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***Review article***

# Harnessing polyploidy for vegetable crop improvement: strategies and applications

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## Abstract

**In the evolution and diversification of plant species, polyploidization is the most common event. Polyploidy, also known as whole-genome duplication (WGD), occurs when a cell or organism has more than two sets of chromosomes per nucleus. Autopolyploidy and allopolyploidy are the two types of polyploidy. The former refers to chromosomal/genome duplication within the same species (AAAA), and the latter refers to genome hybridization followed by chromosome doubling. Scientists are becoming more interested in ploidy because of its benefits in genomic flexibility and long-term functional alterations, as well as its selective ability to respond to environmental changes. The "gigas" effect, is the most visible result. Colchicine, a popular mitotic inhibitor, causes polyploidy in plants by blocking chromosomal segregation during cell division. Ploidy can be detected by using a variety of markers, including morphological, physiological, and molecular ones (counting chromosomes and estimating nuclear genome size using flow cytometry). Watermelon (Pusa Bedana and Arka Madhura), Cassava (Sree Harsha), and Palak (Pusa Jyoti)are among the vegetables that have benefited from polyploidy. As a result, polyploids have a lot of potential for use in breeding programs, particularly in terms of yield and tolerance.**

**Keywords:** Autopolyploids, Allopolyploids, Chromosome doubling, Gigas effect, Whole-genome duplication

The most omnipresent phenomenon for the evolution and diversification of plant species ispolyploidization (Parisod *et al*. 2010; Sattler *et al*. 2016). Polyploidy is the heritable condition of possessing more than two complete sets of chromosomes (Comai 2005). Triploid (3n) and tetraploid (4n) refer to plants containing three and four sets of chromosomes, respectively. Many crop plants have undergone polyploidy, which ranges from 30-70 percent in angiosperms, during the evolutionary process (Chen 2010; Sattler *et al.* 2016). The fertile polyploids not only supplement the species diversity but also an anchorage for polyploidy breeding (Kazi 2015). Some basic terms must be defined before comprehending polyploidy. The letter "x" is used to refer to the basic chromosome number of the ancestor of a polyploid. "2n", refers to the total number of chromosomes. A diploid organism (non-polyploid) is represented as 2n = 2x (Heslop-Harrison, 2013). A somatic cell has 2n chromosomes, whereas gametes only have a haploid (n) set of chromosomes (Otto and Whitton 2000). Whole-genome duplication not only produces variations in the genome (epigenetic changes and modulated gene expression) but also multiplies the copies of existing genes that influence the external characters of the species (Chen *et al*. 2020).

Vegetable crops with increased ploidy levels frequently display higher genetic diversity with anatomical and morphological changes that have resulted in increased size, vigour, biomass, yield and also possess selective abilities to adapt to environmental changes (stress tolerance and disease resistance). Thus, polyploidizationprovides an opportunity for vegetable improvement that put forward many economic and social benefits (Can 2012). The three kinds of polyploidy that have been

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identified are autopolyploidy, allopolyploidy, and segmented allopolyploidy (Stebbins, 1947). In the first one, there is a duplication of a chromosome/genome within the same species (Stebbins 1947). Allopolyploids have two or more different genomes andcan result through the hybridization of two separate species, which is linked to genome doubling (Stebbins 1947; Grant 1975). The third one, *i.e.*, segmental allopolyploids, carries more than two incompletely distinct genomes which can lead to the formation of both bivalents and multivalents during chromosome pairing (Stebbins 1947; Levin 2002; Madlung 2013).

Polyploidy gained much importance during the early part of the twentieth century. One of the earliest examples of natural autopolyploidy was the gigas mutant in *Oenothera lamarckiana* (Ramsey and Schemske 1998). In 1916, Wrinkler experimented with Solanum vegetative grafts and chimeras and discovered that some of the plants obtained were polyploid. *Primula kewensis* (sterile interspecific hybrid through chromosome doubling) was the classical example of allopolyploidy (Digby 1912; Dar *et al*. 2017). Tetraploid and octoploid cells in the cortex and pith of Vicia faba have been reported (Ramsey and Schemske 1998; Dar *et al*. 2017). Antimitotic drugs can be used to artificially produce polyploids, with colchicine being one of the most widely utilized (Blakeslee and Avery 1937; Planchais *et al*. 2000). In contrast to their diploid counterparts, induced polyploids exhibit higher flexibility, tolerance to diverse stresses (biotic and abiotic), and a longer reproductive period with increased photosynthetic and genetic action (Gantait and Mukherjee 2021).

