

## FROM GENOME DUPLICATION TO CROP ADVANCEMENT: A COMPREHENSIVE REVIEW OF PLANT POLYPLOIDY

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### ABSTRACT

Polyploidy, the condition in which an organism possesses more than two complete sets of chromosomes, is a widespread phenomenon in plants that plays a central role in evolution, speciation, and crop improvement. It can arise naturally through processes such as hybridization, whole-genome duplication, or the formation of unreduced gametes, and it can also be induced artificially using chemicals like colchicine or oryzalin to enhance desirable traits in crops. Polyploids are classified as autopolyploids, originating within a single species, or allopolyploids, arising from hybridization between distinct species. Ancient (paleo-) and recent (neo-) polyploidization events have contributed to genome plasticity, diversification, and rapid adaptation, leading to enhanced organ size, biomass, stress tolerance, and resistance to pests and diseases. Key crops such as wheat, cotton, and canola owe much of their productivity, resilience, and genetic diversity to polyploidy. Beyond its agricultural importance, polyploidy plays a major role in driving plant speciation and environmental adaptation, providing a vital genetic mechanism for sustaining crop productivity under climate change and increasing global food demand.

**Keywords:** Polyploidy; Polyploidization; Speciation; Evolution; Stress tolerance, Crop Improvement

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### 1. INTRODUCTION

The diversification and evolution of plants have been powered by polyploidy. It is a very common phenomenon in the kingdom of plants in which an organism possesses more than two sets of complete chromosomes. It is estimated that nearly 70% of flowering plants experienced polyploidy events during their evolutionary period (Manzoor et al., 2019). It is more common in plants and less so in animals. Polyploidy has also been used by plant breeders in the last few decades to enhance the strength and resistance to biotic and abiotic stresses and to induce new traits in plants (Touchell et al., 2020). Polyploidy has been used in plant breeding to polish the traits and desired characteristics in different crops like sugarcane, sugar beet, watermelon, and wheat. Besides the boost in biomass and yield production, these plants are also used as an energy source (Corneillie et al., 2019). According to the parental chromosomal condition, after polyploidization, polyploids can be divided into two major groups, i.e., paleo- and neo-polyploids. Paleo-polyploids are also known as ancient polyploids, are species that experienced Whole Genome Duplication (WGD) about millions of years ago. Over time, their duplicated DNA has experienced extensive gene loss, mutations, and chromosomal rearrangements, which led to diploidization, where the genome structurally and functionally resembles that of a diploid species. As a result, although these organisms are ancestrally polyploid, they are now considered diploids (MacKintosh & Ferrier, 2018). On the other hand, neopolyploids are species that are newly developed through polyploidization and still give clear evidence of having extra chromosome sets. Neopolyploids can either be allopolyploids or autopolyploids (Zhang et al., 2019). They have played a significant role in the process of speciation and evolution of plants. Polyploidization often seems to be linked with increases in vigor and adaptation of the newly formed polyploid to the new conditions. The competitive advantage of polyploids over their diploid progenitors is mostly related to transgressive segregation, i.e., the formation of extreme phenotypes and increased vigor. Polyploidy has polished plant breeding by inducing traits that enhance crop performance. It involves either the duplication of chromosomes within one species (autopolyploid) or combining chromosomes from two species (allopolyploid) (Mackay et al., 2021). These genome changes make plants more adaptable, with advantages like larger fruits, better biotic and abiotic stress resistance, and altered flowering times. Plant breeders use synthetic polyploids to enhance yield and develop varieties adapted to challenging environments. With polyploidy present in the majority of angiosperms (flowering plants), its application holds significant potential for enhancing agricultural productivity and addressing food security challenges (Zhang et

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al., 2020). Understanding the chromosomal basis of polyploidy is essential to fully harness its benefits. In cytogenetics, the basic chromosome number refers to the number of distinct chromosomes in a single complete set, while the somatic chromosome number indicates the total chromosomes found in non-reproductive cells. In diploid species, the basic chromosome number generally equals the haploid number found in gametes. However, in polyploid species, particularly those that have undergone ancient whole genome duplication, the relationship becomes more complex, with multiple sets of chromosomes present. These structural changes in the genome, shaped by polyploidization and subsequent diploidization, contribute to the enhanced genetic diversity and adaptability that make polyploids so valuable in plant breeding. However, polyploidy is of two basic types (Rong et al., 2005; Li et al., 2021). Autopolyploids arise from genome duplication within a single species, whereas allopolyploids result from the combination of genomes from two or more related species (Mauricio et al., 2012). These modifications have important ecological and evolutionary consequences, especially for introduced plant species.

## 2. CLASSIFICATION OF POLYPLOIDY AND ITS ROLE IN CROP IMPROVEMENT

Polyploidy is defined as the presence of more than two complete sets of chromosomes in an organism. It is classified based on various criteria, such as the origin of chromosome sets, mode of formation and level of ploidy. The main types are

