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ADVANTAGES OF POLYPLOID PLANTS IN CLIMATE CHANGE OR EXTREME HABITATS ACCORDING TO ITS DIPLOIDS
– A REVIEW–

NESRIN ORCEN*[1)]

Department of Field Crops, Faculty of Agriculture, Ege University, Bornova, Izmir, 35100, Turkey;

E-mail: nesrin.orcen@ege.edu.tr

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ABSTRACT

Polyploid organisms are those containing more than two paired sets of chromosomes. Polyploidy is occurs in many plants and some animal species but is particularly widespread in the angiosperms. Polyploidy has attract attention researchers for almost a century and today it well knows that polyploidy has had a role in the evolution of all angiosperms. Despite its widespread occurrence, the direct effect of polyploidy on evolutionary success of a species is still largely unclear. Over the years, many hypotheses have been proposed to put functionality into increasing content of a duplicated genome. These hypotheses include the fact that doubling of the genome provides significant advantages over a polyploid, and these advantages allow polypoids to develop in environments that challenge the diploid progenitors of polyploidies Genome doubling, or polyploidy, is a major factor accounting for duplicate genes found in most eukaryotic genomes. Polyploidy has considerable effects on duplicate gene expression, including silencing and up- or downregulation of one of the duplicated genes. Genome doubling confers distinct advantages to a polyploid and that these advantages allow polyploids to thrive in environments that pose challenges to the polyploid's diploid progenitors. Studies of naturally polyploid plants have shown that polyploids have advantages over diploids in terms of stress resistance. This article revisits these long-standing questions and explores how the integration of recent genomic developments with ecological, physiological and evolutionary perspectives has contributed to addressing unresolved problems about the role of polyploidy. Although unsatisfactory, the current conclusion has to be that despite significant progress, there still isn't enough information to unequivocally answer many unresolved questions about cause and effect of polyploidy on evolutionary success of a species. In the future, it will make more direct connections between the effects of polyploidy on the genome and the responses this condition elicits from the organism living in its natural environment. Such information will assist crop breeders and lead to an enhanced understanding of polyploid-generated angiosperm diversity. Ploidy can be an important criterion for selecting plant populations for use in genetic rescue, restoration and revegetation projects, including in habitats affected by climate change.

INTRODUCTION

Polyploids are organisms whose genomes consist of more than two complete sets of chromosomes. There are three major types of polyploids: autopolyploids, allopolyploids and segmental allopolyploids. In autopolyploids all genomes are identical or very similar and arise via genome duplication within the same species. Allopolyploids, contain two or more distinct genomes, and can arise via hybridization of two different species accompanying with genome doubling (Grant, 1975). Segmental allopolyploids carry more than two partially differentiated genomes, which can lead to the formation of both bivalents and multivalents during chromosome pairing in meiosis (Stebbins, 1947).

Different mechanisms have been proposed to explain how polyploids arise in nature. Two major pathways are known to lead to polyploidy in plants: somatic doubling and formation of unreduced reproductive cells. Somatic doubling is associated with mitotic events such as endomitosis or endoreduplication, which may occur either in a zygote cell or in apical meristematic tissues, giving rise to mixoploids or even completely polyploid organisms. Despite being constantly used to attain artificial polyploids, somatic doubling is supposed to have a minor role in the origin of natural polyploid organisms. In gametic non-reduction, fusion of two gametes, of which at least one contains a non-reduced, full somatic complement of chromosomes, can lead to polyploidy. Somatic doubling may occur in zygotic, embryonic or sporophytic tissue. Spontaneous genome duplication in those tissues can thus also produce viable polyploidy offspring via gamete formation in the duplicated sectors (Ramsey and Schemske, 1998). Polyploidization in general is now believed to have occurred at least once during the evolutionary history of all angiosperms (Jiao et al., 2011) and it has been suggested as a major driving force of plant evolution (Soltis and Soltis, 2009). Itis not clear why polyploidy is so abundant in angiosperms, particularly when its occurrence in gymnosperms, considered to be sister to angiosperms, is so low. Indeed, polyploidization has been described as a process leading to instantaneous speciation (Mayr, 1963) because a single generation event such as the hybridization between two species with subsequent somatic doubling, or the fusion of unreduced gametes is enough to quickly establish barriers that prevent gene flow between the new polyploid and the old progenitor species, and can lead to reproductive isolation (Ramsey and Schemske, 1998).

