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Role of polyploidy in improvement of vegetable crops: A review

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ABSTRACT

Polyploidy, the condition of having more than two sets of chromosomes plays a significant role in the improvement of vegetable crops. This phenomenon can occur naturally or be induced artificially and has proven to be a valuable tool in enhancing desirable traits in crops. Polyploidy can lead to increased vigour, size and resistance to environmental stressors as well as improved nutritional quality and disease resistance. The review explores the mechanisms by which polyploidy influences vegetable crops including its effects on plant morphology, fertility and yield. Additionally, it highlights the methods of inducing polyploidy such as the use of colchicine, other chemical agents and the potential challenges associated with polyploid breeding. Recent advances in molecular biology and genomics have further explained the genetic basis of polyploidy providing new opportunities for the development of improved vegetable cultivars. This review also discusses the future prospects of polyploidy in vegetable crop breeding focusing on its potential to address food security challenges by improving crop productivity and resilience.

Keywords: *Colchicine, Disease resistance, Desirable traits, Gigas effect, Polyploidy, Molecular biology.*

Introduction

Polyploidy refers to the condition in which an organism or cell contains more than two complete sets of chromosomes per nucleus. This may include diploids (two sets), triploids (three sets), tetraploids (four sets), and higher levels of ploidy. The discovery of polyploidy dates back to 1907 and is one of the more significant mechanisms of higher plant diversity and speciation [44]. It has been seen in at least 50 % of known angiosperm species and very rare in gymnosperm species [45]. It leads to genetic variability and forms the basis of plant improvement [7].

Polyploid breeding is the process of improving crop plants genetically by manipulating their fundamental set of chromosomes. This approach enhances various traits, including yield, quality and resilience across a range of plant species [35]. The most common result of polyploidy in plants is genome duplication. It leads to the gigas effect which occurs when polyploid organs such as roots, leaves, tubers, fruits, flowers and seeds enlarge in comparison to their diploid progenitors. Triploids have three sets of chromosomes and are sterile resulting in seedless fruits but in some cases, they may be fertile e.g. spinach. Watermelon's seedless nature has been widely cultivated. Tetraploids are useful in overcoming self-incompatibility and are used for making distant crosses or are used directly as a variety.

Polyploidy takes place in nature at low frequency. Polyploidy can be generated artificially using chemicals and other techniques but it can also happen impulsively. Colchicine is an alkaloid that is isolated from *Colchicum autumnale* seeds and buds. It prevents spindle formation which stops sister chromatids from moving to the opposite poles. As a result, the cell's chromosomal count doubles because the resulting restoration nucleus contains all of the chromatids. Polyploidy is beneficial for small-fruited species including cherries, grapes as well as green vegetables and tuber crops that propagate asexually. Additionally, it can boost secondary metabolite production in medicinal plants. This review summarizes the importance and benefits of polyploidy both naturally and artificially occurring in vegetable crops.

History

The history of polyploidy in vegetable crops is marked by significant evolutionary and agricultural implications. Research indicates that nearly all angiosperms have undergone at least one polyploidization event contributing to their morphological and ecological diversity [15]. This phenomenon has been harnessed in agriculture particularly in crops like *Brassica napus*, which arose from hybridization and subsequent chromosome doubling enhancing traits such as yield and stress resistance [5]. GIGAS MUTANT in *Oenothera* described by [24] was the first variation in chromosome number which was a natural autotetraploid (4n). He decapitated the shoots and some of the shoot buds arising from the callus thus produced were tetraploid. [27] first described the chromosome doubling by the action of Colchicine. In 1940-1950 a shift towards allo-polyploidy emphasizing hybridization's significance over phenotypic effects [34]. Polyploid crops often exhibit increased size and resilience making them more suitable for diverse environments [17]. Recent genomic studies have revealed complex interactions within polyploid genomes influencing gene expression and crop traits [5].

