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Polyploidy: an evolutionary and ecological force in stressful times

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Abstract

Polyploidy has been hypothesized to be both an evolutionary dead-end and a source for evolutionary innovation and species diversification. Although polyploid organisms, especially plants, abound, the apparent nonrandom long-term establishment of genome duplications suggests a link with environmental conditions. Whole-genome duplications seem to correlate with periods of extinction or global change, while polyploids often thrive in harsh or disturbed environments. Evidence is also accumulating that biotic interactions, for instance, with pathogens or mutualists, affect polyploids differently than nonpolyploids. Here, we review recent findings and insights on the effect of both abiotic and biotic stress on polyploids versus nonpolyploids and propose that stress response in general is an important and even determining factor in the establishment and success of polyploidy.

Introduction

Polyploidy, that is having multiple sets of chromosomes as a consequence of whole-genome duplication (WGD), has been studied for over 100 years, especially in flowering plants, dating back to the classic work of Hugo de Vries, Øjvind Winge, Cyril Darlington, and G. Ledyard Stebbins, Jr (Soltis et al., 2014a). Because of the well-known detrimental effects arising from doubling one's entire chromosome set, most WGD events are not successful, as new polyploids are typically not better adapted than their diploid parent(s). Genomic instability, mitotic and meiotic abnormalities, and minority cytotype exclusion (Levin, 1975; Comai, 2005; Madlung et al., 2005; Morgan et al., 2020) are all expected to quickly remove new polyploids from the population.

Nevertheless, there are numerous polyploid organisms around us; even those currently considered diploids usually bear signatures of a polyploid ancestry (Wendel, 2015; Van de Peer et al., 2017). Furthermore, several of these ancestral polyploidy events can be traced back to the origin and diversification of major plant lineages, including angiosperms, core eudicots, monocots, orchids, grasses, composites, and legumes (Van de Peer et al., 2017). The same holds true in animals, such as vertebrates, and fishes (Taylor et al., 2003; Le Comber and Smith, 2004; Dehal and Boore, 2005), suggesting an important role for polyploidy in promoting phenotypic diversity (Soltis and Soltis, 2009; Landis et al., 2018; Leebens-Mack et al., 2019). In fact, polyploidy is now

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generally considered to be a common mode of speciation with far-reaching ecological and evolutionary consequences, not only in plants, but also in many other eukaryotes. In addition, polyploid organisms or polyploid populations are often considered more resilient to extreme environments because of their increased genetic variation and the buffering effect of their duplicated genes, which has led to an increased recognition of the short-term adaptive potential of polyploidy (Van de Peer et al., 2009, 2017; Doyle and Coate, 2019).

The number of extant plant species recognized as polyploids exceeds that of ancient WGDs by several orders of magnitude (Van de Peer et al., 2017), although many additional ancient WGDs continue to be uncovered by applying genomic and transcriptomic deep sequencing methods to more lineages of life (Godden et al., 2019; Leebens-Mack et al., 2019). Nevertheless, because relatively recent (i.e. the last few million years) polyploid species are so prevalent, one might expect to find evidence of substantially more ancient WGDs. The many examples of recurrent polyploidy (Soltis and Soltis, 1999), the existence of many polyploids of fairly recent origin (Barker et al., 2016), and mounting evidence of widespread cryptic polyploid species (Soltis et al., 2007; Laport and Ng, 2017) would appear to contrast with the evidence of relatively few ancient polyploidy events, certainly within the same lineage (Van de Peer et al., 2017; Wong et al., 2020). This result is perhaps not surprising in that polyploidy is prevalent, but not all successful polyploidizations will ultimately lead to major species diversification over the longer term (Arrigo and Barker, 2012; Soltis et al., 2015). Notwithstanding, most plant lineages show evidence for one or few established ancient WGDs (Leebens-Mack et al., 2019; Wong et al., 2020). For example, all extant angiosperms have at least one ancient WGD in their ancestry, with some lineages having experienced several additional rounds of genome doubling over time. What is fascinating, however, is that the establishment or long-term survival of many of these WGDs is not random, but instead coincides with major periods of global climatic/geologic change and/or periods of mass extinction (Van de Peer et al., 2017; Novikova et al., 2018; Cai et al., 2019; Koenen et al., 2020; Wu et al., 2020), i.e. periods of major stress (Figure 1).

The recurring association involving polyploidy, gene duplication, and stress (Doyle and Coate, 2019) is evident at multiple levels and stages. From an agricultural standpoint, duplicated genes resulting from polyploidy appear to have been key to crop domestication and the evolution of stress resistance (Renny-Byfield and Wendel, 2014). It is also well-known that stress can trigger polyploidy (Ramsey and Schemske, 1998); concomitantly, there are also strong indications that polyploidy confers a selective advantage under stressful or changing environmental conditions (Van de Peer et al., 2017). Moreover, an increasing number of studies describes how biotic stress and interactions with, for instance, pathogens and herbivores, affect polyploids in different ways than their related diploids (Hannweg et al., 2016;
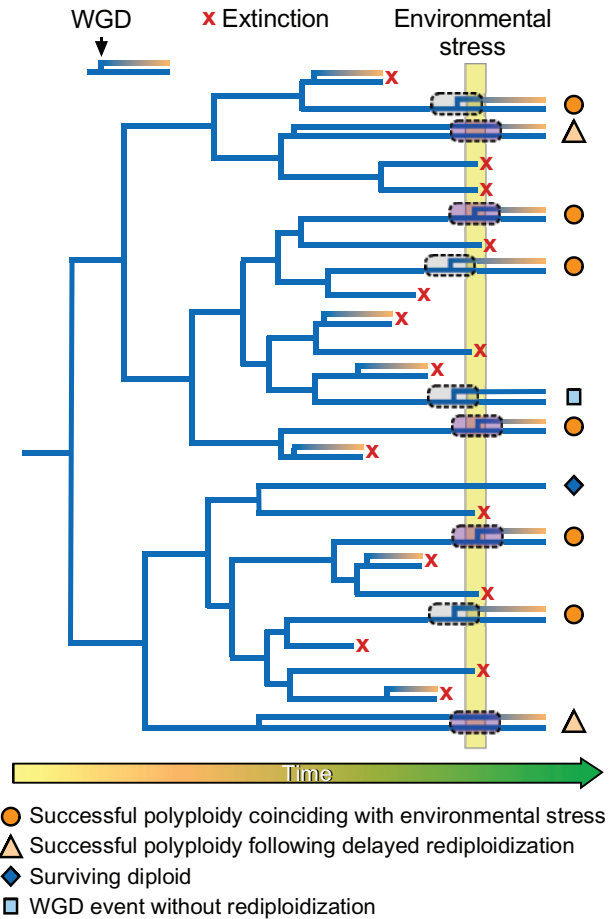

Figure 1 The nonrandom establishment of WGDs. Red crosses represent extinction, while orange circles represent successful polyploidy coinciding with environmental stress, and light orange triangles represent successful polyploidy following delayed rediploidization [responsible for lag times between the WGD event and its exerted effects {Schranz et al., 2012; Robertson et al., 2017}]. The dark blue diamond represents a diploid having survived environmentally challenging conditions. The two branches descending from a WGD event represent the duplicated genome, while the changing color in one branch denotes the divergence (and diploidization) of the subgenomes. Gray squares represent WGDs that coincide (purple) or seem to coincide (light gray) with a period of global change or extinction. If polyploidy by itself (without rediploidization, functional divergence of genes, or rewiring of networks) enables evolutionary innovation (e.g. through short-term gene expression changes, epigenetic remodeling), WGDs might become established even in the absence of rediploidization (represented by the light blue square). See text for details.

