

This is a post-peer-review, pre-copyedit version of an article published in *Molecular Plant*. The final authenticated version is available online at: <https://doi.org/10.1016/j.molp.2019.12.003>

“Winter Is Coming”: How did Polyploid Plants Survive?

Zhen Li^{1,2} and Yves Van de Peer^{1,2,3,*}

¹ Department of Plant Biotechnology and Bioinformatics, Ghent University, 9052 Ghent, Belgium

² VIB Center for Plant Systems Biology, 9052 Ghent, Belgium

³ Centre for Microbial Ecology and Genomics, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria 0028, South Africa

*Correspondence: Yves Van de Peer (yves.vandeppeer@psb.vib-ugent.be)

Cold and dark periods have descended on Earth several times in geological history. One such period characterized the Cretaceous-Paleogene (K-Pg) boundary, following a meteor impact near Chicxulub in Mexico, about 66 million years ago, which caused dust, sulfate aerosols, and soot particles to be ejected into the atmosphere. This in turn led to a so-called “impact winter,” inhibiting photosynthesis and causing a global collapse of terrestrial and marine food webs, leading to the extinction of 60%–70% of plants and animals (Alvarez et al., 1980). Different from animals that might still be able to find shelter and detritus food in a harsh environment, plants are sessile and require (lots of) light for photosynthesis. How did they survive in a time of prolonged darkness and decreasing temperatures (Vellekoop et al., 2016)?

Interestingly, analyses of plant genomes have shown that most of current flowering plants are the descendants of ancestral polyploids. Furthermore, many of these ancient polyploidization (or whole-genome duplication [WGD]) events were dated around the K-Pg boundary (Vanneste et al., 2014). These observations made evolutionary biologists wonder whether polyploid plants had a greater chance of surviving environmental turmoil and extinction events than their diploid progenitors. A recent study by Wu et al. (2019) attempted to attribute the survival of polyploid plants to the expansions of specific genes and gene families responding to environmental stressors that have acted around specific times in evolution, such as cold and reduced light stress during the cataclysmic extinction event at the K-Pg boundary (Figure 1).



Figure 1. Artist Impression of the “Impact Winter” on Earth as a Result of the K-Pg Impactor. Wu et al. (2019) found genes in extant plants with functions in cold and dark response retained in excess following genome duplications at the K-Pg boundary, possibly helping with their survival. The figure was modified (with permission) from “Nouveau niche” by Patrick Morgan (as the cover of *Nat. Rev. Genet.* (2009) Volume 10, Issue 10).

Polyploids are often considered as evolutionary dead ends because they have to compete with their diploid progenitors in the same habitat, while the onset of polyploidy is often detrimental and causes mating difficulties, meiotic abnormalities, and genomic instabilities (Van de Peer et al., 2017). However, polyploids are also viewed as “hopeful monsters,” and they seem to have the ability or potential to invade a wide range of ecological environments that are new or inappropriate to their diploid progenitors. Polyploid plants seem more tolerant to abiotic stress than their diploid progenitors; for example, they are often able to grow in colder, drier, and high-saline environments (Madlung, 2013). From studies on recently formed polyploids, evidence is accumulating that the increased plasticity and adaptation of polyploidy to environmental conditions is related to changes in the expression of genes involved in stress and hormone signaling pathways (Van de Peer et al., 2017).

