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Ploidy manipulation in fruit crops: A Review

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ABSTRACT

Meiotic abnormalities associated with the development of spindle fibres give rise to the phenomenon known as polyploidy. Polyploids may occur naturally or can be induced by artificial means. Overall, polyploidy manipulation is one of the most promising strategies in plant breeding and has been used for a long time to increase the production of many crop plants. Numerous plants typically exhibit polyploidy, which has been recognised as a significant phenomenon in the assessment of plants. Polyploid plants may experience morphological, anatomical, and physiological alterations as a result of ploidy modification that alters nuclear DNA content, gene expression, and developmental processes. In general, polyploid plants have bigger organs, more biomass, higher yields, and improved resistance to biotic and abiotic challenges. They also have higher levels of primary and secondary metabolites. Also, polyploidy often result in reduced fertility due to mitotic error and allows the production of seedless fruits. Ploidy manipulation is recognized as one of the most important technique applied in plant breeding because quick genetic improvement is achieved through the formation of synthetic polyploids. Therefore, polyploidization is an ideal tool for breeding to produce new cultivars since it usually promotes traits like high yield, larger vegetative and floral traits which are desirable for agronomical purposes. In this review we will be discussing about Ploidy manipulation, methods to induce polyploidy and importance of Ploidy manipulation.

1. Introduction

When it comes to bananas and other fruit crops with a limited genetic base, ploidy manipulation is a crucial technique for increasing variability. It has broad implification for growing larger fruit sizes and disease resistant plants. Climate change causes greater temperatures, drought and salinity, all of which are major threats to agriculture (Korres*et al*., 2016), affecting growth,production of crop and quality of fruit, especially in dry and semiarid regions surrounding the Mediterranean region(DE Ollas *et al*.,2019). Ploidy manipulation can be a better tool because polyploids promote better adaptation under these conditions due to their unique phenotypic characters and genome plasticity (Leitch and Leitch, 2008).Ploidy refers to number of set of chromosome and manipulation refers to change in number of set of chromosome. When an organism have more than two complete sets of chromosomes in each cell nucleus, it is said to be polyploid, and it is thought to be a significant factor in evolution of plants and diversification (Soltis *et al*., 2009). Polyploids are abundant in nature, and they serve as a key mechanism for adaptation and speciation. A few basic terms must be defined in order to comprehend ploidy modification. "x" represents the basic set of chromosomes, while "2n" represents the total number of chromosomes in a somatic cell. The number of chromosomes in a somatic cell is double that of the haploid number (n) in gametes. The majority of organisms with nuclei are diploid (2n), which means they have two sets of chromosomes, one from each parent.Most

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eukaryotes have diploid somatic cells, but through the process of meiosis, they produce haploid gametes (Todd *et al.*, 2017). Polyploidy occurs naturally in nature due to a variety of factors such as meiotic or mitotic failures, as well as the union of unreduced (2n) gametes (Comai*et al.*, 2005). Both autopolyploid and allopolyploid plant species can be found in the wild and in cultivated (Xun*et al.*, 2011). Induction of polyploidy is a rapid way for overcoming a hybrid species sterility during plant breeding and an effective strategy for developing more drought-tolerant cultivars, which is critical for future food production sustainability (Rauf *et al* 2016). The growing popularity of citrus fruits and their resistance to abiotic challenges has underlined the need to devise an effective method for producing seedless citrus types that can withstand these changes in the environment (oustric*et al.*, 2020). The ploidy level modification may be an efficient technique to improve tolerance to drought in plants and obtain seedless fruits (Miri 2020). Chromosome doubling is frequently associated with morphological alterations. Chromosome doubling has been shown to affect traits like leaf size and thickness, inflorescence size and quantity, internode length, stomata size and plant height. Size and biomass have both been linked to increases in polyploidy. One of the most efficient ways to grow seedless plants is to cross a diploid with a synthetically produced tetraploid to produce triploids (plants with three sets of chromosomes) (Ranney, 2006). For a number of different species, this strategy has worked. Additionally, chromosome doubling made the interspecific triploid fertile.