Hias et al., 2018). In addition, cellular polyploidy (endoreduplication) is an induced response to stress in normally diploid organisms that may mitigate the effects of stress (Pacey et al., 2020a; Zedek et al., 2020).

In this Review, we discuss the connection between polyploidy (both auto- and allo-polyploidy) and stress, both in terms of formation and survival. We emphasize current views on how polyploidy might confer an advantage when dealing with both abiotic and biotic stress. By stress, we mean strain on an organism resulting from adverse or

demanding circumstances and more specifically environmental factors that cause stress, including abiotic factors (e.g. soil, temperature, water availability) and biotic factors (e.g. predators, pathogens). We highlight recent studies that provide a better understanding into how and why polyploids might better adapt to changing environments, why they might be able to escape periods of extinction better than diploids, and why they respond to biotic agents differently than diploids. We will not discuss—at least not in any detail—the many different ways in which gene or genome duplicates can evolve novel gene functions (neofunctionalization) or acquire tissue-specific or temporally segregated functions (subfunctionalization), how remnants of ancient duplication events can be discovered, and how a polyploid genome undergoes fractionation and diploidizes. We will instead refer the reader to several excellent publications on these topics (e.g. Wolfe, 2001; Taylor and Raes, 2004; Van de Peer, 2004; Conant and Wolfe, 2008; Blischak et al., 2018; Mandakova and Lysak, 2018; Wendel et al., 2018; Doyle and Coate, 2019).

Polyploidy and the stress connection

Polyploidy and abiotic stress

Signs from the past

WGD is often considered an evolutionary dead-end, particularly under stable conditions (Comai, 2005; Oberlander et al., 2016; Van de Peer et al., 2017; Figure 1). However, ancient WGDs are not randomly distributed over time, but rather appear to overlap with periods of dramatic global change, the most apparent of which coincides with the Cretaceous-Paleogene boundary (K-Pg; Fawcett et al., 2009; Vanneste et al., 2014; Cannon et al., 2015; Levin and Soltis, 2018; Koenen et al., 2020). Several possible explanations come to mind. First, the opportunity for the formation of new polyploid species might increase subsequent to a cataclysmic event. It has long been recognized that the levels of unreduced gametes can increase in response to external stimuli, such as environmental stress (Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998). A high frequency of unreduced gametes is associated with temperature stress in fish and amphibians (Mable et al., 2011), and particularly in plants (Ramsey and Schemske, 1998; Mason et al., 2011; Pecrix et al., 2011; De Storme et al., 2012). The effect of stress on unreduced gamete formation is not limited to present-day plants. Indeed, increased levels of unreduced pollen from fossil plants were observed at the Triassic–Jurassic transition, which corresponds to the fourth of the five major extinction events (Kurschner et al., 2013), while abnormal gymnosperm pollen (Foster and Afonin, 2005) and lycophyte spores (Visscher et al., 2004) have been reported during the Permian–Triassic transition, corresponding to the third major extinction event. Second, during stressful times or during times of mass extinction, WGDs have an elevated probability of successful establishment because of increased mutational robustness as well as increased genetic and epigenetic variation, in turn raising the adaptive potential of a polyploid species. The buffering effect against (deleterious) mutations, altered gene expression, epigenetic remodeling, sub-, and/or neofunctionalization, and/or the rewiring of more complex gene regulatory networks (GRNs) following WGD can subsequently provide a selective advantage to the new polyploid in a changed environment, possibly through the derivation of novel traits. In both cases (the origin of new polyploids and the persistence of polyploid lineages), the dating of WGD events will coincide with the period of environmental change (Figure 1). However, for autopolyploids, Robertson and co-authors suggested that delayed diploidization might explain "lag-times" between the occurrence of WGDs and their potential effects (Robertson et al., 2017). Delayed diploidization occurs as long as any two of the four chromosome sets resulting from a WGD pair randomly during meiosis, leading to recombination between them and thus preventing sequence and functional divergence between homoeologs (also called ohnologs). Consequently, homoeolog divergence as well as the potential for evolutionary innovation is also delayed (Figure 1). Only during or after chromosomal diploidization (leading to disomic inheritance) can the subgenomes start to diverge (as do their genes), causing a putative evolutionary effect or selective advantage of WGD. Therefore, the "Lineage-specific Ohnolog Resolution" or "LORe" model may provide a plausible framework to explain how the functional and evolutionary outcomes of genome doubling, and particularly its contribution to extinction avoidance, may be constrained from arising for millions or tens of millions of years after the WGD event (Schranz et al., 2012; Robertson et al., 2017). Thus, WGDs with delayed diploidization, as predicted by the LORe model, may be predicted to be quite a bit younger than they actually are, namely at the age they exert an effect—e.g. during environmental turmoil—rather than at the time they occurred. Therefore, the so-called "waves" of ancient polyploidy, coinciding with challenging or stressful conditions, might also be artificially enriched with WGDs (Figure 1).

Several other, more recent epoch boundaries have also been proposed to align with periods of extensive WGD (Estep et al., 2014; Kagale et al., 2014; Huang et al., 2016; Novikova et al., 2018; Cai et al., 2019; Sessa, 2019). Analysis of WGD events across seed plants (Leebens-Mack et al., 2019) indicates multiple waves of genome doubling corresponding not only to the K-Pg, but also the Middle Miocene Disruption as well as the Paleocene–Eocene Thermal Maximum (Soltis and Landis, unpublished data). The clustering of polyploidy events in association with worldwide, geologically significant events seems to affirm the importance of environmental conditions in the promotion/survival of polyploidy (Levin, 1983; Soltis and Soltis, 2014; Doyle and Coate, 2019).

