

## Review Article

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**Corresponding Author:**

**\*Dr. Rajesh Yadav**

Department of Pharmacy, SRMS,  
College of Engg. and Tech.,  
Bareilly, U.P.  
India.

Tel No: +919410294357,  
+919458702562



e-mail: [raj\\_ishu78@rediffmail.com](mailto:raj_ishu78@rediffmail.com)

# Needs and Necessity of Polyploidy in Medicinal Plants

Rajesh Yadav\*, Nita Yadav<sup>1</sup>

### ABSTRACT

Polyploids are organisms with multiple sets of chromosomes in excess of the diploid number. Polyploidy is common in nature and provides a major mechanism for adaptation and speciation. Approximately 50-70% of angiosperms, which include many crop plants, have undergone polyploidy during their evolutionary process. Flowering plants form polyploids at a significantly high frequency of 1 in every 100,000 plants. Many studies have been carried out to understand the nature of polyploidism. The polyploid condition may bring about several advantages compared to the diploid state. Polyploids often show phenotypes that are not present in their diploid progenitors or exceed the range of the contributing species. Some of these traits may play a role in heterosis or could favor adaptation to new ecological niches. Advances in genomics and sequencing technology may create unprecedented opportunities for discovering and monitoring the molecular effects of polyploidization. Through this review, we provide an overview of technologies and strategies that may allow an in-depth analysis of polyploid genomes. After introducing some basic aspects on the origin and genetics of polyploids, we highlight the main tools available for genome and gene expression analysis and summarize major findings. In the last part of this review, the implications of next generation sequencing are briefly discussed. The accumulation of knowledge on polyploid formation, maintenance, and divergence at whole-genome and subgenome levels will not only help plant biologists to understand how plants have evolved and diversified, but also assist plant breeders in designing new strategies for crop improvement.

**Key-words:** Gene expression, Next generation sequencing, Transcriptomics, Biological invasions, Genome size, Genome duplication

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<sup>1</sup>Department of Pharmacy, SRMS, College of Engg. and Tech., Bareilly, U.P.

## INTRODUCTION

One of the remarkable features of living material is their ability to perpetuate themselves. However, the ever dynamic nature of the surrounding environment has imposed upon plants, much like other organisms, various evolutionary and selective bottlenecks necessitating the adoption of ways and means by organisms to keep their “race going”. A concept which gains prominence in this regard is that of hybridization and has been an area of much fascination since the eighteenth century. Stebbins defined hybridization as the “crossing between individuals belonging to separate populations which possess different adaptive norms”<sup>1</sup>. Polyploidy, a prime facilitator of speciation and evolution in plants and to a lesser extent in animals is associated with intra and inter-specific hybridization. The purpose of this paper is to give a broad overview of the phenomenon of polyploidy in its entirety in plants ranging right from a brief historical background to where it stands today. Given the importance of polyploidy in speciation this will be looked into a little more in detail compared to other aspects of polyploidy.

So what is polyploidy? It refers to a definite arithmetic relationship between the chromosome numbers of related organisms. It has been defined as the possession of three or more complete sets of chromosomes and has been an important feature of chromosome evolution in many eukaryotic taxa including plants, yeasts, insects, amphibians, reptiles, fishes and even the mammalian genome. Polyploidy is present to at least to some extent in most members of the plant kingdom being more common in some and rather rare in others. The fact that it is widespread many plants is also kind of exemplified by the wide variations in chromosome numbers with chromosome numbers ranging from  $2n = 4$  to 500 in angiosperms to  $2n=6$  to 226 in monocots. Thousands of angiosperm species have 14 to 15 pairs of chromosomes<sup>2</sup>.

