

Surviving the K-T mass extinction: New perspectives of polyploidization in angiosperms

Douglas E. Soltis¹ and J. Gordon Burleigh

Department of Biology, University of Florida, Gainesville, FL 32611

Although it has long been recognized that polyploidy (now often referred to as genome doubling) has played a major role in angiosperm evolution (1), analyses of genomic data have dramatically increased interest in the function of polyploidy in shaping plant genome structure and diversity (e.g., reviewed in refs. 2–5). Whereas early estimates largely based on chromosome counts suggested that perhaps 30–50% of all angiosperms may be polyploids, modern genome studies prompted the stunning realization that all or nearly all angiosperms likely have polyploidy in their evolutionary history (e.g., ref. 6). For example, analyses of the small *Arabidopsis* genome, the putative “ideal” diploid, revealed 2 or 3 rounds of genomewide duplication (7, 8), and an estimated 59% of the duplicated genes over the last 350 million years are the result of whole genome duplications (WGDs) (9). There is also evidence of ancient WGD events in basal angiosperm lineages, near the origin of the eudicots, and in numerous other lineages including *Vitis*, *Carica*, and *Populus* (reviewed in ref. 10). This evidence for the pervasive influence of polyploidy throughout plant evolutionary history raises new questions about the evolutionary consequences of polyploidy in plants and has prompted a dramatic resurgence in the view of polyploidy as a major evolutionary force.

In this issue of PNAS, Fawcett et al. (11) propose that genome doubling helped numerous plant lineages survive the Cretaceous-Tertiary (K-T) mass extinction. This intriguing hypothesis illustrates the modern polyploidy paradigm, which attributes enormous genomic versatility and concomitant evolutionary success to polyploid lineages (4). Using a novel method to date ancient genome duplications, Fawcett et al. estimated that ancient polyploidy events occurred at the same time (≈ 65 Mya) in several diverse angiosperm lineages, suggesting the possibility of a shared common causal factor. Interestingly, this estimate corresponds with the K-T boundary. Hence, they propose that genome doubling was a catalyst for the survival and/or diversification of many angiosperms after the mass extinction event that occurred ≈ 65 Mya. Similarly, the

correspondence of ancient polyploidy events to the origin of many species-rich plant clades, including Fabaceae, Asteraceae, eudicots, monocots, and even angiosperms has also sparked specula-

Fawcett et al. suggest that polyploidy ameliorated extinction risks during the K-T.

tion about the role of polyploidy in major bursts of plant diversification (see ref. 10). In the light of such speculation, it is striking to recall that several decades ago, polyploids were commonly viewed as “evolutionary dead ends” (reviewed in ref. 12).

Identifying and Placing Ancient Polyploidy Events

However, before we accept the ubiquity of polyploidy at the major events of plant evolutionary history, it is important to appreciate the difficulty of identifying and placing ancient genome duplications. Polyploidy is followed by rapid gene loss and chromosomal rearrangements that erase evidence of genome doubling (13), and the older a genome duplication, the more difficult it is to detect. One commonly-used approach for detecting ancient polyploidy is to examine the age distribution of pairs of duplicated (paralogous) genes within a genome (7, 13). If gene duplication and loss occurs at a constant rate, there should be an exponential decrease in the number of pairs of duplicated genes as they get older or more diverged. In contrast, genome duplication should result in an overrepresentation of duplicated gene pairs that are similarly diverged, corresponding to the time of the genome duplication event. The date of the genome duplication can be estimated from the amount of divergence between the overrepresented gene pairs based on silent (synonymous) substitution rates. Such analyses can take advantage of large EST datasets that are available for many plants, and thus, they have been very useful for identifying many ancient plant genome duplications