**Origin**

It has been the subject of several reviews in the last century aimed at explaining the causes and effects of polyploidy (Stebbins 1947; Harlan and de Wet 1975; Ramsey and Schemske 1998; Soltis and Soltis 1999 Otto and Whitton 2000).To explain how polyploids originate in nature, various processes have been proposed. Polyploidy in plants is caused by two primary routes: somatic doubling (mitotic nondisjunction) occurs in zygotic, embryonic or sporophytic tissue and the formation of unreduced reproductive cells (non- reduction during meiosis) (Madlung 2013; Sattler *et al*. 2016). Aside from genetic regulation, a variety of environmental factors have contributed to the development of unreduced gametes such as temperature, water-deficient, wounding and nutrient shortage (Ramsey and Schemske 1998). The formation of unreduced gametes can lead to bilateral polyploidization (fusion with another unreduced gamete) or unilateral polyploidization (fusion of an unreduced gamete with a reduced one) (Sattler *et al*. 2016). The two processes that lead to the production of unreduced gametes are cytologically known as first division restitution (FDR) and second division restitution (SDR). During the FDR, there is no chromosome pairing in zygotene or pachytene and/or non-segregation of homologous chromosomes in anaphase I, resulting in two non-sister chromatids with approximately the same heterozygosity level as their parents, whereas in SDR, sister chromatids do not segregate in anaphase I, resulting in the formation of dyads or triads and will have a lower level of heterozygosity as compared to its parents (Bretagnolle and Thompso, 1995; Ramanna and Jacobsen 2003). Other mechanisms that led to the development of polyploid plants are: meiotic or mitotic failures, polyspermy (fertilization of the egg by two male nuclei), and endoreduplication (replication of the DNA but no cytokinesis) (Ramsey and Schemske 1998; Otto and Whitton 2000; Comai 2005; Song *et al*. 2012; Dar *et al*.2017). Chromosome doubling in the zygote or in some apical meristems produces complete polyploids and polyploid chimeras, respectively (Dar *et al*. 2017).

**Autopolyploidy**

Traditionally, autopolyploids were considered to occur from the doubling of structurally similar, homologous genomes within a single species (AAAA) (Parisod *et al*. 2010). They occur naturally in low frequencies and can be artificially induced by a variety of techniques including: heat and chemical treatments, decapitation, and selection from twin seedlings (Dar *et al*. 2017). Artificially, they are originated using colchicine ($C_{22}H_{25}O_6$), an alkaloid from the autumn crocus (*Colchicum autumnale*) as shown in Table 1, which disrupts the spindle mechanism in mitosis, thereby preventing the migration of duplicate chromosome (Blakeslee and Avery 1937). The meristematic tissue is the most vulnerable to colchicine treatment. Tetraploid crop like potato (Wakchaure and

**Table 1. Induction of polyploidy by applying colchicine**

| Method of application | Optimum treatment | Reference |
|---|---|---|
| Colchicine solution is poured over the entire plant. | 0.1; 96 hours | Vichiato *et al.* 2014 |
| Seeds that have been immersed in a colchicine solution | 0.05%; 24 hours | Balode, 2008 |
| Colchicine is applied to seedlings using cotton plugs. | 0.4 %; 3 days | Anurita and GirJesh, 2007 |
| Colchicine was administered to the apical meristems in drops. | 0.006% for 3 successive days | Talebi *et al.* 2017 |

Ganguly 2016) and hexaploid crop like sweet potato are examples of natural autoploids. Meiotic failure occurs in autopolyploidy, leading tothe generation of unreduced gametes, which eventually result in the formation of multivalent (*e.g.*, Tetraploids have quadrivalents or bivalents in addition to certain trivalent and univalent) (Dar *et al.* 2017).

The "gigas" effect, which results in individuals having larger leaves, roots, flowers, fruits, and seeds than their diploid counterparts, was the most common consequence of autopolyploid production (Sattler *et al.* 2016; Stebbins 1950). But sometimes, there is reduction in the fertility of autopolyploids as compared to their diploid progenitors (Ramsey and Schemske 2002). During the research on crops, it was observed that genome doubling in autopolyploids contributes prompt acquisition of novel traits (*e.g.*, increased cell size and gene expression, changes in physiology and ecological tolerance) (Levin 2002; Ramsey and Schemske 2002; Paterson 2005). Autopolyploidy induction is mainly limited to crops cultivated for their vegetative organs and those with vegetative propagation due to the low rates of viable seed production (Paterson, 2005) with an exception of triploid watermelon as in this case, low number of seeds is a desirable characteristic (Crow 1994). Furthermore, autopolyploids may impact stress tolerance, including nutrient insufficiency, drought, water deficit, temperature, pests, and diseases (Levin 2002). Autopolypoids have higher levels of heterozygosity than diploids due to polysomic inheritance (Moody *et al.* 1993; Osborn *et al.* 2003). In autotetraploid maize (Randolph 1942), potato (Mendoza and Haynes 1974), and alfalfa (Mendoza and Haynes 1974), higher levels of heterozygosity have been associated with increased vigour. Autopolyploidy's two key triumphs in crop development are the formation of triploids and tetraploids.

