International Research Journal of Plant and Crop Sciences (IRJPCS) ISSN: 1711-3490, Vol. 7(3), pp. 230-236, August, 2022. Available online at www.advancedscholarsjournals.org © Advanced Scholars Journals

Review paper

Polyploidy and its importance in modern plant breeding improvement

Werkissa Yali

Ethiopian Institute of Agricultural Research, Chiro National Sorghum Research and Training Center, Chiro, Ethiopia
Corresponding Author's Email: workissayali@gmail.com

Accepted 31st May, 2022.

Polyploidy is defined as having more than two sets of chromosomes, and it has long been recognized as a major driver of plant evolution and speciation. A creature with more than two haploid sets of chromosomes is known as a polyploid. Polyploidization has considerably aided plant breeding and agriculture improvement. Polyploidy is likely one of the most important mechanisms of plant adaptation, having been researched extensively over the previous century. It occurs frequently in both plants and mammals. One evolutionary mechanism aids speciation, diversification, and adaptation to changing environmental conditions. Polyploidy is currently an interesting research topic for understanding agricultural plant evolution and utilizing its diversity in crop breeding. The most common use of polyploidy is to overcome or remove sterility in hybrids created via interspecific or inter-generic hybridization or remote cross. Significant economic and societal benefits have resulted from the invention and application of polyploidy breeding. Polyploidy is induced in numerous agricultural plants using diverse ways. The purpose of this paper is to assess polyploidy, classification, and its application in plant breeding.

Key words: polyploidy, crop improvement, Autopolyploidy, Allopolyploidy, chromosome

INTRODUCTION

Polyploidy occurs when an organism's cells have more than one pair of (homologous) chromosomes. It is a heritable phenomenon in which a cell nucleus has more than two complete sets of chromosomes, and it is quite frequent in plants (Comai, 2005). Most polyploids contain an even number of chromosomal sets, with four being the most prevalent (tetraploidy), which has been thought to be a one of a kind phenomena in plant evolution and diversification (Madani *et al.,* 2021). In general, all organisms have a consistent chromosomal number, which is determined by the species (Ohbayashi *et al.,* 2019).

Plant breeding and crop enhancement have benefited greatly from polyploidization (Corneillie *et al.,* 2019). Plant breeding plays a significant part in the improvement of plant traits. This is necessary for the successful and cost-effective development of the new variety (Nadeem *et al.,* 2018). Plant breeding is a technique for extracting desirable traits from a variety of sources. For crop enhancement, many sorts of breeding procedures have been created (Gao, 2021). Plant breeders can assist farmers in increasing food production by developing new cultivars that are more suited to their farming methods, but these cultivars must be able to provide the essential plant inputs for the requisite crop yields (Bradshaw, 2017).

Polyploidy is a major driver in both wild and farmed plant evolution (Sattler *et al.,* 2016). Polyploid organisms often have more vigor than their diploid cousins and, in some situations, surpass them in multiple ways. Polyploidy is a fascinating phenomena in plants that has served as a crucial evolutionary and speciation pathway (Van de Peer *et al.,* 2021). Polyploid organisms have more than two copies of each chromosome, which is a situation that is rarely tolerated in animals but is common in plants (Bourke *et al.,* 2018). In the evolution of many plant species, polyploidization is a crucial step. Intraspecific genome duplication (autopolyploidy) or hybridizing divergent genomes and chromosomal doubling (allopolyploidy) can produce an additional set of chromosomes (Zhang *et al.,* 2019).

Polyploidy can occur in a variety of ways in nature (Ranney, 2006). Due to a disruption in mitosis, a somatic (non reproductive) mutation might arise, resulting in chromosomal doubling in meristematic cell(s) that will give rise to a polyploid shoot. Polyploidy was discovered more than a century ago (Strasburger, 1910) and has remained a source of fascination and discussion ever since (Buggs *et al.,* 2011). For complex organisms, diploidy (having two copies of each chromosome) is considered the chromosomal "ground state" or norm (Bourke, 2018).

