

Hopeful Monsters: Evolutionary Relevance and Ecology of Polyploid Plants in the Arctic

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Polyploidy is a bizarre phenomenon whereby a large amount of genetic material accumulates within the nucleus of a single cell, forming utterly complex genomes. Plants in particular tend to be extremely variable in genome size and withstand more dramatic mutations than animals. Whole genome duplication forms polyploid gametes and individuals. It is quite common in flowering plants, whereas it is observed only in a few animal species. Yet, polyploid plants occur naturally and are the rule rather than the exception in alpine or polar habitats such as the Arctic. It is difficult to understand why the multiple genomes per cell are not reduced, even though selection forces against polyploids are so strong.

The purpose of this paper is to discuss the ecological and evolutionary significance of polyploids and to give a brief explanation of how polyploids are formed and in which ways polyploidisation influences the ecology of flowering plants in general. This paper will also discuss the role polyploids play in the evolution of higher plants before accounting for the relevance of polyploids in arctic ecosystems in particular. Ultimately, I discuss possible explanations for the frequency of polyploids in the circumarctic flora and describe their role as genetic buffers which counteract genetic pauperisation in glacial periods.

Genetic Mechanisms of Polyploidy

The heritable condition of possessing more than two complete sets of chromosomes is called polyploidy. This is contrary to haplo- and diploid cells: Tissues or organisms that have one or two complete sets of chromosomes respectively. The total number of chromosome sets tends to be highly variable in polyploid flowering plants, but it seems that even numbers of chromosome sets are the most common (Comai, 2005).

Pathways leading to the formation of polyploids are numerous, but can be divided into two major categories based on the origin of the different chromosome sets. Commonly, duplication of a genome within or between populations of a single species is referred to as autopolyploidy, whereas the condition of bearing two or more chromosome sets of different evolutionary origin is called allopolyploidy (Comai, 2005; de Wet, 1971). Allopolyploids may form by hybridisation between two polyploid races, ecotypes, or species that often originated from hybrids themselves (Comai, 2005). Formation of polyploids is quite common among angiosperms at an estimated frequency of 1 per 100,000 (Ramsey & Schemske, 1998). Physical factors, such as extreme shifts in temperature or exposure to toxic substances, are able to inhibit reductional division or induce polyploidy in somatic cells

by acting upon the plant, especially in vegetative tissues (de Wet, 1971; Tischler, 1942). Many errors can occur in vegetative parts, due to the high number of cell divisions taking place. This will subsequently lead to mitotic failures, eventually causing the formation of polyploid ramets that can become independent from the mother plant and may start to reproduce sexually (Ramsey & Schemske, 1998). This can be confirmed by the fact that the frequency of polyploids is highest in plant families where vegetative propagation by runners, stolons, or root sprouts is common (Ramsey & Ramsey, 2014), like Rosaceae (rose family) and Poaceae (true grasses).

Polyploidy in the Arctic

The frequency of polyploid plants is particularly high in the Arctic. This vast, environmentally challenging biome is characterised by a harsh climate and low biodiversity. Arctic flora is known to be sensitive to climatic oscillations, such as repeated glaciations, changes in temperature and resource availability (Brochmann et al., 2004). It is, for example, known that plants follow the movement of retracting glaciers and that the composition of Arctic plant communities that have persisted for a long time can change rapidly following sudden changes in average temperature (Eidesen et al., 2013).

Arctic plant species are generally widespread and known to have an intricate evolutionary history. Highly self-pollinating and inbreeding plant populations are common; evolution of Arctic plants is driven mainly by hybridisation and whole genome doubling (Brochmann et al., 2013). It is estimated that 73.7 percent of all species of mainly and exclusively Arctic taxa are polyploids (Brochmann et al., 2004). Large-scale phytogeographical studies in the 1940s revealed that the amount of polyploids among flowering plants is correlated with distance from the equator (Lynch & Conery, 2000; Löve & Löve, 1943). More DNA is found per individual with increasing latitude, in spite of a drastic decrease in overall number of species from the equator to the poles (Bennett, 1976; Brochmann et al., 2004; Löve & Löve, 1943).