The phenomenon of polyploidy gained much of what it is today during the early part of the twentieth century. One of the early examples of a natural polyploid was one of De Vries's original mutations of *Oenothera lamarckiana*. The first example of an artificial polyploid was by Winkler (1916) who in fact introduced the term polyploidy<sup>2</sup>. Winkler was working on vegetative grafts and chimeras of *Solanum nigrum* and found that callus regenerating from cut surfaces of stem explants were tetraploid. Digby had discovered the occurrence of a fertile type *Primula kewensis* from a sterile inter-specific hybrid through chromosome doubling but failed to realize its significance in the context of polyploidy<sup>3</sup>. Though unaware of the ‘Primula type’ fertile hybrid, Winge, from his studies on the chromosomal counts of *Chenopodium* and *Chrysanthemum* found that chromosome numbers of related species were multiples of some common basic number; he subsequently proposed a hypothesis that chromosome doubling in sterile inter-specific hybrids is a means of converting them into fertile offsprings<sup>3</sup>. This was subsequently verified by various workers in artificial inter-specific hybridizations of *Nicotiana*, *Raphanobrassica* and *Gaeleopsis*. Finally the colchicine method of chromosome doubling was developed by Blakeslee and Avery and became an important tool for the experimental study of polyploidy<sup>4</sup>.

Before going ahead what is the main significance of polyploidy in brief? As pointed out at the very outset it is recognized as one of the main process in the evolutionary history of plants and to some extent other organisms. Though differences do exist with regard to the nature of its role and the relative importance of different kinds of polyploidy, an understanding of the ways in which polyploidy operated in the past to produce new species and races may provide useful insights to improving our cultivated plants. In fact many of our crop species, including wheat, maize, sugar cane, coffee, cotton and tobacco, are polyploid, either through intentional hybridization and selective breeding (e.g. some blueberry cultivars) or as a result of a more ancient polyploidization event (e.g. maize)<sup>5</sup>. Added to it, a technological advance in the analysis of genome structure and function has made it possible to better analyze the genetic consequences of genome duplication. The importance of polyploidy in such diverse fields such as cytogenetics, physiology, breeding, cytotaxonomy and biogeography in conjunction with new possibilities put forth by various molecular techniques has all spurred a resurgence of interest in issues of origin and establishment of lineages<sup>6</sup>.

**Origin of Polyploids:** There are various modes for the origin of polyploids. These mainly include mechanisms such as somatic doubling during mitosis, non-reduction in meiosis leading to the production of unreduced gametes, polyspermy (fertilization of the egg by two male nuclei) and endoreduplication (replication of the DNA but no cytokinesis). Endoreduplication however, is more similar to somatic doubling and is therefore not viewed as a separate mechanism by some authors<sup>2</sup>. These mechanisms are reviewed in greater detail below<sup>7</sup>.

Chromosome doubling can occur either in the zygote to produce a completely polyploid individual or locally in some apical meristems to give polyploid chimeras. Somatic polyploidy is seen in some non-meristematic plant tissues as well. (eg: tetraploid and octoploid cells in the cortex and pith- *Vicia faba*)<sup>8</sup>. In somatic doubling the main cause is mitotic non-disjunction. This doubling may occur in purely vegetative tissues (as in root nodules of some leguminous plants) or at times in a branch that may produce flowers or in early embryos (and may therefore be carried further down). Spontaneous somatic chromosome doubling is a rare event and the only well documented instance of the same was in case of tetraploid *Primula kewensis* which arose by somatic doubling in certain flowering branches of a diploid hybrid. The phenomenon of chromosome doubling in the zygotes was best described from heat shock experiments in which young embryos were briefly exposed to high temperatures. Zygotic chromosome doubling was first proposed by Winge and the spontaneous appearance of tetraploids in *Oenothera lamarckiana* and amphidiploid hybrids in *Nicotiana* were shown to be a result of zygotic chromosome doubling<sup>8,9</sup>.

A second major route of polyploid formation involves gametic “non-reduction” or “meiotic nuclear restitution” during microsporogenesis and megasporogenesis resulting in unreduced 2n gametes. Non reduction could be due to meiotic non-disjunction (failure of the chromosome of separate and subsequent reduction in chromosome number), failure of cell wall formation or formation of gametes by mitosis instead of meiosis. The classic example, *Raphanobrassica*, originated by a one step process of fusion of two non-reduced gametes<sup>10</sup>. The production of non-reduced gametes has been shown to be rather common in *Solanum sps.*<sup>11</sup>.