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Classification

Types of Polyploidy:

Autopolyploidy: This occurs when an organism has multiple sets of chromosomes derived from a single species. It is common in many vegetable crops, such as cabbage and broccoli where whole-genome duplications have been documented (Table 1) [18]. Autopolyploidy plays a significant role in enhancing the traits of various vegetable crops particularly in terms of stress tolerance and morphological improvements. This phenomenon involves the duplication of an organism's own genome, leading to increased genetic material that can enhance adaptability and yield. Autopolyploidy has been linked to improved salinity stress tolerance in leguminous crops as it enhances physiological and molecular responses to osmotic and ionic imbalances [21]. The multigenic response in polyploid plants includes the production of compatible solutes and antioxidants which help mitigate the effects of environmental stressors [25].

Allopolyploidy: This involves the combination of chromosome sets from different species often resulting from hybridization events. This type is prevalent in Brassicaceae vegetables enhancing genetic diversity and adaptability [20]. Allopolyploidy plays a significant role in the evolution and breeding of vegetable crops enhancing genetic diversity and agricultural traits. This process involves the hybridization of different species, leading to genome doubling and the formation of new polyploid species. Allopolyploidy often arises from spontaneous hybridization which can lead to favorable interactions between homoeologous genes, enhancing traits such as yield and stress resistance. Allopolyploidy can result in nonadditive gene expression due to genetic rearrangements and epigenetic modifications which may enhance adaptability to environmental changes [8]. This can also lead to genomic fractionation which can influence species diversity and the evolutionary trajectory of crops like tomatoes and sweet potatoes (Table 1) [46].

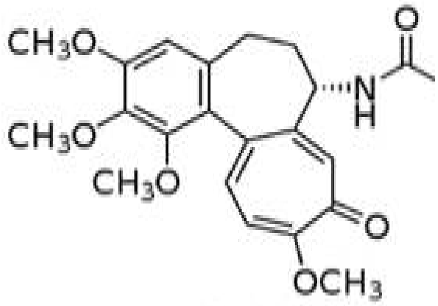
Spontaneous Polyploidy: Some vegetables like certain Apiaceae and Cucurbitaceae, can undergo spontaneous haploid genome duplication which can bypass the need for chemical treatments [11]. It occurs naturally in various vegetable species contributing to genetic diversity and potentially enhancing desirable traits. The mechanisms behind spontaneous polyploidy include processes such as endoreduplication and nuclear fusion, which can happen during different developmental stages of the plants. This process involves the duplication of the genome without cell division leading to polyploid cells. It has been observed in crops like cucumber where spontaneous polyploidy was quantified at 2.2% in greenhouse studies [33]. Recent studies have documented spontaneous triploidy in cassava highlighting its occurrence in traditional cropping systems and its implications for crop evolution [36]. Spontaneous polyploidy contributes to genetic variation which is crucial for breeding programs aimed at improving yield and resilience in vegetable crops [10].

Induction of polyploidy

Inducing polyploidy in vegetable crops is a critical method for enhancing agricultural traits and improving crop resilience. Various techniques have been developed including chemical treatments, plant growth regulators and spontaneous genome doubling.

Chemicals like colchicine, oryzalin and trifluralin are commonly used to induce polyploidy by disrupting normal cell division leading to chromosome doubling (Table 2) [11]. The effectiveness of these agents depends on concentration, exposure time and the developmental stage of the plant with optimized protocols yielding higher polyploidization rates [31].

Structure of colchicine



Colchicine

Plant Growth Regulators: The application of plant growth regulators can facilitate polyploidization by enhancing physiological responses in plants promoting adaptation to environmental stresses [16]. Understanding the molecular pathways influenced by these regulators is crucial for developing robust polyploid crops [16].

Spontaneous Genome Doubling: Some vegetable crops exhibit spontaneous haploid genome duplication which can bypass the need for chemical treatments (Table 2). This phenomenon is observed in various families like Apiaceae and Brassicaceae [11].

Examples of polyploidy induced in vegetables

Induced Polyploidy in Black Pepper

In a study on black pepper (*Piper nigrum* L.) a tetraploid cultivar named Panniyur-1 was developed using 0.05% colchicine treatment on open-pollinated seeds resulting in plants with 104 chromosomes and enhanced vigor [29].