In Oenothera, the gigas mutant, an autotetraploid, the first polyploidy was discovered (Miri, 2020). Polyploidy is seen in a wide range of plant taxa, and recent advancements in whole-genome sequencing have enabled extensive examination of recent and ancient polyploidisation processes in an increasing number of plant lineages (Mandáková & Lysak, 2018). Polyploids are particularly frequent among cultivated crops, which has sparked interest in learning more about them (Gonzalo, 2022).

Evolutionary significance of polyploidy

Polyploidy can be caused by a variety of reasons or by different means (Miri, 2020). During the embryo's early stages of development, chromosome doubling, union or fusion of the gametes, one or both of which may be unreduced in chromosome number for any reason (Song *et al.,* 2012). A triploid is formed when two male gametes combine with a single egg cell in rare occasions. Despite this, abnormal cell division can result in polyploidy (Schinkel *et al.,* 2017). The ability of polyploidy to swiftly develop new vigorous forms is traditionally credited with its evolutionary significance. Increased ploidy causes almost rapid reproductive isolation from parental species (Hegarty *et al.,* 2008).

The self-incompatibility mechanism is frequently disrupted by changes in ploidy level, allowing self-fertilization, which is notably common among plants (Stone, 2002). A polyploid benefits from gene redundancy because copies of genes can gain new functions while keeping the old ones. Polyploids have a better ability to disguise harmful mutations and are less likely to suffer from inbreeding depression (Otto, 2007).

Polyploidy can result from aberrant cell division during mitosis or, more typically, during metaphase I of meiosis (it might result from chromosomes failing to split during meiosis or from more than one sperm fertilizing an egg) (Potapova & Gorbsky, 2017). In addition, several substances can cause it in plants and cell cultures: the most well-known is colchicine, which can cause chromosomal doubling, though its use may have other, less evident side effects. Oryzalin will also double the amount of chromosomal content already available (Dhooghe *et al.,* 2011).

Polyploidy has played a significant role in higher plant evolution. Approximately 30% to 70% of today's angiosperms are polyploid, and many of them are unique in that they combine the diploid nuclear genomes of two or more ancestral species or genera (allopolyploids) (Soltis & Soltis, 2009). Evolution can be divided into two stages. Hereditary variation occurs first, followed by selection of genetic variants that will be passed down to future generations most successfully. In higher plants, polyploidy is a prominent aspect of chromosomal evolution (Levin, 1983).

