

Tanvir-Ul-Hassan Dar · Reiaz-Ul Rehman

Polyploidy: Recent Trends and Future Perspectives

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1.1 Introduction

Polyploidy refers to the presence of more than two genomes per somatic cell. Generally, the polyploid organism would have multiple sets of chromosomes or either the combination of chromosome sets found in same species or a closely related diploid species. Polyploid organisms can arise spontaneously by the chromosome duplication of somatic cells, or they can arise during meiosis due to non-disjunction of homolog chromosomes giving rise to diploid gametes (Ramsey and Schemske 2002). Polyploidy can also be induced artificially in the laboratory by drug treatment of the cells of an organism which inhibits the cell division, e.g. colchicine. In nature the polyploidy exists in organisms in either all or some somatic cells. The prevalent occurrence of polyploids suggests that polyploidy confers some selective advantages over diploidy. Some of the advantages can be enhanced vigour, increased heterozygosity, novel variation and production of new genotypes and allelic sub-functionalization (Salmon et al. 2005; Udall and Wendel 2006; Abbott et al. 2007; Anssour et al. 2009; Dar et al. 2013). The ancestral condition of any eukaryote is now suspected to have gone through polyploidization and re-polyploidization (Blanc et al. 2003; Bowers et al. 2003; Tuskan et al. 2006; Jaillon et al. 2007). The return of many genes back to single copy with disomic chromosomal inheritance and, in some cases, to smaller genome size and reduced chromosome numbers can occur through diploidization. Diploidization mechanisms include events such as chromosomal translocations, deletion of repetitive sequences and gene silencing (Pontes et al. 2004; Han et al. 2005; Gaeta et al. 2007; Mandáková et al. 2010).

Being one of the best known mechanisms for rapid mode of speciation, polyploidy has an important role in the formation of new species (reviewed in Otto and Whitton 2000; Doyle et al. 2008; Leitch and Leitch 2008). Hybridization and sympatric speciation through polyploidy are well-established phenomena in plants and have played significant roles in the evolution and ‘macro-diversification’ of flowering plants (Soltis and Soltis 2009). Fawcett et al. (2009) suggest that polyploidy helped numerous plant lineages survive the Cretaceous-Tertiary (K-T) mass

extinction. It has also been found that duplicate genes increase gene expression diversity in closely related species and allopolyploids, thereby facilitating morphological and adaptive evolution (Wang et al. 2004; Adams and Wendel 2005; Ha et al. 2009); Vamossi and Dickinson (2006) provided an analysis linking polyploidy and species richness in Rosaceae; based on comparisons of diversification rates, Soltis and Soltis (2009) suggest that genome doubling may have led to a dramatic increase in species richness in several angiosperm lineages, including Poaceae, Solanaceae, Fabaceae and Brassicaceae. These and other such findings negate the long-held belief that polyploids are commonly ‘evolutionary dead ends’ (for review see Soltis and Soltis 1993). This prompts one to believe that, as a process of speciation, polyploidy holds great promise for future to make up for the unprecedented loss of biodiversity being faced all over the world.

Initially, polyploids gained attention because of their unique cytogenetics and reproductive isolation from diploids (Blakeslee 1921; Jorgensen 1928). Subsequently, it was recognized that polyploids also exhibit distinctive phenotypic traits, pertaining to morphology, anatomy, physiology, reproductive characters, phenology and overall life history, which differentiate neo-polyploids from their progenitor diploids (Pal and Khoshoo 1977; Hahn et al. 1990). ‘Gigas’ characteristics, such as sturdier foliage, thicker stems and enlarged reproductive structures, which are typically less numerous in the diploid progenitors, are some of the common characteristics of neo-polyploids. Compared to their diploid ancestors, neo-polyploids have been reported to often show increase in the size of individual cells, reduced branching, variations in the contents of various substances, slower growth and development, relatively later and longer flowering and reduction of pollen and seed fertility (see Stebbins 1950; Ramsey and Schemske 2002).