**Autopolyploidy's evolutionary course**

Top panel: Genome doubling occurs because of cross-fertilization between individuals, either by the direct fusing of two unreduced gametes (one-step creation) or as a two-step process of cross-fertilization between an unreduced gamete and a triploid intermediate (triploid bridge). In natural populations, spontaneous doubling is uncommon. Central panel: Genome doubling causes genetic and epigenetic alterations, which lead to structural and functional reorganization until full diploidization is achieved in the long run. These genetic mechanisms are associated with the development, establishment, and growth of autopolyploid lineages in wild populations (Parisod *et al.* 2010). The practical applications of autopolyploidy are as under:

**Triploid Seedless watermelon**

The first triploid seedless watermelon was developed by Dr. Khiara and Nishiyama (Kazi 2015) by treating a normal diploid plant (2x=22) with a tetraploid plant (4x=44) using antimitotic agent *i.e.*,colchicine as shown in Figure1 and thus triploid progeny is produced by using the pollen of the diploid (triploid does not produce viable pollen for pollination and fruit development) to pollinate the stigma of the induced tetraploid (Crow 1994; Pal and Bal 2020). As a result, diploid plants were planted in the same region as triploids to supply the requisite pollen for seedless fruit development (Crow 1994). Seedless watermelons are gradually gaining favour among Indian customers. Through colchiploidy, Kerala Agricultural University (KAU), Trichur, has generated a stable tetraploid line of watermelon called 'KAU-CL-TETRA-1. By crossing this tetraploid line with diploid males, notably CL-4 (red-fleshed) and CL-5 (yellow-

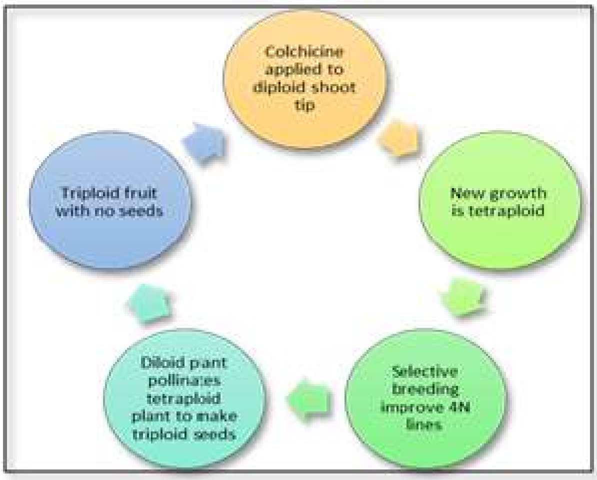


**Figure 1: Formation of triploid seedless watermelon**

fleshed), two triploid hybrids, Shonima and Swarna, have been created. Both hybrids have been approved for cultivation in Kerala (Thayyil *et al*. 2016).

**Triploid sugar beet**

Sugar beet comes in diploid (2x = 18), triploid (3x = 27), and tetraploid (4x = 36) forms, and is a major sugar producer in temperate climates (Smulders *et al*. 2010). Male diploid sterile plants are crossed with tetraploid pollinators or by reciprocal crossing, *i.e*., between male tetraploid sterile plants and diploid pollinators, to generate triploid sugar beet (Kinoshita and Takahashi 1969). Sugar beets that are triploid have larger roots and produce more sugar per unit area (Dabholkar 2006).

**Triploid asparagus**

The most economically important Asparagus species is *Asparagus officinalis* L. (2n = 2x = 20), which is also the only one cultivated as a vegetable crop worldwide. It does, however, have a limited genetic base. As a result, it's critical to introduce agronomically relevant features from wild relatives, thereby expanding the breeding gene pool. In asparagus, a triploid cultivar has been described from crossings between the tetraploid landrace 'Morado de Huetor' and a diploid commercial cultivar (Castro *et al*. 2012).

**Tetraploid turnip**

Hua-bing *et al*. (2011) investigated a series of physiological characteristics to see if a tetraploid turnip (cv Aijiaohuang, 4n) and its diploid parent (cv. Aijiaohuang, 2n) were tolerant to salinity stress. Tetraploid turnips adapted better to a high salt medium (200 mmol $L^{-1}$) and had a higher $K^+$ / $Na^+$ ratio in the roots, higher glutathione concentration, and antioxidant activity in the leaves, according to the findings.