Signs from the present

The close relationship between stress and polyploidy is also supported by present-day polyploids; there is a long history

of association between polyploidization and abiotic stress, particularly adaptation to extremely dry and cold environments (Stebbins, 1949; Ehrendorfer, 1980; Levin, 1983; Folk and Soltis, 2020; Lourkisti et al., 2020). Numerous studies have suggested an association between dry habitats and polyploidy across diverse lineages of land plants, with polyploids occupying drier habitats than observed for the diploids in those same clades (te Beest et al., 2012; Gunn et al., 2020). Polyploidy increases in frequency from the equator to the poles (Rice et al., 2019); within the Arctic, the frequency of higher order polyploids increases with latitude (Brochmann et al., 2004). In the context of adaptation to drought stress, genome doubling has been shown to lead to changes in transpiration, water use efficiency, photosynthetic rate, phenology, antioxidant response, and morphology (Maherali et al., 2009; Deng et al., 2012; Soltis and Soltis, 2014). For example, naturally occurring tetraploid Arabidopsis (*Arabidopsis thaliana*) plants exhibit increased salt tolerance compared to diploids (Chao et al., 2013). Both tetraploid rice (*Oryza sativa*) and citrange (*Citrus sinensis* L. Osb. x *Poncirus trifoliata* L. Raf.) have an increased tolerance to salt and drought stress as a result of WGD, which affects the expression of genes involved in stress and phytohormone response pathways (Yang et al., 2014b; Ruiz et al., 2016). Similarly, tetraploid rootstock-grafted watermelon (*Citrullus lanatus*) plants are more tolerant to salt stress than are diploid plants (Zhu et al., 2018). Although the physiological, cellular, and genomic responses to stress are more frequently documented for polyploids (see further), the exact molecular processes underlying these responses still remain to be discovered (Fox et al., 2020).

Polyploidy and Stress, a Universal Connection?. Higher abiotic stress tolerance has also been demonstrated in fungi and animals. For instance, experimental evolution studies in yeast (*Saccharomyces cerevisiae*) have shown that genome duplication can confer a fitness advantage during stressful conditions (Selmecki et al., 2015). Diploid frog species of the genus *Neobatrachus* are currently geographically isolated, whereas tetraploid *Neobatrachus* species can occupy harsher environments and are distributed more widely across Australia; polyploidy-mediated gene flow and hybridization may promote the adaptive advantage of the tetraploids in the face of climate change (Novikova et al., 2020). Another example involves the initial establishment and subsequent radiation of polyploidy in cyprinid fish, likely triggered by environmental and climate changes associated with the uplift of the Tibetan Plateau. Moreover, uniquely retained homoeologous genes that confer adaptation to harsh environments were identified (Li and Guo, 2020). WGD in an ancestor of the giant African snail (*Achatina immaculata*) was estimated to have occurred ∼70 Mya, possibly coinciding with the K-Pg extinction event (Liu et al., 2020). Although terrestrial adaptation of these snails was initiated before WGD, specific homoeologs encoding hemocyanins, involved in O_2 transport, and genes involved in gluconeogenesis were retained after WGD, enhancing the capacity for gas exchange and glucose homeostasis in aestivation (animal dormancy during a dry or hot season). WGD may have facilitated terrestrial adaptation by increasing the survival rate in the stressful transition from water to land (Liu et al., 2020).

Polyploidy and biotic stress
Plant–antagonist interactions

Aside from abiotic stress, organisms experience biotic stress in various forms, including attacks by pathogens, predators, or herbivores, and competition with other species of the same trophic level. Changes in anatomical structures, growth regulators, and other physiological processes associated with WGD are predicted to alter these interactions and may increase the ability of a polyploid to resist or tolerate damage, or to garner shared resources. For instance, models predict that polyploidy can increase resistance within the gene-for-gene systems that underlie many host–pathogen interactions or where genotype × genotype interactions are important (Oswald and Nuismer, 2007). In a test of this model, synthetic neopolyploids of a monogenic resistant apple cultivar (*Malus × domestica*) exhibited increased resistance to apple scab (*Venturia inaequalis*) compared to diploid cultivars (Hias et al., 2018). Another study found that synthetic tetraploid garden impatiens (*Impatiens walleriana*) showed improved resistance to downy mildew (*Plasmopara obducens*) relative to diploid plants (Wang et al., 2018b). Similarly, Hannweg et al. found that synthetic tetraploids of the Livingstone potato (*Plectranthus esculentus*) were more resistant to root-knot nematodes than diploids (Hannweg et al., 2016). Comparable findings have been reported in animal systems. In experimental (bath) inoculations of diploid and triploid Atlantic salmon (*Salmo salar* L.) with salmonid alphavirus, symptoms of the disease appeared more slowly in the triploids than in the diploids, although there was no difference in viral loads between ploidies (Moore et al., 2017). Interestingly, Harms et al. (2020) found in lab bioassays that triploid genotypes of the Eurasian wetland weed, *Butomus umbellatus*, had larger leaf lesions than diploids in response to several pathogens (Keane et al., 2014), indicating their lower resistance compared to diploid genotypes, although in the field triploids had ∼50% lower disease incidence than diploids, suggesting that plant–pathogen interactions may be modified by climatic differences in pathogenicity or in the regional pool of pathogens. Pathogens themselves may also shift ploidy during infections, such as with *Phytophthora infestans* that led to the Great Irish potato famine (Li et al., 2017) or, more recently, a pathogen that increasingly infects European honeybees (Peters et al., 2019), evoking the possibility for ploidy-driven coevolutionary dynamics.

Increased abiotic tolerance exhibited by polyploids may make them better competitors than diploid relatives, especially under limited resources or marginal habitats (Segraves, 2017; Baduel et al., 2018; Harms et al., 2020). For instance, while triploid genotypes of the Eurasian wetland weed, *Butomus umbellatus*, were more poorly adapted than

diploids under some conditions, Harms et al. concluded that their increased root: shoot ratios made them better-adapted competitors than diploids over several years (Harms et al., 2020). In a 5-year study in China with diploid, tetraploid, and hexaploid canadian goldenrod (*Solidago canadensis*), polyploidization and rapid evolution post-introduction contributed to increased competitive ability in polyploids and influenced the outcome of community succession (Wu et al., 2019).

Biotic interactions can ameliorate stress

How plants respond to abiotic stresses such as drought or limited essential nutrients, or to biotic stresses such as pathogens and herbivores (Figure 2), may be mediated by mutualistic interactions with bacteria (e.g. rhizobia that inhabit root nodules) and fungi (e.g. root-associating mycorrhizae or leaf endophytes; for review, see Acuna-Rodriguez et al., 2020). If polyploids have enhanced interactions with mutualists, they may then be able to tolerate stresses that their related diploids cannot. In this way, mutualisms may

also contribute to polyploid success by enabling or reinforcing abiotic niche differentiation from diploids. For instance, theory shows that increasing mutualistic partner breadth can expand the range of abiotic tolerances for a species (Batstone et al., 2018) and thus may facilitate the ability of a polyploid to differentiate its abiotic niche from that of diploids (a potential prerequisite for polyploid speciation (Thompson and Lumaret, 1992). Moreover, if polyploids modify the local soil microbiome in ways that feed back to enhance their own growth, but not that of diploids, they may amplify their own persistence while suppressing other species, as predicted by niche construction theory (Albuquerque et al., 2019).