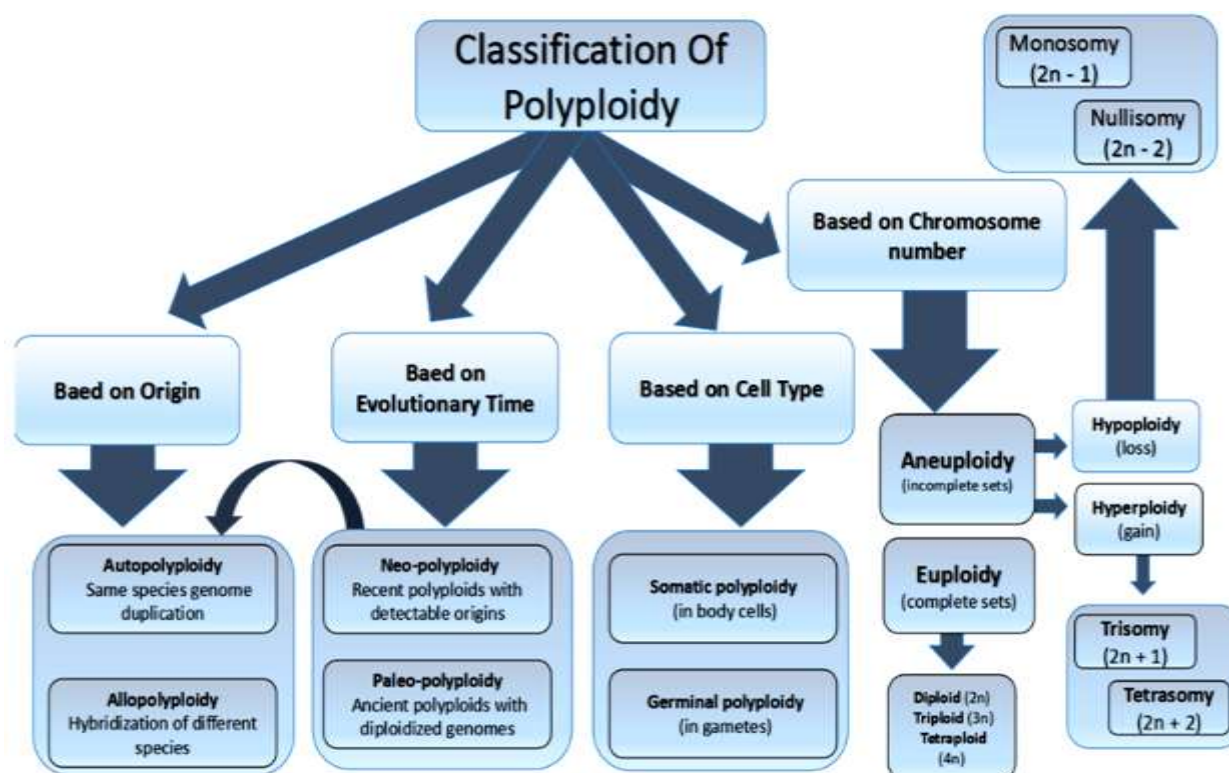
### 2.1. Autopolyploids vs. Allopolyploids: Impacts on Plant Evolution and Agriculture

Polyploidy, the condition of having more than two complete sets of chromosomes, can arise through various mechanisms that result in two primary types based on the origin, i.e., autopolyploid and allopolyploid (<https://www.britannica.com/science/polyploidy>). Autopolyploidy occurs within a single species when chromosome duplication takes place without hybridization, typically due to meiotic or mitotic errors. This process leads to the formation of plants with multiple sets of homologous chromosomes, which increases the cell size, a trait beneficial in certain agricultural aspects (Lv et al., 2024). Examples include autotetraploid crops like alfalfa (*Medicago sativa*), banana (*Musa spp.*), and potato (*Solanum tuberosum*), where increased ploidy level usually enhances traits like tuber size and biomass production. Allopolyploidy occurs when hybridization between two distinct species is followed by chromosome doubling, resulting in a stable and fertile polyploid organism. Compared to their diploid ancestors, allopolyploids typically display increased genetic diversity, hybrid vigor (heterosis) and enhanced adaptability to a wide range of environmental conditions. These characteristics make allopolyploids particularly valuable in crop breeding and improvement efforts (Osabe et al., 2012). However, not all allopolyploids are immediately stable or fertile after formation; some require multiple generations of selection and genome reorganization to achieve full stability. Additionally, the degree of adaptability and vigor can vary depending on the species involved and the specific environmental conditions (Soltis & Soltis, 2009). Many important crops, such as bread wheat (*Triticum aestivum*), cotton (*Gossypium hirsutum*), and oilseed rape (*Brassica napus*), are natural or synthetic allopolyploids. As such, allopolyploidy plays a crucial role in plant evolution and breeding, providing opportunities to enhance yield, stress tolerance and disease resistance in crops (Farhat et al., 2023).

### 2.2. Evolutionary Types of Polyploidy and Their Roles in Plant Diversification

Based on evolutionary history of genomic duplication, polyploidy can be classified in two major types. The first one is paleo polyploidy, and the other one is neo polyploidy. These two types of polyploidy mainly elaborate the genomic evolution, diversification of species (Heslop-Harrison et al., 2023) and the enhancement of the new traits in the plant, making them more diversified and adaptive than nonpolyploid plants. Paleo polyploidy is basically a type of polyploidy in which there is a whole genomic duplication that occurred millions of years ago during the early evolution of the plants (Wu et al., 2020). These polyploidy events usually seem to be similar to one another, but they are very distinct from each other. It is proved from recent studies that many angiosperms, including soybean, maize, and Arabidopsis, had undergone paleo polyploidization one or more times, and that contributed a lot to the diversification of the gene family's versatility of metabolic activities and morphological complexities. Such events are believed to have played a fundamental and significant role in the rapid and widespread diversification of certain species within a short period of time (Van de Peer et al., 2017). On the other hand, neopolyploidy describes the recent or newly occurring polyploidization events or activities, typically within the last few thousand or million years. These are rapidly observable because there is a limitation in the time for the reshuffling of the genome (Soltis & Soltis, 2016). The neopolyploids often show a condition that is known as genomic instability. In this condition, there are frequent mutation events in the genetic material of the cell, which can cause problems in the cell's ability to do its function correctly. It can cause problems like chromosome rearrangements and epigenetic changes (Edger et al., 2025b). Despite of these difficulties, neopolyploids have the ability of rapid adaptations and played a significant role in this speciation. For example, many crop species, such as bread wheat (*Triticum aestivum*), which is hexaploid, cotton (*Gossypium hirsutum*), and *Brassica napus*, are considered neopolyploids because they have evolved recently through allopolyploidy followed by the process of

maintaining the structure of their genetic material. There are some researchers who recognize another event of polyploidy, which is known as mesopolyploidy. This is the condition between two extremes, i.e., neopolyploidy and paleopolyploidy, which represents the intermediate-aged duplication of the genome (Fig. 1). Several families of the plants such as Brassicaceae exhibit mesopolyploidy, where the ancient polyploidy activities occurred almost ten Million years ago but they still maintain the partially genome identity (Mandakova et al., 2017).