Polyploid Ecology

Polyploids generally share great morphological similarity with diploids, but they tend to occur in more extreme environmental conditions and climates than their diploid counterparts (Lewis, 1966; Ramsey & Ramsey, 2014). Polyploids usually occupy niches where the exposure to physical stress is high, for example in extremely wet and halide marshes, alpine areas or other hostile environments such as the Arctic (Hagerup, 1932). This indicates greater environmental adaptability compared to diploids. Furthermore, polyploids tend to be perennial rather than annual, spend more energy on growing and multiplying vegetatively (Gustafsson, 1948) and are commonly associated with a greater tendency to bypass sexual reproduction by self-pollination or apomixis (Comai, 2005). These features are greatly beneficial in the Arctic ecosystem. They increase the invasiveness of polyploids, which makes them well equipped to expand into and colonise new habitats (Weiss-Schneeweiss et al., 2013). De novo formation of polyploids poses an important problem, since the whole process of genome duplication often happens in the habitat of the parental diploids. Once it has become a polyploid, an individual needs to compete immediately with its progenitors (de Wet, 1971). Thus, invasiveness should be seen as a trait not only associated with polyploidy but moreover as a characteristic that is selected positively amongst polyploids (Soltis & Soltis, 2000).

Trade-Offs Associated With Polyploidy

The metabolic costs of possessing and maintaining an enormous genome such as in polyploids are huge. Bigger genomes require more energy during each round of genome replication during the synthesis phase in the eukaryotic cell cycle. Naturally, this process takes longer in polyploids than in diploids, leading to generally slower growth rates in plants that have undergone genome doubling (Otto, 2007). High chromosome numbers give rise to many possible difficulties in meiosis or mitosis, resulting in disorganised segregation or even loss of chromosomes during cell division (Comai, 2005). This is an issue es-

pecially for anorthoploid individuals having an uneven number of chromosomes. It is thought that plants having an odd number of nucleic genomes are doomed to an evolutionary dead-end of infertility, due to their inability to form gametes that contain a stable amount of genetic information (Comai, 2005; Otto, 2007). Moreover, polyploidisation increases the number of non-coding DNA. This, in some cases, can be involved in gene regulation, resulting in metabolic irregularities caused by interaction of the different genomes leading to improper expression of genes in different developmental stages (Adams & Wendel, 2005). Thus, it seems puzzling that polyploids are more abundant in the Arctic and other extremes than in more hospitable environments where resources are scarce.

Duplication of a diploid genome entails that every gene is present twice per cell, causing high redundancy of genes (Comai, 2005). Thereby, polyploid populations maintain a higher number of heterozygotes than diploids. Heterozygosity has the advantage that deleterious or recessive lethal alleles are masked by dominant, functional ones. Highly polyploid and heterozygote populations tolerate higher levels of self-fertilisation (Soltis & Soltis, 2000). This effect is very important in populations where the effective population size is small and inbreeding is common: a small effective population size favours the loss of alleles by random genetic drift. Polyploidisation can buffer this effect by maintaining high genetic diversity in areas where introduction and maintenance of new genetic variation by gene flow and sexual reproduction is a rare event. This is a demanding issue in the Arctic. Practical absence of seed dispersal vectors and pollinators paired with low rates of seed survival strongly select for vegetative spread and asexual reproduction, which is often entirely clonal or apomictic (Brochmann et al., 2004). Moreover, heterozygosity leads to heterosis, which means that higher performance is shown by a hybrid compared to its progenitors (Comai, 2005). Especially the effect of genes that act in a dose-specific manner is amplified by a great magnitude, simply because of the higher number

of gene copies available to expression (de Bodt et al., 2005). Extra gene copies provide a canvas for experimentation when it comes to adaptability and evolution (Comai, 2005). Some gene copies can retain their original function whereas others mutate and are sacrificed to natural selection if not positively contributing to the individuals' fitness. It is important to note that no new genes are added to a population by any kind of polyploidisation event. This does not necessarily need to be a disadvantage. In fact, the formation of polyploids provides "genetic continuity" (de Wet, 1971) to populations that are in danger of losing their environmental adaptations by intermixing with distant populations, a phenomenon known as outbreeding depression. Arctic ecosystems demand a high degree of specialisation, such as cold tolerance and a well-timed life cycle, due to the short growing season. Gene pools of northern Arctic plant populations can be contaminated by invaders or pollen from southern or subarctic populations adapted to milder environments, thus weakening the hardiness of their relatives.