Table1: Selection of polyploids crops for agricultural interest

Crop	Ploidy	Agronomic traits
Apple	3x,4x	Dwarfness and increased size
Citrus	4x	Drought and salinity tolerance
Grape	3x,4x	Seedlessness and fruit size increased
Loquat	3x,4x	Increased size of fruit
Mango	4x	Increased fruit size
Persimmon	6x	Increased fruit size
Pomegranate	4x	Increased fruit size
Sweet cherry	3x	Dwarfism

Source: Ruiz *et al.*, 2020

2. Ploidy Classes and modes of origin

Kihara and Ono described two different classes of polyploids: “autopolyploids,” which arise within populations of individual species, and “allopolyploids,” are the product of interspecific hybridization.When the basic set (X) of chromosomes of the same genome is duplicated several times during meiosis, this condition is known as autopolyploidy. This condition arises naturally when unreduced gametes are fused.(Mason and Betley 2015).Allopolyploids are further sub-divided into two classes: one is true allopolyploids and the second is segmental allopolyploids. True allopolyploids arises when hybridization occur between distantly related species (Sattler *et al.*, 2016). here, the opposite chromosome complements do not pair with each other, that results in the formation of bivalents during meiosis and in a disomic inheritance pattern. But in case of, segmental allopolyploids hybridization between closely related species having partially different genomes(Savacine*etal.*,2020 and Stebbins, 1950).A single genome's chromosomes differ from one another in appearance, gene content, and homology; individuals of a single genome do not have a predisposition to mate with one another. A diploid species has two genomes, a triploid three, and a tetraploid four, and so on. Heteroploids are individuals who have chromosome numbers other than the diploid (2x, not 2n) number. Aneuploidy refers to a change in chromosome number that affects one or more chromosomes of the genome.

The aneuploid alterations are defined in relation to the species somatic chromosomal number (2n rather than 2x). As a result, aneuploid individuals derived from diploid and polyploid species use the same terminology. Euploidy is a type of heteroploidy that involves one or more entire genomes. By defination, euploid chromosomal counts are an exact multiple of the concerned species fundamental chromosome number, but aneuploid chromosome numbers are not. Nullisomic aneuploids have one chromosome pair missing (2n-2), whereas monosomic aneuploids have only one chromosome missing (2n-1) (Islam 1954). Two chromosomes are missing in a double monosomicindividual;however, the two chromosomes belong to two separate chromosome pairs (2n-1-1). Trisomic individuals have one additional chromosome (2n+1), while double trisomic individuals (2n+l+1) have two extra chromosomes, each belonging to a distinct chromosome pair (Dar and Wani 2017). Tetrasomic (2n+2) refers to an individual who have an additional set of chromosomes. The chromosome number in euploids is a perfect multiple of the basic or genomic number. Autopolyploid occurs when all of the genomes of a polyploid species are identical, and the scenario is referred to as autopolyploidy. Allopolyploids, on the other hand, have two or more unique genomes. Euploids can have three (triploid), four (tetraploid), five (pentaploid), six (hexaploid), seven (heptaploid), and eight (octaploid) or genomes making up their somatic chromosome number.They are referred to as autotriploid, autotertaploid, autopentaploid, autohexaploid, autoheptaploid, autooctaploid, and so on in the event of autopolyploidy, and as allotriploid,allotetraploid, allopentaploid, allohexaploid, alloheptaploid, allooctaploid. Amphidiploid is a type of allopolyploid that contains two copies of each genome and, as a result, behaves like a diploid during meiosis (Sorres*et al.,* 2021).