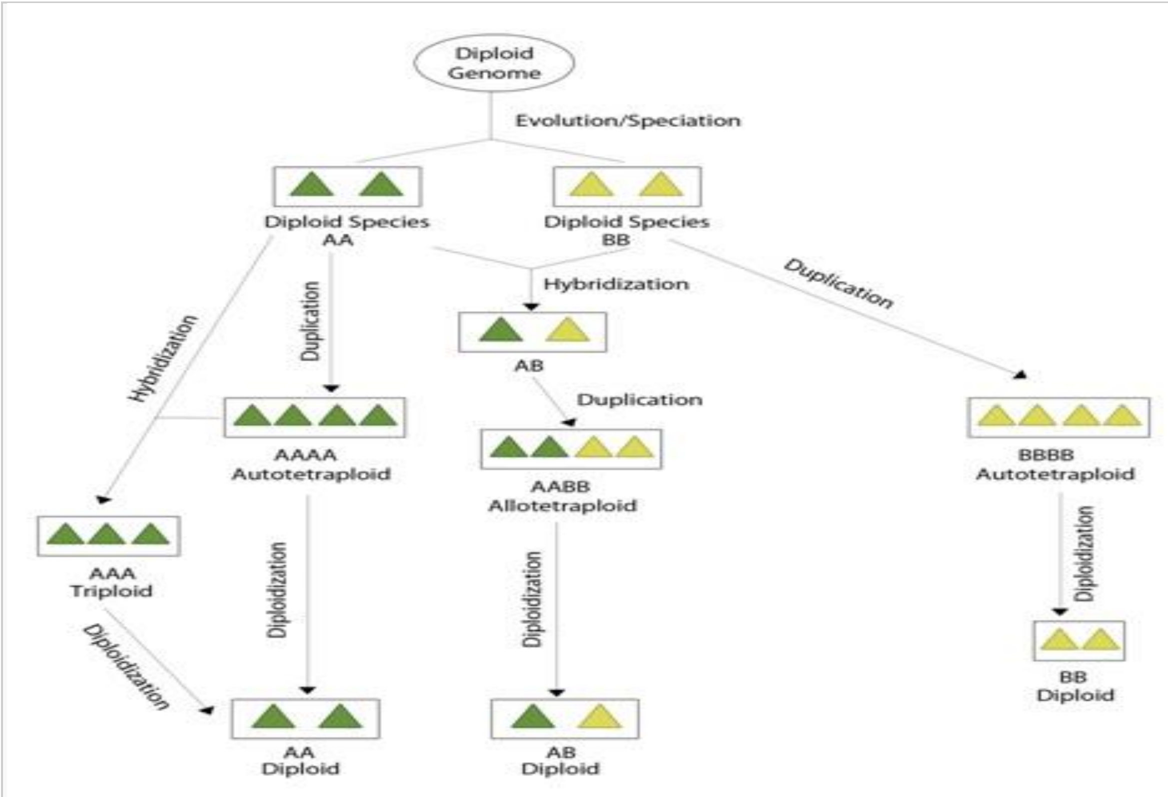
Polyploidy induction

Sexual polyploidization or somatic doubling can be used to create polyploids. In plants and animals, chromosome doubling is linked to a lack of cell division after mitotic doubling (Song *et al.,* 2012). Sexual polyploidization was widely employed for producing polyploids until the discovery of colchicine in the 1930s. This approach has been successfully employed in breeding projects for potato, alfalfa, red clover, yams, roses, lilies, and a variety of other economically important plants (Stoskopf *et al.,* 2019). Sexual polyploidization is based on the fusion of unreduced reproductive cells and can be unilateral (fusing one reduced and one unreduced gamete) or bilateral (fusing both unreduced gametes) (Sattler *et al.,* 2016).The main advantage of inducing sexual polyploids rather than somatic polyploids is that they combine the genetic effects of increased ploidy levels (i.e., genome buffering, increased levels of gene expression, neofunctionalization) and meiotic recombination (i.e., genetic variability through independent segregation and crossing over), allowing for the maintenance of high levels of heterozygozygosity (Comai, 2005).

Polyploidy induction procedures have been established for a variety of crop species. In vitro polyploidization with colchicine, an antimitotic drug, has been one of the most important applications for artificial polyploidy induction since its discovery (Suhaila, *et al.,* 2015). When significant levels of heterozygozity are necessary, sexual polyploidization via the fusing of unreduced reproductive cells is also used. Initial expectations for polyploidy induction for plant improvement were high, especially following the discovery of colchicine (Sutherland, 2017). Polyploids are also useful for reestablishing the fertility of sterile hybrids and for genetic transfer between species where direct cross is not possible (Rieseberg & Willis, 2007).Polyploidy will be artificially created by inhibiting mitosis, which is a common practice in plant breeding. In order to promote polyploidy in some crops, high temperatures are required. Polyspermy, in which one egg is fertilized by numerous male nucleuses, is an uncommon mode of polyploid development that is regularly observed in orchids (Eng & Ho, 2019).

Applications of polyploidy in plant breeding

Polyploidy induction has proven to be a reliable method for improving plants. Polyploidy episodes have definitely played a significant influence in plant evolution and



speciation. Polyploids include many vegetatively propagated flowers and fruits, as well as crop plants (Dhooghe *et al.* 2011; Corneillie *et al.*,2019). Plant polyploidy appears to be connected with obvious phenotypic changes such as increased vigor and adaptability of the newly generated polyploid to unfamiliar environments (Levin, 1983; Sattler *et al.*,2016). These intriguing characteristics of polyploid people have sparked a renewed interest in creating artificial polyploids (Dhooghe *et al.,* 2011; Sattler *et al.,* 2016).

