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Review

Cytogenetics and Consequences of Polyploidization on Different Biotic-Abiotic Stress Tolerance and the Potential Mechanisms Involved

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Abstract: The application of polyploidy in sustainable agriculture has already brought much appreciation among researchers. Polyploidy may occur naturally or can be induced in the laboratory using chemical or gaseous agents and results in complete chromosome nondisjunction. This comprehensive review described the potential of polyploidization on plants, especially its role in crop improvement for enhanced production and host-plant resistance development against pests and diseases. An in-depth investigation on techniques used in the induction of polyploidy, cytogenetic evaluation methods of different ploidy levels, application, and current research trends is also presented. Ongoing research has mainly aimed to bring the recurrence in polyploidy, which is usually detected by flow cytometry, chromosome counting, and cytogenetic techniques such as fluorescent in situ hybridization (FISH) and genomic in situ hybridization (GISH). Polyploidy can bring about positive consequences in the growth and yield attributes of crops, making them more tolerant to abiotic and biotic stresses. However, the unexpected change in chromosome set and lack of knowledge on the mechanism of stress alleviation is hindering the application of polyploidy on a large scale. Moreover, a lack of cost–benefit analysis and knowledge gaps on the socio-economic implication are predominant. Further research on polyploidy coupling with modern genomic technologies will help to bring real-world market prospects in the era of changing climate. This review on polyploidy provides a solid foundation to do next-generation research on crop improvement.

Keywords: cytogenetics; stress; polyploidy; fluorescent in situ hybridization; genomic in situ hybridization

1. Introduction

The duplication of single or combined differentiated genomes is known as polyploidy. Autopolyploid arises from the doubling of structurally similar, homologous (AAAA) genomes within a single species, while allopolyploids arise through interspecific hybridization and subsequent doubling of nonhomologous (AABB) genomes [1–3]. Aneuploid genomes have incomplete chromosome sets, which occur naturally in plant populations and are induced by chemical and physical agents [4–6]. Differences in the number of chromosomes [7–9] and phenotypic differences [10–12] have been verified using molecular cytogenetic methods. These differences increase allergic diversity [13] and heterozygosity [14] by genome buffering, resulting in novel dose effects. For instance, wheat, canola, cotton, peanut, soybean, and tobacco [1,6,15,16] have been identified as domesticated crops.

Several chemical and gaseous agents are currently used to induce polyploidy. The most widely used agents are colchicine and oryzalin, though colchicine has been suggested to be avoided due to its carcinogenic properties [17]. The common consequences of induced polyploids are increased cell size as well as whole plant size, reduced fertility, and heterosis [18]. In modern breeding, cytoplasmic male sterility often occurs in F1 progenies, where N_2O gas treatment (~6 bar, 48 h) plays a significant role in restoring fertility [19]. Similarly, pre- and post-fertilization barriers can be minimized through embryo rescue, particularly in flowering ornamentals, such as *Lilium and Hibiscus* [20–23]. Currently, polyploidization is vital in creating crop diversity and producing fruits, vegetables, and flowers most sought after by consumers.

Due to climate change and global warming, plants experience multiple abiotic stresses such as salinity [24–27], drought [28–30], temperature [31–34], and biotic stresses such as insect pests [35–37] and diseases. These stresses threaten crop production by disrupting plants' physiological and biochemical processes. Polyploidy offers several advantages amid stress situations, which are described in previous studies. However, the underlying mechanism and holistic understanding are still missing.

Several studies assessed polyploidy, but cytogenetic evaluations of polyploids and their effects on crop physiology remain uncertain. Therefore, polyploidy's roles in plant development, mechanisms and assessment processes, plant physiology changes, biotic-abiotic stresses, challenges, and prospects are outlined here. This study aims to help to recognize possible interactions between polyploids and to establish a consistent assessment.