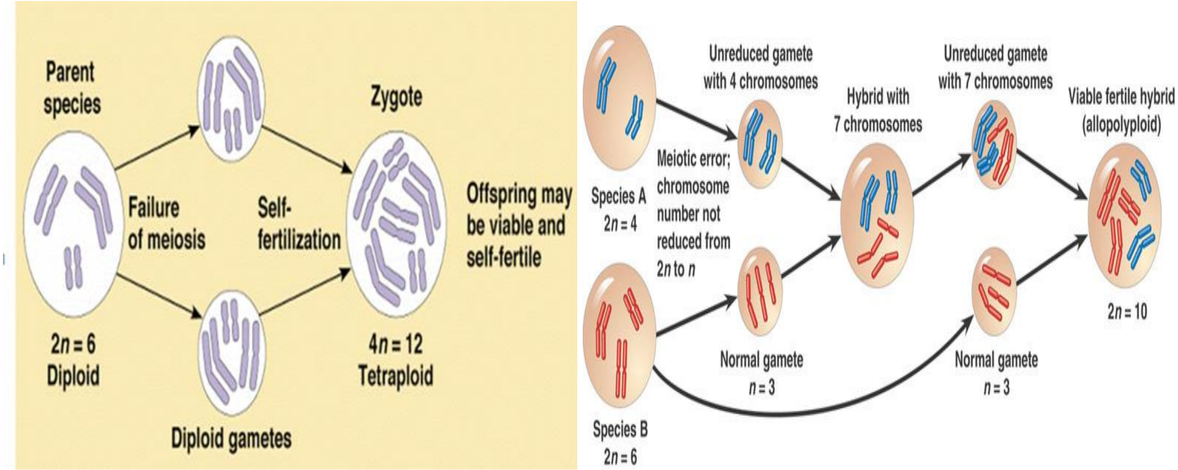


Figure1. Formation of auto and allopolyploids (Sahoo and Kaluram, 2019)

Table 2. Different Polyploids in Fruit crop

Autopolyploids	**Examples**
Autotriplods	Tahiti lime
Autotetraploids	Aonla, Bael, Lithchi, Jackfruit, Phalsa, Umranber
Autohexploids	Persimmon and Kiwifruit
Autopolyploids	**Examples**
Allotetraploid	Mango
Allohexaploid	European Plum
Allooctaploid	Vellaicolumban and strawberry

3. Methods to Induce Polyploids

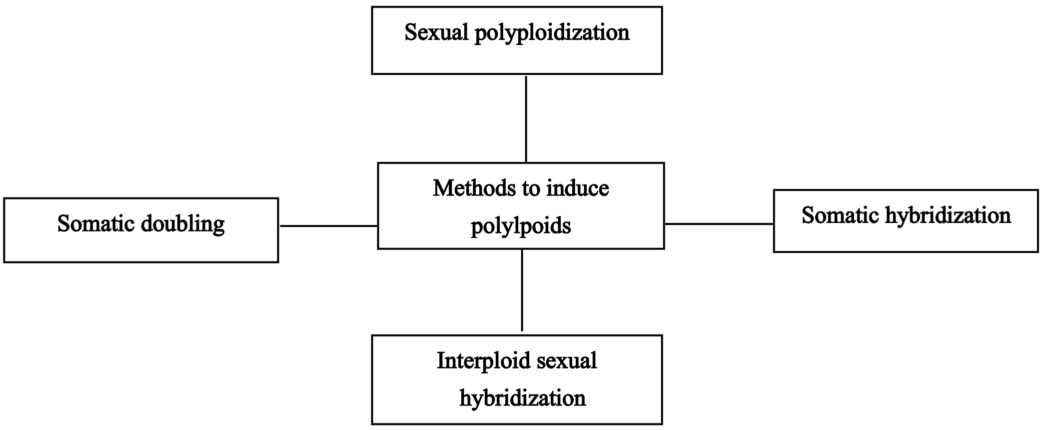
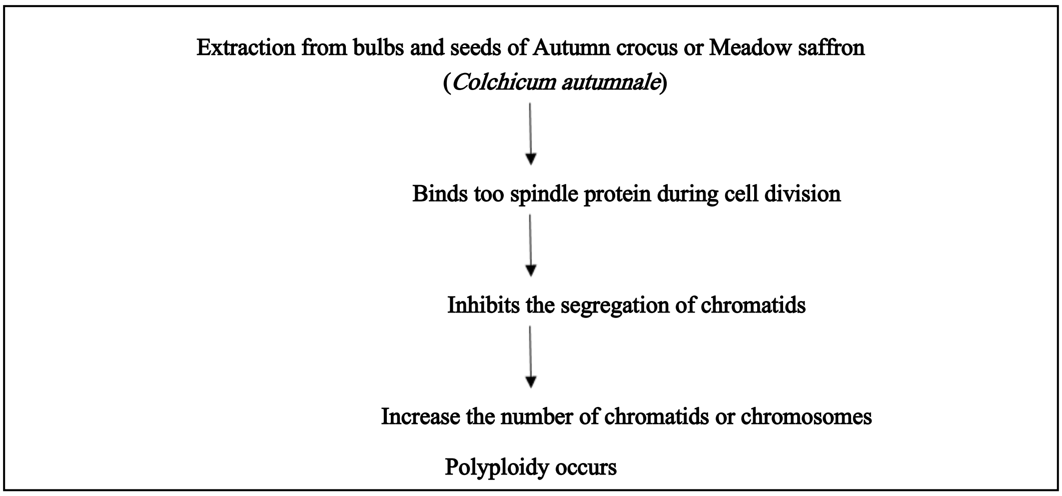