**Fig. 1:** Classification of polyploidy in plants based on origin, evolutionary history, chromosome number and cell type. Classification of polyploidy in plants can be categorized based on four key criteria: origin (autopolyploidy vs. allopolyploidy), evolutionary history (paleopolyploidy, mesopolyploidy, neopolyploidy), chromosome number (euploidy vs. aneuploidy), and cell type (somatic vs. germinal polyploidy). Each classification highlights distinct mechanisms and evolutionary or practical implications in plant development, adaptation, and breeding.

### 2.3. Euploidy and Aneuploidy: Chromosome Number Variations in Polyploidy

Polyploidy is further classified on the basis of a change in the chromosome number. It is especially considered when it is studied in relationship with the basic set of the chromosome. The basic set of the chromosome is denoted by X (Masterson, 1994). This classification of polyploidy helps to differentiate between euploidy and aneuploidy. Aneuploidy is a condition in which the number of chromosomes in a cell is not an exact multiple of the basic set (X) due to the gain or loss of one or more individual chromosomes. Meanwhile, euploidy is a condition where the basic set is the exact multiple of the total number of chromosomes. The number of chromosomes in a basic set is called the monoploid number (x). The normal conditions are “1x” haploid or “2x” diploid. Polyploids (>2x) represent a deviation from diploidy but are common and often advantageous in plants. Haploid number (n) refers only to the number of chromosomes in gametes (Torres & et al., 2007). For example, if we talk about hexaploidy in the polyploidy, we have results of hexaploid bread wheat (*Triticum aestivum*). It has 42 chromosomes, and 6 is the basic set number; it exhibits all the properties derived from the three ancestral genomes (AABBDD). It shows greater adaptability, diversification, and high yield (Wang et al., 2021). In aneuploidy, the basic set “X” is not the exact multiple of the total number of the chromosomes (Heslop-Harrison et al., 2023). There is a gain or a loss in the number of the chromosomes in aneuploidy. Aneuploids usually have abnormal distribution of chromosomes. Aneuploidy further includes hyperploidy and hypoploidy. Hypoploidy is a condition where there is a loss of one or more chromosomes and consists of two types, i.e., monosomy (2n-1) and nullisomy (2n-2). Hyperploidy is a condition where there is gain of one or more chromosomes and it includes events like Trisomy, tetrasomy and polysomy etc. (Wang et al., 2023).

#### 2.4. Polyploidy by Cell Origin: Implications for Plant Phenotypes and Breeding

Polyploidy can also be classified on the basis of the cell type in which the replication of the genome occurs. It is broadly categorized into two types, one of which is somatic polyploidy, which is also known as mitotic polyploidy (Pachakkil et al., 2016) and the other one is germinal polyploidy, which is also known as meiotic polyploidy. This classification mainly focuses on how polyploidy affects the development, reproduction, and evolution of the plant (Anatskaya & Vinogradov, 2022). Somatic polyploidy is the replication of the whole genome during the process of mitosis in non-reproductive cells (Darmasaputra et al., 2024). This process is specifically common in the epidermal layer of the plant and the endosperm tissues. In horticulture, artificially induced somatic polyploidy has been exploited to produce large organs and leaves and to enhance the quality of fruits, flowers, and vegetables with the help of artificial polyploidization and hybridization (Jafarkhani Kermani & Emadpour, 2019).

On the other side, the Germinal polyploidy occurs in the germinal cells, for example, pollens and ovules. It occurs through the abnormal distribution of chromosomes or error in meiosis. It is important for the formation of polyploids, including both allopolyploids and autopolyploids (Zhang et al., 2019). Germinal polyploidy ultimately results in the transfer of polyploid genomes further to the next generation, and it plays a significant role in the process of speciation, diversification, and domestication of plants. The main distinction between somatic and germinal polyploidy is very important in both fundamental and applied plant sciences. Somatic polyploidy often focuses on phenotypic modification, and it is limited to the individual plants, not to the population, while germinal polyploidy can result in long-term evolutionary changes and is of great importance in plant breeding programs (Otto & Whitton, 2000). The development of polyploids in specific tissues is increasing very rapidly, as it is seen as a strategy by which plants manage their cell size, tissue function, and metabolic capacity. For example, the high level of polyploidy in the cells of root cells has been linked with the enhanced stress tolerance and growth under difficult and challenging environments (Ruiz et al., 2020).

### 3. CHROMOSOME SET VARIATION IN PLANTS: NATURAL ORIGINS AND ARTIFICIAL INDUCTION

Polyploidy is a situation of having more than two complete sets of chromosomes, and it can occur through both natural pathways and by artificial induction. Understanding the difference between natural and artificial polyploids gives us significant insights into the adaptation, speciation, diversification, and advancements of plants (Pelé et al., 2018). Natural polyploids are developed automatically in nature through various events such as hybridization followed by the doubling of chromosomes, some errors in the meiosis during cell division, and unreduced gamete formation. These polyploids are often considered the important carriers for evolution and diversification of the plants. Many modern crops, such as hexaploid bread wheat and tetraploid cotton, are considered natural polyploids (Farhat et al., 2023). They all are formed through the ancient hybridization of their related species, showing greater heterozygosity and ecological adaptability (Alix et al., 2017). Artificial polyploidy is induced intentionally under controlled conditions to enhance the desirable traits in the plants (Hegarty et al., 2013). There are certain chemicals that are used to induce artificial polyploidy and for the doubling of the chromosome. For example, colchicine and oryzaline disturb normal mitotic spindle formation, which leads to the doubling of the chromosome in a nonreproductive cell. These artificially induced polyploids are used in many fields of agriculture, such as plant breeding, in genetic research, and in horticulture for the enhancement of traits such as large flower size, large vegetable size, and large organs (Ruiz et al., 2020). Polyploidy is very common in the Poaceae family, which is also known as the grass family. Polyploidy has shaped the process of evolution and diversification in the graminaceae family of plants. The role of artificial and natural polyploids in the evolution of plants is remarkable, as they made the grass family greatly adaptable to the environment and genetically diverse to a great extent (Stebbins, 2010).