Another route may involve non-reduction occurring in one of the germ lines (pollens or the eggs). A tetraploid individual can then result from a two-step process (sometimes referred to as a triploid bridge mechanism) from the fusion of an unreduced 2n gamete with a reduced 1n gamete to give a 3n zygote followed by the subsequent fusion of a 3n gamete with a normal 1n gamete in the next generation to give rise to a tetraploids individual (as in artificial *Galeopsis tetrahit*)<sup>12</sup>.

The production of non-reduced gametes is also a function of the environment and genotype. eg: adverse growing conditions were shown to favor an increase the number of non-reduced gametes in *Gilia*. An example of the influence of genotype in modulating the production of non-reduced gametes can be seen in case of maize wherein the gene “*elongate*” on chromosome 3 was found to increase the proportion of diploid eggs produced<sup>13</sup>. Studies on unreduced gametes in both plants and animals are getting easier with the use of rapid screening techniques such as flow cytometry, chromosome painting and other genomic techniques<sup>14</sup>.

Polyspermy is observed in many plants but its contribution as a mechanism for polyploid formation is rather rare except perhaps in some orchids<sup>15</sup>. Endoreduplication is a form of nuclear polyploidization resulting in multiple uniform copies of chromosomes. It has been known to occur in the endosperm and the cotyledons of developing seeds, leaves and stems of bolting plants. In animals it occurs in certain tissues such as the liver cells, and megakaryocytes (the cells which give rise to the thrombocytes)<sup>16</sup>.

**Miscellaneous factors promoting Polyploidy:** There are a number of other factors favoring polyploidy include (but not limited to), the mode of reproduction, the mode of fertilization, the breeding system present, the growth habit of the plant, size of chromosomes etc. These are looked into in a little more detail below.

Polyploidy seems to be favored in long lived/perennial plants possessing various vegetative means of propagation (eg: *Fragia*, *Rubus*, *Artemisia*, *Potamogeton* etc.) and in those with frequent occurrences of natural inter-specific

hybridizations. Various possible reasons have been advanced by various workers to account for the above phenomenon; one of the widely accepted ones' being the enhanced chances of somatic doubling made possible in plants with enhanced lifespan and vegetative means of reproduction.. Cross fertilization and allogamy were argued to be factors favoring polyploidy. Autogamy however was thought to restrict it. There have been opposing views as well on the same. For example in the tribe *Midinae* (Compositae) polyploidy was found to be highly developed in the autogamous genus *Madia* but almost absent in the allogamous species of *Layia* and *Hemizonia* <sup>17</sup>. As regards latitude and altitude, the proportion of polyploids has been found to increase with latitude and altitude; but this has not always been found to be true with respect to altitude. Various reasons which have been put forth to explain the above trend in the distribution of polyploids some of them being the better adaptability of polyploids to colder climates and changes that might have taken place in the Pleistocene period etc.

Various ecological factors also have a bearing on the distribution of polyploids eg: polyploids were found to be more frequently distributed in wet soils and meadows as opposed to more stable habitats with drier soils or forest communities respectively. With regard to the breeding system since the main mode of origin of allopolyploids in annuals is by the fusion of unreduced gametes, the presence of an outcrossing breeding system tends to reduce the chances of union of unreduced gametes. A perennial growth habit tends to favor polyploidy as opposed to an annual growth habit, probably due to the fact that having a long life span increases the chances that rare events will occur (e.g. polyploidization following hybridization), and allows for mating between polyploids and their offspring<sup>18</sup>.

A reciprocal relationship has been observed between cell size, chromosome size and chromosome numbers in polyploids. Added to these a few other factors related to the genotype and the environment which had been looked into during the discussion on "the production of unreduced gametes" also come into play in.