In nature, polyploidy is used to domesticate a variety of important crops. Polyploidization episodes are frequently connected with gains in vigor and adaptability of the newly produced polyploid to unfamiliar environments, according to phylogenetic methods (Alix *et al.,* 2017). Polyploids have a competitive advantage over their diploid progenitors due to transgressive segregation, or the production of extreme phenotypes, as well as greater vigor. Polyploids, particularly allopolyploids, have numerous evident advantages, such as larger nutritive organs, faster metabolism, more secondary metabolites, and enhanced stress resistance, according to studies on the growth and biochemical characteristics of natural polyploid plants (Van de Peer *et al.,* 2009).

Polyploidy is so frequent in both natural and man-made systems. Polyploid production has been used in the breeding of a variety of crops, as polyploid plants are expected to have larger organs (Manzoor *et al.,* 2019). In some circumstances, polyploid plants also have disease resistance, delayed flowering, and lower fertility. These phenotypes are thought to be advantageous. Treatment with substances including colchicine, pronamide, trifluralin, oryzalin, and amiprophos methyl has been studied for chromosomal doubling. These substances stop cells from dividing after chromosome doubling, resulting in polyploid cells. As a result of these chemical treatments, chromosome doubling has happened, allowing for the production of higher ploidy plants (Hoshino *et al.,* 2011).

Based on the phenotypic and molecular characterization of neoplyploids, it has been hypothesized that after polyploids form, they must overcome the obstacle of instability before becoming adapted and joining the evolutionary fray as efficient competitors of their diploid relatives (Kovalsky & Sols Neffa, 2015). Polyploids play a variety of roles in plant breeding: Autopolyploids have a higher vegetative growth rate but a lower seed production rate. This means that autopolyploid induction would be more effective for plant vegetative portions like fodder or roots, but not for seed. Autopolyploids created from diploids with fewer chromosomes have been more successful (Fu *et al.,* 2014).

Plants that are polyploid have three or more sets of homologous chromosomes. A genome duplication event has resulted in an increase in the number of chromosomes in these plants. There are two types of polyploidy, depending on the origin of the genome duplication event: autopolyploids, which are formed from multiplication of a diploid genome (intra-species), and allopolyploids, which are derived through hybridization followed by doubling of the two haploid genomes. Despite this distinction, both forms of polyploids benefit from a genomic buffering effect supplied by their genetic information being doubled (Mable *et al.,* 2011).Because of this buffering, epigenetic changes, as well as the gain and loss of DNA sequences, have little or no effect on the organism's viability, whereas they increase genetic variation, allowing the genome to evolve. The increased chromosome number and additional genomic interactions and genetic alterations often result in superior properties in polyploid plants compared to their diploid counterparts, making polyploid plants superior to diploid plants (Corneillie *et al.,* 2019).

Because many crop species are allopolyploids, knowing the evolutionary ramifications of (allopolyploidy is critical to our understanding of crop plant domestication, agricultural improvement, and flowering plant natural history (Wendel & Grover, 2015). Crops have revealed a variety of evolutionary processes that affect polyploid genomes, including rapid and significant genome reorganization, fractionation, gene conversion, genome downsizing, transgressive gene expression alterations, and sub- and/or neofunctionalization of duplicate genes, among others (Doyle & Coate, 2019). These genomic alterations are frequently accompanied with heterosis, resilience, and increased crop output, all of which are regarded to be essential factors in polyploid agricultural success (Renny Byfield & Wendel, 2014).

In polyploid crop improvement, mutation breeding uses the concepts of gene redundancy and mutation tolerance in two ways. Polyploids can endure harmful allele alterations after mutation, and they have a higher mutation frequency due to their huge genomes, which arise from their genes being duplicated (Gao, 2021). When trying to generate mutations in diploid cultivars that do not yield enough genetic variation following a carcinogenic treatment, the high mutation frequencies observed in polyploids may be used. This method has been employed in the mutation breeding of Achimenes sp. (nut orchids) by first producing autotetraploids with colchicine treatment, then using fast neutrons and X-rays to induce mutations (Wang *et al.,* 2012).Polyploidy has great promise for agricultural improvement, as it may allow plant breeders to more precisely control polyploid genomes and achieve excellent results (Sattler*et al.,* 2016).