Induced Polyploidy in Broad Bean

Research on *Vicia faba* demonstrated that soaking seeds in colchicine at varying concentrations (up to 4%) for 9 to 18 hours successfully induced triploid and tetraploid plants. These polyploid plants exhibited significant morphological changes including larger stomatal sizes and altered growth rates [28].

Polyploidy in Leguminous Crops

Colchicine-induced polyploidy in legumes has shown improvements in morpho-physiological traits, such as enhanced root and shoot growth which are crucial for drought stress tolerance. The study highlighted the dose-dependent nature of colchicine application and its effectiveness in improving crop resilience [26]. (Table 3)

Genomic and cytogenetic consequences of polyploidy

Genomic Changes

Polyploidy results in the duplication of entire genomes which can lead to increased genetic diversity and novel traits known as gene duplication [9]. Changes in gene expression can occur without alterations in DNA sequence affecting how plants respond to environmental stresses [9]. In polyploids, rDNA sequences may undergo concerted evolution leading to the loss or conversion of parental sequences over time [39].

Cytogenetic Implications

Polyploidy can induce chromosomal changes such as translocations and deletions which may enhance adaptability [9]. Over time, polyploids may revert to a diploid-like state, impacting their genetic behaviour and stability [9]. Methods like flow cytometry and fluorescence in situ hybridization (FISH) are essential for evaluating polyploidy and its effects on plant morphology [2].

Polyploidy offers advantages such as increased adaptability and resilience to stress, it also poses challenges including potential fitness costs associated with genetic load and the complexities of maintaining genomic stability [3].

Polyploidy role in improvement of vegetables

Polyploidy plays a significant role in the improvement of vegetable crops by enhancing various agronomic traits and expanding genetic diversity (Table 5). This phenomenon characterized by the presence of multiple sets of chromosomes can be induced artificially or occur naturally leading to increased biomass, stress tolerance and beneficial secondary metabolites in crops [41]. Polyploid crops, such as wheat and Brassica species exhibit superior yield and biomass compared to diploids [41]. Polyploidy contributes to greater resilience against environmental stresses like drought and salinity, making crops more adaptable to climate change [41].

Breeding Strategies

Breeders utilize synthetic methods to create novel polyploid varieties, overcoming genetic barriers and enhancing trait transfer between species [41]. Methods such as spontaneous haploid genome duplication and antimitotic treatments are employed to induce polyploidy in vegetable crops [11].

Molecular and genomic tools in polyploidy research

Molecular and genomic tools have significantly advanced the study of polyploidy, a prevalent phenomenon in plants that involves whole-genome duplication. These tools are crucial for understanding the complex genetic architecture and evolutionary dynamics of polyploid organisms. Despite the challenges posed by polyploidy such as multiple alleles and mixed inheritance patterns, recent developments in molecular and genomic technologies have opened new avenues for research. Next-generation sequencing (NGS) technologies have revolutionized the study of polyploid genomes by enabling comprehensive genome and gene expression analyses. These technologies facilitate the exploration of polyploid formation, maintenance and divergence at both whole-genome and sub-genome levels [1]. The development of genome-wide molecular markers has improved the understanding of plant domestication and evolution, revealing the repeated occurrence of polyploidization and associated genomic changes such as gene loss and silencing [12]. Some commercially cultivated polyploid varieties in vegetable crops are shown in Table 6:

Population Genomics and Genetic Mapping

New software tools have been developed to infer population structure and ancestry in mixed-ploidy data sets, addressing the shortage of tools for polyploid population genomic analysis. Polyploid genotyping, genetic and physical mapping and quantitative trait analysis are facilitated by tools that estimate marker allele dosage, establish linkage phases and perform genome-wide association studies (GWAS) and quantitative trait locus (QTL) analyses [4].