**Classification of Polyploids:** Kihara & Ono (1926) first described two distinct types of polyploids: "autopolyploids" and "allopolyploids". Autopolyploidy is the doubling of the same chromosome set while allopolyploidy is the product of inter-specific hybridization; it is the product of doubling in a species hybrid and is therefore a polyploid containing separate sets of non-homologous chromosomes. The frequency of multivalent formation at synapsis was initially emphasized as a criterion for distinguishing auto- and allopolyploidy<sup>18</sup>. Later other basis for classification was also put forth. But nevertheless the classification of a plant into an auto or allotetraploid simply based on criteria such as resemblance in external morphology to some diploids, the behavior of chromosomes at meiosis etc. does not give any information as to the behavior or phylogenetic origin of the species and may therefore be of little practical value. More extensive classifications were subsequently given by other workers (Simonet, Lilienfield and Clausen, Keck and Hiesey) and the classification has expanded ever since. Below is generally accepted classification of the different classes of polyploids<sup>19-21</sup>:

**Autopolyploids:** Here the genomes coming together in the polyploid are identical. Here again they may be a strict /true autopolyploid (AAAA) or an *interracial autopolyploid* (AAAA). Autopolyploids are also called polysomic polyploids and can occur at the level of triploidy or anywhere upwards.

**Amphiploid:** This was a term coined by Clausen, Keck and Hiesey (1945) and includes true allopolyploids, segmental allopolyploids and autoallopolyploids and aneuploids.

A true allopolyploid or a disomic polyploid is a polyploid species derived from hybridization of parents that had structural dissimilarity between their basic genomes. These can occur at any level from tetraploidy upwards. eg: AA X BB → AABB

In a segmental allopolyploid the genomes in the species are partially homologous to each other and therefore exhibit partial multivalent formation. eg: A<sub>1</sub>A<sub>1</sub> X A<sub>2</sub>A<sub>2</sub> → A<sub>1</sub>A<sub>1</sub>A<sub>2</sub>A<sub>2</sub>

Autoallopolyploids are polyploids which combine the characteristics from both autopolyploids and allopolyploids, such as. eg:AA X BBBB → AABBBB

Aneuploids involve the gain or loss of single chromosomes

**Paleopolyploid:** This refers to an ancient polyploid that later became a diploid again due to sequence divergence between duplicated chromosomes as in the human genome. They generally have large basic chromosome numbers.

**Neopolyploids:** newly formed auto and allopolyploids. A polyploid could have individuals with a series of ploidy levels within the species thereby giving rise to a 'ploidy series'. The ploidy series may consist of individuals with even or odd multiples of the basic chromosome number(eg: *Chrysanthemum* (x=9); series 2x, 4x, 6x, 8x,10x) or odd multiples of the basic chromosome number ( eg: *Crepis occidentalis* (x=11); series 2x, 3x, 4x, 5x, 7x and 8x forms)<sup>19</sup>. Aneuploid series represent succession of allopolyploids based on different basic chromosome numbers. (eg: *Stipa* 2n=22,24,28,32,36....82). Dibasec polyploids are the sum of two different diploid numbers (eg: *Brassica oleracea*( 2n=18) and *Brassica campestris* (2n=20) and their tetraploid derivative *B. napus* (2n =4x=38)<sup>21</sup>.

Polyploids often tolerate the loss of one or more chromosome pairs which at times may give rise to modified polyploid series, what Darlington called a 'polyploid drop'(eg: a modified series found in *Hesperis* where different species have gametic numbers of n =7,14,13 and 12)<sup>22</sup>.

**Consequences/Implications of polyploidy/Polyploidy and the evolution of new species:** Polyploidy has been regarded as a major force in evolution and speciation. It is estimated that between 47% and 70% of angiosperm species are polyploid and this shoots up to as high as 95% in Pteridophytes (reaches the highest known levels in the plant kingdom). Polyploidy is rather common in some families like Rubiaceae, Compositae, Iridaceae, Gramineae etc. It is uncommon but present in other families such as Caesalpiniaceae, Passifloraceae and Fagaceae. Homosporous pteridophytes are found to have higher base numbers as compared to heterosporous types. Again the highest percentage is found in perennial herbs and a smaller proportion is found in annuals and woody plants<sup>23</sup>. It has been studied to a lesser extent in thallophytes (algae) but polyploids have been also observed in Cladophora and Chara. A few cases of polyploidy have been observed Rhodophycophyta and Phaeophycophyta. In bryophytes mosses seems to be a classical example for the occurrence of natural and artificial polyploids but is rather uncommon in liverworts. Stebbins even pointed out to inter-generic differences in the frequency of polyploids and cited the example of *Saliaceae* where polyploidy was common in *Salix* but rare in *Populus*. In Gymnosperms it is rare. It is unknown in cycads and *Ginkgo* but is known in *Ephedra*, *Pseudolarix amabilis* and *Sequoia sempervirens*.

