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Current Opinion in Plant Biology

Of dups and dinos: evolution at the K/Pg boundary

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Fifteen years into sequencing entire plant genomes, more than 30 paleopolyploidy events could be mapped on the tree of flowering plants (and many more when also transcriptome data sets are considered). While some genome duplications are very old and have occurred early in the evolution of dicots and monocots, or even before, others are more recent and seem to have occurred independently in many different plant lineages. Strikingly, a majority of these duplications date somewhere between 55 and 75 million years ago (mya), and thus likely correlate with the K/Pg boundary. If true, this would suggest that plants that had their genome duplicated at that time, had an increased chance to survive the most recent mass extinction event, at 66 mya, which wiped out a majority of plant and animal life, including all non-avian dinosaurs. Here, we review several processes, both neutral and adaptive, that might explain the establishment of polyploid plants, following the K/Pg mass extinction.

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Current Opinion in Plant Biology 2016, **30**:62–69

This review comes from a themed issue on **Genome studies and molecular genetics**

Edited by **Yves Van de Peer** and **J Chris Pires**

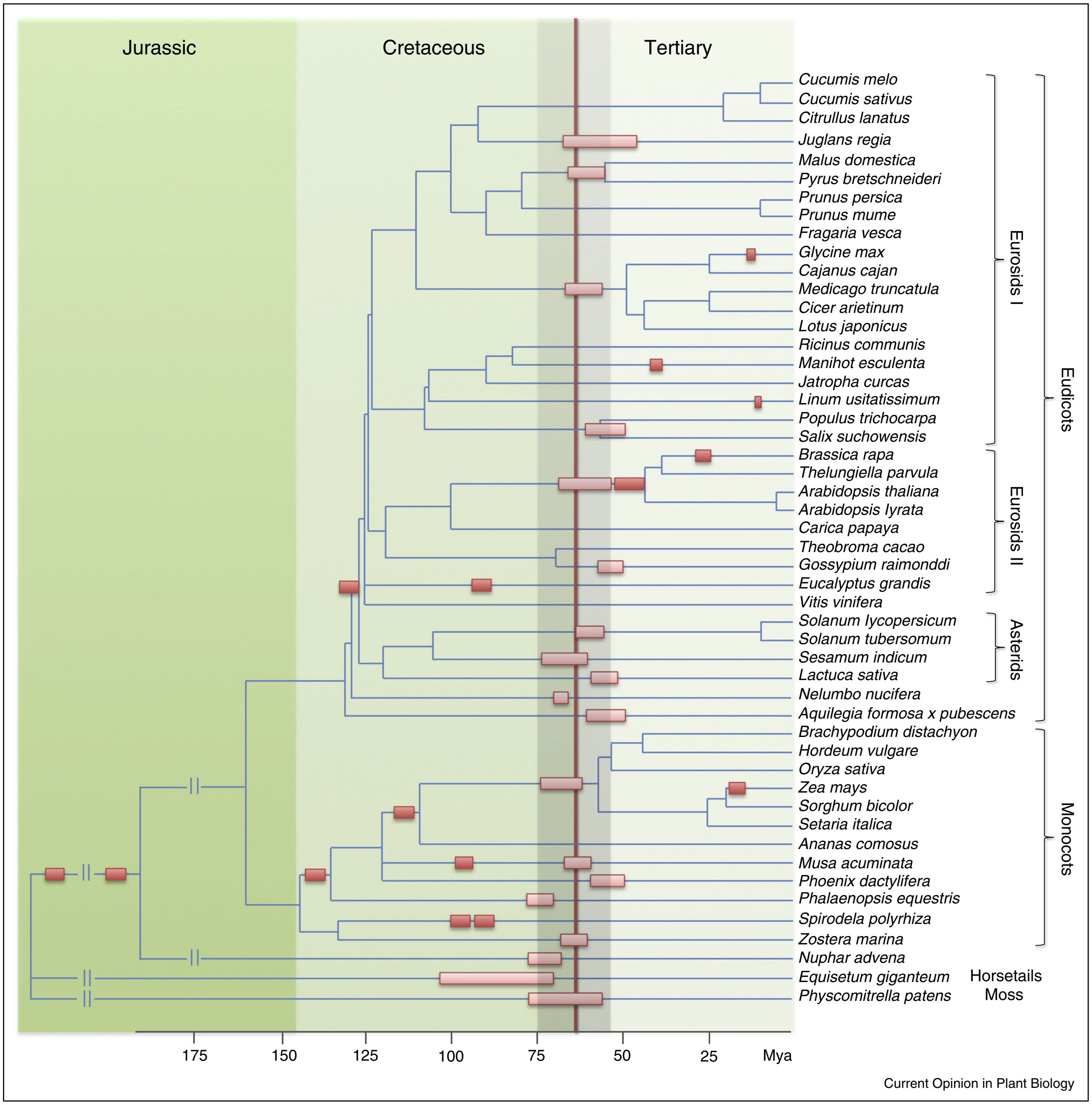
http://dx.doi.org/10.1016/j.pbi.2016.01.006