2. Role of Polyploidy in Modern Plant Breeding

Plant breeders modify crop traits using multiple tools, including polyploidization, to satisfy market demand. This technique creates intense phenotypes and high vigor, making it one of the most potent crop enhancement methods [38]. In addition, some plants have a specific demand for their specific traits, such as seedless fruits in grapevine and banana, which can be achieved through polyploidization [39,40]. Polyploidy results in higher heterozygosity and genome redundancy that are considered advantageous for improving crop plants over conventional plant breeding tools [41,42].

Interspecific hybridization helps to increase the diversity of crops and helps them adapt to new environments [43]. For example, Allopolyploid Triticale is a manufactured crop developed by crossing hexaploid bread wheat and rye to achieve specific goals (e.g., high yield, grain quality, less disease, and stress tolerance) [44,45]. In addition, bridge hybridization is done to transfer genes from one ploidy stage to another if a direct crossover is not feasible. Creation of diversity is one of the most important tasks to develop a crop variety where polyploidy has the efficacy to enhance crop diversity [46,47].

Polyploidy is common in newly domesticated crops [48]. In many cultivated crops, polyploidy has been observed in the speciation process and is now commonly used to create new species selected for features [3]. Unreduced gametes result in plant polyploidy and are used in crop breeding. Polyploidy increases the chromosome number, which helps plants tolerate the mutation by allelic modifications [49,50]. Chromosome deletion-related polyploidy breeding and substitution can produce targeted traits. We have seen many examples of successful cultivation influenced by polyploidy breeding. For example, seedless triploid watermelons, tetraploid red clovers, ryegrass, rye, and many ornamental plants have been developed or improved using polyploid breeding [17,51].

In summary, the main benefits of polyploidy are related to improving the use of heterozygosity. It buffers the effect of gene redundancy in mutations and, in some cases, facilitates reproduction by self-fertilization or asexual means [52]. It has a significant influence on farmers and food security issues.

3. Induction of Polyploids

The recurrence and frequency of polyploidization in plant species make polyploidization an influential research area [53] in which a major step is to select traits in plants [54]. The occurrence of polyploidy in plants was discovered about a century ago. Because of the widespread occurrence of polyploids in wild and cultivated plants, it is important for plant breeders and evolutionary biologists. In the past, antimitotic reagents-induced polyploids have not directly contributed to crop improvement. On the other hand, sexual polyploids (unreduced 2n gametes) are more relevant for crop improvement in many cases. Two pathways cause polyploids: mitotic polyploidization and meiotic polyploidization [55].

Mitotic polyploidization depends on doubling somatic tissue where homoeologous chromosome recombination occurs [56]. The first mitotic polyploidization was introduced in 1930 [57]. This activation polyploidization was tested on plants in vitro [55]. Colchicine, oryzalin, trifluralin, amiprophos-methyl, N_2O gas treatment, and caffeine have recently been used as antimitotic reagents [17]. Colchicine is an alkaloid from wild meadow saffron and was the most used as an antimitotic reagent. Oryzalin is a potent herbicide from the Dow AgroScience, USA toluidine chemical band [17,58]. Wetting roots or auxiliary buds or shoots with a colchicine solution of a specific concentration and duration resulted in the successful development of polyploids in many crop species [57,59], as shown in Figure 1. Previous studies successfully applied in vitro chromosomes doubling of colchicine and oryzalin for starch, fodder beet, ryegrass, oriental melon, watermelon, and red clover [17,60].