Polyploidy may increase quantity or quality aspects of mutualistic associations (Powell and Doyle, 2016; Anneberg and Segraves, 2019; Forrester and Ashman, 2020). For instance, during legume–rhizobium interactions, bacteria fix atmospheric nitrogen into a metabolizable form for the plant in exchange for carbon provided by the plant within root nodules (Figure 2, A and B). Ancient polyploidy is hypothesized
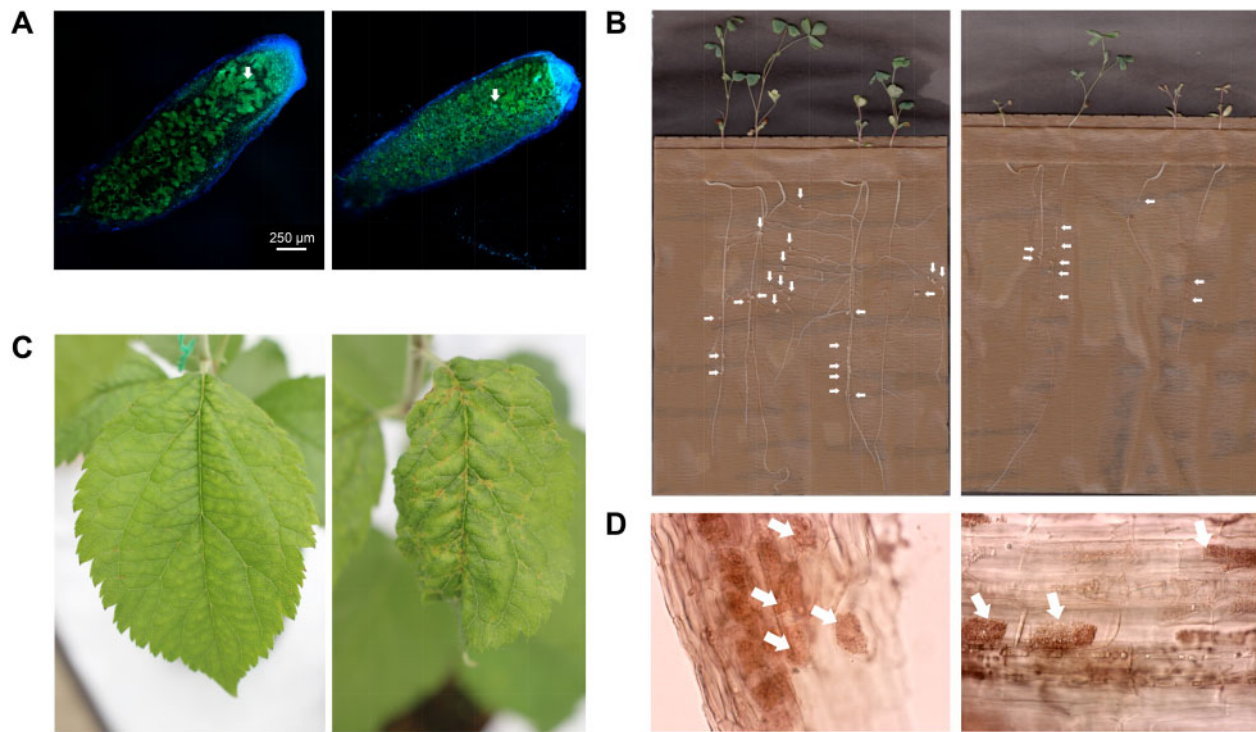

Figure 2 Representative examples of the effects of polyploidy on mutualistic and antagonistic species interactions. (A, B, and D), Examples of mutualistic interactions. (C), Antagonist interaction. (A) Root nodules of synthetic neotetraploid (left) and diploid (right) alfalfa (*Medicago sativa* subsp. *caerulea*) inoculated with rhizobia (Forrester and Ashman, 2020). The autotetraploid plants produced nodules that were 20% larger than diploids and these housed symbiosomes—each with enlarged bacteroids (white arrows)—that were nearly twice the size of those present in diploids. Nodules are stained with SYTO 13 bacteroid fluorescence is depicted in green and plant autofluorescence in blue, 10× lens was used for viewing. (B) Tetraploid (left) alfalfa subsp. *sativa* and diploid (right) alfalfa subsp. *caerulea* showing root nodule production (Forrester et al., 2020). Autotetraploid alfalfa produced more than twice as much total root nodule biomass (white arrows pointing to individual nodules) than diploids, and this leads to higher shoot biomass. (C) Tetraploid (left) and diploid (right) apple (*Malus × domestica* cultivar G58) response to infection by the ascomycete fungus *Venturia inaequalis* causing apple scab disease (Hias et al., 2018). Visual symptoms and PCR quantification of *V. inaequalis* decreased in the neotetraploid relative to its diploid progenitor. (D) Tetraploid (left) and diploid (right) poker alumroot (*Heuchera cylindrica*) roots colonized by mycorrhizae fungal arbuscules (the nutritional-exchange structures; Anneberg and Segraves, 2019). Tetraploids show higher colonization rates, as measured by total arbuscules (arrows pointing to arbuscules in each image) than diploids. 200× magnification. Photo credits: (A and B) N. Forrester, (C) N. Hias, and (D) T.J. Anneberg.

to have enhanced this mutualism by increasing the diversity of signaling factors that function in the establishment and maintenance of the interaction in legumes having this symbiosis (Doyle, 2011; Powell and Doyle, 2016, 2017). Changes in root architecture induced by recent polyploidy can also enhance infection rates and increase the total number of nodules produced and number of nitrogen-fixing bacteria hosted (Forrester and Ashman, 2020). Moreover, the "gigas" effect of polyploidy (Stebbins, 1971) can immediately increase nodule size and expand the internal interface for nutrient exchange, as evidenced in synthetic (neo) tetraploid alfalfa subsp. *caerulea* (Forrester and Ashman, 2020; Figure 2, A and B). Such an effect can increase the efficiency of nitrogen fixation by rhizobial symbionts and thus the amount of nitrogen provided to the plant (Forrester and Ashman, 2020). Lastly, in a test of whether polyploids associate with a wider range of mutualists or gain greater benefits from those with which they do associate, Forrester et al. (2020) exposed diploid and tetraploid alfalfa lineages to a range of bacterial symbionts and found similar niche breadth, but observed that tetraploids attained greater fitness enhancement and maintained this over a larger range of symbionts than diploids.

Root–mycorrhizae associations are widespread and aid plants in obtaining phosphorus, tolerating drought, and provide resistance to root pathogens. Although only recently a focus of study, a positive effect of polyploidy on mycorrhizae colonization has been observed in some cases (Anneberg and Segraves, 2019). In particular, in poker alumroot, tetraploids displayed greater colonization by fungal hyphae and arbuscules, the nutrient exchange structures, than their diploid progenitors (Anneberg and Segraves, 2019; Figure 2D). Although other types of mutualisms (e.g. plant-growth-promoting bacteria in the rhizosphere) are known to assist plant tolerance to stresses such as salt, heavy metals, or pathogens (Rilling et al., 2019) and ploidy-mediated changes in root exudates are predicted to modify these communities (Segraves, 2017), knowledge of how polyploidy affects these processes is lacking. Interestingly, while stress tolerance is often noted as a pathway to invasion for polyploids, potentially accounting for their predominance as invasive species (te Beest et al., 2012; Baduel et al., 2018), another mechanism may be through suppression of the soil microbiome beneficial to natives (Inderjit and Cahill, 2015) via allelopathic root exudates. Whether invasive polyploid plants are especially adept at these remains to be seen. In a 5-year study of diploid and polyploid goldenrod, soil from plots previously inhabited by diploids was significantly different in terms of nutrients, microbes, and soil nematodes relative to soil inhabited by tetraploid or hexaploid plants (Wu et al., 2019), suggesting that polyploidization can affect rhizosphere processes. If these changes in the rhizosphere feed back to benefit the polyploid, they may facilitate polyploid invasion and persistence.