Classification

In general, all creatures have the same chromosomal number, which is determined by the species. Plants, on the other hand, may experience number changes in their chromosomes. The chromosomal composition of polyploids can be used to classify them. Polyploidy, or having more than two genomes per cell, is a common way of plant species creation (Vimalav *et al.,* 2021).

Euploidy

Euploidy (polyploidy) is a shift in the number of chromosomes that can involve the loss or gain of the entire set of chromosomes (Firbas & Amon, 2014). Euploids are polyploids containing several copies of a species' entire complement of chromosomes. Euploids can be classed as autopolyploids or allopolyploids based on their genomic composition. Tetraploidy is the most prevalent euploidy kind (Comai, 2005).

Autopolyploidy

Autopolyploid occurs when all of the genomes of a polyploid species are identical, and the scenario is referred to as autoploidy. Autoploidy had only played a modest influence in plant evolution (Soltis *et al.,* 2007). Autopolyploids make only a small percentage of today's crop species. Autopolyploids and autoploids are the same thing. They have several copies of the same genome's basic set (x) of chromosomes (Bharadwaj, 2015). Autoploids are created naturally by the union of unreduced gametes, but they can also be created artificially. The Autopolyploids have several copies of the same genome's basic set of chromosomes. The merger of unreduced gametes occurs naturally, but it can also be purposefully generated.They happen naturally as a result of chromosomal doubling (Van de Peer *et al.,* 2017). In autoploids, chromosome doubling has different effects depending on the species. In ornamentals and forage grasses, spontaneous chromosomal doubling has resulted in improved vigor. For example, ornamentals like tulips and hyacinths, as well as forage grasses like ryegrasses, have produced improved cultivars as a result of spontaneous chromosomal doubling (Bukhari & Kour, 2019).

The presence of more than two homologous chromosomes in autopolyploids may lead to the creation of multivalent during meiosis. The offspring of a cross between two autopolyploids will have a different ratio than the typical Mendelian cross due to non-preferential pairing (Sattler *et al.,* 2016). Autoploids are created naturally by the union of unreduced gametes, but they can also be created artificially. Several methods can be employed to determine the ploidy status of induced polyploids. Chloroplast count in guard cells, morphological features like leaf, flower, or pollen size, and flow cytometry are among them (Lewis, 1980). Autopolyploidy is essential in crop improvement because it allows monoploids (haploids) to produce homozygous diploid lines by chromosome doubling in two years, greatly reducing the time and labor necessary for isolation of inbreeds and pure lines. It also allows triploids to produce seedless fruits (Kumar, 2006).

Allopolyploids

Allopolyploidy occurs when all of the genomes of a polyploid species are not similar (Flagel & Wendel, 2010). The genomes of allopolyploids come from two or more species. (For example, AA, BB). Allopolyploids are made up of genomes from completely unrelated species. They are caused by the fusing of unedited gametes from different species, or by the conjugation of two or more genomes followed by body doubling. Strawberry, wheat, seed rape, and mustard are some of the most important natural alloploid crops (Acquaah, 2012).

Chromosome doubling in F1 hybrids between two distinct species belonging to the same genus or two different genera most likely produced today's allopolyploids. Because they are synthesised by man from two distinct genus or species of plants, allopolyploids generated by man are known as synthetic allopolypoids. The genetic ratios in an allotetraploid are determined by each individual's constitution. Homoeologues are groups of chromosomes that are connected to one another. Both homoeologues would need to be mutant to express a recessive trait if they both had homoeologous gene copies that are expressed similarly. Duplicate gene ratios would normally be detected in these scenarios (Birchler, 2012).

Individuals of hybrid origin are referred described as allopolyploid. The analysis of pairing and inheritance patterns is widely used to determine which class an individual belongs to. True and segmental allopolyploids are the two sub-classes of allopolyploids. Hybridization between distantly related species is required for the production of true allopolyploids. Because the divergent chromosome complements do not mate with each other in this situation, bivalents are formed during meiosis, resulting in a disomic inheritance pattern. Segmental allopolyploids, on the other hand, are the result of hybridization between closely related species with partially distinct genomes (Sattler *et al.,* 2016).