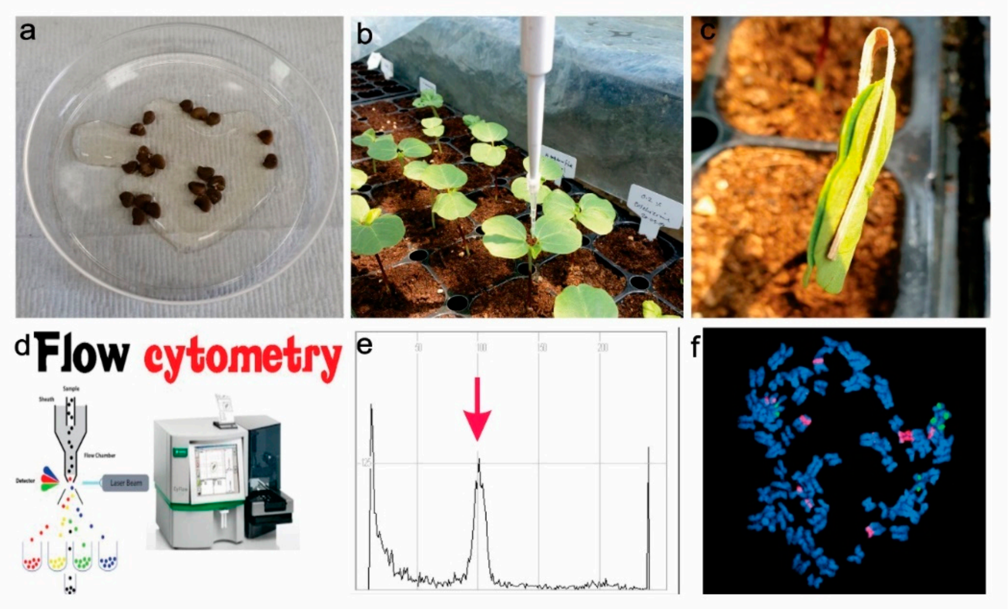

Figure 1. Mechanism of in vivo polyploidization; (**a**). Seeds soaking (6–24) hours with colchicine (0.01–0.2)%, (**b**). Colchicine treatment (10–20 µL) 10 days in the young leaves, (**c**). Leaves binding with clips for maximum chemical attachment, (**d**). Flow cytometry analysis for ploidy level assessment, (**e**). Ploidy level assessment by a histogram, (**f**). Hibiscus ploidy assessment using chromosome number; and 5S rDNA (green) and 18 rDNA (red) signals.

In vitro polyploidization showed better performance than the success rate of in vivo polyploidization in sugar and fodder beet, ryegrass, and red clover [55,59]. Table 1 provides a list of crops, vegetables, and ornamental and medicinal plants treated with chromosome antimitotic agents for chromosome duplication using different methods and protocols.

Table 1. Commonly used methods for polyploidization in vitro.

Plants	Treatment	Most Successful Method	References
Vegetables			
Allium	Callus	Colchicine 2.5 mM, 1/2 days	[60]
Citrullus lanatus	Germinating seedlings	2,6-Dinitroaniline 65.5 µM, 24 h	[61]
Manihot esculenta	Axillary node cuttings	Colchicine 5 mM, 48 h	[62]
Smallanthus songifolius	Nodal segments	Oryzalin 25 µM, 8–48 h	[63]
Ornamentals			
Buddleja	Nodal sections	Oryzalin 25 µM, 3 days	[64]
Dieffenbachia	Shoot clumps	Colchicine 1.25 mM, 24 h	[65]
Dracaena deremensis	Callus	Oryzalin 144.5 µM, 48 h	[66]
Hypericum	Callus	Oryzalin 30 µM, 3–9 days	[67]
Lagerstroemia indica	Nodal buds	Colchicine 750 µM 24 h	[68]
Rhododendron	Micro-shoots	Oryzalin 150 µM, 24 h	[69]
Rosa	Shoots tips, nodal sections	Oryzalin 5 µM, 1 day	[70]
Rosa rugosa	2 or 10mm nodes	Oryzalin 2.5 µM, 48 h	[71]
Syringa	Nodal sections	Colchicine 0.05–0.25 mM, 1–2 Days	[72]
Alocasia	Shoot tips	Oryzalin 289 µM, 24 h	[73]
Alstroemeria	Plantlets	Colchicine 5–15 mM, 6–24 h	[74]
Cattleya	PLB	Colchicine 1.25 mM, 8 days	[75]
Cyclamen	Tuber segments	Colchicine 0.25 mM, 4 days	[76]
Lilium longiflorum	Scale	Surflan (0.1 mM oryzalin), 3 h	[77]
Tulipa gesneriana	Flower stem dices	Oryzalin 2.88–120 µM, 2–24 h	[78]
Watsonia lepida	Shoots	Oryzalin 120 µM, 24 h	[79]
Zantedeschia	Shoot cultures	Colchicine 1.25 mM, 1–4 days	[80]
Aromatic, medicinal plants			
Astragalus membranaceus	Apical buds	Colchicine 5 mM, 36 h	[81]
Bixa orellana	Cotyledonary nodes from seedlings	Oryzalin 15 µM, 15 days	[82]
Colophospermum mopane	Seeds	Colchicine 2.5 mM, 48 h	[83]
Dioscorea zingiberensis	Apical buds	Colchicine 3.75 mM, 24 h	[53]
Humulus lupulus	Apical buds	Colchicine 1.25 mM, 48 h	[84]
Zingiber officinale	Shoot tips	Colchicine 5mM, 8 days	[85]