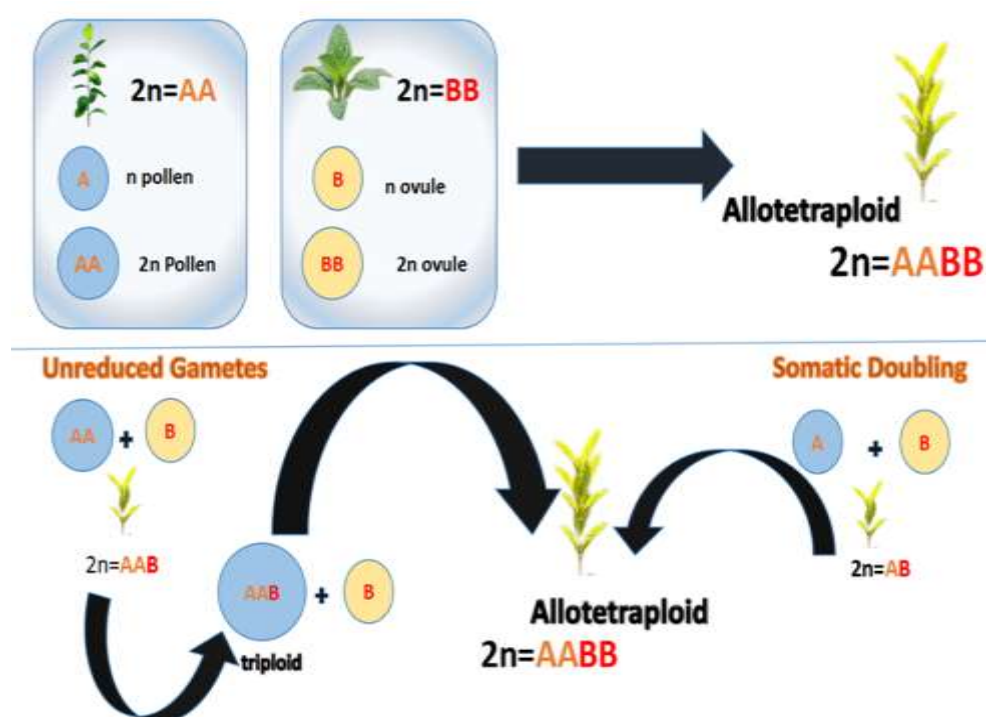
### 4. MECHANISMS UNDERLYING THE FORMATION OF GENOME MULTIPLICATION: NATURAL, ARTIFICIAL, AND HYBRIDIZATION PATHWAYS

The formation of polyploidy involves numerous complex processes at the molecular and cellular levels, ultimately resulting in a phenomenon that both natural and artificial methods can induce (Hegarty et al., 2013). This formation by natural and artificial methods mainly contributes to the evolution of gene expression in plants (Mutti et al., 2017), and plays a significant role in speciation and the improvement of crop polyploidization for desirable traits. Mechanisms that are widely recognized in the formation of polyploids include the unreduced gamete formation, somatic doubling of the chromosome, and interspecific hybridization followed by the duplication of the whole genome. Focusing on these mechanisms, the first mechanism for the formation of polyploids is the production of unreduced gametes (Fig. 2). These are  $2n$  in number, which have somatic chromosome numbers



instead of gametic chromosome numbers ( $n$ ) due to some error during cell division and meiosis. These two unreduced gametes are able to fuse with other gametes (reduced or unreduced) to form polyploids (Pelé et al., 2018). These unreduced gametes contribute as diploid chromosomes ( $2n$ ) instead of a haploid chromosome set ( $n$ ). There are some reasons for the production of unreduced gametes, which later on play a significant role in the formation of polyploids (Clo et al., 2022). There are certain reasons for the formation of polyploids. The first one is the failure of homologous chromosomes to separate during meiosis I, which leads to the formation of diploid gametes. The second reason is the failure of two sister chromatids of one chromosome to separate during meiosis II, which also leads to the formation of unreduced gametes. The production of unreduced gametes can result in the formation of both autopolyploids and allopolyploids. When an unreduced gamete fuses with a normal haploid gamete, it produces a triploid, which is the autopolyploid. The other situation is the fusion of an unreduced gamete with another unreduced gamete ( $2n+2n$ ). It will result in the formation of tetraploid. For example, several plants, like banana and potato, are formed by the production of unreduced gametes (Ramsey & Schemske, 1998). Unreduced gametes from different species can be hybridized, and it can result in the formation of allopolyploids. For example, hexaploid wheat, also known as bread wheat, is formed by the hybridization of tetraploid wheat and diploid grass (Li et al., 2014). And another way of the formation of polyploids is somatic doubling of chromosomes. It occurs both naturally and can be induced artificially using different chemicals, oryzaline and colchicine (Jeloudar et al., 2019). These agents usually disturb the normal formation of spindle fiber during mitosis. It causes the failure to segregate and separate the chromosomal set during mitosis; therefore, there is the doubling of chromosomes within a single cell and nucleus (Darmasaputra et al., 2024). This method is widely used in different breeding programs for the formation of synthetic polyploids (Pachakkil et al., 2016).

