polyploids have been so successful is a question that has generated important research activity in the last decade (reviewed in Wendel, 2000; Osborn *et al.*, 2003; Chen, 2007; Doyle *et al.*, 2008; Van de Peer *et al.*, 2009), accompanied by increasing national and international collaborative efforts through funded networks and international meetings. The International Polyploidy Conference held in London in April 2003 (Leitch *et al.*, 2004) provided an opportunity to evaluate the progress made during the 25 years since the first International Conference,

Polyploidy: Biological Relevance (Lewis, 1980) held in 1979 in St Louis, MI, USA. Significant advances have continued to be made towards an understanding of polyploid genome functioning and evolution over both the short-term (in young or neo-polyploids) and long-term (in paleopolyploids). The importance of recent findings from this timely and fast-evolving area was no more evident than at the latest gathering, the International Conference on Hybridization, Polyploidy and Biodiversity that was held in Saint-Malo (France), 17–20 May 2009 (<http://www.icphb2009.univ-rennes1.fr/>). In this special issue, *New Phytologist* recognizes these advances by bringing together current ideas and findings about plant polyploidy in a series of research reviews and accompanying original research articles.

Polyploid species may be formed through a diversity of mechanisms in natural populations (unique or multiple origins, via one-step or stepwise) involving one progenitor species (i.e. autopolyploids) or divergent parental lineages (i.e. allopolyploids). Although autopolyploidy has long been considered as less prevalent than allopolyploidy, there are reasons to ask whether genome multiplication represents an evolutionary advantage *per se* (Parisod *et al.*, this issue, pp. 5–17). Likewise, although estimating the time of origin of polyploid species is an important evolutionary issue, current procedures need to be handled with caution to avoid spurious conclusions (reviewed in Doyle & Egan, pp. 73–85).

Once formed, neopolyploid plants face an immediate challenge during meiosis: the different sets of chromosomes are usually sufficiently similar to one another that recombination may lead to complex meiotic configurations which are prone to generate unbalanced gametes, aneuploid progenies (Mestiri *et al.*, pp. 86–101) and chromosome rearrangements (Szadkowski *et al.*, pp. 102–112), and hence to impair fertility (reviewed by Gaeta & Pires, pp. 18–28). Precise control of meiotic crossovers (an important facet of meiotic recombination) is therefore a prerequisite for meiotic and reproductive stability in polyploids. This can be achieved either through random processes, accelerated by subfunctionalization (partitioning of homeologous gene expression in different tissues or developmental stages) or neofunctionalization (when one of the homeologous gene copies evolves a new function with a selective advantage) (Le Comber *et al.*, pp. 113–122) or through the involvement of genes that contribute to the cytological diploidization of autopolyploid and allopolyploid species (Cifuentes *et al.*, pp. 29–36). Interestingly, none of these processes necessarily impair the occurrence of noncrossover

(i.e. the second product of meiotic recombination), as detected in synthetic and natural allotetraploid cotton (Salmon *et al.*, pp. 123–134).

The merger of divergent genomes in allopolyploids also represents a form of 'genomic shock' that may cause increased transposable element (TE) activity (reviewed in Parisod *et al.*, this issue, pp. 37–45). Emerging evidence suggests that amplification of TEs during the first generations following polyploidy may be restricted to a few TEs (e.g. young active elements), such as Tnt1 in synthetic allotetraploid *Nicotiana tabacum* (Petit *et al.*, pp. 135–147), while most others are rapidly targeted by epigenetic changes following hybridization in allopolyploids (Parisod *et al.*, 2009). Transposable element activity notably leads to the production of specific classes of small interfering RNAs (siRNAs) that are differently contributed by the maternal and paternal genomes and may lead to an epigenetic hybrid barrier (Martienssen, pp. 46–53). Of note, TEs are not the only repetitive sequences that are prone to rapid evolutionary changes, as demonstrated by the unexpected rate of satellite repeat replacement in allopolyploids of *Nicotiana* (Koukalova *et al.*, pp. 148–160).

Significant progress has been made in understanding changes of gene and genome expression in polyploids compared with their parents, including expression dominance from one parent, transgressive expression levels compared with parents, and modulation or silencing of transcriptional activity of homeologous subgenomes in nascent (e.g. *Spartina*, Chelaifa *et al.*, pp. 161–174; and *Tragopogon*, Buggs *et al.*, pp. 175–183) or long-evolved (e.g. *Gossypium*, Flagel & Wendel, pp. 184–193) polyploids. Interestingly, genome duplication *per se* (in autopolyploids) seems to have limited effects on global genome expression, although it may significantly impact less complex regulatory pathways (Pignatta *et al.*, pp. 194–206). These observations are in agreement with the theory that the stoichiometry/connectivity of multisubunit complexes is a major determinant driving the ability of duplicated genes to evolve (Birchler & Veitia, pp. 54–62). There is also evidence that some changes in gene and genome expression are epigenetically controlled. For example, the down-regulation of microRNA (miRNA) biogenesis was shown to induce developmental changes in resynthesized *Arabidopsis* allotetraploids (Lackey *et al.*, pp. 207–215). Likewise, small RNAs are likely candidates for explaining proteomic changes in resynthesized *Brassica napus* allotetraploids that otherwise exhibit mainly additive transcriptomes of their parents (Marmagne *et al.*, pp. 216–227).

Increasingly, data are documenting the link between the regulation of gene expression and phenotypic changes following allopolyploid speciation. Evolution of tandem gene duplications at the *Flowering Locus C* (FLC) and the divergence of corresponding putative regulatory upstream sequences have increased expression diversity and flowering

time variation in *Arabidopsis* allotetraploids (Nah & Chen, pp. 228–238). Transcriptional changes of floral gene regulators were found to be associated with photoperiod-dependent floral reversion in the natural allotetraploid *A. thaliana*, thus increasing the plasticity of this species (McCullough *et al.*, pp. 239–250). Increased plasticity of mating systems was also demonstrated in natural and synthetic allohexaploid *Senecio cambrensis* (Brennan & Hiscock, pp. 251–261). Finally, the importance of gene flow across ploidy levels causing increases in phenotypic variation and adaptation in natural populations is revisited and shown to occur in *Senecio* (reviewed in Chapman & Abbott, pp. 63–71).

As data accumulate from different biological systems, much progress is being made towards understanding the respective impacts of hybridization (i.e. genome merger), genome duplication (polyploidy *per se*) and subsequent evolution following allopolyploid and autopolyploid speciation. Experimentally resynthesized polyploids from model systems in a known genetic context, and comparisons with their corresponding natural species, are providing invaluable insight into the nature and tempo of the mechanisms involved. The rapidly evolving tools (e.g. next-generation sequencing technologies), allowing large-scale investigations of genomes, epigenomes and transcriptomes, offer promising opportunities to extend our knowledge in natural populations of previously under-explored wild species from various plant lineages, thus providing both a precise and a broader picture of the important evolutionary process of polyploidy.

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Malika L. Ainouche^{1*} and Eric Jenczewski²

¹UMR CNRS 6553 Ecobio, University of Rennes 1, Bât. 14 A, Campus de Beaulieu, 35042 Rennes Cedex, France;

²INRA, Institut Jean-Pierre Bourguin, Station de Génétique et amélioration des plantes, Route de Saint-Cyr, 78 026 Versailles Cedex, France

(*Author for correspondence: tel +33 2 23 23 51 11; email malika.ainouche@univ-rennes1.fr)

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