In spite of the prevalence of high rates of polyploidy in many of the plant species there have been opposing views on the as well on relative contribution of polyploidy towards the process of speciation. These are exemplified in the statements below:

...polyploidy has contributed little to progressive evolution.

....polyploidy, far from playing a secondary role in evolution, has provided the additional, uncommitted gene loci necessary for major steps in the evolution of animals<sup>24</sup>.

The field of polyploidy therefore formed an area of interest and controversy for more than 50 years. The application of molecular techniques is now contributing to reshape many of our traditional tenets of polyploidy which is looked into in greater detail in some of the sections below.

The evolutionary forces involved in speciation can broadly be grouped into those producing variation and those tending to fix it. The forces mainly contributing to bring about variation include hybridization and novel mutations while those tending to fix it include selection with wide outcrossing, inbreeding by self fertilization and selection, inbreeding by assortative mating etc. The variation generating and variation fixing forces can be combined in



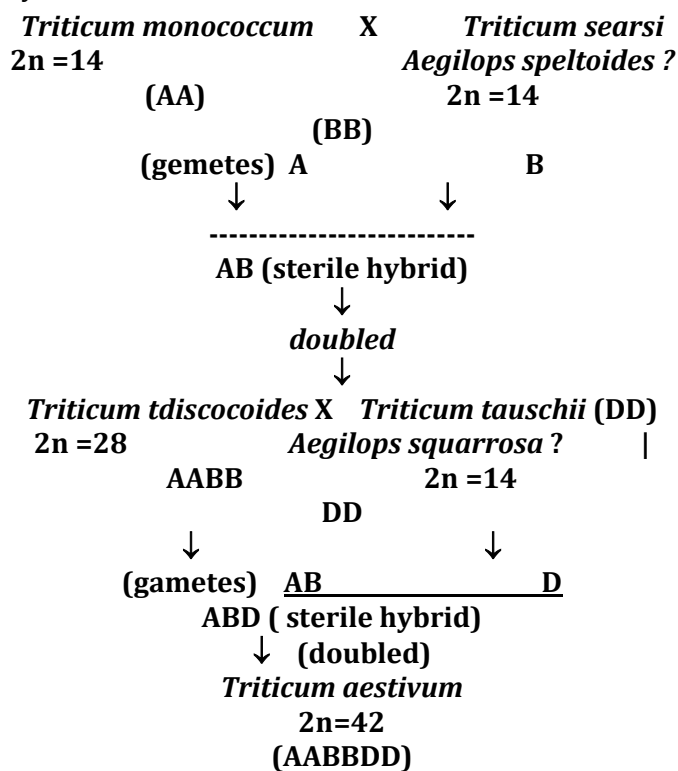
various permutations and combinations. The process of polyploidization can essentially be seen as a variation generating force involving extensive intra and inter-specific hybridizations as mentioned earlier. Naturally occurring inter-specific hybrids, presumably F1s occur in all major groups of plants. Examples for artificially induced polyploids range from the classical *Raphanobrassica* example of Karpechenko to many of the modern crop plants. The classic intergeneric cross between *Raphanus* (radish,  $2n=18$ ) and *Brassica* (cabbage,  $2n=18$ ) caused the formation of a sterile F1 hybrid with only univalents. However subsequent chromosome doubling resulted in a fertile allotetraploid, *Raphanobrassica* ( $2n=36$ ), which behaved similar to normal diploids and therefore provided a clear example of how hybridization between two species followed by chromosome doubling could cataclysmally (cataclysmic evolution) bring about the creation of a new species. Though an artificially created allopolyploid species, it definitely epitomized all criteria required of a legitimate species encountered in nature. *Primula kewensis* also represented another example of an artificial allotetraploid created from a previously sterile hybrid (got from a cross between two diploid species)<sup>25</sup>.