Another mechanism for polyploid formation in nature involves hybridization following polyploidization. This is commonly observed in allopolyploids, which arise from distantly related species. Newly formed hybrids after polyploidization are often initially sterile due to errors in chromosome pairing during cell division. However, fertility can be restored once homologous chromosomes properly pair. This process is exemplified in allopolyploid crops such as hexaploid bread wheat and tetraploid cotton. In these cases, hybridization after polyploid formation can initially produce sterile offspring, but subsequent polyploidization stabilizes the genome and enables sexual reproduction, ultimately allowing the hybrid to transmit its genome to the next generation. This process of polyploidization restores the fertility of the hybrid and gives it characteristics like novelty and plasticity to the genome (Wei et al., 2019), and as a result, the hybrid shows the characteristics that were absent in their parents but introduced by the events of polyploidy after hybridization. This process leads to the induction of hybrid vigor and desirable traits due to the doubling of chromosomes, or polyploidization. Due to these benefits, this process is widely used in plant breeding programs to develop new breeds and varieties with tolerance, greater adaptability, higher abiotic and biotic stress tolerance. good yield and novel traits (Chen, 2010).



**Fig. 2:** Mechanisms of polyploid formation: somatic doubling and unreduced gamete fusion. It illustrates how chromosome doubling in somatic cells and the fusion of unreduced gametes contribute to the development of polyploid plants.

#### 4.1. Enhancing Plant Traits Through Chemical-Induced Genome Doubling

Polyploidy can be introduced in plants by chemical induction; there are certain chemicals, such as colchicine and oryzalin, that are used to induce polyploidy artificially in the plants (Jeloudar et al., 2019). Chemical induction of polyploidy is a widely used and successful technique for artificially doubling chromosome numbers. In many programs, it provides a direct route to form polyploids with our desirable and improved traits. This method is usually used in different fields of agriculture, such as plant breeding and genetics, horticultural sciences and biotechnology. This induction gives plants novelty (Nieto Feliner et al., 2020) and plasticity (Wei et al., 2019) to their genome and gives them novel traits such as high yield and improved stress tolerance, restores the fertility in hybrids, and makes them more successful than other nonpolyploids. Some factors on which the success of artificial induction of polyploidy depends are the methods of application of treatment, the species of the plant that has been chosen, and the stage of development of the tissue that you have used. This artificial induction by using different chemicals has shown many advantages. Such as large flower size and greater stability. large fruit size and disease resistance in triploid seedless hybrid species such as banana, and watermelon (Silva et al., 2022).

The process used for the artificial induction of polyploidy includes material or explants, such as seeds, meristematic tissues, roots, or callus. The second step is treating the explant with the chosen chemical, such as colchicine or oryzaline, then screening them carefully and identifying the cells with successfully doubled chromosomes (Niazian & Nalouisi, 2020). The identification of polyploids involves the counting of chromosomes and different analyses, such as the DNA analysis. morphological changes are also observed phenotypically, such as large stomatal size and thickness of leaves (Jeloudar et al., 2019) etc. Along with some advantages, there are some challenges that we usually face during artificial induction of chromosome polyploidy and doubling of chromosomes, such as unintended mutations and somaclonal variations, which later on cause the undesirable development of certain abnormal activities (Chen, 2010). But besides these challenges, the chemical induction of polyploidy is of great significance in plant trading programs for the improvement of crops and introduction of desirable and novel traits in the plants, such as gigantism. Improved stress tolerance in the plants (Li et al., 2024), higher yields than non-polyploids through manipulation of the ploidy level of the plant, and it made them improved in aspects of quality, quantity, resilience, and tolerance. In short, it is a milestone in plant breeding programs.

#### 4.2. The Prevalence and Importance of Polyploidy in Plant Evolution

Polyploidy, the presence of more than two chromosome sets, is widespread in plants and plays a major role in their evolution, diversification, speciation, and adaptation. Nearly every plant species is believed to have experienced polyploidy, with around 50 such events identified across various families during plant evolution. (Zhang et al., 2019). About 30 to 70% of angiosperms are considered to have undergone the phenomenon of polyploidization once in their evolutionary time. The condition of the genome arises from 2 main phenomena, which are autopolyploidy and allopolyploidy. Autopolyploidy involves the duplication of the whole genome within a single species (Lv et al., 2024) and allopolyploidy is a condition of duplication of the genome from two distant species (Farhat et al., 2023). It results from the hybridization of two distantly related species followed by the chromosomal doubling. This process of polyploidization has resulted in the development of many species that are very important in agriculture, such as bread wheat (Zhao et al., 2020), which is hexaploid; cotton, which is tetraploid; and many more, such as tetraploid oats and canola. Besides the challenges it faced in the beginning, such as instability of the genome and errors in meiosis and mitosis, it has been very successful over time as it went on.