Finally, if the ability of polyploids to tolerate stresses increases through either direct physiological effects or through indirect effects via altered mutualistic interactions

or soil biota feedbacks, this increase may change the entire network of species interactions within the community and thus have cascading effects on community structure and resilience (Segraves, 2017). Because communities are the building blocks of ecosystems, and polyploids dominate in some ecoregions more than others (Rice et al., 2019), these changes in stress tolerance may impact nutrient cycling at the level of global biomes. Polyploidy may be selected to enhance mutualisms between animals and other organisms (including those that are not related to abiotic stress). For instance, changes in flower size with polyploidy can lead to more or unique interactions with pollinators (see Roccaforte et al., 2015) that will cascade to affect the structure of the community more broadly. Community-level effects that can be traced to stress response, however, remain another poorly studied area in the broad realm of polyploidy consequences. Nevertheless, the above studies and discussions present intriguing evidence that polyploidy can ameliorate biotic stress, but also illustrate the context-dependency of outcomes of biotic antagonistic and mutualistic interactions.

Stress-induced cell-level polyploidy

Endoreduplication, the result of cell cycle activation without mitosis, leads to tissue-level polyploidy in an otherwise diploid organism (Neiman et al., 2017). Cells that are endopolyploidized often have specific and programmed roles during normal development (Schoenfelder and Fox, 2015; Kolarčik et al., 2020). In plants, well-known examples of specialized endopolyploid cells include fibers and leaf hairs (De Veylder et al., 2011). Endoreduplication has also been proposed to be a plastic response to mitigate the effects of stress (Scholes and Paige, 2015; Bhosale et al., 2018) that may be heritable, and thus a potential target for natural selection. Endoreduplication within plant cells is stimulated by abiotic stresses (e.g. high UV, low temperature, drought, or soil contaminants; Scholes and Paige, 2015) and antagonistic biotic interactions (e.g. disease or herbivory; Smant et al., 2018; Paige, 2019), but also by mutualistic interactions that involve damage to tissues (mycorrhizal fungi and nitrogen-fixing rhizobia, Carotenuto et al., 2019). In animals, endoreduplication is stimulated by damage (e.g. induced wound healing in *Drosophila melanogaster* epithelium; Losick et al., 2013) and predation (e.g. production of inducible defenses in *Daphnia*; reviewed in Neiman et al., 2017), but can also be common in secretory or growing tissues (Neiman et al., 2017). Endoreduplication, by increasing cell size, as well as gene copy number and thus gene expression or flux through metabolic pathways, may allow for a rapid response to stress (reviewed in Neiman et al., 2017; Paige, 2019). Notably, in response to various biotic interactions that involve penetration of the plant tissue, endoreduplication results in the upregulation of some host genes that normally regulate cell cycle and cellular hypertrophy, suggesting that the involved effectors are generic reactions to cell stress (Smant et al., 2018). In symbiotic interactions, endoreduplication also functions as a means for differentiation and specialization; for instance, both plant and rhizobial symbionts undergo

endoreduplication during nodulation. Indeed, many of the ploidy-related changes in the epigenome in root nodules that house nitrogen-fixing rhizobia are nodule-specific in function (Nagymihaly et al., 2017). Thus, endoreduplication may enhance plant fitness both by mitigating injury and fostering mutualisms, but such plasticity may come with a trade off to whole-organism ploidy (Neiman et al., 2017; Pacey et al., 2020b).

Mechanistically, how can polyploidy mitigate stress?

Physiological and cellular responses to stress

One of the best-known effects of WGD is to increase cell size (Bennett, 1972; Doyle and Coate, 2019). However, the effects of WGD on cell biology are complex and the underlying molecular and physiological mechanisms, as well as the resulting acquired adaptive changes, remain elusive. In some studies, the differences between diploids and polyploids in response to temperature, drought, or salinity stress are attributed to differences in leaf anatomy and/or transpiration rate. For instance, autotetraploid birch (*Betula platyphylla*) seems better able to maintain water pressure under drought conditions, which is attributed to anatomical differences in leaves. Li et al. observed that polyploids have fewer stomata per unit area, while they also have thicker upper and lower epidermises and more pubescence, which all tend to reduce water loss (Li et al., 1996). Further in birch, Zhang et al. (2016) noticed remarkably different pit-level anatomical traits in polyploids, favoring greater hydraulic safety than their congeneric diploid species and likely contributing to an overabundance of polyploid birch in more stressed habitats. However, the opposite has also been observed. Analysis of leaf anatomy in fireweed (*Chamerion angustifolium*) revealed morphological adjustments for tolerating water deficiency in diploids in the form of closely packed mesophyll cells and small conduits in the midvein, making diploid *C. angustifolium* more tolerant to drought than hexaploid plants (Guo et al., 2016).

In Arabidopsis, alterations in cell proliferation and organ size in tetraploids potentiate plant tolerance to salt and drought stresses and decrease transpiration rate, likely through controlling stomatal density and closure, abscisic acid (ABA) signaling, and reactive oxygen species (ROS) homeostasis (del Pozo and Ramirez-Parra, 2014). Indeed, transcriptome deep sequencing (RNA-seq) analysis revealed that the expression of genes involved in redox homeostasis, ABA and stress response was affected (del Pozo and Ramirez-Parra, 2014). In Japanese honeysuckle (*Lonicera japonica*), water stress decreased net photosynthesis rate, stomatal conductance, and transpiration rate of both diploid and tetraploid cultivars. Water stress also decreased electron transport rate, effective quantum yield of photosystem II, photochemical quenching, and starch content, but increased nonphotochemical quenching and contents for total soluble sugars, proline, and malondialdehyde (Li et al., 2009). However, tetraploid *L. japonica* showed higher resistance to water stress than diploid species, and physiological responses were less affected in the tetraploid than the diploid. Morphological and anatomical analysis further revealed that the tetraploid had a smaller total plant leaf area, higher leaf mass per unit area, thicker epidermis and palisade tissue, as well as denser pubescence. The suite of specialized structures altered by WGD likely led to greater capacity in dealing with drought stress (Li et al., 2009).

Hexaploid bread wheat (*Triticum aestivum*) is generally more salt tolerant than its tetraploid progenitor emmer (*Triticum turgidum*). After allohexaploidization, hexaploid wheat acquired a stronger capacity to retain sodium ions (Na^+) within its roots, likely contributing to its higher salt tolerance (Yang et al., 2014a). Similarly, polyploid Arabidopsis accessions are more tolerant to salt stress and better mediate potassium (K^+)/Na^+ homeostasis under saline conditions than their respective diploid progenitors (Chao et al., 2013). However, the reasons behind this ploidy-determined differential K^+/Na^+ homeostasis regulation are still largely unknown. Compared to its diploid ancestor, hexaploid morning glory (Ipomoea trifida) efficiently prevents K^+ efflux from the meristematic root zone under salt stress through plasma membrane K^+ permeable channels, which have low sensitivity to ROS like hydrogen peroxide (H_2O_2). Moreover, hexaploid *I. trifida* efficiently excludes Na^+ from the elongation and mature root zones under salt stress, because of the high sensitivity of plasma membrane calcium ions ($Ca2^+$) permeable channels to H_2O_2 (Liu et al., 2019b). However, additional studies are required to unravel the molecular mechanisms underlying this highly cell type-specific ion transport in the roots of hexaploid *I. trifida* (Liu et al., 2019b).