Polyploidy and Evolution

Recent large-scale molecular studies conducted on several angiosperm genomes revealed the importance of polyploidisation on plant evolution by displaying that the fraction of recent angiosperms whose ancestors underwent whole genome duplication once in the past is much higher than anticipated. It has been shown that so-called paleopolyploids are found in great number throughout all angiosperm families and genera, and support the hypothesis that the entire angiosperm lineage diversified during a series of polyploidisations around the Cretaceous–Paleogene boundary extinction event, roughly 66 million years ago (Linder & Barker, 2014; Vanneste et al., 2014). This is consistent with the theory of polyploids as good invaders and colonisers that form in situations of severe physical stress (Linder & Barker, 2014; Vanneste, Maere, & van de Peer, 2014). This provides an idea of what kind of environmental conditions may have ruled the earth in a time where many taxa



were wiped out completely. More recent paleopolyploidisations happened during later major environmental shifts such as the expansion of steppes in the Miocene (Estep et al., 2014), particularly in true grasses (Poaceae). Polyploidy is, in that way, an important driving force in plant evolution. The fact that it primarily is preserved in the Arctic accredits this region great importance for plant evolution (Brochmann & Brysting, 2008).

Although most of the recent plant lineages developed from polyploid ancestors, many diploids are found among recent angiosperms. Obviously, lots of genetic information has been lost over time and polyploids gradually evolved back into diploids. What was the fate of these duplicated genes? As previously mentioned, maintenance of huge genomes is incredibly resource demanding and thereby very costly. Eventually, duplicated genes or even entire chromosome segments are merged together or lost unless they are essential in gene regulation or acquire new functions by mutation (Adams & Wendel, 2005; de Bodt, Maere, & van de Peer, 2005). Selection favouring the most effective genomes will thereby reduce ploidy level, gene redundancy and downsize genomes over time. Thus, retained genes will rearrange and chromosome sets will merge until diploidy is restored (Lynch & Conery, 2000; Soltis et al., 2014).

Discussion

It has been suggested that polyploids are more adapted to extreme climates and show greater hardiness than diploids (Hagerup, 1932; Tischler, 1942). The most straightforward explanation is that polyploidisation itself causes greater resistance to the harsh climate ruling the Arctic (Löve & Löve, 1943). The formation of polyploids is thereby thought to be an evolutionary strategy diploids are forced to make use of when the environment becomes hostile (Stebbins, 1984). This hypothesis implies a strong correlation between latitude and plants with duplicated genomes, also within the Arctic. However, several highly Arctic areas do not show this distributional pattern at a smaller scale. Alaska is such an example. There, frequency and degree of polyploidy is highest in southern and central habitats, whereas northern regions around

the Bering Strait are rich in diploids (Johnson & Packer, 1965). In fact, polyploids are mostly found in areas recently uncovered by ice. These provide niches with difficult growing conditions: wet, unstable and severely disturbed soils with a fine texture as well as shallow permafrosts (Johnson & Packer, 1965). This suggests that it is the degree of previous glaciation that primarily determines the frequency of polyploids in the Arctic (Stebbins, 1984).