Significance and Achievements

There have been numerous studies on polyploidy in the improvement of vegetable crops, which are summarized below:

[40] examined the characteristics of diploid, triploid and tetraploid tiny gourds. The triploid flowering time was 38 days, while the diploid took 40 and the tetraploid took 42 days. Additionally, triploid plants produced 15.25 kg/vine/year, significantly larger than diploid plants. Triploid fruits were larger than diploid fruits which were medium-sized. Triploid fruits contained fewer phenols making them more flavoured.

[42] investigated the effects of colchicine on beans and found an increase in root length, shoot length and number of lateral roots at all concentrations (5, 10, 15, 20 and 25 ppm) as compared to the control. Similarly the pod circumference increased significantly at 5 ppm concentration compared to the control. Colchicine concentrations of 5 ppm (148.8±28.93) and 10 ppm (109±16.81) resulted in significantly larger seed/pod weights than the control (59.75±4.8).

[20] investigated the impact of varying ploidy levels in four brinjal cultivars. Tetraploid accessions displayed decreased glycoalkaloid concentration compared to diploids during fruit set. At harvest no substantial difference was noticed.

[23] found that tetraploid pumpkin plants had descending female flower nodes. Tetraploid fruits weighed 2.9 kg and diploid fruits weighed 2.2 kg. Tetraploid fruits had approximately 30 seeds per fruit while diploid fruits had 122 seeds. Tetraploid plants showed a 90 % increase in photosynthetic rate and a 50 % rise in flavonoids content.

[32] recorded effects of colchicine on the survival rate and found that after being treated with 0.1 % colchicine for 12 hours, 415 seedlings out of 500 seeds were obtained with a survival rate of 83 %, and 32 seedlings were proven to be tetraploid by chromosomal counting with an induction rate of 7.7 %. The tetraploid plants show "gigas" effect i.e., an increase in size of both vegetative and reproductive parts.

[43] investigated shoot regeneration ability in diploid and tetraploid garlic and discovered that as the duration time and concentration of colchicine increased in diploid, the total explant viability and shoot regeneration ability (regenerated shoots per explant, RSE) decreased, whereas tetraploid induction rates did not.

[13] investigates the morphological and biochemical characteristics of 17 red ginger genotypes, including 14 Indian and the released cultivar IISR Varada. The findings revealed a substantial difference in growth, yield and quality characteristics between the red ginger genotypes and IISR Varada. Polyploidy induction in vitro was shown to be more efficient than in vivo, yielding five tetraploids (2n=44). The maximum tetraploidy induction was seen after 48 hours of treatment with 0.10 % colchicine in vitro. The induced tetraploids showed increased vigour, improved morphological and stomatal characteristics and higher yields.

Future Prospects

The potential of polyploidy in vegetable breeding is vast and largely untapped. Advances in genomics and molecular tools now allow precise identification and manipulation of polyploid genomes, opening avenues for developing vegetables with improved yield, stress tolerance and nutritional quality. Polyploid induction and hybridization can accelerate the creation of novel vegetable varieties with enhanced disease resistance, abiotic stress adaptation and extended shelf-life. Additionally, studying naturally occurring and synthetic polyploids can provide insights into gene expression regulation, epigenetic modifications and genome stability, which are critical for sustainable crop improvement. With the integration of CRISPR/Cas and other genome-editing technologies, polyploid breeding could enable targeted trait enhancement without extensive backcrossing. Overall, polyploidy offers a promising strategy for diversifying vegetable germplasm and meeting the challenges of global food security, climate change and consumer demand for high-quality produce.

Table 1: Classification of vegetables based on ploidy level

Vegetable crop	Type of Polyploidy	Chromosome Number (2n)	Natural or Induced	Reference
Potato	Autotetraploid	4x = 48	Natural	**[38]**
Onion	Allopolyploid	2n = 16	Induced	**[6]**
Carrot	Diploid	2n = 18	Natural	**[19]**
Cabbage	Amphidiploid	2n = 18	Natural	**[37]**