That being said, direct evidence on how ancient WGD events contributed to adaptations in a particular geological period is hard to come by. Also, it remains unclear to what extent knowledge obtained from studying novel polyploids could be transferred to study adaptation of ancient polyploids during extreme environmental shifts. Wu et al. (2019) approached these questions from a comparative genomics perspective by analyzing 24 angiosperm genomes, for which WGDs have been well described in the literature. After ascribing WGDs to several clearly marked periods in time and focusing on duplicate genes originated from these WGDs in different angiosperm lineages, they find that the biased retention of certain classes of genes is similar among lineages. These overly retained genes tend to respond to environmental stressors, such as coldness, salt, and water deprivation. They further describe that not all transcription factors (TFs) have similar chances to be retained, but that those involved in response to abiotic and biotic stresses seemed to be over-retained following WGD. Specifically, TFs originating from WGDs around the K-Pg boundary and acting in cold-response and shade-avoidance pathways have survived and are still present in many species. Thus, there seems to be a correlation between the genes that tend to be retained from ancient WGD events and those playing essential roles in the adaptation of novel polyploids to extreme environments.

Although Wu et al. (2019) observe subfunctionalization in the retained TFs, this process needs time to evolve and hence could not exert short-term effects in the fast-changing environment at the K-Pg boundary. Instead, polyploidization may confer enhanced abilities to a polyploid in responding to abiotic stresses straight away through increasing gene expression and cell size. The expression profiles and potential roles of TFs in novel polyploid plants remain elusive. Hou et al. (2018) compared distributions of gene expression ratios of aneuploids (trisomy) and polyploids (triploid and tetraploid) with the diploid *Arabidopsis*. They showed that aneuploids show greater modulation in expression than polyploids, and TFs are significant contributors to expression discordance in aneuploids showing trisomy. Hou et al. (2018) also illustrated that the overall expression of genes changes with increased cell size in a ploidy series. Together, their results suggest that TFs may play critical roles in the regulatory stoichiometry of gene expression in polyploids. Therefore, the specific retention of TFs involved in dealing with abiotic and biotic stresses subsequent to different WGDs in a certain time period, as observed by Wu et al. (2019), seem in line with the regulatory roles of TFs, which might elevate gene expression after WGD events. In addition, the increased cell size per se can change the surface-to-volume ratio of a cell, so it would affect physiological processes and might further help polyploids survive in harsh environments or during times of environmental turmoil (Doyle and Coate, 2019).

Wu et al. (2019) propose a potential link between the retention of genes linked to specific processes following WGD, and the adaptation of plants during geological epochs, but several issues remain to be

addressed. First, it remains to be seen how well supported the(ir) classification of WGD events into three clearly separated geological periods is. The wave of polyploidizations close to the K-Pg boundary is based on analyses of a large number of plant genomes and transcriptomes (Van de Peer et al., 2017); however, the limited number of WGD events used in Wu et al. (2019) to delineate more ancient and more recent WGD waves might affect the reliability of their analyses. Recently, the One Thousand Plant Transcriptomes (1KP) Initiative has proposed many more WGD events across the green plants (Leebens-Mack et al., 2019), some of which could potentially help supporting the two WGD waves proposed by Wu et al. (2019). Second, although perhaps responding to coldness and darkness after the meteor impact at the K-Pg boundary, the specific TFs could be retained initially just as a by-product of polyploidizations – a regulatory spandrel, *sensu* Freeling (2017). They might, for instance, be preserved by dosage constraints at first (Birchler, 2019) and then selected by environmental stressors in a later period. Also, climate change following the K-Pg boundary was probably not restricted to cold and dark. Indeed, as recent studies suggest, periods of global warming, both at the end of the Cretaceous (Petersen et al., 2016) and during post-impact early Paleogene (MacLeod et al., 2018), might have prevailed.

In short, the paper of Wu et al. (2019) provides an interesting study about how polyploids might have adapted to a changed environment, about 66 million years ago, by the biased retention of genes acting in processes necessary to deal with decreased temperatures and light. If true, WGDs might actually have been instrumental for the survival of species during times of extinction—as suggested before (see Van de Peer et al., 2017 and references therein)—while their diploid progenitors were no longer well-adapted and went extinct.

FUNDING

Z.L. is funded by a postdoctoral fellowship from the Special Research Fund of Ghent University (BOFPDO2018001701).

ACKNOWLEDGMENTS

No conflict of interest declared.

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