Recurrent glacials eradicate vegetation in vast areas thereby separating populations from each other, a process generally known as vicariance. As a consequence, the populations adapt independently to different environmental conditions in spatially separated refugia, diverging into different ecotypes, races or even species. Glacial expansion followed by separation of populations is a form of bottleneck event. Only a few individuals survive the disruption event, leading to little genetic variation in the respective populations that survive in ice-free refugia (Brochmann et al., 2004). Severe inbreeding and loss of genetic variation by genetic drift can be counteracted by increasing the amount of genetic diversity carried per individual. Genetic buffering can be exemplified by the Arctic grass *DuPontia fisheri* s.l., which is a species complex from which hexaploids ($2n = 6x = 42$ chromosomes), dodecaploids ($2n = 12x = 84$) and even decaoctoploids ($2n = 18x = 126$) are reported (Brysting et al., 2004). Individuals from all ploidy levels are found in the same areas, indicating that the entire Arctic was first colonised by hexaploids, which constantly form higher polyploids in habitats they occupy during interglacials. Because *D. fisheri* is the result of an allopolyploidisation (Brochmann et al., 2004), no recombination is happening between the different genomes of this plant, which in the long run has led to fixed heterozygosity.

During interglacials, secondary contacts between these polyploidal populations become established in contact zones vacated by ice. Previously separated populations start to intermix again, leading to the formation of autopolyploid hybrids. Polyploidy facilitates not only the persistence of rare alleles against glaciation, but also the formation of entirely new species when the living conditions for plants turn to the better.

One example of such a recently emerged, allo-tetraploid hybrid species is the Oslo Saxifrage (*Saxifraga osloensis*). The distribution of this species is limited to the contact zone of its parental diploid parents, *Saxifraga adscendens* and *Saxifraga tridactylites*. It is believed that *S. adscendens* and *S. tridactylites* survived the last glaciation in separate refugia in continental Europe. When the ice retreated, both species expanded northwards to Scandinavia and hybridised there, eventually resulting in the newly formed *S. osloensis* (Brochmann et al., 2004).

The impact of vicariance events such as glaciations on the frequency of polyploids and ploidy level can also be demonstrated on a large scale covering the entire Arctic. In North America, angiosperm taxa restricted to the areas around the Bering Strait are richer in diploids than plants restricted to the previously glaciated region bordering the Atlantic Ocean (Brochmann et al., 2004). Beringia acted as a refuge during the glacials of the Pleistocene where plants, both di- and polyploids, were forced to retreat to during cold periods (Eidesen et al., 2013). The higher ratio of polyploid to diploid taxa in the Beringian region indicates that it was particularly polyploid individuals that re-colonised the Atlantic region after the ice sheets retracted northwards. Studies conducted on polyploid model organisms indicate that long distance dispersal is a trait that might be associated with whole genome, however the ultimate cause for why polyploids seem to be better colonisers and invaders still remains to be revealed (Linder & Barker, 2014). Polyploidy may lead to increased masking of disadvantageous or

even lethal alleles and better adaptability to new ecological conditions due to greater amounts of genetic material and hence greater variation in plant metabolism (Linder & Barker, 2014; Soltis & Soltis, 2000). Climatic oscillations contribute in that manner not only to the regional extinction of plants, but also to the maintenance of considerable genetic variation by favouring the formation of polyploids and creating niches they can invade (Brochmann & Brysting, 2008; Brochmann et al., 2004).

Conclusion

The study of polyploids is crucial to understanding the mechanisms that formed the circumpolar flora. It is the degree of glaciation during the last ice age and the position of regions that acted as refugia during glacials which has to be considered in order to explain distributional patterns of polyploid plants within the Arctic. It was in Arctic refugia that polyploids persisted during ice ages as “hopeful monsters” that escorted genetic information through bottlenecks. During times of severe inbreeding, polyploids maintained genetic diversity, thus keeping the Arctic flora from genetic impoverishment. Arctic polyploids are of great importance for the flora of the northern hemisphere and demonstrate that ample amounts of genetic diversity exist above the polar circle. In a time where global warming threatens the existence of the Arctic ecosystem, it is important to develop conservation strategies that stress the role of polyploids as an evolutionary motor. Safeguarding polyploids and their habitats ensures that their plentiful genetic diversity will be carried on into the future.

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