Analysis of whole genome sequences shows that the long-term establishment of ancient organisms that have undergone whole genome duplications (WGDs, paleopolyploids) has been rare, even for flowering plants, where the majority of ancient WGDs have been observed [1]. Indeed, during the last 150–200 million years of plant evolution, some lineages have experienced maybe four to five WGDs, but most no more than one or two (Figure 1). On the other hand, tens of thousands of now-living species, both plants and animals, are polyploid, and contain multiple copies of their genome. For example, it has recently been estimated that ~43% of the ~3700 Brassicaceae species may be neopolyploids [2]. The apparent paucity of ancient genome duplications and the existence of so many species that are currently polyploid provide an interesting and fascinating enigma. Part of this observation can probably be explained by the fact that because evolutionary relationships form a tree, with most ancient lineages extinct, there are simply fewer places on the 'older' parts of the tree to observe a polyploidy event than on the tips of the tree. It is possible that we see relatively few ancient WGDs because only a few of the lineages that existed at those times have survived to the present for us to observe them. Nevertheless, it remains true that even for plant lineages that have not gone extinct and have existed for a long time, the total number of established ancient WGDs is usually very limited.

Thus, although the prevalence of WGDs has been firmly established, their attributed importance remains controversial [3]. Despite being considered by many as an evolutionary dead end [4,5], at some time in evolution, organisms that have undergone WGDs have unequivocally had an adaptive advantage, because so many descendants share the same duplication event. Well-known examples are for instance ancient genome duplications at the base of the flowering tree [6], but also at the base of the dicots [7], the monocots [8,9], and on branches leading to important plant families [10,11••,12,13].

A question that has received much attention of late is whether these older genome duplications have survived by coincidence or because they did occur, or were selected for, at very specific times, for instance during times of major ecological or environmental upheaval, and/or periods of extinction [3]. Indeed, it has been proposed that chromosome doubling conveys greater stress tolerance by for instance fostering slower development, delayed reproduction, longer life span, and greater defense against pathogens and herbivores. Furthermore, polyploids have also been considered to have greater ability to colonize new or disturbed habitats [14••]. There is thus growing evidence that WGDs might be correlated with so-called major events in evolution. One of the most striking cases is a wave of WGDs in flowering plants at the Cretaceous–Paleogene (K/Pg) boundary [3,11••,15], as outlined in Figure 1. This boundary is marked by a bolide impact near Chicxulub (Mexico) and a possibly impact-induced increase in Deccan flood volcanism (India) [16], which caused, among others, the extinction of all non-avian dinosaurs and massive disruption of plant communities with an estimated extinction of 30–60% of plant species and global deforestation [17,18]. Many of the WGDs

Figure 1



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Schematic tree showing the evolutionary relationship between plants for which the genome sequence has been published. WGDs described in previous studies [9,11••,12,13,84–86] are mapped onto the tree (red and pink rectangles). WGDs estimated between 55 and 75 million years old (shaded area around the K/Pg boundary, red line) are indicated by pink rectangles. See text for details.

clustered around the K/Pg extinction event are at the base of some of the largest and most successful extant plant families suggesting that polyploidy appears to be correlated with plant survival through the K/Pg boundary [3].