It remains to be seen to what extent commonalities—with respect to morphological and physiological alterations—exist for different cells and cell types and/or different organisms after polyploidization (Fox et al., 2020). In addition, further studies are necessary to explore the exact molecular and genetic mechanisms shaping condition-dependent morphological and physiological changes in polyploid species.

The genomic response to stress
Long(er) term effects

The reasons for a close relationship between stress and polyploidy have been the subject of considerable speculation, and several hypotheses have been proposed. As stated earlier, most polyploids arise through the formation of unreduced gametes (Ramsey and Schemske, 1998; Mable et al., 2011; Bomblies and Madlung, 2014). However, while increased formation of polyploids in response to stress is one thing, surviving major global change or cataclysmic events is another thing entirely. The K-Pg extinction event likely resulted from a combination of factors, including increased volcanism and in particular the impact of an asteroid near Chicxulub in the Yucatan peninsula (Mexico; Renne et al., 2015). These cataclysmic events ejected dust, sulfate

aerosols, and soot particles into the atmosphere, which affected photosynthesis and seed germination during a time of prolonged darkness and dropping temperatures (Vellekoop et al., 2016), resulting in the extinction of up to 70% of all plant species (Nichols and Johnson, 2008). Research suggests that transcription factors with functions in mediating responses to low temperature and shade avoidance, the two main stresses resulting from the K-Pg extinction event, were preferentially retained following WGDs at the K-Pg boundary (Wu et al., 2020). If this finding is correct, the expansion of specific gene families and the resulting dosage effects, or sub- or neofunctionalization of new genes, may have facilitated adaptation to these greatly changed conditions. Biased retention of, in particular, genes with regulatory and developmental functions subsequent to WGDs has been known for many years (Blanc and Wolfe, 2004; Maere et al., 2005) and has been considered by some a mere regulatory or developmental spandrel, a byproduct of the WGD (Freeling, 2009; Birchler and Veitia, 2012). Transcription factor genes, signal transducer genes, developmental genes, and genes encoding proteins that act in multiprotein complexes are retained, not necessarily because of an immediate selective advantage, but mostly because they are important to maintain stoichiometry or gene balance (Freeling, 2009; Birchler and Veitia, 2012; Song et al., 2020). However, given sufficient time, genes can evolve novel functions, facilitating adaptation to the changed environment.

Recent work using an agent-based computational framework built to simulate biological evolution suggested that artificial nonpolyploids perform better than polyploids under stable environments, whereas the opposite holds for unstable or "stressed" environments (Yao et al., 2019, see also Cuypers and Hogeweg, 2014). The evolutionary trajectories of individual genomes in terms of sequence and encoded GRNs were interpreted as follows. Random mutations cause changes in the genome and its associated GRNs. This phenomenon is expected to be amplified in more complex GRNs, such as those arising from WGD, featured by a duplicated number of nodes (i.e. genes or alleles) and an exponential increase in the number of edges (i.e. interactions). Therefore, under stable environments, such random mutations in polyploid genomes will propagate widely throughout the network and will often be maladaptive or detrimental. In contrast, in unstable or stressful environments, these (bigger) changes or disturbances in GRNs may actually provide the substantive changes necessary for survival (Yao et al., 2019; Carretero-Paulet and Van de Peer, 2020).

Duplication of entire genomes and their GRNs immediately creates redundant modules in the genome. Modules are represented by subnetworks within the global GRN that are formed by highly connected genes that are co-expressed and/or co-regulated by the same set of key regulators, while establishing sparser connections with genes from different modules (De Smet and Van de Peer, 2012; Clune et al., 2013; Espinosa-Soto, 2018). There are different ways redundant

modules created through WGD may facilitate evolutionary innovation and rapid adaptation to novel environments. First, network redundancy after WGD may help buffer against deleterious mutations, contributing to the genetic or mutational robustness of the organism (Keane et al., 2014). Second, by increasing the absolute dosage of all genes in a pathway (but see Song et al., 2020), WGD can lead to increased fitness under conditions that require elevated fluxes for certain pathways (Van Hoek and Hogeweg, 2009; Bekaert et al., 2011; Hudson et al., 2011; Wu et al., 2020). Third, the probabilities of rewiring biological networks formed by multiple connected genes into specialized metabolic, regulatory, or developmental pathways increase if all involved genes are duplicated together by means of WGD and co-evolve partitioned subfunctions, such as interaction partners or expression domains. This pattern, designated as network subfunctionalization (Blanc and Wolfe, 2004; Conant et al., 2014), has been demonstrated in plants (De Smet et al., 2017). Similarly, modularity increases the probability of rewiring newly duplicated networks into novel biological pathways, a pattern consistent with network neofunctionalization (Sato et al., 2012; Edger et al., 2015; De Smet et al., 2017). The complex and modular structure of duplicated GRNs allow both a wider and faster exploration of phenotypic space and resulting fitness landscapes, ultimately offering increased possibilities for evolutionary innovation and adaptation in a (rapidly) changing environment. Finally, in autopolyploids, each gene is not truly duplicated in a genetic sense, but rather acts as a single locus with up to four alleles segregating within each individual subgenome (tetrasomic inheritance). Although this is different from allopolyploids, the end effects might be very similar. Just as there will be higher gene dosage in autopolyploids because of the additional production of gene products because of the duplication of alleles (Song et al., 2020), there is an increase in the number of edges and nodes, whether between genes or alleles. Of course, one might argue that the effects described above may be different (and perhaps stronger) for allopolyploids, where there are two completely independently evolving loci, and thus less homogenization through recombination, but this needs further study.