The contribution of natural polyploidy to the creation of new species can best be seen from the stories of various crop plants such as wheat (*Triticum aestivum*), tobacco (*Nicotiana tabacum*), and upland cotton (*Gossypium hirsutum*) to name a few.

The origin of allohexaploid bread wheat (*Triticum aestivum*) occurred from three diploid grass species coupled with chromosome doubling as shown in the figure below (Flow chart1)<sup>26</sup>.

The New World cottons ( $2n=52$ ) are also supposed to have risen from an allopolyploidization event between Asiatic cottons ( $2n=26$ ) and American cottons ( $2n=26$ ).

Similarly many of the mustard species such as *Brassica juncea* ( $2n=36$ ), *B.napus* ( $2n=38$ ) etc are supposed to have risen from inter-specific crosses between *B.nigra* ( $2n=16$ ) and *B.campestris* ( $2n=20$ ) and *B.oleraceae* ( $2n=18$ ) and *B.campestris* ( $2n=20$ ) respectively.



**Flow chart 1:** The role of polyploidy in the evolution of new species; the origin of bread wheat.

Having looked into some specific examples as to how polyploid was involved in some of the early speciation events in may be useful to review in brief some of the traditional views on polyploidy and restructuring of some of these which have been made possible by modern molecular techniques.

Long polyploid events were considered rare and most of the polyploid species were thought to have single origin. Polyploids in general were regarded to have the ability to colonize a wider range of habitats and survive better in harsh and unstable climates as compared to their diploid progenitors probably due to increased heterozygosity and genic and biochemical flexibility provided by the presence of additional alleles<sup>27</sup>. Due to the 'buffering effect' of multiple genomes, mutations and recombination etc. they were thought to contribute lesser to the development of new adaptive complexes than diploids. (considering equal mutation rates in diploids and polyploids). There again, allopolyploids were considered a major force in evolution while autopolyploids on the other hand were considered rare and rather maladaptive<sup>28</sup>. But as mentioned earlier many of these views on seem to be undergoing transformation largely due to data available from molecular approaches such as RFLPs, GISH, chromosome painting etc. Polyploids in fact are thought to represent a relatively frequent class of mutation, one that occasionally establishes within populations when its phenotypic effects are relatively mild. Or conversely polyploidy may be common because polyploid species may evolve faster or in more novel directions<sup>29</sup>.

Most of the polyploid species are now seen to be of multiple origin with a few exceptions such as *Arachis hypogea* and salt water grass (*Spartina anglica*). The exact extent of multiple origins is unknown but in most cases is thought to be underestimated. Studies on recent allopolyploidy in *Tragopogon* indicate that multiple origins can occur frequently over a short time and area. (just past about 50 years in a small region of eastern Washington). The concept of recurrent polyploidization and subsequent further interbreeding of genotypes is best seen in the Arctic flora. Multiple polyploid events from genetically and morphological differentiated diploid populations yield a complex of different genotypes at the ploidy level and these genotypes in turn ultimately come into contact and hybridize.

Another discovery is the occurrence of extensive genomic reorganization in polyploids. Chromosome painting, genetic mapping and comparative genetics have shown the occurrence of extensive intra and intergenomic reorganizations. Nine intergenomic translocations were detected in allotetraploid tobacco (*Nicotiana*), Soybean, an ancient tetraploid also revealed significant intra-chromosomal rearrangement. In another experiment by Song *et al.* using synthetic polyploids of *Brassica* to study the evolution of early generations after polyploidization, it was found that extensive genomic changes were detected in F5 as compared to the F2 plants as indicated by the loss/gain of parental restriction fragments and also by the appearance of new fragments. Transposable elements (TE) might also facilitate genome restructuring since duplicates of all genes in polyploids might buffer them from the deleterious consequences of transposition and TE will tend to multiply and be maintained. (eg: in cotton the spread of A genome repeats to D genome is thought to be mainly by transposition)<sup>27</sup>.