Although auto- and allopolyploidy share the property of duplicated genomes, the difference in their compositions has important consequences. In autopolyploids, chromosomes generally pair as multivalents during meiosis, while in allopolyploids bivalent pairing between chromosomes of the same original genome is prevalent (Stebbins, 1947), resulting largely in the maintenance of two separate genomes. However, the more closely genomes in the allopolyploid are related, the more likely it is for homoeologs (the chromosomes duplicated by allopolyploidy) to pair (Levin, 2002), resulting in chromosomal exchanges between the two genomes.

Polyploids are often widely distributed and their tendency to be common in fluctuating environments has been a matter of interest since the 1930s and 1940s. The causes of their success remain under debate. Changes in DNA content may alter key ecological traits such as seed size by changing the size, number and geometry of cells. Changes in gene copy number may increase biochemical flexibility and promote homeostasis in stressful environments by enabling spatial and temporal partitioning of gene expression among homeologues or, in the case of autopolyploids, via maintenance of allelic diversity across loci on homologous chromosomes. Genetic consequences such as the occurrence of transgressive phenotypes, chromosomal rearrangements, the masking of deleterious alleles and changes to DNA methylation may also contribute to polyploid advantage in extreme habitats. These can occur rapidly in allopolyploids, and may become important in autopolyploids over time. Understanding how polyploidy enhances plant fitness in stressful environments is of immense practical as well as theoretical significance. As climate change threatens the stability and persistence of vegetation globally, the ability to improve the adaptive capacity of existing or restored plant populations via assisted gene flow or the selection of provenances based on their expected performance under projected climate regimes is seen as a crucial link in the maintenance of biodiversity and ecosystem services. Despite its prevalence in natural plant populations, however, variation in ploidy has rarely been used as a basis for selecting pre-adapted genotypes for conservation work.

Despite the interest in polyploidy there are many long-standing, yet still unanswered questions about the significance of genome doubling, especially in the areas of ecology, physiology and evolution (Soltis et al., 2010). In this review, discuss how recent genomic developments have improved the debate over these questions. It is intended to pay special attention to areas where complementary approaches of different disciplines are becoming synergistic and the continuous integration of the genome with ecological and organizational knowledge will help to solve unresolved problems in the future.

ADAPTATION OF POLYPLOIDS PLANT TO EXTREME ENVIRONMENTS

The question of whether polyproids are better adapted to stressful environments was raised early. Given the hypothesis that polyploids can thrive relative to their diploid progenitors, polyploids have been studied for their morphological, physiological and developmental differences from diploids to find correlative evidence that might explain observations of higher stress endurance. Morphological differences between diploids and polyploids are the larger cell sizes in polyploids (Melaragno et al., 1993) including those of the stomata (Speckman et al., 1965; Masterson, 1994; Hodgson et al., 2010; Orcen and Emiroğlu, 2013). Changes in stomatal pore size in response to polyploidy could suggest an effect of genome duplication on the water relations of the plant. A lower density of stomata in polyploids compared with diploids as found in Betula ayrifera (birch) could on the other hand reduce or offset any differences in the overall gas exchange rates. Integrative and experimental approaches to questions regarding the adaptive role of polyploidy in responses to the environment are still rare. Maherali et al. (2009) compared natural diploid, tetraploid and colchicine-induced neotetraploids of fireweed (Chamerion angustifolium) to study the effect of genome doubling on water relations. The researchers reported larger stomata, increased stem and vessel diameter, and decreased specific hydraulic conductivity in both types of tetraploids over the diploids, but noted that the established tetraploids showed significantly greater drought tolerance than the similarly responding diploid and neotetraploid, suggesting that drought tolerance In another recent study with an examining the ecophysiological implications of an altered morphology in polyploids, Li et al. (2012) examined the underlying mechanisms of cell size variation in diploid and tetraploid Arabidopsis thaliana with molecular tools. Using quantitative PCR, these authors queried expression differences in 34 cell cycle regulating genes and reported significant differences in the expression of three inhibitors of cyclin dependent kinases (ICK1, 2, 5) between diploids and tetraploids. These results suggest a mechanism by which altered gene expression levels of select genes could have direct results on the morphology and ecology of the plant. The results by Li et al. (2012) set the stage for follow-up experiments that could, for example, test if experimentally altered gene expression of ICK1, 2 and 5 has direct or proportional consequences on stoma size and if so, if variable stoma sizes have proportional effects on the water relations of the plant. It would also be of great interest if the described changes in transcriptional activity are the same in different populations of polyploids derived from separate polyploidization events, or if they are stochastic changes. If changes in gene expression levels of specific genes in multiple separately induced polyploids could directly be linked to physiological or morphological changes in polyploids compared with their parents, this would indicate that genes exist, which are directly and consistently regulated by genome doubling.