As crop species, allopolyploids have fared better than autopolyploids. Allopolyploids make up a large portion of today's crop species. Allopolyploidy has played a significant role in the evolution of plants. For example, allopolyploidy was important in the evolution of bread wheat, Triticum aestivum. The process of allopolyploidy can be utilized to create new crop species. For example, Triticale and Raphanobrassica. Allopolyploids have two or more unique genomes and can be formed by hybridizing two separate species at the same time (Madlung, 2013).

Aneuploidy

Aneuploidy is a change in the number of chromosomes that can involve the loss or increase of one or more chromosomes. The occurrence of an abnormal number of chromosomes in a cell is known as aneuploidy. Aneuploids are polyploids with one or more particular chromosome(s) added or subtracted from the total number of chromosomes that normally make up a species' ploidy (Acquaah, 2012; Ramsey and Schemske, 1998). During the meiosis of euploids, univalents and multivalents develop, resulting in aneuploids (Acquaah, 2012). Plants with these meiotic aberrations have a lower vigor. The number of chromosomes gained or lost is used to classify aneuploids.

Table 5.2: Classification of aneuploids

Term	Chromosome number
Monosomy	2n-1
Nullisomy	2n-2
Trisomy	2n+2
Tetrasomy	2n+2
Pentasomy	2n+3

CONCLUSIONS

Polyploids produce a variety of outputs, including plant evaluations. Polyploidy success is determined by parental DNA sequencing, gene silencing, maternal and paternal effects, larger ecological adaption, and more heterozygosity. Domestication, natural selection, and artificial section of polyploids have resulted in a higher percentage of polyploidy plants in nature, as well as several popular and highly productive plants. Polypliod plants have more genomic and genetic diversity than other plants. Early varieties, seedless fruits, sterile lines, productive crops, resistance, and therapeutic plants are all possible with polyploidy plants. As a result, polyploidy not only combats hunger, but also alleviates poverty. Polyploidy is also important for humans, as evidenced by the fact that many of the most important crop species are polyploid. The numerous effects of polyploidy found in natural populations have piqued plant breeders' interest in using artificial polyploidy as a crop enhancement strategy.

Studies on wild polyploids are becoming more common as genome sequencing and contemporary molecular biology and bioinformatics techniques advance. Polyploidy in plant breeding broadens the potential base of variability by increasing the number of genes that can mutate; on the other hand, it adds genetic diversity to variability in the plant kingdom, and deleterious recessive mutations may be covered up to a greater extent by their dominant alleles in polyploidy. The use of polyploid in crop development is an example of gene transfer from wild to cultivated species via a bridge species. Synthetic allopolyploidy has resulted in the creation of new crop species.

Conflict of Interest

The author declare that they have no conflict of interest with any organization in relation to the subject of the manuscript.

REFERENCES

Acquaah G (2012). *Principles of Plant Genetics and Breeding.* Wiley-Blackwell.

Alix K, Gérard PR, Schwarzacher T, Heslop-Harrison JS (2017). Polyploidy and interspecific hybridization: partners for adaptation, speciation and evolution in plants. *Annals of botany*, *120*(2), 183-194.

Bharadwaj DN (2015). Polyploidy in crop improvement and evolution. In *Plant biology and biotechnology* (pp. 619-638). Springer, New Delhi.

Bourke PM (2018). *Genetic mapping in polyploids* (Doctoral dissertation, Wageningen University and Research).

Bourke PM, Voorrips RE, Visser RG Maliepaard C (2018). Tools for genetic studies in experimental populations of polyploids. *Frontiers in plant science*, *9*, 513.

Bradshaw JE (2017). Plant breeding: past, present and future. *Euphytica*, *213*(3), 1-12.

Buggs RJ, Soltis PS, Soltis DE (2011). Biosystematic relationships and the formation of polyploids. *Taxon*, *60*(2), 324-332.

Bukhari R, Kour H (2019). Polyploidy in agriculture: With special reference to mulberry. *J. Pharmacogn. Phytochem*, *8*, 1795-1808.