Figure 2. Methods to Induce Polyploids

- **Sexual Polyploidization**: Sexual polyploidization is an oldest method which is used to generate polyploids. This requires one of the parents having non-reduced gametes (typically 2n). Production of 1st division restitution and 2nd division restitution are the primary mechanisms in plants for diploid gamete production) (De Storme and Geelen, 2013). Because in this case the 1st or 2nd meiotic divisions fail and results in restituted nuclei with a somatic chromosomal number (Park *et al.*, 2007). As a result, the genetic implications of FDR and SDR 2n gamete production procedures differ, which is important to consider when breeding polyploids because it has a direct impact on the progeny's genetic makeup. Non-sister chromatids are present in FDR 2n gametes. Based on the extent of chromosome interference, parental heterozygosity restitution (PHR) rates range from hundread percent for loci adjacent to the centromere to 60–70 percent for loci far from the centromere when crossover occurs. In case of fruits formation of non-reduced gametes has been seen in the genus Annona which contains edible fruits such as cherimoya (*A. cherimola* Mill.) and sugar apple (*A. squamosa* L.), after uncommon polyploid progenies were observed (Martin *et al.*, 2019).
- **Interploid sexual hybridization**: Another way for Ploidy manipulation is through interploid sexual hybridization, that includes crossing plants having different ploidy levels. Using 2x × 4x, 4x × 2x, or 2x × 3x crosses to restore triploid (3x) plants is a typical method. However, it has the disadvantage of frequently failing to produce endosperm, resulting in abortion of seed (Birchler, 2014). As a result, embryo rescue technique is an essential strategy for interploid cross breeding (Wang *et al.*, 2016); it has been used widely in several fruit crops, including apple (Dantas*et al.*, 2006), citrus (Aleza*et al.*, 2012), and grape (Wang *et al.*, 2016, Sun *et al.,* 2011 and Li *et al.*, 2015) which gave an overview of the aspects that could influence its effectiveness.
- **Somatic Doubling**: In this method chromosome duplication take place in non-germ cells which generate autopolyploids or allopolyploids. Antimitotic chemicals like as colchicine, trifluralin, and oryzalin can chemically induce duplication in this method due to a mitotic failure. In crops which have nucellar embryony, such as citrus and mango (*Mangifera* spp.) species, however, spontaneous somatic duplication events in the nucella may result in the natural formation of tetraploid (4x) embryos that can be selected from seedlings (Galan-Sauco*et al.*, 2001; Aleza*et al.*, 2011). The success of somatic duplication is depends on the development of an effective protocol, type of explant, agent dose of antimitotic chemical, time of treatment, and *in vitro* regeneration conditions. Secondary effect induced by chemical treatments are chimeras. Ploidy level of various organs on each regenerant explant must therefore be further verified using this procedure, which typically entails morphological analysis, karyotyping, or analytical flow cytometry techniques. This method has been widelyused for Ploidy manipulation in crop breeding, as shown by Sattler *et al.* (2016). The most used antimitotic drug for creating polyploids is colchicine, an alkaloid obtained from meadow saffron (*Colchicum autumnale*) (Planchais *et al.*,2000). The binding of colchicine to a- and b-tubulin dimers, inhibition of microtubule polymerization during the cell cycle, and suppression of chromosomeor chromatid movement during anaphase all contribute to its mechanism of action. As a result, cytokinesis will also be impaired, leading to the creation of cells with double chromosomes. It has low affinity for plant tubulins and must be used at millimolar concentrationfor effective poly-ploidy induction in plants (Dhooghe *et al.*, 2011).