(e.g., refs. 6, 14, and 15). However, it can be difficult to interpret the age-distribution graphs (14), and molecular rate heterogeneity among lineages and genes makes it difficult to precisely date the divergence times of genome duplications. Phylogenetic comparisons may help to place ancient polyploidy more precisely. For example, in the simplest approach, the divergence of a pair of paralogous genes from one species can be placed relative to its common ancestor with a second taxon by comparing the paralogous genes with homologs from the second taxon and an outgroup (e.g., ref. 8). Still, phylogenetic comparisons are limited by the taxonomic breadth of available genomic sequence data. Fawcett et al. (11) take a novel approach to date ancient polyploidy that combines phylogenetic comparisons and methods for dating duplications that do not assume a constant rate of molecular evolution (16). This method arguably results in the most precise estimates of the timing of many ancient polyploidy events to date; however, the combination of rapid gene loss after polyploidy, lack of genomic data from a broad taxonomic sample, and the inherent methodological challenges mean that the picture of ancient polyploidy in plants is still very incomplete. Thus, because even small variations in the estimates of the timing or phylogenetic placement of ancient polyploidy can greatly affect interpretations of the evolutionary consequences of ancient polyploidy, it is important to be cautious before ascribing too much significance to these inferences.

The Consequences of Polyploidy

Another crucial part of untangling the role of polyploidy in plant evolution is to determine the possible consequences of polyploidy. Indeed, there are many possible mechanisms that could link polyploidy to diversification and adaptation. Levin (17) for example, provocatively suggested that polyploidy could propel a population into a “new adap-

Author contributions: D.E.S. and J.G.B. wrote the paper.

The authors declare no conflict of interest.

See companion article on page 5737.

¹To whom correspondence should be addressed. E-mail: dsoltis@botany.ufl.edu.

tive sphere” as a result of the numerous fundamental changes that accompany genome doubling. Numerous genetic, biochemical, physiological, and morphological changes that have been attributed to polyploidy also have been considered the underlying causes for the success of these plants in nature (e.g., refs. 2–5 and 18). Specifically, there is strong evidence that gene and genome duplication result in subfunctionalization, new gene functions, epigenetic changes, and altered gene expression. Many physiological and developmental processes are impacted by genome doubling, including carbon dioxide exchange rates, hormone levels, photosynthetic rates, and water balance. Other studies indicate that plant polyploidy can have profound effects on mating systems and interactions with animal herbivores and pollinators (19). Finally, polyploidy is among the few unambiguous mechanisms for sympatric speciation, which in itself may increase rates of diversification.

Although the incredible diversity of possible consequences of polyploidy suggest that it can be an important mechanism for adaptive evolution, they also make it easy to ascribe an important adaptive role for polyploidy in nearly any evolutionary context. The adaptive scenarios involving ancient polyploidy take advantage of the supple nature of polyploid hypotheses. For example, explanations relating polyploidy to the diversification of angiosperms link polyploidy to mechanisms that increase speciation rates, whereas Fawcett et al. (11) suggest that polyploidy ameliorated

extinction risks during the K-T. Both scenarios could be correct but it is important to note that there is no direct evidence for either.

Although much of the discussion of ancient polyploidy in plants is still speculative, it provides the missing links needed to form a comprehensive picture of polyploidy throughout plant evolution. Thus far, evolutionary analyses of ancient polyploidy have rarely integrated insights from more recent polyploidy events, and conversely, studies of recent polyploidy have rarely considered ancient patterns of polyploidy. Even the term ancient polyploidy is imprecise and suggests a distinction from just “polyploidy,” and we propose using “cryptic polyploidy” to describe genome duplication events that are not apparent by superficial comparison of chromosome numbers among closely-related species. Studies of recent polyploid populations and genetic studies of synthetic polyploids doubtlessly will help further reveal the adaptive mechanisms and consequences of polyploidy, and these insights may help evaluate adaptive hypotheses of ancient polyploidy. Alternately, a comprehensive comparative phylogenetic study that incorporates both ancient and more recent polyploidy may help uncover broad-scale patterns and correlates of evolution associated with polyploidy throughout plant history. We suggest that such comparative studies follow the lead of Vamosi and Dickinson’s (20) groundbreaking analysis linking polyploidy and species richness in Rosaceae.