Short-term effects

Although some of the processes described above (rewiring of GRNs, sub- or neofunctionalization of genes and networks) take time to exert an effect, genetic variation can also increase immediately upon polyploidization, through the combination of parental genotypes, changes in gene expression, genomic shock, and by epigenetic remodeling (Renny-Byfield and Wendel, 2014; Soltis et al., 2015; Panchy et al., 2016; Van de Peer et al., 2017; Wendel et al., 2018; Qiu et al., 2020). The degree of genomic and transcriptomic changes following WGD is lower in autopolyploids than in allopolyploids, but is highly variable both within and between species in both polyploid types (Wendel, 2015; Spoelhof et al., 2017). Abiotic stress can lead to dramatic

changes in the transcriptome of polyploids compared to diploid progenitors (Dong and Adams, 2011; Visger et al., 2019). There is now a vast literature on the influence of genome doubling on gene expression (primarily in allopolyploids, but also in autopolyploids), with most insights garnered via RNA-seq analyses (Chen, 2007; Doyle et al., 2008; Grover et al., 2012; Conant et al., 2014; Yoo et al., 2014; Wendel, 2015; Lian et al., 2020; Nieto Feliner et al., 2020; Qiu et al., 2020). Patterns of gene expression in an allopolyploid can, in part, be the simple addition of its diploid parents. However, many polyploids deviate from the expectations whereby parental gene expression patterns are combined in the allopolyploid. Gene silencing and nonadditive gene up- or down-regulation may occur. A new or young allopolyploid may exhibit novel patterns of gene expression (Grover et al., 2012; Coate et al., 2014; Griffiths et al., 2019), as well as expression level dominance of one parental genome over the other (Yoo et al., 2014; Alger and Edger, 2020). In addition, gene expression differences among duplicate genes present in an allopolyploid are a legacy of expression differences that were already present in the progenitor diploid species (Buggs et al., 2014). In autopolyploid Arabidopsis accessions, a recent study showed that immediate transcriptomic response to genome doubling appears to follow the gene balance hypothesis independently of long-term selective pressures (Song et al., 2020). Overall transcriptome size does not exhibit a simple doubling in response to genome doubling, but instead individual gene dosage responses are highly variable, indicating that expression is not strictly coupled with gene dosage. Nonetheless, putative dosage balance-sensitive gene groups (such as genes encoding multiprotein complexes or genes encoding interacting proteins and metabolic networks) exhibit smaller and more coordinated dosage responses than do putative dosage-insensitive gene groups, suggesting that constraints on dosage balance operate immediately following WGD and that duplicate gene retention patterns are shaped by selection to preserve dosage balance (Song et al., 2020). Also, alternative splicing (AS) has emerged as an important mechanism for generating transcriptomic variation and is very important in stress responses across eukaryote life, including the green lineage (Staiger and Brown, 2013). Significantly, several studies have shown that AS patterns change rapidly following polyploidization and that some or even many of the changes in AS are linked to abiotic stress (Zhang et al., 2010; Zhou et al., 2011; Tack et al., 2014).

Rapid changes in gene expression and epigenetics (see below) following polyploidy may provide the polyploid with an almost immediate selective advantage compared to its diploid progenitors. Indeed, the effects of genome doubling on the phenotype or life history traits can directly affect their chance of survival under stressful conditions. As an example, Godfree et al. determined that tetraploids produced more viable seed and heavier seed than did diploids in kangaroo grass (*Themeda triandra*), thus increasing fitness and survival under stress (Godfree et al., 2017). More recently, in the same diploid–tetraploid complex, polyploidy was shown to have a direct effect on seed, dormancy, and seedling characteristics (Stevens et al., 2020). Furthermore, tetraploids produced heavier, more viable seed sets that stayed dormant longer under stress, enabling plants to avoid germination under stressful conditions. Furthermore, once they did germinate, tetraploid seedlings were larger and grew faster than did the diploids and were thereby able to outcompete their diploid relatives. Also in *T. triandra*, it was recently shown that polyploidy appears dominant in hot and dry regions, indicative of ploidy-based adaptive responses to climate (Ahrens et al., 2020). In wheat, higher ploidy levels are associated with higher photosynthetic capacity and stronger morpho–physiological adaptation (Mao et al., 2018). Because polyploid complexes are common in the grasses (Visser and Molofsky, 2015), it would be interesting to know how phenomena such as increased seed viability, seed dormancy, and increased photosynthetic capacity relate to increasing ploidy. Polyploidy has similarly been associated with adaptation to cold stress, facilitating dwarf phenotypes, rapid growth under favorable conditions, and asexual reproduction (te Beest et al., 2012; Freeling, 2017; Syngelaki et al., 2020). It is not difficult to imagine how such traits would provide an advantage under stressful situations, or have increased adaptive potential during or subsequent to cataclysmic events such as those responsible for mass extinction events (Crow and Wagner, 2006).

Stress and epigenetic response

A growing body of evidence points to the importance of epigenetic modifications that accompany WGD. These epigenetic changes can modify homoeologous gene expression patterns, alter networks of gene expression patterns, and may be accompanied by a burst in transposable element (TE) activation. This latter phenomenon has been mainly described for allopolyploids (Parisod et al., 2009; Glombik et al., 2020), although some have reported bursts in TE activation in autopolyploids as well (Bardil et al., 2015; but see Baduel et al., 2019). Ultimately, these changes may facilitate adaptation by new polyploids to their local environment, which includes various stress adaptations (Song and Chen, 2015; Ding and Chen, 2018; Wendel et al., 2018). A study of diploid and autopolyploid alpine buttercup (*Ranunculus kuepferi*) shows an epigenetic impact of genome doubling on the methylation profile and associated response to cold (Syngelaki et al., 2020). In Arabidopsis hybrids, stress induces the expression of stress–response genes that are normally repressed; the expression of these genes—likely under epigenetic control—allows hybrid plants to combat stress and recover faster than their parents after stress conditions are removed. This role for the timing and operation of stress responses in hybrids is similar to gene expression and growth vigor observed in allopolyploid Arabidopsis (Ni et al., 2009; Miller et al., 2015).

The formation of polyploids significantly increases the complexity of GRNs and transcriptional regulation, which is expected to be reflected in higher-order chromatin

structures as well. However, there is little known about three-dimensional (3D) genome structure and its dynamics during polyploidization. By studying 3D genome architectures for both diploid and tetraploid cotton, Wang et al. (2018a) found that by comparing each subgenome in tetraploids with its extant diploid progenitor, genome allopolyploidization contributed to the switching of A/B compartments and the reorganization of topologically associated domains (TADs; Lieberman-Aiden et al., 2009; Lupianez et al., 2015; Dixon et al., 2016). The authors showed that the formation of TAD boundaries during polyploidization preferentially occurred in open chromatin, coinciding with the deposition of active chromatin marks. Furthermore, analysis of inter-subgenomic chromatin interactions revealed the spatial proximity of homoeologous genes, possibly associated with their coordinated expression (Wang et al., 2018a). Although canonical TADs have not been detected in Arabidopsis, hundreds of genomic regions were identified with properties similar to those of TADs (Wang et al., 2015). Allopolyploid Swedish cress (*Arabidopsis suecica*) showed pronounced expression differences between both parental subgenomes that strongly correlated with chromatin compaction differences between the two homoeologous genomes (Zhu et al., 2017). TAD-like structures have been identified in several additional plant species (Dong et al., 2017), and recent studies have demonstrated the existence of TADs in rice (Dong et al., 2018). Whether analogous compaction differences occur in the homologous genomes of an autopolyploid is as yet unknown (Doyle and Coate, 2019). Likely, there is thus an effect of genome polyploidization on the spatial organization of chromatin, and consequently on gene regulation and gene expression (Jiao et al., 2018; Wang et al., 2018a). To what extent this plays a role in differences between diploids and polyploids, and in their response to stress, needs further work.

What about the proteome?