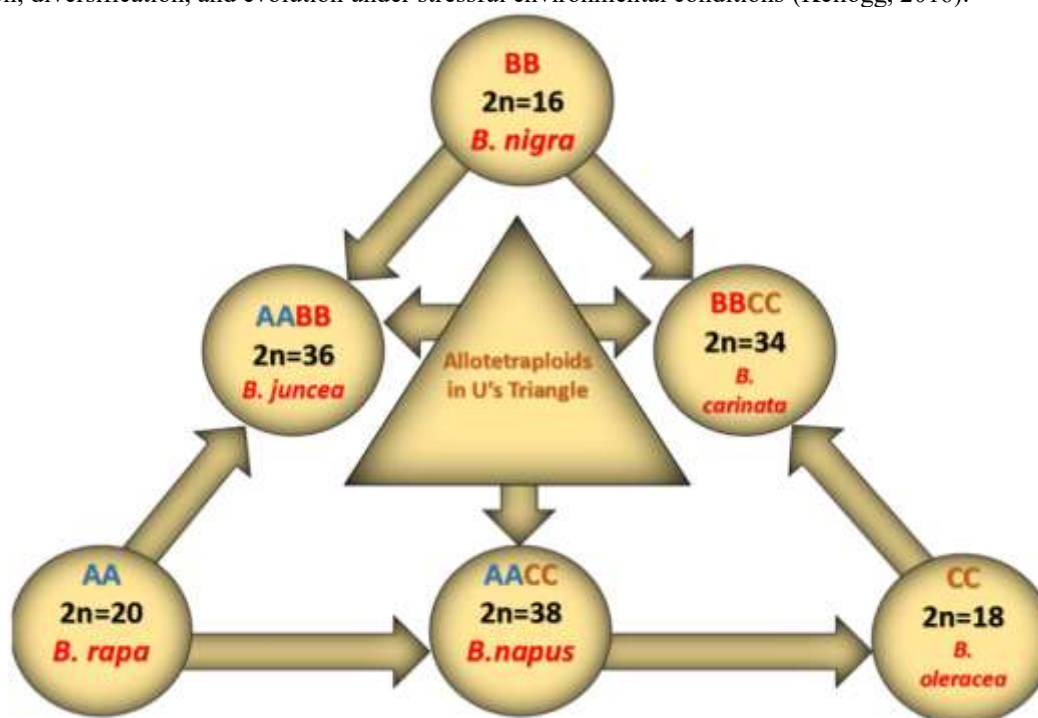
#### 4.3. Polyploidy-Driven Speciation and Diversification in Plants: Evidence from Allopolyploidy and Brassica

Polyploidy had played a vital role in this process of speciation in the plants and their diversification (Heslop-Harrison et al., 2023). It has always served as nature's driver and the most important mechanism of speciation. It is most commonly observed in angiosperms, in the plants that produce seeds and flowers. By the replication of the whole genome, polyploidy is considered as a fundamental requirement for the process of speciation and origination of new species followed by evolution (Alix et al., 2017) and the introduction of novel traits and in making them more diverse from non-polyploids, as it always facilitated the diversity and the process of speciation. In many cases it has been observed that when a polyploid makes a cross with their diploid relatives, it results in the unbalanced formation of the gametes, and it often reduces fertility. This process effectively separates the polyploids and non-polyploids reproductively. That isolation makes polyploids more independent, following their evolutionary pathway, forming a species without need of gradual changes (Becker et al., 2022). Moreover, the allopolyploidy, which comes from the hybridization followed by whole genome duplication, can merge very distant genetic makeups from two different species by combining their novel traits. The merger makes novel and genetic makeup and combinations, which leads to increased heterogeneity and heterosis. This is the property that often gives allopolyploids a very good advantage over their ancestors. It is noticed that *Brassica napus* (Cheng et al., 2014), which is known as canola, and *Triticum aestivum*, which is a bread wheat, are the perfect examples of successfully made allopolyploid species that merge through the process of genome merging and bring diversity to these

allopolyploids (Farhat et al., 2023).

Focusing on the Brassica family, the Brassica genus gives us a classical model of speciation in the Brassica family through allopolyploidy. As it is mentioned in the diagram of the U triangle, in this family there are three diploid species and they served as progenitors that gave rise to the three distinct allotetraploid species through interspecific hybridization and doubling of chromosomes. A cross between *Brassica rapa* and *Brassica nigra* results in the formation of *Brassica juncea*, while hybridization of *Brassica rapa* and *Brassica oleracea* led to the formation of *Brassica napus*. Similarly, *Brassica carinata* originated from the hybridization of *Brassica oleracea* and *Brassica nigra* (Fig. 3). This polydization gave interspecific hybrids the ability to restore fertility and to introduce all genetic combinations that increased the adaptability, quality of oil, and performance of these allotetraploids. This Brassica triangle mainly demonstrates how polyploidy served in the speciation of the Brassica genus.

It also has been observed through the recent studies that the polyploidization creates novelty and regulatory complexity in plants due to these changes. This change highlights the divergence required for the process of speciation, diversification, and evolution under stressful environmental conditions (Kellogg, 2016).



**Fig. 3:** Speciation in the Brassica genus illustrated by U's Triangle. The diagram shows how interspecific hybridization and genome doubling among three diploid species (*B. rapa*, *B. nigra*, and *B. oleracea*) led to the formation of three allotetraploid species: *B. juncea*, *B. carinata*, and *B. napus*, highlighting the evolutionary role of allopolyploidy in this genus.

## 5. POLYPLOIDY IN NATURE: EVOLUTIONARY AND AGRICULTURAL ADVANTAGES

Although polyploidy is more common in plants than animals, it offers several important advantages in both. In plants, it enhances vigor and size, often resulting in larger fruits, flowers, and greater biomass due to hybrid vigor or heterosis. Polyploidy also improves adaptation to environmental stress such as drought, salinity, and high temperatures. It contributes to genetic diversity, evolution, and speciation in plants (Otto & Jeannette, 2000). Some polyploids show stable fertility, which supports successful reproduction. In agriculture, they are used in breeding programs to achieve traits like larger fruit, better seed quality, and higher yield. Examples of polyploid crops include wheat, cotton, oats, and strawberries. They may also have improved taste and nutritional content compared to non-polyploids.

### 5.1. Polyploidy as a Key Driver of Stress Resilience and Trait Enhancement in Plants

Polyploidy has emerged as an amazing mechanism in enhancing the stress tolerance against biotic and abiotic factors in the plants (Tossi et al., 2022). Whole chromosome duplication enhances physiological novelty (Nieto Feliner et al., 2020), and enables polyploids to better withstand biotic and abiotic stresses than diploids (Sattler et al., 2016). Polyploids often exhibit exceptional adaptations such as thick leaves, larger stomata and increased

biomass in fruits and shoots that enhance stress tolerance under harmful environmental conditions. They also improve nutrient uptake and transport efficiency. Additionally, polyploids play a vital role in regulating gene expression due to extensive genetic modifications, which further support their resilience to environmental stress (Van de Peer et al., 2021). One of the key advantages of polyploidy is the increased genetic material, which allows masking harmful mutations and enhances overall functionality and flexibility. Enhanced stress tolerance in polyploids is primarily due to changes in gene expression and metabolic adjustments. These changes can activate stress-responsive genes and alter metabolism, helping polyploids cope with environmental stress (Mutti et al., 2017). Studies have also shown that artificially induced polyploidy enables plants to better cope with stressful conditions and harmful environments. Artificial polyploids exhibit increased drought tolerance, improved resistance to pathogens and pests, and altered growth patterns that support survival under stress (Coate et al., 2022).