Another example of WGDs that might be correlated with decisive moments in plant evolution has recently been described by Estep *et al.* [19••]. These authors showed a wave of allopolyploidizations in C_4 grasses coincident with the worldwide expansion of C_4 grasslands. Grasses using C_4 photosynthesis rose to ecological dominance and displaced C_3 grasslands starting in the Late Miocene, after an earlier decrease of atmospheric CO_2 levels in the Oligocene and a forest-to-C_3-grassland transition in the

Early-Middle Miocene [20]. In the ecologically dominant and economically important grass tribe Andropogoneae (which includes maize (*Zea mays*), sorghum, and sugarcane (*Saccharum officinarum*)), the authors found at least 32% of the ~1200 species to be allopolyploids. More remarkably, these are the result of a minimum of 34 distinct polyploidy events, most of which occurred during the expansion of the C_4 grasslands. Polyploidy hence also seems to be correlated with dominance of C_4 over C_3 grasses and large-scale displacement of the latter [19••]. Other evidence for a major role of polyploidy (alone or in conjunction with hybridization) in plant invasion success has been accumulating in recent years [14••,21–23]. For instance, Pandit *et al.* [24] compared ploidy levels among rare and invasive plant species on a worldwide scale, and found that polyploids are 20% more likely to be invasive than closely related diploids.

Clearly, the correlations of polyploidization with both plant survival at the K/Pg boundary and plant invasiveness in general are related, as the plant survivors of the K/Pg mass extinction event turned into plant invaders and recolonizers of the post-cataclysmic, low-plant diversity environment. The signature of the WGDs that got established around the K/Pg boundary could thus stem from these polyploidization events being linked to plant survival, being linked to plant invasiveness post-survival, or both. In each case, the particular WGDs could have been adaptive, that is, enhancing survival and/or invasiveness, while also more neutral processes could have led to an increase in the production or occurrence of plant polyploids [11••]. Examples of the latter could be environmental stress causing an increase in unreduced gamete formation [25], or contact/overlap between divergent expanding populations or species causing an increase in hybridization and allopolyploid formation. Likely, it has been a (potentially species-specific and environment-specific) mixture of all of the above.

In the following, we elaborate on several processes, neutral and adaptive, that associate WGD with plant survival and/or invasiveness, and which could individually or in combination be responsible for the observed pattern of plant (genome) evolution at the K/Pg boundary. We review some of the supporting evidence and particularly highlight some recent studies that investigate the adaptive role of polyploids in this context using experimental or modeling approaches.

Survival and extinction in devastated plant populations (aka out-surviving dinosaurs)

Polyploidy undoubtedly can have detrimental effects on phenotype, and these have long been recognized [4,26]. For instance, genomic instability, mitotic and meiotic abnormalities, and gene expression and epigenetic changes following polyploidization [27–29] — often collectively termed 'genomic shock' — can lead to increased sterility and decreased fitness, at least for polyploids within stable populations of well-adapted diploid progenitors. Nevertheless, stable polyploids can commonly be found in many natural plant populations because polyploidization occurs at relatively high frequency in plants, and some polyploid lineages do stabilize and avoid immediate extinction [30–34].

During the environmental and ecological upheaval at the K/Pg boundary, existing or naturally occurring polyploids could have had higher survival or lower extinction rates than the existing diploids [3,35]. The massive loss of plant life likely resulted in more fragmented, isolated and small populations, which could suffer from the negative effects of genetic bottlenecks such as increased drift and inbreeding. Polyploidy could have provided several benefits in such populations. An immediate advantage of a newly formed polyploid is the creation of redundant genes, which has the effect that deleterious recessive alleles can be masked [21,36]. This could, at least temporarily, reduce inbreeding depression [37,38]. Gene redundancy could also increase robustness (the buffering of genetic or environmental perturbations), at the gene and/or network level [38–40]. Increased genetic robustness could result in lower genetic load in polyploids compared to diploids, but could also potentially be opposed by the larger mutational target size and by dosage balance constraints once deleterious mutations accumulate [41,42]. That polyploids could have higher fitness in harsh conditions and increased stress tolerance (environmental robustness) has been proposed repeatedly and is supported by a number of studies (reviewed in [14••], see also [43•]), as well as by the observation that present-day polyploids, particularly younger ones, tend to occur more in disturbed environments [44,45]. To which extent environmental robustness is promoted by gene duplicates and/or redundancy or is the result of other mechanisms is, however, unclear. Another characteristic of small populations is that the strength of selection is reduced and thus some deleterious mutations may effectively be neutral. This could result in a smaller disadvantage of polyploids with decreased fitness compared to their diploid progenitors.