- **Somatic hybridization:** One of the oldest methods of loidy modification through protoplast fusion is somatic hybridization. This approach was created to manage the crossing of species barriers; this allows the full genomes of two different parents to be combined in a one cell resulting in a polyploid hybrid plant. This approach can be used to create polyploids that have not been created through meiotic recombination processes. Thus, resultant progenies combine the entire genomes of both parents, as well as all of the dominant parental traits, irrespective of heterozygozity, and thus overcome reproductive biology's limitations. Meanwhile, on crops with a long juvenile stage, the likelihood of combining all desired traits in a sexual recombinant hybrid is much lower and slower (Dambier*et al.*, 2011Ollitrault and Navarro, 2012).The application of this method in many crops is hampered by difficulties in protoplast isolation, culture and plant regeneration. It is, however, an integral part of a number of citrus breeding programmes around the world, both for scion and rootstock breeding (Grosser *et al.*, 2000; Dambier*et al.*, 2011; Grosser and Gmitter, 2011). Artificial polyploids can be used as breeding material or as prospective new varieties once they've been obtained. As a result, in order to maximise the potential of each newly produced genotype, their potential benefits and drawbacks must be considered in relation to their intended application. Triploids produce larger seedless fruit, but they have restricted fertility, which often serves as a roadblock to continued development.Resynthesizing a 3x variety with improved parents is one technique to add desired features such as disease resistance a posteriori (de Carvalho-Santos *et al.*, 2019). More crucially, triploid crops must be able to trigger a parthenocarpic fruit set, which can be initiated by hormonal therapies, accelerated by pollination, or caused by epigenetic manipulation (Joldersma and Liu, 2018). Natural parthenocarpy is relatively common among cultivated species, particularly on trees, hybrid plants, and polyploids (Picarella and Mazzucato, 2019).

4. **Phenotypic characters induced by Ploidy manipulation**

   Phenotypic variations that are indued by polyploidy are following:

- **Polyploids have increase in cell and organ size**:Different modifications are observed in polyploids, including phenotypic changes at the organ level in plants as a result of polyploidy (Beest*et al.*, 2012). In comparison to diploids, polyploids have larger cell and organ sizes. Some of the most common unique qualities include thicker and greener leaves due to increased biomass production, higher water content in leaves, thicker and smaller roots, and a dwarf phenotype (Motosugi*et al.*, 2002; Padoan*et al.*, 2013; Ruiz *et al.*, 2016 Wang *et al.*, 2016). The composition of cell walls is also affected by ploidy modification. However, this does not always result in a change in the overall size of the plant (Corneillie*et al.*, 2019). Polyploids, such as citrus, typically have larger blooms and seeds.
- **High biomass in polyploids**:Polyploids produce more biomass than diploids, resulting in the growth of thicker leaves (Hennig *et al.*, 2015; Denaeghel*et al.*, 2018). There is debate about whether ploidy modification generates different alterations in woody species' primary and secondary growth. While these two criteria are often connected in diploid species, the regulatory systems that coordinate plant organ growth differ between many diploids and autotetraploid trees, with autotetraploids showing dwarfism but higher biomass than their 2x counterparts. As a result, some scientists propose genome duplication as a beneficial breeding technique for tailoring crops for biomass output, as shown in the model plant Arabidopsis (Corneillie*et al.*, 2019).