**Allopolyploidy**

The prefix 'allo' indicates that the ploidy solely includes non-homologous chromosomes (Wakchaure and Ganguly 2016). Allopolyploids, also known as alloploids, were originated from the hybridization of two or more genomes followed by chromosome doubling or by fusing of unreduced gametes from different species (Ramsey and Schemske 1998; Acquaah 2007; Jones *et al*. 2008; Chen 2010). Rapeseed and mustard are examples of important natural alloploids. (Acquaah 2007; Chen 2010). It is crucial to distinguish the origins of genomes in allopolyploid, hence each genome is assigned a separate letter (*e.g*., Nagaharu explained the origin of the cultivated mustards (Brassica species), in the triangle of U with each species represented by a distinct letter) (Bellostas *et al.* 2007; Nelson *et al*. 2009). Further, there are two subclasses of allopolyploids: true and segmental allopolyploids. If hybridization occurs between distantly related species, then there is the formation of bivalents during meiosis in a disomic inheritance pattern which ultimate giverise to true allopolyploids (Sattler *et al.* 2016). On the contrary, if hybridization occurs between closely related species with partially differentiated genomes, it will result in the formation of segmental allopolyploid (Stebbins 1950). Sometimes allopolyploids are also formed by a two-step process i.e., formation of a triploid bridge (the fusion of reduced 1n gamete with unreduced 2n gamete gives rise to 3n zygote followed by the subsequent fusion of 1n reduced gamete with 3n gamete in the next generation (Dar *et al*. 2017). The increasing number of alleles of a given gene mask detrimental recessive mutations and hence protects against fitness loss (Gu *et al*. 2003). The second benefit is polyploids' ability to outperform their diploid counterparts due to heterosis (Birchler *et al*. 2010). The neo-functionalization or sub-functionalization that leads to ecological niche expansion is the third and most crucial advantage (Adams and Wendel, 2005; Moore and Purugganan, 2005; Lynch 2007). Okra (2n=130) is a natural amphidiploid (Joshi and Hardas1956) that results from chromosome doubling in a hybrid between *Abelmoschus tuberculatus* as one parent and *Abelmoschus ficulneus* as the other probable parent (Lata *et al*. 2021). The important applications of allopolyploidy are enumerated as under:

1. **Contribution of ploidy in the evolution of new species:**

**Amphidiploid *Brassica* species**

*Brassica* contains 330 genera and 3800 species, making it the most important genus (Bailey *et al*. 2006; Huang *et al*. 2016). The six key cultivated species are *Brassica rapa, Brassica juncea, Brassica nigra, Brassica carinata, Brassica oleracea,* and *Brassica napus*. Based on artificial inter-specific hybridization experiments, a well-known model, U's triangle, was proposed to demonstrate the genetic links among these six species (Figure 2; Nagaharu U's triangle, 1935). *B. rapa* (AA, 2n = 2x = 20), *B. nigra* (BB, 2n = 2x = 16), and *B. oleracea* (CC, 2n = 2x = 18) are the three fundamental diploid species, and three allotetraploid species, *B. juncea* (AABB, 2n = 4x = 36), *B.carinata* (BBCC, 2n = 4x = 34), and *B.napus* (AACC) are formed through natural hybridization and chromosome doubling (Chalhoubetal 2014; Yang *et al*. 2016).

**Hakuran**

An artificially manufactured interspecific hybrid and a promising breeding bridge plant created by crossing Chinese cabbage with cabbage and combining the heading qualities of both parents. Bacterial soft rot resistance and low-temperature sensitivity were introduced from common cabbage and Chinese cabbage, respectively. Hakuran is self-incompatible, although it is cross-compatible with other Brassica species (Nishi 1981).

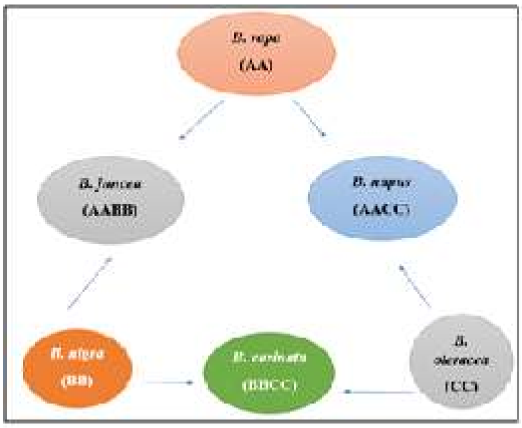


**Figure 2: Brassica U's triangle**

***Cucumis hytivus***

*Cucumis hytivus (Cucumis hystrix × Cucumis sativus)*, a novel synthetic Cucumis (Cucurbitaceae) species resulting from interspecific hybridization via embryo culture and chromosome doubling. It has many advantages, including resistance to root-knot nematodes, sticky stem blight, downy mildew, and low temperature and irradiance tolerance (Chen and Kirkbride 2000).