Polyploidy is often accompanied with a switch to selfing or apomixis (asexual reproduction) [46,47]. This may increase the chances of polyploids to survive or help avoid extinction for the following reasons. In small populations, strong selection for the most efficient reproductive mode may operate [48,49]; polyploids could be able to respond to such selection, or be selected for if variation in reproductive strategy preexists in the population. Asexual or selfing polyploids may have an advantage if suitable mating partners are scarce, and they would overcome the minority cytotype disadvantage inherent to polyploids [50]. A shift to asexuality or self-fertilization also releases a polyploid from recombination load which could temporarily further reduce its genetic load compared to its diploid sexual progenitors [51], and this in addition to its potential gain in mutational robustness mentioned above.

Existing allopolyploids can exhibit heterosis, or hybrid vigor [29], and fixed heterozygosity, resulting in a strong competitive advantage over diploid progenitors [26], particularly in bottlenecked populations. Several other potential advantages of polyploids over diploids related to enhanced survival in harsh or new conditions have been described, particularly with regard to plant invasiveness (e.g., reviewed in [14••]). Among them are morphological changes leading to, for example, higher seed mass and seedling vigor; niche differentiation, where polyploids favor drier and more open habitats; changes in biotic interactions which may result in, for example, higher pathogen resistance [52,53] or lower insect herbivory in polyploids [54]. There are several examples from the literature on plant invasions that show pre-adaptation of existing polyploids to become invasive, for example, by allowing them to avoid or mitigate founder effects when established in the invasive range, or by possessing simply by chance a divergent phenotype that is close to the optimum under the new environmental conditions [1,14••,23,32]. The underlying mechanisms or processes are the same or similar to the ones outlined above, thus they may be applicable to also facilitate pre-adaptation of existing polyploids to survive in small populations in a drastically changed environment.

(Neutral) drivers of increased plant polyploidization (aka out-duplicating dinosaurs)

Apart from the potential survival benefits that existing or naturally occurring polyploids might have had at the K/Pg boundary, more neutral processes could have contributed to the observed establishment of polyploids by passively or actively increasing the frequency with which polyploids were created. We will briefly review two of these.

Unreduced gamete production is most probably the major mechanism of polyploid formation in plants [30], and it has recently been suggested that it may constitute an evolutionary mechanism for plant speciation and/or stress-response [11••,55••]. A substantial number of studies have documented that environmental stress and/or fluctuations (particularly, heat and cold stress and fluctuating temperatures, but also stresses such as herbivory or disease) trigger increased formation of unreduced gametes [25,30,56,57]. Additional support for this link comes from the discoveries of increased numbers of unreduced fossil gametes from the time of the End Triassic (fossil pollen from an extinct conifer group [58•]) and End Permian extinction events (fossil gymnosperm pollen and lycophyte spores [59,60]). Importantly, unreduced gamete production is a highly heritable trait and genetic variation for the ability to produce unreduced gametes exists for selection to act on [61,62]. These and other [11••,55••] lines of evidence all point to unreduced gamete formation and hence polyploidization as a potential evolutionary survival mechanism in response to environmental and/or ecological disaster. Oswald and Nuismer [32] developed a mathematical model in which polyploids with no intrinsic fitness benefits arise in a diploid population at low frequency. Their results showed that in a rapidly changing but not in a constant environment a higher rate of unreduced gamete formation increased the probability of polyploids to replace their diploid progenitors. Alternatively, or in addition to being increased mechanistically, the relative frequency of unreduced gametes could have also been increased more neutrally at the K/Pg boundary by the more dominant role of genetic drift under small population sizes. In small post-cataclysm plant communities this could have led to (even) higher numbers of unreduced gametes by random chance events, thereby increasing the probability of matings leading to polyploidy [63].