The discovery of frequent ancient polyploidy in plants has undoubtedly shifted the perceptions of the significance of polyploidy and spurred increased interest in the study of this process in plants. The exciting hypotheses generated from studies of ancient polyploidy such as that by Fawcett et al. (11) reveal how mysterious this major, although oddly common, genomic change is in plants. Ultimately, it may be impossible to determine whether polyploidy enabled plant lineages to survive the massive K-T extinctions, but the adaptive hypotheses born from such speculation may be very relevant to understanding the current patterns of plant diversity and perhaps patterns in the future. For example, if polyploidy allowed certain plant lineages to survive and adapt during the tremendous global changes of the K-T period, does polyploidy confer a similar advantage in the current period of global warming? However, caution is in order in attributing too much evolutionary power to polyploidy, and we must be careful not to let the exuberance surrounding the identification of more and more ancient polyploidy events inflate explanations for the adaptive significance of polyploidy. As Stebbins (1) early noted, polyploids are complex and generalizations are difficult to make. There may be important morphological, physiological, and ecological consequences of polyploidy (17), but these may vary from group to group and differ depending on the mode of polyploidization (2, 5).

1. Stebbins GL (1950) *Variation and Evolution in Plants* (Columbia Univ Press, New York).
2. Tate JA, Soltis DE, Soltis PS (2005) Polyploidy in plants. *The Evolution of the Genome*, ed Gregory TR (Elsevier, San Diego), pp 371–426.
3. Adams KL (2007) Evolution of duplicated gene expression in polyploid and hybrid plants. *J Hered* 98:136–141.
4. Leitch AR, Leitch IJ (2008) Genomic plasticity and the diversity of polyploid plants. *Science* 320:481–483.
5. Doyle JJ, et al. (2008) Evolutionary genetics of genome merger and doubling in plants. *Annu Rev Genet* 42:443–461.
6. Cui L, et al. (2006) Widespread genome duplications throughout the history of flowering plants. *Genome Res* 16:738–749.
7. Vision TJ, Brown DG, Tanksley SD (2000) The origins of genomic duplications in *Arabidopsis*. *Science* 290:2114–2117.
8. Bowers JE, Chapman BA, Rong J, Paterson AH (2003) Unraveling angiosperm genome evolution by phylogenetic analysis of chromosomal duplication events. *Nature* 422:433–438.
9. Maere S, et al. (2005) Modeling gene and genome duplication in eukaryotes. *Proc Natl Acad Sci USA* 102:5454–5459.
10. Soltis DE, et al. (2009) Polyploidy and angiosperm diversification. *Am J Bot* 96:336–348.
11. Fawcett JA, Maere S, van de Peer Y (2009) Plants with double genomes might have had a better chance to survive the Cretaceous–Tertiary extinction event. *Proc Natl Acad Sci USA* 106:5737–5742.
12. Soltis DE, Soltis PS (1993) Molecular data facilitate a reevaluation of traditional tenets of polyploid evolution. *Crit Rev Plant Sci* 12:243–273.
13. Lynch M, Conery JS (2000) The evolutionary fate and consequences of duplicate genes. *Science* 290:1151–1155.
14. Blanc G, Wolfe KH (2004) Widespread paleopolyploidy in model plant species inferred from age distributions of duplicate genes. *Plant Cell* 16:1667–1678.
15. Barker MS, et al. (2008) Multiple Paleopolyploidizations during the evolution of the Compositae reveal parallel patterns of duplicate gene retention after millions of years. *Mol Biol Evol* 25:2445–2455.
16. Sanderson MJ (2002) Estimating absolute rates of molecular evolution and divergence times: A penalized likelihood approach. *Mol Biol Evol* 18:101–109.
17. Levin DA (1983) Polyploidy and novelty in flowering plants. *Am Nat* 122:1–25.
18. Otto SP (2007) The evolutionary consequences of polyploidy. *Cell* 131:452–462.
19. Thompson JN, Nuismer SL, Merg K (2004) Plant polyploidy and the evolutionary ecology of plant/animal interactions. *Biol J Linn Soc* 82:511–519.
20. Vamosi JC, Dickinson TA (2006) Polyploidy and diversification: A phylogenetic investigation in Rosaceae. *Int J Plant Sci* 167:349–358.