The above-said genomic changes induced by polyploidy are thought to influence the transcriptome, metabolome and proteome, which can change the phenotype and ecology of the individuals (Leitch and Leitch 2008). Song et al. (1995) reported changes in genomic organization of the synthetic allotetraploid of *Brassica* sp. and detected nonadditive inheritance of genomic fragments. Both the loss of parental genome fragments and the gain of new fragments were observed. Allotetraploids of wheat have also displayed genomic changes immediately after hybrid formation (Feldman et al. 1997; Ozkan et al. 2001; Shaked et al. 2001; Town et al. 2006). These findings, besides explicitly negating the long-standing perception that polyploids are evolutionary dead ends, not dynamic (Wagner 1970), suggest that polyploidy is almost a universal phenomenon.

Polyploids are of four main types, viz. auto-, allo-, segmental and auto-allopolyploids (Stebbins 1947). Autopolyploid organisms have similar genome which arises by genome duplication thus resulting in multiple similar sets of chromosomes (Stebbins 1947; Lewis 1980). In allopolyploid organisms two or more divergent chromosome sets get merged (Stebbins 1947; Grant 1975). The segmental allopolyploids are formed from the two or more partially different genomes giving rise to bivalents and multivalents during chromosome pairing. In auto-allopolyploids, both auto- and allopolyploids get combined (Table 1.1).

Table 1.1 Classification of polyploidy

Type	Description	Genomic constitution	Example
<i>Autopolyploidy</i>	A polyploid having multiple sets of identical genomes	AAAA	<i>Solanum tuberosum</i> , <i>Zea perennis</i>
<i>Allopolyploidy</i>	A polyploid having multiple sets of different genomes	AABB	<i>Triticum aestivum</i> , <i>Gossypium hirsutum</i>
<i>Segmental allopolyploids</i>	A polyploid having multiple sets of similar but not identical genomes	A ₁ A ₁ A ₂ A ₂	<i>Aesculus carnea</i> , <i>Delphinium gypsophilum</i>
<i>Autoallopolyploids</i>	A polyploid produced by the combination of autopolyploidy and allopolyploidy	AABBBB	<i>Helianthus tuberosus</i>

1.2 Historical Perspective

Etymologically, polyploidy is composed of two words: *poly*, Greek for many/more than two, and *ploudeus*, ending of cytological terms relating to the number of sets of chromosomes, derived from Greek *idios* (private, peculiar, individual) by way of Weismann's term *Id*, introduced in German in 1893 to designate the hereditary germplasm, and Strasburger's term haploid (single id, gametophyte) and diploid (double id, sporophyte), introduced in German in 1905 (Stearns 1992). The phenomenon is one of the earliest cytogenetic characteristics to be studied in greater detail (Stebbins 1950). Probably for the first time, *Oenothera gigas* De Vries was recognized to be a tetraploid mutant of *O. lamarckiana* (Lutz 1907; Gates 1909). Kuwada (1911) wrote on an early interest in putative chromosome duplication in maize (*Zea mays*). Winkler (1916) is said to have introduced the term polyploidy, when he artificially made a tetraploid form of *Solanum nigrum*, perhaps the first laboratory production of a polyploid type. Meanwhile, multiples of a basic chromosome number were revealed in many plant genera, such as *Drosera* (Rosenberg 1909), *Dahlia* (Ishikawa 1911) and *Chrysanthemum* (Tahara 1915). Digby (1912) found that the fertile *Primula kewensis* (a sterile interspecific hybrid *P. verticillata* × *floribunda*) could occur by doubling its chromosome number. Winge (1917) compared chromosome numbers of related species in *Chenopodium* and *Chrysanthemum* and found that in both cases, they are multiples of a common basic number. This led him propose a fruitful hypothesis that hybridization followed by polyploidy is a method for the origin of species. Winge's hypothesis was soon confirmed by the artificial production of several other species through interspecific hybridizations, notable among them being the classical combination of radish and cabbage, *Raphanobrassica* (Karpechenko 1927, 1928), and the evidence that *Spartina townsendii* is derived from the cross of *S. alterniflora* × *stricta* (Huskins 1931a,b). Simultaneously, interspecific hybridization was noticed in some other important genera, such as *Triticum* (Sakamura 1918; Sax 1922), *Rosa* (Tackholm