Another, related process that could have resulted in neutrally increased levels of polyploids is intensified hybridization around the time of the K/Pg boundary. The (re)expansion of decimated and fragmented plant populations and (re)colonization of desolated or deforested habitats is likely to have caused both intraspecific and interspecific hybrid formation within new contact zones. Hybridization can lead to (see below) or is at least closely associated with polyploidization, as the latter stabilizes hybrids affected by genomic shock [64], and prevents hybrid sterility or restores sexual reproduction [21]. Consistently, hybridization is common in regions currently affected by plant invasions (e.g., [65,66]), and a recent meta-analysis showed a high percentage of polyploids among invasive and weedy plant hybrids [22]. There is some evidence that suggests that the high rate of allopolyploidizations in C_4 grasses, mentioned earlier, is driven by the expansion of the grasslands which led to hybridizations between divergent diploid progenitor species [19••]. Furthermore, interspecific hybrids themselves have markedly increased levels of unreduced gamete production, thus facilitating allopolyploidization [30], and unreduced gametes are themselves also being involved in hybridization events [55••].

Enhanced evolvability of polyploid plant survivors (aka adaptive blooming in a dinosaur-free world)

Whichever of the processes outlined in the previous two sections generated new, or maintained or increased existing levels of plant polyploids, these polyploids could possess or have an increased capacity to gain adaptive advantages in their stressed, changing or new environment, enabling selection to reinforce or drive polyploid establishment. Such higher adaptive potential of polyploids has long been recognized and discussed [10,14••,26,45,67]. Most explanations center around the creation of genetic variation by WGDs leading to increased phenotypic variability and/or plasticity [68–71], or even to novel phenotypes, for example, more extreme, transgressive ones [72,73]. Under new and challenging conditions, this variation then provides 'fuel' for evolution and could thus result in polyploids having a higher capacity for adaptation than their diploid progenitors. Consequently, polyploidy has been associated with the tolerance of a broader range of ecological and environmental conditions, and increased invasion and colonization success, with some evidence supporting each of these ([24,70]; examples in te Beest *et al.* [14••]). Such attributes could certainly have been advantageous for exploiting a devastated global ecosystem, potentially explaining the clustering of WGDs at the K/Pg boundary, as suggested before [11••,15]. Similarly, the recurrent allopolyploidizations in C_4 grasses could have allowed range expansions and thus driven formation of global C_4 grasslands, one of the most remarkable examples of biome evolution; this is an alternative hypothesis to the opposite, grassland expansions driving polyploidization, as described in the previous section [19••,20].

Two sources of increased genetic variation in polyploids are most commonly recognized: genomic shock (see above) and introgression. Polyploids could also harbor higher levels of pre-existing cryptic or standing genetic variation. WGDs create genetic redundancy, which could lead to an increase in genetic robustness. Both enlarge neutral genotype space and allow for the buildup of cryptic genetic variation [74–77]. Adaptation from such pre-existing genetic variation can be fast (compared to adaptation from new beneficial mutations); for instance, it has recently been shown that selection on standing genetic variation drove early adaptation in flowering time in a colonizing population of (the non-polyploid) Pyrenean Rocket [78].

Direct tests of the hypothesis that WGDs can enhance or accelerate evolutionary adaptation to new or changing environments are difficult to conduct and therefore rare. Selmecki *et al.* [79••] recently used an experimental evolution approach to test the effect of yeast ploidy on the speed of adaptation to a nutrient-limited environment. They found that tetraploid yeast showed significantly faster adaptation than diploid or haploid yeast, and that tetraploidy increased the amount of genetic variation within a population. Using mathematical modeling they attributed the higher rate of adaptation in polyploids to increased frequency and fitness effects of beneficial mutations in these populations, and whole-genome sequencing supported post-WGD genomic instability as one of the sources of these mutations. Another elegant experimental study used field transplant experiments to compare fitness of both wild hexaploid and artificial neohexaploid wild yarrow (*Achillea borealis*) against fitness of wild tetraploid *Achillea borealis* in the hexaploid dune habitat [80]. The results suggest that both WGD per se as well as post-WGD evolution conferred adaptation to the novel dune habitat. Cuypers and Hogeweg [81,82•] developed a computational model of simple metabolic dynamics in a virtual unicellular organism and used population-based simulations to study evolutionary and genomic consequences of WGDs. A major aim was to investigate if WGDs could increase the ability of model organisms to adapt to a wide range of new environments. They found that establishment of WGDs was very common in the initial standard environment before the change, but that only a minority of populations established subsequent WGDs during adaptation to one of the new environments after the environmental change, with establishment of WGDs being particularly rare in rapidly re-adapting populations [82•]. Nevertheless, the authors claim that WGDs did improve the ability of populations to adapt to a changed environment. However, 80% of the majority of populations that did *not* establish WGDs during re-adaptation were equally able to adapt to a changed environment, and often more rapidly. Due to these incongruities and because we believe the experimental design and analysis was inadequate to test the above hypothesis, we feel that the results and conclusions of this study should be treated with caution. For example, in their simulation protocol neither the occurrence, nor the number, nor the timing of WGDs before the environmental change was a controlled independent variable, but any of these could have had an effect on the ability to adapt to the environmental change. More importantly, we also suspect that those few post-change WGDs that did establish in populations and led to a higher adaptability did so almost exclusively only in a specific subset of new environments whose characteristics — high enzyme degradation rates — gave organisms with WGDs a 'built-in' advantage.