Comai L (2005). The advantages and disadvantages of being polyploid. *Nature reviews genetics*, *6* (11), 836-846.

Corneillie S, De Storme N, Van Acker R, Fangel, JU, De Bruyne M, De Rycke, R, Boerjan, W. (2019). Polyploidy affects plant growth and alters cell wall composition. *Plant Physiology*, *179*(1), 74-87.

Dhooghe E, Van Laere K, Eeckhaut T, Leus L, Van Huylenbroeck J, (2011). Mitotic chromosome doubling of plant tissues in vitro. *Plant Cell, Tissue and Organ Culture (PCTOC)*, *104*(3), 359-373.

Doyle JJ, Coate, JE (2019). Polyploidy, the nucleotype, and novelty: the impact of genome doubling on the biology of the cell. *International Journal of Plant Sciences*, *180*(1), 1-52.

Eng WH, Ho WS (2019). Polyploidization using colchicine in horticultural plants: a review. *Scientia horticulturae*, *246*, 604-617.

Firbas P, Amon T (2014). Chromosome damage studies in the onion plant Allium cepa L. *Caryologia*, *67*(1), 25-35.

Flagel LE, Wendel JF (2010). Evolutionary rate variation, genomic dominance and duplicate gene expression evolution during allotetraploid cotton speciation. *New Phytologist*, *186*(1), 184-193.

Fu D, Xiao M, Hayward A, Fu Y, Liu G, Jiang G, Zhang H (2014). Utilization of crop heterosis: a review. *Euphytica*, *197*(2), 161-173.

Gao C (2021). Genome engineering for crop improvement and future agriculture. *Cell*, *184*(6), 1621-1635.

Gonzalo A (2022). All Ways Lead to Rome Meiotic Stabilization Can Take Many Routes in Nascent Polyploid Plants. *Genes*, *13*(1), 147.

Hegarty MJ, Hiscock SJ (2008). Genomic clues to the evolutionary success of polyploid plants. *Current biology*, *18*(10), R435-R444.

Hoshino Y, Miyashita T, Thomas TD (2011). In vitro culture of endosperm and its application in plant breeding: approaches to polyploidy breeding. *Scientia horticulturae*, *130*(1), 1-8.

Kovalsky IE, Solís Neffa VG (2015). Análisis de la progenie de individuos productores y no productores de gametos masculinos no reducidos de Turnera sidoides (Passifloraceae). *Boletín de la Sociedad Argentina de Botánica*, *50*(1), 23-33.

Kumar N (2006). *Breeding of horticultural crops: principles and practices*. New India Publishing.

Levin DA (1983). Polyploidy and novelty in flowering plants. *The American Naturalist*, *122*(1), 1-25.

Lewis WH (1980). Polyploidy in species populations. *Polyploidy*, 103-144.

Mable BK, Alexandrou MA, Taylor MI (2011). Genome duplication in amphibians and fish: an extended synthesis. *Journal of zoology*, *284*(3), 151-182.

Madani H, Escrich A, Hosseini B, Sanchez-Muñoz R, Khojasteh A, Palazon J (2021). Effect of polyploidy induction on natural metabolite production in medicinal plants. *Biomolecules*, *11*(6), 899.

Mandáková T, Lysak MA (2018). Post-polyploid diploidization and diversification through dysploid changes. *Current Opinion in Plant Biology*, *42*, 55-65.

Manzoor A, Ahmad T, Bashir, MA, Hafiz IA, Silvestri C (2019). Studies on colchicine induced chromosome doubling for enhancement of quality traits in ornamental plants. *Plants*, *8*(7), 194.

Miri SM (2020). Artificial polyploidy in improvement of horticultural crops. *Journal of Plant Physiology and Breeding*, *10*(1), 1-28.

Nadeem MA, Nawaz MA, Shahid MQ, Doğan Y, Comertpay G, Yıldız M, Baloch FS (2018). DNA molecular markers in plant breeding: current status and recent advancements in genomic selection and genome editing. *Biotechnology & Biotechnological Equipment*, *32*(2), 261-285.