Although studies of the proteome and the consequences of polyploidy remain in their infancy, it is noteworthy that the proteome does not always mirror the transcriptome (Soltis et al., 2016b). This finding is important in that so much of our current understanding of genetic-based diversity is derived from transcriptome data. In some cases, the polyploid produces qualitative and/or quantitative nonadditive protein patterns compared to the parents of the polyploid, while in others, novel protein production patterns have been observed (Soltis et al., 2016b). Allopolyploids generally combine the protein contributions of their diploid parents, but there is also evidence of one parental genome being dominant. Autopolyploid plants usually are qualitatively identical to their diploid parent, but show quantitative protein differences. Importantly, emerging data show that the proteome and post-translational modifications of proteins play a direct role in the plant immune response (Liu et al., 2019a). For example, Wang et al. (Wang et al., 2013) showed an increased proteomic and physiological response to salt stress in autopolyploid black locust (*Robinia pseudoacacia*) compared to

the diploid progenitor. More studies of the proteome of polyploids and diploid progenitors(s) in response to stress are crucial.

Stress and ecological niche: toward an integration of biotic and abiotic stress response

Given the responses of polyploids to both abiotic and biotic stresses at the cellular and/or organismal levels, it seems likely that responses to stresses might manifest at the landscape scale. Indeed, long standing views on polyploids, especially allopolyploids, suggest that they may have broader ecological amplitude than their diploid progenitors. For example, the higher frequency of polyploids in the Arctic and alpine areas relative to the temperate regions of the Northern Hemisphere was interpreted as evidence for greater stress tolerance, broader ecological niches and possibly even greater colonizing ability in polyploids compared to diploids (e.g. Ehrendorfer, 1980). Although these distributions might also be tied to a higher frequency of formation in habitats in the Arctic/alpine areas following deglaciation (due to increased frequency of unreduced gamete formation in harsh environments and/or novel contact between previously separated diploid species; e.g. Stebbins, 1950, 1984; Novikova et al., 2018; Zozomová-Lihová et al., 2020), latitudinal and elevational gradients in polyploid frequency persist and suggest that polyploids may indeed be better able to cope with harsh environments (Abbott and Brochmann, 2003; Brochmann et al., 2004; Rice et al., 2019). Moreover, ecological divergence from the parental species is generally considered a prerequisite for establishment of a nascent polyploid (Levin, 1975; Fowler and Levin, 1984). Although limited, studies of autopolyploids suggest that the polyploid may escape minority cytotype exclusion through ecological divergence in microhabitat, phenology, pollinators, parasites, or mycorrhizae (Ramsey and Ramsey, 2014; Marchant et al., 2016; Segraves, 2017); even fewer such fine-scale empirical analyses have been reported for allopolyploids.

A polyploid may exhibit ecological niche conservatism with its parental species or it may diverge and exhibit niche expansion, niche contraction, niche intermediacy, or niche novelty (Castro et al., 2020). The application of ecological niche models to the study of polyploids provides a glimpse into the effect of abiotic stresses on both auto- and allopolyploids at the landscape scale. Models for a polyploid and its diploid progenitor(s) generally demonstrate extensive niche overlap between the polyploid and its parent(s), whether an auto- or allopolyploid (Glennon et al., 2012, 2014; Godsoe et al., 2013; Theodoridis et al., 2013; Marchant et al., 2016; Visger et al., 2016; Gaynor et al., 2018), but many polyploids also tend to diverge at least slightly from one or both parents as well. Of course, at present, ecological niche models for plants generally incorporate only abiotic features of climate, elevation, and perhaps soil and land cover, but we can aspire toward incorporating biotic components of the environment as well, from microbiomes to pollinators to herbivores and more. Such models would integrate biotic

and abiotic stressors across space and time and thereby permit macroecological and macroevolutionary perspectives on stress response in polyploids. We encourage further study to evaluate more examples of polyploids and their parents to address the relative role of biotic and abiotic stresses in shaping polyploid distributions (Harbert et al., 2014; Rice et al., 2019; Baniaga et al., 2020).

Conclusions

Both individual species, as well as entire ecosystems, can experience stressful conditions; individual plants can be attacked by herbivores or pathogens, while cataclysmic events and/or rapid global change can devastate entire communities. While the effects of all sorts of stress, whether biotic or abiotic, (particularly) on plants are widely documented—see the many excellent reviews on this topic (Erb and Reymond, 2019; Wilkinson et al., 2019; Zhang et al., 2019; Kerchev et al., 2020; Van zelm et al., 2020)—the potential for polyploidy as a stress-tolerance enhancer is much less widely recognized (Fox et al., 2020) and has been based largely on anecdotal evidence (Madlung, 2013; Van de Peer et al., 2017; Doyle and Coate, 2019; Yao et al., 2019; Stevens et al., 2020). Nevertheless, the notion that polyploidy can facilitate response to both abiotic and biotic stresses and that WGD can act as a buffer to mitigate their effects (Van de Peer et al., 2017) is increasingly gaining support. The circumstances and the extent to which polyploidy might confer a selective advantage under stressful conditions, however, as well as the mechanisms underlying the responses to stress-related phenomena, might differ greatly and clearly need further study (Fox et al., 2020).

In a stable environment, gradual changes can successfully explain the divergence and optimization of evolutionary processes. In contrast, when the environment drastically changes, in a short geological time frame, gradual evolution may not keep pace, and existing species may run out of time to adapt and will disappear. Polyploidy might provide a way out of these periods of rapid environmental change and intense stress by enabling swift adaptation to a rapidly changing environment (Crow and Wagner, 2006; Van de Peer et al., 2009; Levin and Soltis, 2018). Gene and genome duplications have been suggested as possible explanations underlying so-called saltational jumps in evolution, consisting of many sudden mutations from one generation to the next (Soltis et al., 2014b, 2016a; Soltis and Soltis, 2014). Indeed, the duplication of genes and particularly the duplication of entire genomes immediately create redundant informational entities or modules in the genome, offering possibilities for a more substantial change and a wider exploration of genotypic and phenotypic space (Conant and Wolfe, 2006; Yao et al., 2019; Carretero-Paulet and Van de Peer, 2020). In a constant environment, organisms are likely to be fairly well-adapted, undergoing only further slow optimization over time; in a changing environment, polyploidy provides a mechanism for more extensive changes. Although such polyploid individuals might initially have

difficulty competing with their diploid progenitors, for reasons explained elsewhere (Comai, 2005; te Beest et al., 2012; Van de Peer et al., 2017; Baduel et al., 2018), they could "take their chances" under different conditions or in different contexts. Increased genomic and genetic variation evoked by WGD thus forms a fertile substrate allowing evolution to explore more diverse options, possibly explaining those bigger jumps sometimes observed in evolution. Again, such evolvability (see Payne and Wagner, 2019) might only be successful when the existing environmental conditions have been (seriously) disrupted. Once new environmental conditions have stabilized, the increased evolvability through WGD will become less important in further optimizing the system, and selection on a more complex system might again be constrained. Considering polyploidy in the evolutionary history of organisms might thus indeed be one additional way of explaining large leaps or major transitions that have occurred in the past, as suggested by Susumu Ohno 50 years ago (Ohno, 1970).

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