In addition to gene restructuring, in a polyploid organism there could be several fates for redundant genes including regulatory or functional divergence which will preserve the increased gene number but may also lead to 'copy number dependent gene silencing'; an epigenetic change. Extensive silencing may finally cause a polyploid to no longer appear to be structured as an allopolyploid as in *Zea mays*. Gene silencing from epigenetic modifications is thought to be reversible. Also it has long been held that polyploid species have the ability to colonize a wider range of habitats and survive better in harsh and unstable climates (better heat, cold drought resistance etc. But an opposing view has been presented by Stebbins who postulated that the better ability is due to secondary contacts between previously isolated populations which generate more aggressive and adapted gene combinations that have been buffered and maintained. In a 39 year experiment with diploid and tetraploid *Ehrharta erecta* he found that the polyploid was inferior in behavior to their diploid ancestors under field conditions.

The high rates of polyploid occurrence has been looked into and explained on different grounds. Incompatible gene or chromosome combinations that may be brought together in allopolyploid genomes cannot be easily flushed out

through Mendelian segregation and the elimination of such DNA sequences and the alteration of DNA methylation patterns permit fertility restoration in some allopolyploids<sup>30</sup>.

Another contradicting view in the context of polyploids with respect to evolution is the fact that autopolyploids are not maladaptive to evolution. Important genetic attributes such as increased enzyme multiplicity and increased allelic diversity in fact make them a strong success in nature.

**Other consequences of polyploidy:** The effects of polyploidy on evolution have been one of the one key areas of focus of many workers and authors. Nevertheless polyploidy does have implications on various other aspects some of which are looked into below<sup>28-30</sup>.

**Cytology:** Polyploids in general tend to have larger cells compared to their diploid progenitors. As regards the effect of polyploidy on the volume of the cell there seem to be conflicting reports with some stating the lack of any effect cell volume while others reporting an increase in cell volume (upto eight times that found in haploids). Overall there seems to be a reduction if the surface area to volume ratio which in turn has a bearing on enzymes such as ornithine transcarbamylase, tryptophan synthase, invertase and acid phosphatase related to cell volume and cell surface area respectively. Metabolism and growth seems to be rather retarded in polyploids due to altered geometric relations between the nucleus and the rest of the cell. An inverse relationship between DNA content and development rate has also been found. Polyploids also seem to have reduced number of cell divisions during development<sup>28</sup>.

**Gene activity:** There have been reports of variable results with regard to the effect of polyploidy on gene activity, the total RNA and protein contents. Differential amplification of RNA cistrons were reported with increasing ploidy levels in *Datura innoxia* and autotetraploid tomato. With regard to effect of chromosome doubling on enzyme behavior “ambiguous” results have been reported. The levels of various enzymes involved in the electron transport chain, photosynthesis and photorespiration were found to increase, decrease or remain unchanged in autotetraploid tomatoes. The CO<sub>2</sub> exchange rate has generally been reported to decline with ploidy level but has been found to increase in *Festuca arundinacea*<sup>29</sup>.

The effects of chromosome doubling may exhibit differences between gametophytes and sporophytes of the same species and also between different strains within the same species.

**Growth substances:** As regards the effect of polyploidy on various growth hormones lower contents of abscisic acid and an auxin like substances were found in autotetraploid *Lycopersicon pimpinellifolium* as compared to diploids<sup>29</sup>.

**Water balance:** Higher water content and a lower osmotic pressure was found in autotetraploid tomatoes and also in *Petunia*. Not much was known about differences in the rates of water uptake but it was found that transpiration rates were lower in polyploids<sup>28</sup>.

**Responses to different stress:** Parameters such as whole plant weight, relative water content etc. decrease to smaller extent in polyploids as compared to diploids. Generally polyploids seem to be more tolerant to drought than their diploid progenitors. But contradictory views have been presented by Stebbins who observed that tetraploids of *Ehrrharta erecta* persisted only on shady well drained soils whereas the diploids survived in more harsh environments. As regards cold tolerance it was found that autotetraploids of *Brassica campestris*, *Raphanus sativus* and a few others were more cold resistant while tetraploids of *Trifolium repens* were less resistant. Polyploids plants were also found to be more resistant to mutagenesis and irradiation. Polyploids seem to be more



tolerant to poor soils, since most of them are slow growers and therefore have more modest nutrient requirements. Most polyploids in general are more resistant to pathogens and pests due to enhanced production of various secondary plant metabolites. Polyploids are also more resistant to herbicides, which may be due to increased heterozygosity and increased genetic redundancy<sup>30</sup>.