**Raphanobrassica**

Karpechenko (1927), developed Raphanobrassica viable hybrid (artificial alloploid) by crossing radish (*Raphanus sativus*, n=9) and cabbage (*Brassica oleracea,* n=9).The goal was to create a plant with radish roots and cabbage leaves. By accident, a fertile amphidiploid (4n=36) with cabbage roots and radish leaves was created by spontaneous chromosomal doubling (Bharadwaj 2015).

**Polyploid onion**

McCallum (1988), used colchicine to treat $F_1$ of *Allium cepa × Allium fistulosum* and reciprocal crosses, and found a $C_2$ population with good seedling vigour and cold hardiness at Beltsville during the winter, compared to normal diploids.

2. **Bridge crossing**

Another breeding approach that takes advantage of polyploids is bridge crossing. When ploidy levels induce sexual incompatibilities between two species, intermediary crosses can be used to produce fertile bridge hybrids, followed by chromosomal doubling. For onion breeding, *Allium fistulosum* has several beneficial agronomical features. Direct sexual hybridization of *A. fistulosum* for onion breeding is problematic. As a result, we investigated whether using *A. roylei* as a bridging species in a bridge cross could be a realistic alternative (Khrustaleva and Kik 1998).

3. **Polyploids are employed for mutation breeding**

Polyploids are utilized for mutation breeding because, despite their ability to withstand harmful cistron alterations after mutation, they require a higher mutation frequency due to their huge genomes, which result from the duplicated condition of their bountiful chromosomes (Gaul 1958). The high mutation frequencies found in polyploids could be used to try to generate mutations in diploid cultivars that don't produce enough genetic variation when subjected to an agent treatment. This method has been used to generate mutants ofthe hot water plant species(nut orchids). It is the first to develop autotetraploid after being treated with colchicine and exposed to X-rays. During this research, autotetraploid were discovered to have a 20-40 times higher mutation frequency than diploid varieties with big genomes (Broertjes 1976).

**4. Genetics effects**

**4a. Cell and body size changes**

Polyploid cell sizes typically rise in tandem with genome doubling and increases in genetic resources. Plants may use a variety of ways to deal with the increased cell size that comes with polyploidy. Polyploid plants have the same number of cells as diploid plants, which allows them to grow larger organs and bodies (Mable 2004; Gregory and Mable 2005).

**4b. Genomic Shift**

The novel polyploid's primary distinguishing characteristics are genomic instability and fast recombination, in an endeavourto establish the peaceful coexistence of several genomes within one nucleus. Within five generations of artificial synthetic polyploid Brassica hybrids, for example, substantial genomic rearrangements and fragment loss were detected (Song 1995; Comai 2000; Chen *et al.* 2007).

**4c. Gene expression changes in polyploids**

Polyploids undergo alterations in gene expression, including gene silencing, up-regulation or down-regulation of expression, non-functionalization, sub-functionalization, and neofunctionalization, in addition to chromosomal structural changes. Both genetic and epigenetic processes are essential (Chen 2007; Song 2012).

**4d. Diploidization**

The allopolyploid generally undergoes diploidization to maintain stability following genome merging and doubling, to eliminate a wide spectrum of incompatibilities. Because homoeologous chromosomes may pair during meiosis, preventing the generation of functional gametes, allopolyploids frequently exhibit bivalent rather than multivalent chromosome pairing, indicating a diploid-like meiotic behaviour (Song 2012).

**Disadvantages**

Polyploidy alters the structure of the genome and the arrangement of cells. It imposes several significant constraints on cell cycle events (mitosis, meiosis), cell physiology (metabolism, growth), gene expression regulation, and genome stability.

**Ploidy level measurement**

Traditionally, meristematic tissue chromosomes (i.e., root tips during the metaphase phase of cell division) are counted to determine ploidy levels. There are numerous indirect approaches for determining ploidy: the number of chloroplasts in the stomatal guard cell can be counted. The length of the stomata can be measured (the longer the stomata, the higher the ploidy). Pollen grain diameter can also be used to determine ploidy levels. Flow cytometry has recently been the most widely used and accurate method. It determines the amount of nuclear DNA in plants (Pal and Bal 2020).