Ohbayashi R, Nakamachi A, Hatakeyama TS, Watanabe S, Kanesaki Y, Chibazakura T, Miyagishima SY (2019). Coordination of polyploid chromosome replication with cell size and growth in a cyanobacterium. *MBio*, *10*(2), e00510-19.

Otto SP (2007). The evolutionary consequences of polyploidy. *Cell*, *131*(3), 452-462.

Potapova T, Gorbsky GJ (2017). The consequences of chromosome segregation errors in mitosis and meiosis. *Biology*, *6*(1), 12.

Ramsey J, Schemske DW (1998). Pathways, mechanisms, and rates of polyploid formation in flowering plants. Annu Rev Ecol Evol Syst 29:467–501.

Ranney TG (2006). Polyploidy: From evolution to new plant development. In *Combined proceedings international plant propagators' society* (Vol. 56, pp. 137-142).

Renny-Byfield S, Wendel JF (2014). Doubling down on genomes: polyploidy and crop plants. *American journal of botany*, *101*(10), 1711-1725.

Rieseberg LH, Willis JH (2007). Plant speciation. *Science*, *317*(5840), 910-914.

Sattler MC, Carvalho CR, Clarindo WR (2016). The polyploidy and its key role in plant breeding. *Planta*, *243*(2), 281-296.

Schinkel CC, Kirchheimer B, Dullinger S, Geelen D, De Storme N, Hörandl E (2017). Pathways to polyploidy: indications of a female triploid bridge in the alpine species Ranunculus kuepferi (Ranunculaceae). *Plant Systematics and Evolution*, *303*(8), 1093-1108.

Soltis DE, Soltis PS, Schemske DW, Hancock JF, Thompson JN, Husband BC, Judd WS (2007). Autopolyploidy in angiosperms: have we grossly underestimated the number of species?. *Taxon*, *56*(1), 13-30.

Soltis PS, Soltis DE (2009). The role of hybridization in plant speciation. *Annual review of plant biology*, *60*, 561-588.

Song C, Liu S, Xiao J, He W, Zhou Y, Qin Q, Liu Y (2012). Polyploid organisms. *Science China Life Sciences*, *55*(4), 301-311.

Stone JL (2002). Molecular mechanisms underlying the breakdown of gametophytic self-incompatibility. *The Quarterly Review of Biology*, *77*(1), 17-32.

Stoskopf NC, Tomes DT, Christie BR, Christie BR (2019). *Plant breeding: theory and practice*. CRC Press.

Suhaila AS, Norihan MS, Norwati M, Azah MN, Mahani MC, Parameswari N, Fuad YM (2015). Aquilaria malaccensis polyploids as improved planting materials. *Journal of Tropical Forest Science*, 376-387.

Sutherland BS (2017). *Interploid reproductive isolation in the Campanula rotundifolia polyploid complex* (Doctoral dissertation, Ph. D. dissertation, University of Virginia, Charlottesville, Virginia, USA).

Van de Peer Y, Ashman TL, Soltis PS, Soltis DE (2021). Polyploidy: an evolutionary and ecological force in stressful times. *The Plant Cell*, *33*(1), 11-26.

Van de Peer Y, Maere S, Meyer A (2009). The evolutionary significance of ancient genome duplications. *Nature Reviews Genetics*, *10*(10), 725-732.

Van de Peer Y, Mizrachi E, Marchal K (2017). The evolutionary significance of polyploidy. *Nature Reviews Genetics*, *18*(7), 411-424.

Vimala Y, Lavania S, Lavania UC (2021). Chromosome change and karyotype differentiation–implications in speciation and plant systematics. *The Nucleus*, *64*(1), 33-54.

Wang TL, Uauy C, Robson F, Till B (2012). TILLING in extremis. *Plant biotechnology journal*, *10*(7), 761-772.

Wendel JF, Grover CE (2015). Taxonomy and evolution of the cotton genus, Gossypium. *Cotton*, *57*, 25-44.

Zhang K, Wang X, Cheng F (2019). Plant polyploidy: origin, evolution, and its influence on crop domestication. *Horticultural Plant Journal*, *5*(6), 231-239.