  Fruit quality: Ploidy manipulation induces the formation of seedless fruit and favoursvigour when triploidy is used (Wang *et al.*, 2016). While triploids breeding for seedlessness has resulted in the development of remarkable variations in some plants, such as grapevine and citrus, some triploid apples and citrus limes contain seedy fruits that are less appealing. Polyploidy increases fruit size in grape and kiwi (Shengjian*etal.*, 2005; Wu *et al.*, 2012).Xue*et al.* (2017) reported that the length, weight and shape index were increased in the tetraploid *Malus pumila* fruits by 11.9, 23.6 and 21.5, respectively. Compared with the diploid plants, tetraploid *Ziziphus jujuba* had significantly bigger and heavier fruit, showing 40.56 % increase in weight (Wang *et al.*,2019)

5. **Importance of Ploidy Manipulation:** Ploidy manipulation is regarded as an important method for genetic improvement in a variety of crops, with the goal of developing novel polyploid types or enhancing interspecific hybrid fertility (Dhooghe *et al.*, 2011; Sattlser*et al.*, 2016; Denaeghel*et al.*, 2018; Parsons *et al.*, 2019).Polyploid plays an important role in breeding due to their reduce seeds, increase in fruit size and tolerance to biotic and abiotic stress. Ploidy manipulation is one of the key elements driving evolution in higher plants. Wendel and Doyle, 2005; Hollister *et al.*, 2012).Conferring genotypic plasticity by increasing the number of copies of the genome (autopolyploidy) or adding different genomes

(allopolyploidy), thereby increasing their potential for adaptation and promoting their selection (Leitch and Leitch, 2008). Polyploidy according to Ramsey (2011) promotes adaptive evolution to changing environmental conditions by allowing duplicate genes to express differently (Dong and Adams, 2011). Diploid polyploidization allows the utilisation of valuable variability in diploid bananas that would otherwise be unavailable for breeding. When it comes to human-made polyploidy, however, only a few events have been commercially successful such as in 2009, the Chinese government published 'Chenguang,' a novel tetraploid *Chinese jujuba* cultivar generated using colchicine on the stem apex of the diploid 'Linyilizao.' Autotetraploid kiwi (*Actinidia chinensis* Planch), auto-allopolyploid apple (*Malus spp.* Mill), banana (*Musaspp.*), and grape (*Vitis* spp.) (Ping et al.,2012) had bigger fruits and improved fruit quality (Motosugi *et al.*, 2002; Wu et al., 2012). With the exception of polyploidy variants such as the triploid "Tahiti" lime, citrus trees are mainly diploid (2n = 2= 18). Because of their inviable seeds, triploid cultivars are uncommon in nature, resulting in a dearth of progeny. Triploid plants, on the other hand, will be effective for boosting phenotypic and organoleptic traits that are commercially significant in the fresh fruit market, thanks to their seedlessness and rapid growth. Triploidy is one of the key breeding procedures utilised in citrus cultivars to develop unique seedless fruit (Recupero et al., 2005; Aleza et al., 2012; Navarro et al., 2015). Excessive number of seeds in citrus makes it unappealing to the consumers. Seedlessness has been successfully achieved through ploidy manipulations as triploidy is associated with sterility 3x: spontaneous, 2x crosses, endosperm culture, somatic hybridization (2x+1x), 4x × 2x crosses(Esen and Soost, 1972). The interploidal hybridization (4x × 2x) most effective and is commonly used to produce seedless triploids. Ploidy manipulation by crossing of tetraploid with diploid yielded some valuable triploid like Oroblanco and Melogold.

6. Conclusion

Ploidy manipulation is one of the most common phenomenaof diversity, adaptation and evolution in floweringplants. The several advantages of polyploidyobserved in natural species indicate that polyploidshave a more advantage over diploids.Ploidy manipulation can be utilized to develop varieties in fruit crops which have a narrow genetic base.It will facilitate in development of drought and stress tolerant fruit varieties. Ploidy manipulation is a useful tool for improving the crop plants. Since no direct genetic manipulation is involved, the varieties developed will be acceptable and welcomed by the masses. Ploidy manipulation is associated with extensive structural,developmental, physiological and biochemicalchanges in plants that result in wide variation inthese traits. Therefore, it can be concluded thatPloidy manipulation provides new options for plant breeders to induce ex vitro and in vitro syntheticpolyploids.

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