**Table 2. The varieties of vegetable crops developed using polyploidy**

| Crop | Variety | Feature |
|---|---|---|
| Watermelon | Arka Madhura | TSS 13-14 percent, higher shelf life, and transit quality, appropriate for year-round cultivation under protected conditions, yields 50-60 t/hectare |
| Watermelon | Pusa Bedana | Aborted embryos and fake, rudimentary, barely discernible seeds characterize this seedless triploid hybrid. |
| Cassava | Sree Harsha | Plants are triploid and non-branching, yielding 35-40 t/ha and containing 39.05 percent starch. |
| Palak | Pusa Jyoti | Tetraploid with large, thick, soft, succulent dark green leaves, fast rejuvenation, and yields of 50 tonnes per hectare. |

## Conclusion

Polyploidy is a valuable tool to employ in breeding programs. Polyploidy causes plant gigantism, which is especially helpful for vegetative crops like potatoes, sweet potatoes, taro, and green vegetables. Polyploidy can be used to create new plant types with improved disease resistance, adaption, yield, and quality. With distantly related species, polyploidy helps to overcome fertilization obstacles. Triploidy is used to achieve seedlessness. Polyploidy is a widespread phenomenon in vegetable crops that has a significant impact on plant evolution.

**Future prospects**

Initially, polyploidy drew interest because of its distinct cytogenetics and reproductive isolation, but it was quickly discovered that polyploids also exhibited unusual phenotypic features and hybrid vigour, both of which are beneficial to agriculture. Polyploidy species that arise from heterozygous diploid progenitors may be a significant source of genetic variation. It is possible to generate new crops, transmit interspecific genes, and track the origins of crops. Despite the risk of displaying unwanted traits and the potential for a variety of obstacles, polyploidy breeding will unveil many of the plant's mysteries. In the realm of vegetable breeding, unveiling the evolution of crop plants and exploiting their variety is currently an intriguing research topic.

**Conflict of interest:** The authors declare no conflict of interest in relation to this research article.

## References


Acquaah G. 2007. Principles of plant genetics and breeding. Wiley-Blackwell, Malden.

Adams K and Wendel J. 2005. Polyploidy and genome evolution in plants. *Current Opinionin Plant Biology*, 8, 135-141.doi: 10.1016/j.pbi.2005.01.001. PMID: 15752992

Anurita D and Girjesh K. 2007. Morphogenetic analysis of colchitetraploids in *Impatiens balsamina* L. *Caryologia*, 60, 199-202.doi: 10.1080/00087114.2007.10797937

Bailey CD, Koch MA, Mayer M, Mummenhoff K, O'Kane SL and Warwick SI. 2006. Toward a global phylogeny of the Brassicaceae. Molecular Biology and Evolution, 23, 2142-2160. doi: 10.1093/molbev/msl087

Balode A. 2008. Applying colchicine and oryzaline in *Lilium* L. polyploidization. Latvian Journal of Agronomy **11:** 22-28.

Bellostas N, Sorensen JC and Sorensen H. 2007. Profiling glucosinolates in vegetative and reproductive tissues of four Brassica species of the U triangle for their biofumigation potential. Journal of the Science of Food and Agriculture **87:** 1586-1594.

Bharadwaj DN. 2015. Polyploidy in crop improvement and evolution. Plant Biology and Biotechnology: Plant Diversity, Organization, Function and Improvement. p. 619-638.

Birchler JA, Yao H, Chudalayandi S, Vaiman D and Veitia RA 2010. Heterosis. The Plant Cell **22:** 2105-2112.

Blakeslee AF and Avery AG 1937. Methods of inducing doubling of chromosomes in plants by treatment with colchicine. Journal of Heredity **28:** 393-411.

Bretagnolle FA and Thompson JD 1995. Gametes with the somatic chromosome number: mechanisms of their formation and role in the evolution of autopolyploid plants. New Phytologist **129:** 1–22.

Broertjes C 1976. Mutation breeding of autotetraploid Achimenes cultivars. Euphytica **25:** 297-304.

Can S 2012. Polyploid organisms. Science China Life Sciences **55:** 301-311.

Castro P, Gill J, Cabrera A and Moreno R 2012. Assessment of genetic diversity and phylogenetic relationships in Asparagus species related to *Asparagus officinalis.* Genetic Resources and Crop Evolution **60:** 1275-1288

Chalhoub B, Denoeud F, Liu S, Parkin IA, Tang H and Wang X 2014. Plant genetics. early allopolyploid evolution in the post-neolithic *Brassica napus* oilseed genome. Science **345:** 950–953.

Chen JF and Kirkbride JH 2000. Anew synthetic species of Cucumis (Cucurbitaceae) from interspecific hybridization and chromosome doubling. Brittonia **52:** 315-319.

Chen JT, Jeremy C and Geoffrey M 2020. Editorial: Artificial Polyploidy in Plants. Frontiers in Plant Science **11:** 621849.

Chen ZJ 2007. Genetic and epigenetic mechanisms for gene expression and phenotypic variation in plant polyploids. Annual Review Plant Biology, **58:** 377–406.

