Polyploidy as a mechanism for surviving global change

The effects of this process have been so far-reaching, and it is so widespread, that anyone who would have a real understanding of species interrelationships and species evolution in the majority of plants must realize the significance and implications of polyploidy and the processes that accompany it.

(Stebbins, 1940)

One of the great paradigm shifts in the plant sciences in the last century has been the recognition of the fundamental role that whole genome duplication (WGD), or polyploidy, has played throughout the evolutionary history of plants. As its name suggests, a WGD event results in a complete doubling of the cell’s genomic complement. Confirming G. L. Stebbins’ early insights on the immense potential of polyploidy to influence species’ evolution, researchers have now found evidence to support the role of WGD in shaping nearly every aspect of plant evolution, from genome and transcriptome structure to gene expression patterns, gene family evolution, and myriad aspects of ecology and physiology (reviewed in Soltis et al., 2014). Much of the work on plant polyploidy has focused necessarily on extant taxa, but phylogenetic approaches have allowed researchers to identify WGDs that occurred putatively many millions of years ago, including in the ancestry of all major land plant and algal lineages examined to date (One Thousand Plant Transcrip- tomes Initiative, unpublished). In this issue of New Phytologist, Cai et al. (pp. 565–576) extend these insights into the past one step further and identify not only a remarkable number of WGD events in the history of the plant order Malphigiales, but a significant correlation between the timing of these events and periods of global climatic change during the Paleocene–Eocene transition and in the late Miocene, c. 56–54 and 7 million yr ago (Ma), respectively.

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Cai et al. employed a suite of methods to identify and date the occurrence of WGD events across the Malphigiales. These approaches typically use multi-gene data from sequenced genomes and transcriptomes to infer the phylogenetic location and probable age of polyploidization events. The authors assembled datasets from 36 ingroup taxa belonging to 21 families representing all major lineages across the order (which includes a total of c. 16,000 species in 36 families; Xi et al., 2012). They first searched for clusters of orthologous genes in these datasets and then used these ortholog clusters to reconstruct a dated phylogenetic tree using penalized likelihood, and a species tree using a summary coalescent approach. Three distinct methods were then applied to identify WGD events: (1) assessment of synonymous substitution rates among paralogs; (2) gene tree reconciliation; and (3) a gene count technique. These procedures identified 22, 24 and 22 WGD events across Malphigiales, respectively, most of which were supported by all three techniques. A Gaussian mixture model determined that these events were not distributed randomly in time and discerned two significant clusters of WGDs, one around the Paleocene–Eocene boundary, c. 56–54 Ma, and one in the late Miocene, c. 7 Ma. A majority of the WGD events inferred in Malphigiales (19 of them) occurred during the Paleocene–Eocene cluster, while a group of five WGDs creates the Miocene peak.

Both the Paleocene–Eocene transition and the late Miocene were periods of worldwide climatic upheaval associated with surges in global temperature (Zachos et al., 2001, 2008). The Paleocene–Eocene thermal maximum (PETM) was the warmest point in the most recent 65 Ma of Earth’s history and saw expansion of rainforest habitats worldwide (Pross et al., 2012), while the Mid-Miocene climatic optimum (MMCO) was a period of heightened seasonality and aridity with accompanying expansion of grassland habitats globally (Estep et al., 2014). Both periods are associated with rapid diversification in numerous plant lineages (Jaramillo et al., 2006; Graham, 2011), and evidence increasingly suggests that these and other past intervals of dramatic global change were also associated with increases in paleopolyploidy in plants. For example, Kagale et al. (2014) and Estep et al. (2014) found evidence for clusters of WGD events across the Brassicaceae and in the grass tribe Andropogoneae, respectively, which both sets of authors dated to the mid to late Miocene. Similarly, Fawcett et al. (2009) and Vanneste et al. (2014) found evidence for numerous independent WGD events across multiple angiosperm lineages that appear to cluster in the early Cenozoic, at or slightly after the Cretaceous–Paleogene (K–Pg) boundary, predating or potentially overlapping the PETM given the uncertainty in age estimates. The K–Pg boundary itself was a period of intense global change associated with the mass extinction event that ended the Age of Dinosaurs; the Chicxulub impactor and its aftermath also had significant impacts on global plant life, with as many as four out of five species of plants thought to have become extinct (Nichols & Johnson, 2008).

Numerous mechanisms have been suggested to explain why WGD may facilitate survival and adaptation during periods of global change (reviewed in Soltis et al. (2014) and Van de Peer et al. (2017)). Many of these involve genomic plasticity and the potential...
for new combinations of genes, genotypes, and regulatory pathways to increase the possible mechanisms by which populations may adapt to rapidly changing environments. Masking of recessive alleles and restoration of appropriate pairing behavior at meiosis can also ‘rescue’ otherwise sterile hybrids and restore fertility, increasing opportunities for hybridization to contribute to evolution. Myriad studies have documented the extensive nature of genome restructuring that can occur following WGD, with the general consensus being that there are infinite possible ways by which an extra genome can generate new raw materials for selection to shape into adaptation. Empirical research on the distributions of polyploid plant species reinforces the results of these genomic and transcriptomic studies, as polyploids have routinely been found to be present at higher frequency than diploids in disturbed and challenging environments, and amongst invasive species (Mable, 2013; Van de Peer et al., 2017).

Although polyploidy is now recognized as a common mechanism of speciation in plants, discussion continues about the relationship between WGD and net diversification rate. One way to characterize the question at the heart of this debate is whether polyploidy should be seen on average to be an evolutionary ‘dead end’ or as a facilitator of diversification. The ever-greater numbers of ancient WGD events identified across the plant tree of life, and the ever-greater numbers of hybridization events, often ending in loss, or extinction. However, those events and lineages that ‘hit it big’ will win the evolutionary jackpot and experience subsequent increases in net diversification. These increases may lag behind the initial WGD event in evolutionary time, a pattern seen frequently enough that Schranz et al. (2012) formalized it as the ‘Radiation Lag-Time’ model of increased diversification following, but separated from, a polyploidy event by up to several million years. While not all major bursts of diversification in plant evolution are associated with polyploidy, the correlation is too strong to ignore the legacy of WGD in shaping plant diversity through time. While Cai et al. did not test directly for a relationship between WGD and changes in net diversification rate across Malpighiales, they do note that overall there appears to be a strong association of WGD with the most diverse clades in the order.

In summary, the results presented by Cai et al. have implications for numerous areas of interest in the ever-growing field of plant polyploidy research. The relationship between WGD and the success of lineages during periods of global change is a particularly compelling avenue that deserves further attention across the plant tree of life. This study on Malpighiales and the multi-pronged approach that Cai et al. used to identify and date WGD events should serve as a gold standard for other researchers wishing to use genomic and transcriptomic tools to study paleopolyploidy in their clades of interest.

References


Key words: climate change, environmental change, paleopolyploidy, polyploidy, whole genome duplication (WGD).