

Emerging trends in polyploidy research

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The Key Word ‘Polyploidy’ (i.e., the presence of more than two chromosome sets/more than two complete genomes in a cell) coined by Winkler in 1916 [25] has lived nearly a Century. Genome sizes in plants are remarkably diverse, with a 2350-fold range from the smallest 63 Mb (in two species of carnivorous *Genlisea*, *G. aurea* ($2n$ =approximately 52) and *G. margaretae* ($2n$ =approximately 40)), to the largest 149 000 MB (in *Paris japonica*, $2n=8x=40$), divided into $n=2$ to n =aprox. 600 chromosomes [1]. The polyploidy phenomenon has intrigued biologists over the years and many attractive hypotheses have been proposed in an attempt to assign functionality to the increased content of a duplicated genome [14, 19–21]. With the advent of newer tools of genetic analysis there has been tremendous resurgence of interest in polyploidy research, and several publishers have brought out special issues of the journals / reference books [4, 6, 12, 17, 18, 22, 24].

Chromosome doubling is brought about by endoreduplication/ $2n$ gametes/inter-genomic hybridization—all constraining genetic stability. That polyploidy can be induced with chemicals such as Colchicine, was first demonstrated by OJ Eigsti in 1935 cited in Blakeslee and Avery [2]. Genome duplication impedes sexual reproduction and may impact growth and development. A change to tetraploid state nearly doubles the cell volume and enhances cell surface area by about 1.5 times, often facilitating development of larger

organs in plants. But in animals there is a tendency to preserve the same body size by reducing the overall number of cells, thus indicating differential effect to polyploidy change across the taxonomic groups [13].

Stebbins and the central tenets of polyploidy in the 1900s

Perhaps no other single person has contributed more to our understanding of polyploidy than George Ledyard Stebbins, Jr., with publications spanning over 70 years from 1929 to 1999 [21]. Stebbins is considered as an architect of the initial models of polyploid evolution who strongly influenced thinking about polyploidy for over 50 years. He popularized five major themes as the central tenets of Polyploid evolutionary thinking [21] i.e., (i) Polyploids are formed at a moderate frequency in angiosperms, for which he provided an estimate of ~30–35 % of all species, most is through allopolyploidy, (ii) Polyploids for the most part are evolutionary “dead-ends” with limited importance in diversification, (iii) Polyploids are formed via a single origin with limited genetic potential exhibiting high degree of genetic uniformity across individuals, (iv) Genetic buffering, resulting from the combination of multiple parental genomes, leads to low rates of fixation of new mutations in polyploids, (v) Autopolyploidy is extremely rare in nature; it is not a help but a hindrance, and has minor role in plant evolution. His strong views regarding the minor role of autopolyploidy had a huge impact, hindering research into this type of polyploidy for decades, until DA Levin [10, 11] emphasized the role of polyploidy in generating novelty at a range of organizational levels and dynamic nature of polyploid genomes. It is now recognized that both allo- and autopolyploidy are common and extremely important in nature [19–21].

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Whole genome sequencing led to paradigm change

With the availability of new genetic tools of DNA based markers, In Situ hybridization, DNA sequencing, there has been tremendous resurgence in polyploidy research that have led to a new paradigm of polyploidy replacing much of the Stebbinsian framework. Complete sequencing of the genome of *Arabidopsis thaliana*, which has a very small genome (thought to be an undoubted diploid owing to low chromosome number—05 pairs and small genome size—157 Mb) revealed presence of numerous duplicate genes, suggesting two or three rounds of ancient genome duplication [3, 23]. In fact all of the angiosperm genomes sequenced exhibit evidence of ancient polyploidy events (Comparative Genomics [CoGe] website, <http://genomeevolution.org/CoGe/>), suggesting occurrence of ancient polyploidy in Angiosperms [5, 7].

Polyploidy, body size and ecological fitness

An exhaustive study conducted on paired set of diploid vs autopolyploid clones differing for their native metabolites revealed that polyploidy differentially influences body size depending upon the pathway steps involved in the production of native metabolites produced by the plant, i.e., a longer metabolite pathway shall have negative affect on the body size of the derived polyploids [9]. Of course, if the polyploids could be made to behave like diploids vis-à-vis their meiotic behavior i.e., diploidization coupled with high fertility, then such polyploid may facilitate fixation of heterozygosity [8]. Further, based on critical analysis on endangered and invasive plants vis-à-vis numerical chromosome change, it is observed that multiple sets of chromosomes is often associated with plant's vigour and the ability to adapt to different environments. This could enable polyploid plants to be more competitive and potentially invasive in a new environment [15, 16].

New paradigm in polyploidy research

Synthesis of the huge data available has led to believe that polyploidy is common and the polyploid genomes are highly dynamic [21] beyond anything that Stebbins and his contemporaries could have predicted. Polyploidy is ubiquitous in green plants, with all angiosperms and all seed plants being of ancient polyploid origin, and autopolyploidy is quite common having major force in plant evolution. Polyploidy empowers invasive potential enabling their reach to newer ecological niches.

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