Chen ZJ 2010. Molecular mechanism of polyploidy and hybrid vigour. Trends in Plant Science **15:** 57-71.

Comai L 2000. Genetic and epigenetic interactions in allopolyploid plants. Plant Molecular Biology **43:** 387–399.

Comai L 2005. The advantages and disadvantages of being polyploid. Nature Reviews Genetics **6:** 835-846.

Crow JF 1994. Hitoshi Kihara, Japan's pioneer geneticist. Genetics**137:** 891–894.

Dabholkar AR 2006. General Plant Breeding. Concept Publishing Company, New Delhi.

Dar J, Beigh Z and Wani AA 2017. Polyploidy: Evolution and crop improvement. Chromosome Structure and Aberrations doi: 10.1007/978-81-322-3673-3_10

Digby L 1912. The cytology of *Primulakewensis* and of other related Primula hybrids. Annals of Botany **26:** 357–388.

Gantait S and Mukherjee E 2021. Induced autopolyploidy- a promising approach for enhanced biosynthesis of plant secondary metabolites: an insight. Journal of Engineering and Biotechnology **19:** doi: https://doi.org/10.1186/s43141-020-00109-8

Gaul H 1958. Present aspects of induced mutations in plant breeding. Euphytica **7:** 275- 289.

Grant V 1975. Genetics of Flowering Plants. Columbia University Press: New York.

Gregory TR and Mable BK 2005. Polyploidy in animals. In: Gregory TR, ed. The Evolution of the Genome. San Diego: Elsevier, 427–517.

Gu Z, Steinmetz LM, Gu X, Scharfe C, Davis RW and Li WH 2003. Role of duplicate genes in genetic robustness against null mutations. Nature **421:** 63–66.

Harlan J R and deWet JMJ 1975. On O. Winge and a Prayer: The Origins of Polyploidy. Botanical Review **41:** 361–390.

Heslop-Harrison JS 2013. Polyploidy. Brenner's Encyclopedia of Genetics (Second Edition) pp-402-403.

Hua-bing M, Si-Si J, Shui-jin H, Xian-yong L, Yuan-long L, Wan-li G and Li-xi J 2011. Comparison between a tetraploid turnip and its diploid progenitor (*Brassica rapa* L.): The adaptation to salinity stress. Agricultural Sciences in China **10:** 363-375.

Huang CH, Sun R, Hu Y, Zeng L, Zhang N and Cai L 2016. Resolution of Brassicaceae phylogeny using nuclear genes uncovers nested radiations and supports convergent morphological evolution. Molecular Biology of Evolution **33:** 394–412.

Jones JR, Ranney TG and Eaker TA 2008. A novel method for inducing polyploidy in Rhododendron seedlings. Journal of American Rhododendron Society **62:** 130-135.

Joshi A and Hardas M 1956. Alloploid Nature of Okra, *Abelmoschus esculentus* (L.) Monech. Nature **178:** (1190).doi: https://doi.org/10.1038/1781190a0

Karpechenko GD 1927. Polyploid hybrids of *Raphanus sativus*×*Brassica oleracea* L. Bull. Appl Bot **17:** 305–408.

Kazi NA 2015. Polyploidy in vegetables. Journal of Global Biosciences **4:** 1774-1779.

Khrustaleva L and Kik C 1998. Cytogenetical studies in the bridge cross *Alliumcepa*× *(A. fistulosum*×*A.roylei).* Theoretical and Applied Genetics **96:** 8–14.

Kinoshita T and Takahashi M 1969. Studies in polyploid varieties of sugar beets, use of cytoplasmic male sterility in the production of triploid hybrids and their performance in trials. Journal of the Faculty of Agriculture, Hokkaido University **56:** 171-186.

Lata S, Yadav RK and Tomar BS 2021. Genomic tools to accelerate improvement in okra (Abelmoschus esculentus). doi: 10.5772/ intechopen. 97005

Levin D 2002. The role of chromosomal change in plant evolution. Oxford University Pres: New York.

Lynch M 2007. The origins of genome architecture. Sinauer: Sunderland, MA.

Mable BK 2004. 'Why polyploidy is rarer in animals than in plants': myths and mechanisms. Biological Journal of the Linnean Society **82:** 453–466.

Madlung A 2013. Polyploidy and its effects on evolutionary success: old questions with new tools. Heredity **110:** 99-104.

McCollum GD 1988. Amphidiploid onion germplasm f-c 8407 and f-c 8432. Hort Science **23:** 918- 919.

Mendoza HA and Haynes FL 1974. Genetic basis of heterosis for yield in the autotetraploid potato. Theoretical and Applied Genetics **45:** 21–25.