Polyploidy significantly enhances desirable traits that are important agronomically and economically. It improves the nutritional performance of crop species. The redundancy of chromosomal sets provides genetic, morphological, and physiological benefits that regulate plant productivity and trait improvement. One notable benefit of polyploidization is the increase in organ size, including seeds, fruit, floral parts, and leaves. This increase in cell volume in polyploid plants compared to diploids is often called the “gigas effect” (Levin, 1983). Plants with larger biomass and greater photosynthetic area contribute more to growth and yield across various crop species. Polyploids also show functional trait divergence from their diploid ancestors in traits like leaf morphology and gas exchange. These differences make polyploids more adaptive and provide agronomic and economic advantages. The benefits of polyploidy extend beyond size and productivity (Koziara-Ciupa & Trojak-Goluch, 2025). Polyploidy often modifies metabolic activities, improving nutritional quality, aroma, and the content of metabolic byproducts. Induced polyploidy has increased concentrations of chemical compounds in medicinal and spice crops, enhancing their commercial value (Thriveni et al., 2024). Thus, polyploidy is considered a key driver of novel traits and genome plasticity due to chromosomal redundancy (Edger et al., 2025a). Polyploidy is also widely used in breeding programs to develop hybrids and improve yield through hybrid vigor. The ability of polyploids to combine traits from multiple ancestors while maintaining genetic stability is essential for creating high-yielding, resilient lines. This makes polyploid plants superior to their diploid counterparts and crucial for addressing global food security challenges under changing and stressful environmental conditions (Ortiz et al., 2024).

## 5.2. Genetic and Metabolic Contributions of Polyploidy in Pest and Pathogen Resistance

Polyploidy significantly increases the ability of the plant to resist pests and different pathogens through its different genetic combinations from its ancestors and progenitors, its changed metabolic activities, and its modified defense system due to advanced genetic combinations. It is specifically valuable in plant breeding when making new varieties with abiotic resistance and biotic stress tolerance, and crop improvement is the key target for the breeders. The presence of more than one copy of a gene in the polyploid plants gives an advantage to the polyploid genome of plant immunity, which is responsible for the recognition of pathogens and giving a response against them. This is due to the duplication of the genome in polyploids, which are able to give a battery response against a range of pests and diseases (Islam et al., 2022). It is observed that the polyploid plants show reduced symptoms for delayed symptoms as compared to deployed when they are exposed to different diseased media such as bacterial, viral, or fungal pathogens. There is another change associated with polyploidy: the altered structure due to the duplication creates a strong physical barrier against insects that prevents them from being fed on by any insect and the entry of pathogens (Thompson et al., 1997). There are certain examples of the polyploids that show strong tolerance and resilience against different diseases that are absent in their diploid relatives, such as canola, wheat, and potato. They have shown enhanced tolerance to diseases such as powdery mildew, bacterial blight, and rust diseases. It is often linked to the expression of novel alleles, which are derived from the combination of different genes during the polyploidization from different species. This change can open a wide range of resistance and reduce the time for the evolution of different harmful pathogen strains (Anatskaya & Vinogradov, 2022).

A well-studied example of this phenomenon is seen in polyploid strawberries (*Fragaria × ananassa*), which exhibit heightened disease resistance due to genomic redundancy and increased allelic diversity. As described by Foltá and Davis (2018), the octoploid genome ( $2n=8x=56$ ) provides multiple copies of defense-related genes, enhancing pathogen recognition and response. For instance, polyploid genotypes show improved resistance to soil-borne pathogens like *Phytophthora cactorum* (crown rot) and foliar fungi such as *Podosphaera aphanis* (powdery mildew). This resilience is attributed to gene dosage effects, where duplicated *R-genes* and *PRR* (pattern recognition receptors) amplify immune signaling. Additionally, epigenetic regulation in polyploids modulates secondary metabolite production (e.g., flavonoids and lignin), further inhibiting pathogen colonization (Nellist, 2018). These mechanisms make polyploid strawberries a robust system for studying and breeding disease-resistant cultivars (Fig. 4).

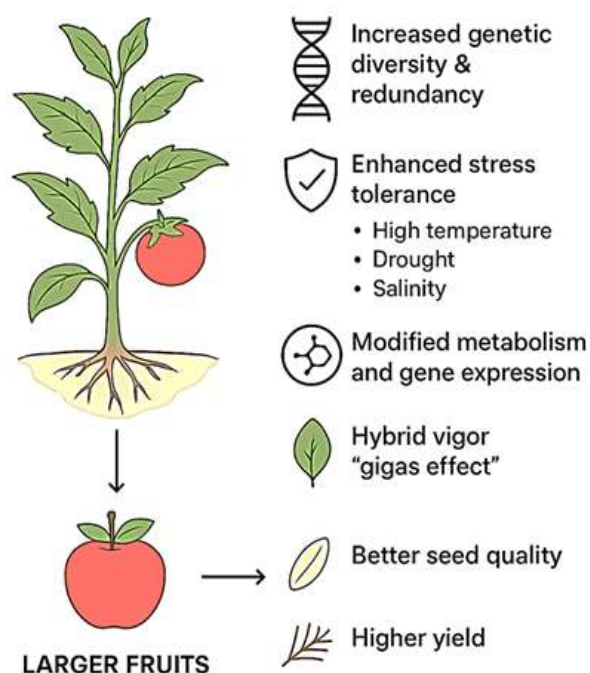
Similarly, polyploidy also plays a crucial role in the evolution and adaptability of major cereal crops, most