**Other aspects:** There seems to be reduced pollen and seed viability in autopolyploids as compared to diploid ancestors. There is an alteration in the primary and secondary metabolism. Autopolyploids of many drug plants have increased quantities of alkaloids per dry weight. Chromosome doubling may also alter the secondary metabolism in a qualitative manner (eg: differences in glycoflavone profiles). Another effect appears to be reduction in the amount of branching, which occurs frequently not universally. Seeds of most tetraploids are larger than those of diploids; however the percent germination may be variable being lower in some (eg: *Lycopersicon esculentum*) or higher in others (*Oryza punctata*). The leaves and other appendages of polyploids in general seem to be more thicker, shorter and broader. Polyploidy also seems to affect incompatibility relationships of some self-incompatible species. Any incompatibility in the diploid parents such as in *Raphanus* and *Brassica* seems to be carried down equally to the autotetraploid also<sup>29</sup>.

**Polyploids in agriculture and horticulture:** Some of the crop plants cited by Stebbins (1950), which are polyploids, include potato, coffee, banana, peanut, tobacco, wheat, oats, sugarcane, plum, loganberry and strawberry<sup>26</sup>. After observing the polyploid nature of different crop plants and also the bigger size and vigour of the same in many cases, plant breeders started getting interested in the artificial induction of polyploids. Though this was initially marred by the lack of a suitable method for the induction of polyploidy, the discovery of the “colchicine method” served to remove this hurdle to a large extent<sup>31</sup>. Polyploids are now found in alsike clover, rey, turnip, dill, spinach, apple, radish, grapes, zinnias, sugarbeets, petunia, *Datura*, *Polulus*, tea, watermelons, various forage grasses etc. to name just a few. It must be pointed out that in many of the seed crops polyploids produced had lower fertility rates than their diploid prototypes also in general there is an optimum range of polyploidy beyond which growth may be depressed with increasing chromosome numbers. But in plants and flowers where seed cost are minor compared to the beauty of the flowers or other valuable features of other plant parts reduced fertility may not be a critical factor<sup>32</sup>.

## CONCLUSION

Polyploidy is an exciting phenomenon with intriguingly, a lot of practical potential. As mentioned earlier it has been an area of interest right from the eighteenth century and continues to be an area of interest as seen from the increasing number of publications being generated continually on various aspects of polyploidy over the last decade. Technological advancement and various molecular tools (such as GISH, RFLP, flow cytometry etc.) seem to be helping us gain better insights into various aspects of polyploidy in plants and animals and also help reshape many of the traditionally held tenets. While it is suggested by some that certain factors such as the high rates of polyploid occurrence in plants, the absence of ethical issues etc. may make plants very good models to elucidate the molecular mechanisms of polyploid formation yet others have suggested a ‘cross-disciplinary’ approach involving both plants and animals in looking into the origin and establishment of polyploids lineages as a more efficient strategy.

Many discoveries of the past in conjunction with the current information being generated seem to be setting the stage for a new series of questions such as the extent of geneflow in polyploid lineages of separate origin, the rapidity of genome restructuring, its prevalence in neopolyploids and the like. Many of our crop plants are polyploids and a number of them have and are being synthetically produced. Yet, it has been impossible to predict with certainty, which diploid genomes when merged will coexist stably, therefore transforming the present ‘hit and miss’ process into a more exact science will form an area of focus in future. Also a more detailed analysis of

gene expression changes in many of the newly formed polyploids could help uncover the impact of new variation on polyploid evolution. An understanding the timing and frequency of changes in many of the newly formed polyploids along with the mechanisms involved in diploidization may also facilitate gain a more thorough insight into the evolutionary impact of rapid genome changes in neopolyploids along with strategies possible for manipulation.

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