Moody ME, Mueller LD and Soltis, D.E. (1993). Genetic variation and random drift inautotetraploid populations. Genetics **134:** 649–657.

Moore RC and Purugganan MD 2005. The evolutionary dynamics of plant duplicate genes. Current Opinion of Plant Biology **8:** 122–128.

Nagaharu U 1935. Genome analysis in Brassica with special reference to the experimental formation of *B. napus* and peculiar mode of fertilization. Journal of Japanese Botany **7:** 389–452.

Nelson MN, Mason AS, Castello MC, Thomson L, Yan G and Cowling WA 2009. Microspore culture preferentially selects unreduced (2n) gametes from an interspecific hybrid of *Brassicanapus* L.× *Brassicacarinata* Braun. Theoretical and Applied Genetics **119:** 497- 505.

Nishi S 1981. Hakuran, an interspecific hybrid between Chinese cabbage and common cabbage. Chinese cabbage Proceedings of the first international symposium: 385-391.

Osborn TC, Pires JC, Birchler JA, Auger DL, Chen ZJ, Lee HS, Comai L, Madlung A, Doerge RW, Colot V and Martienssen RA 2003. Understanding mechanisms of novel gene expression in polyploids. Trends in Genetics **19:** 141–147.

Otto SP and Whitton J 2000. Polyploid incidence and evolution. Annual Review of Genetics **34:** 401–437.

Pal S and Bal S 2020. Polyploidy: a novel technique for improvement of vegetable crops. Agriculture & Food: e-Newsletter 2.

Parisod C, Holderegger R and Brochmann C 2010. Evolutionary consequences of autopolyploidy. New Phytologist **186:** 5-17.

Paterson AH 2005. Polyploidy, evolutionary opportunity, and crop adaptation. Genetica **123:** 191–196.

Planchais S, Glab N, Inze D and Bergounioux C 2000. Chemical inhibitors: a tool for plant cell cycle studies. FEBS Letters **476:** 78-83.

Ramanna MS and Jacobsen E 2003. Relevance of sexual polyploidization for crop improvement: a review. Euphytica **133:** 3–8.

Ramsey J and Schemske DW 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. Annual Review of Ecology, evolution, and Systematics **29:** 467–501.

Ramsey J and Schemske DW 2002. Neopolyploidy in flowering plants. Annual Review Ecology and Systematic **33:** 589–639.

Randolph LF 1942. The influence of heterozygosis on fertility and vigour in autotetraploid maize. Genetics **27:** 163.

Sattler MC, Carvalho CR and Clarindo WR 2016. The polyploidy and its key role in plant breeding. Planta **243:** 281-296.

Smulders MJ, Esselink GD, Everaert I, De-Riek J and Vosman B 2010. Characterisation of sugar beet (*Beta vulgaris* L. *ssp. vulgaris*) varieties using microsatellite markers. BMC Genetics **11:** 41-52.

Soltis DE and Soltis PS 1999. Polyploidy: recurrent formation and genome evolution. Trends in Ecology & Evolution **14:** 348-352.

Song C, Liu S, Xiao J, He W, Zhou Y, Qin Q, Zhang C and Liu Y 2012. Polyploid organisms. Science China Life Sciences **55:** 301-311.

Song K, Lu P and Tang K 1995. Rapid genome changes in synthetic polyploids of Brassica and its implications for polyploid evolution. Proceedings of the National Academy of Science of the United States of America **92:** 7719–7723.

Stebbins GL 1947. Types of polyploids: their classification and significance. Advances in Genetics **1:** 403–429.

Stebbins GL 1950. Variation and Evolution in Plants. Columbia University Press, New York.

Talebi SF, Saharkhiz MJ, Kermani MJ, Sharafi Y and Raouf Fard F 2017. Effect of different antimitotic agents on polyploid induction of anise hyssop (*Agastache foeniculum* L.). Caryologia **70:** 184–193.

Thayyil P, Remani S and Raman GT 2016. Potential of a tetraploid line as a female parent for developing yellow- and red fleshed seedless watermelon. Turkish Journal of Agriculture and Forestry **40:** 75-82.

Vichiato MRDM, Vichiato M, Pasqual M, Rodrigues FA and Castro DMD 2014. Morphological effects of induced polyploidy in *Dendrobiumnobile* Lindl. (Orchidaceae). Crop Breeding and Applied Biotechnology **14:** 154–159.

Wakchaure R and Ganguly S 2016. Chromosomal polyploidy: A brief review. Pharmaceutical and Biological Evaluations **3:** 510-512.

Yang J, Liu D, Wang X, Ji C, *et al*. 2016. The genome sequence of allopolyploid *Brassica juncea* and analysis of differential homoeolog gene expression influencing selection. Nature Genetics: **48:** 1225–1232.