In a other study, the authors analyzed the relative contribution of each gene in homoeologous gene pairs to the overall expression of the gene in the allopolyploid and reported significant differences in their relative contribution to the overall transcription of the pair, depending on both tissue type and environmental conditions (Combes et al., 2012). This study suggested that the allopolyploid has a different, but not necessarily broader, range of responses to changing conditions. It would be interesting to see if the difference in expression could lead to a selective advantage, for example, in a comparative study of wholeplant performance of different individuals in different environments. Homoeologous genes in the allopolyploid Gossypium hirsutum showed differential expression levels of each homoeolog when a variety of abiotic stresses, such as heat or cold, were applied (Liu and Adams, 2007; Dong and Adams, 2011). Also, in the allopolyploid Brassica napus, stressful environmental conditions due a to a change in the identity of splice variants in a significant subset of homoeologous genes when compared to the two parent species B. olaracea and B. rapa. Alternative splicing creates multiple mature mRNAs from a single gene, which can give rise to multiple proteins with different functions. Collectively, these studies provide strong experimental evidence that regulation of gene expression in homoeologs of allopolyploids can be variable in different conditions. Whether such changes in homoeolog regulation are adaptive, again, remains to be shown. Another example for changed responsiveness to stress of allopolyploids relative to its parents comes from Arabidopsis. Here, mRNA stability was compared between allopolyploids and their parent species (Kim and Chen, 2011). Results from this study showed that genes involved in abiotic and biotic stress responses were significantly more likely to also have a differential mRNA decay time when comparing allopolyploids and progenitor species (Wang et al., 2006; Kim and Chen, 2011). These studies suggest that differential posttranscriptional regulation between allopolyploids and their progenitors might modulate the stress response of allopolyploids relative to their parent species and potentially allow survival under altered conditions. Modern molecular studies suggest that replicated homologous genes in allopiploids may migrate subfunctionality by allowing allopiploid to use homologous genes differently for different or variable responses to a series of stressful conditions. This will support the idea that allopopolyidization can lead to a functional increase in response options to a wider range of potentially stressful environmental conditions that can be adapted to evolutionarily. However, in many cases, it is important to note that it lack direct evidence that the variability from polyploid is necessarily due to the evolutionary potential of polyploid populations.

To answer the question whether polyploidy promotes evolution through increased adaptability, more work is required to integrate molecular and ecological approaches to test the role of specific genes on adaptation under field or controlled conditions.

AUTOTETRAPLOIDIZATION ENHANCES DROUGHT STRESS TOLERANCE

Studies of naturally polyploid plants have shown that polyploids have advantages over diploids in terms of stress resistance. The induction of polyploidy is an efficient way to improve drought stress tolerance in plants. For example, polyploid plants of rice are more drought tolerant than its corresponding diploid plant. However, how polyploidy contributes to this adaption at the molecular and physiological level is poorly known.

The changes in characteristics in polyploids are mainly caused by differences in gene expression. Numerous researches focus on identifying changes in the genome expression pattern of allopolyploid materials, and few studies on autotetraploids. In allotetraploids, changes in gene expression are thought to be attributed to the nature of divergent genomes and possible interactions between the various genetic components. In contrast to allotetraploids, alteration in the expression of any allele in autopolyploids may lead to a change in phenotype, because no potential complementation or advantageous sub functionalization could occur.

In many plant species, it has been reported that polyploidization might lead to better adaptation to adverse environmental condition. Some studies focus on the herbaceous plant, polyploid plants of *Coccinia palmata, Dendranthema nankingense, Arabidopsis* and *Oryzea sativa* are more drought tolerant than its corresponding diploid plant.

CONCLUSION

The question of how polyploid affects the evolutionary orbit of a species is still unknown. In response to stress, the about the role of polyploidy or whether genome replication is useful or harmful to evolutionary process have been discussed. Molecular techniques have provided evidence for genomic change at numerous regulatory levels associated with polyploidy. However, in many cases, we still do not know the effect of polyploidy on fitness under different environmental conditions, and there is little evidence that transcriptional and genomic changes actually lead to faster evolution or adaptation in natural populations. What's more, recent phylogenetic studies point to perhaps the opposite. It is possible that natural differences in the types of responses to polyploidization are species specific or stochastic in individuals. These differences may be the reason why some polyploids, such as cotton and soybeans, are so successful and why so many are not. Future phylogenetic studies may distinguish between autoplyploids and allopolyploids, so it would be worthwhile to answer the polyploidy role question per se.

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