Table 2: Methods used for polyploidy induction

Method	Agent	Crop	Efficiency	Remarks	Reference
Colchicine Treatment	Colchicine (0.1–0.5%)	Onion, Garlic, Okra	High	Most widely used method	**[22]**
Oryzalin Treatment	Oryzalin	Potato, Tomato	Moderate	Less toxic alternative	**[23]**
Temperature Shock	Cold/Heat	Lettuce	Low	Limited usage, crop-specific	**[14]**
Endopolyploidy Induction	Gene Editing	Model Plants	Experimental	Emerging technique	**[19]**

Table 3: Different varieties of vegetables induced through polyploidy

Vegetable Crop	Variety	Ploidy Level	Induction Method	Remarks
Brinjal	Arka Kusumakar	4x (Tetraploid)	Colchicine treatment	Higher yield, larger fruit size
Radish	Triploid chinese radish	3x (Triploid)	Colchicine treatment	Sterile hybrid, better texture
Carrot	Pusa Meghali	4x (Tetraploid)	Colchicine treatment	Larger roots, better quality
Okra	Varsha Uphar	4x (Tetraploid)	Colchicine treatment	Increased pod size, delayed maturity
Chilli	Tetraploid Pusa Jwala	4x (Tetraploid)	Colchicine treatment	Larger fruit, increased capsaicin
Watermelon	Pusa bedana	3x (Triploid)	Hybridization of 2x × 4x	Sterile, seedless varie
Beetroot	Pusa Jyoti	4x (Tetraploid)	Colchicine treatment	Higher sugar content, larger root size

Table 4: Effects of Polyploidy on Morphological and Physiological traits

Trait	Diploid Expression	Polyploid Expression	Crop	Reference
Leaf Size	Small	Larger	Tomato	**[22]**
Stomatal Size	Normal	Enlarged	Chili	**[30]**
Flowering Time	Early	Delayed	Cabbage	**[6]**
Biomass	Moderate	High	Spinach	**[14]**

Table 5: Improvement achieved through polyploidy in vegetable crops

Crop	Trait Improved	Type of Polyploidy	Yield Impact	Quality Traits	Reference
Tomato	Fruit Size	Induced Autotetraploid	Increased around 25%	Enhanced Lycopene Level	**[38]**
Brinjal	Disease Resistance	Allopolyploid	Increased around 10%	Firmer Texture	**[30]**
Okra	Fiber Reduction	Tetraploid	Increased around 15%	Tender Pods	**[6]**

Table 6: Commercially cultivated polyploid vegetable varieties

Crop	Variety Name	Ploidy Level	Country of Release	Year	Trait Improved	Reference
Potato	Kufri Chipsona	Tetraploid	India	2005	Chipping quality	**[37]**
Sweet Potato	Beauregard	Hexaploid	USA	1987	High Yield	**[6]**
Broccoli	Green Magic	Tetraploid	USA	2010	Heat Tolerance	**[14]**

Table 7: Challenges and Limitations of polyploidy in vegetable crops

Challenge	Affected Crops	Description	Suggested Solution	Reference
Sterility	Onion, Garlic	Chromosome mismatch leading to reduced fertility	Backcrossing strategies	**[22]**
Unstable Traits	Tomato	Segregation and instability in desired traits	Use of doubled haploids	**[38]**
Hybridization Barriers	Carrot	Ploidy level differences hinder hybrid formation	Bridge crosses	**[19]**

Conclusion

Polyploidy contributes significantly to the enhancement of vegetable crops by promoting desirable characteristics such as larger size, higher yield, improved tolerance to environmental stress and increased resistance to pests and diseases. By inducing polyploidy breeders can introduce beneficial genetic variations that contribute to the development of crops with superior agronomic qualities. Moreover it leads to greater genetic diversity offering new avenues for breeding and adaptation to changing environmental conditions. While challenges such as fertility and chromosomal instability may arise, advances in biotechnology and breeding techniques continue to make polyploidy a valuable tool in crop improvement. Ultimately, the strategic application of polyploidy holds promise for meeting the growing demand for high-quality, sustainable vegetable crops in the face of global agricultural challenges.

Conflict of Interest

The authors declare no conflict of interest.

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