Conclusions

Since the origin of the flowering plants, whole genome duplication events have been identified in many different plant lineages. Strikingly however, in many lineages, which are often over a hundred million years old (see Figure 1), we have evidence for only one (sometimes two, rarely three) WGD event(s) that got established in the long term, although many more WGDs must have occurred during the evolutionary past of these lineages. Even more strikingly, in a majority of cases, this WGD event seems to have occurred close to the K/Pg boundary, shaped by the most recent mass extinction event, about 66 mya, which wiped out a major part of plant and animal life, including all non-avian dinosaurs. Apparently, many plants we are so familiar with (or better their ancestors) had or gained a duplicated genome at that time, which gave them a selective advantage compared to their diploid progenitors, who went extinct.

When we first speculated on the tentative link between some of the known paleopolyploidization events in plants and the K/Pg boundary, and suggested that WGD was linked to plant survival around that time [15], this was met with skepticism because of the limited amount of data available at that time, and because dating ancient events that occurred tens of millions of years ago is not trivial. Therefore, we recently revisited this hypothesis using many more whole genome sequences and more sophisticated models of molecular evolution and tree dating, and concluded that our initial findings were confirmed [11••]. We have also considered the possibility whether dating a majority of WGDs between 55 and 75 mya might be due to technical or methodological issues, rather than reflecting true dates of duplication. Although we could show, with statistical support, that the inferred dates for many of the WGDs are clustered in time [11••,15], a correlation between WGDs and the K/Pg extinction would not hold much significance if WGD events in this time window are simply easier to detect than older or younger WGDs, because, for instance, more ancient events are obscured by more recent events, or because more recent events may be hard to distinguish from other genomic duplication processes. However, we do not believe this to be the case. First, both younger and older WGDs have been reported (see Figure 1) based on K_S age distributions from synonymous substitutions and phylogenomic approaches, two inherently different methods that generally do not suffer from the same methodological issues [3,83]. Second, we do have the bioinformatics tools (e.g., for detecting within-genome colinearity) to see, in most cases, whether multiple rounds of whole genome duplications have occurred and/or how duplicates were generated.

Here, we discussed three, not mutually exclusive, groups of processes that could explain this clustering of WGDs around the K/Pg boundary: (1) existing and/or naturally occurring polyploids had higher survival or lower extinction rates, (2) the rate of polyploid formation increased and hence the relative frequency of polyploids and their chance of fixation, and (3) polyploid survivors of the cataclysm had higher post-cataclysm adaptive and/or invasive potential. Thus, both adaptive and more neutral processes likely contributed to promote the establishment of polyploid plants at a time when a catastrophic event of global scale led to a much more challenging and transformed environment.

Acknowledgements

The authors acknowledge the Multidisciplinary Research Partnership 'Bioinformatics: from nucleotides to networks' Project (no. 01MR0310W) of Ghent University and the European Union Seventh Framework Programme (FP7/2007-2013) under European Research Council Advanced Grant Agreement 322739-DOUBLEUP. We apologize to those whose work could not be cited because of space limitations. We also thank two reviewers for their constructive and insightful comments.

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