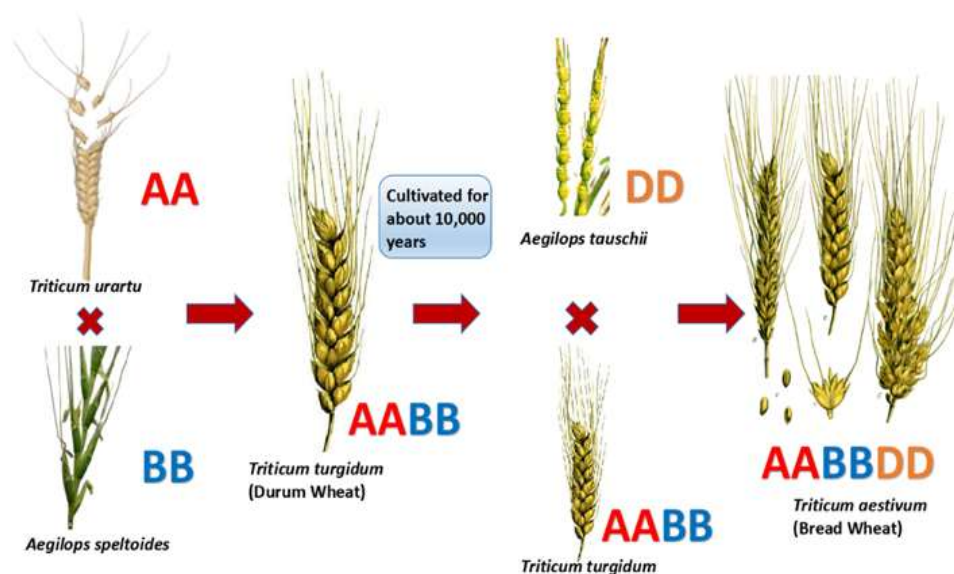
notably bread wheat. As a hexaploid species (6x), bread wheat arose through two successive hybridization and whole-genome duplication events involving three diploid progenitors: *Triticum urartu* (AA genome), *Aegilops speltoides* or a close relative (BB genome) and *Aegilops tauschii* (DD genome) shown in Fig. 5. This complex genomic structure provides vast genetic diversity, enabling increased grain size, improved fertility, and enhanced tolerance to various biotic and abiotic stresses. Additionally, the presence of multiple gene copies helps buffer against harmful mutations, contributing to greater genomic stability and resilience (Li et al., 2014).

## Polyploidy in Nature:

### Evolutionary and Agricultural Advantages



**Fig. 4:** Schematic overview showing how polyploidy enhances genetic diversity, stress tolerance, and metabolism in plants, leading to larger fruits, better seed quality, and higher yield.



**Fig. 5:** Evolutionary pathway of Allotetraploid wheat formation through polyploidy.

Further benefits of polyploidy in wheat have been revealed through recent studies, showing that it enables the expression of diverse alleles from ancestral genomes, which enhances resistance to various diseases and pests. Polyploidy also contributes to stress resilience, including tolerance to cold, drought, and salinity, which is one of

the major factors limiting wheat growth and yield. Bread wheat's multiple chromosome copies have led to gradual genomic modifications that improve its ability to cope with soil salinity (Yang et al., 2014). Additionally, polyploidy supports improved nutritional quality and other adaptive traits, further highlighting the evolutionary advantages of genome duplication (del Blanco et al., 2001). Therefore, breeders are leveraging the polyploid structure of wheat to introduce new traits through induced mutations and wide crosses (Sidhu et al., 2025).

Building on the significant role of polyploidy in wheat, this phenomenon is also crucial in other important crops such as cotton. There are about 50 cotton species, with four cultivated and the rest wild. *Gossypium hirsutum* (upland cotton) is a classic example of successful allopolyploidy. This tetraploid species has 52 chromosomes from hybridization between an old-world A-genome and a new-world D-genome, followed by chromosome duplication, driving its evolution and domestication (Peng et al., 2022). The fusion of A and D genomes in cotton, occurring 1 to 2 million years ago, introduced traits like long, strong fibers and improved quality. This natural polyploidization enhanced fiber quantity, quality, and environmental adaptability, playing a crucial role in the evolution and domestication of cotton plants (Xu et al., 2010). Such modern plant breeding efforts have improved the genetic plasticity through polyploidy, which ultimately supports the production of fiber with enhanced fineness, pest and disease resistance against bollworm and bacterial blight, and tolerance to salinity and drought conditions and other biotic and abiotic factors. These improvements in upland cotton have made it the most successful and widely cultivated cotton species globally, accounting for over 90% of the total commercial cotton production.

## 6. CONCLUSION

Polyploidy is a fundamental and pervasive phenomenon in plants that drives evolution, speciation, and diversification while simultaneously providing valuable avenues for crop improvement. Through both natural mechanisms, such as hybridization, unreduced gamete formation, and somatic chromosome doubling, and artificial induction using chemicals like colchicine or oryzalin, polyploidy contributes to enhanced genome plasticity, heterosis, and the emergence of novel traits. Its impacts are evident in major crops such as wheat, cotton, canola, and strawberries, where polyploidization has improved organ size, biomass, stress tolerance, disease resistance, and overall productivity. By increasing genetic redundancy and diversity, polyploidy enables plants to adapt rapidly to environmental challenges, ensuring both evolutionary success and agricultural resilience. As global food security faces mounting pressures from climate change and population growth, understanding and harnessing polyploidy remains an essential strategy for developing high-yielding, resilient, and nutritionally superior crops.

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