Meiotic polyploidization produces 2n gametes due to the incomplete division of chromosomes [86]. Polyploids that originate through the functioning of 2n gametes are called sexual polyploids, and their usefulness for crop improvement has been demonstrated in potato, alfalfa, and red clover. Introgression can be accomplished by recombination due to genetic crossing-over between alien chromosomes as well as the addition of alien chromosomes in the case of sexual polyploidization in allopolyploids, which is exceedingly difficult or unlikely in the case of colchicine or oryzalin induced allopolyploids. This deviation can occur in plants with normal chromosome pairing as well as in those with disturbed chromosome pairing such as homoeologous recombination of meiotic replication that was seen in *Alstroemeria* [87], *Lilium* [88] and *Gasteria lutzii* × *Aloe aristate* [89]. The process leading to the formation of 2n gamete is called meiotic nuclear restitution during micro- or megasporogenesis. Depending on the meiotic stage at which nuclear restitution occurs, different restitution mechanisms have been recognized, such as first division restitution (FDR), second division restitution (SDR) [90], and novel intermediate meiosis restitution [88]. In FDR, the non-sister chromatids are heterozygous from the centromere to the first convergence point, while preserving heterozygosity in both parents [91]. In SDR, the two sister chromatids are homozygous between the centromere and the first crossover point, and the resulting gametes have lowered heterozygosity levels compared to the parents [92]. In some cases, 2n gametes restitution cannot be classified as FDR or SDR; the word "indeterminate meiotic restitution" (IMR) has been coined to describe it [88]. Furthermore, IMR might be a widespread occurrence in allotriploids, where both bivalents and univalents are most produced.

4. Cytogenetic Evaluation of Induced Polyploids

Traditionally, polyploids have been assessed by morphological examination. Advanced cytogenetic methods such as flow cytometry, genomic in situ hybridization (GISH), and fluorescence in situ hybridization (FISH) are currently used for polyploid evaluation [11,20,22,93].

4.1. Flow Cytometry

Counting chromosomes in an individual cell is the most efficient and accurate way to confirm ploidy. However, the basic number of chromosomes must be identified before counting. Furthermore, chromosomes are confusing regarding mixoploidy because of the smaller size with a higher number of chromosomes, e.g., taxa *Hibiscus* [94] and taxa *Chrysanthemum*.

Flow cytometry may also be the unique method incorporating strong analytical utility to calculate the cell nucleus's physical size and genome [95,96]. Flow cytometry is a comparatively simple and easy method of calculating a polyploid's nuclear DNA material. By measuring the relative DNA content using flow cytometry [97,98], the ploidy level of mediated polyploids can be easily verified (Figure 2). However, flow cytometry has some limitations as it is not precise enough to estimate the exact chromosomes number and is unable to differentiate the variation in chromosomes number compared to the ploidy level.

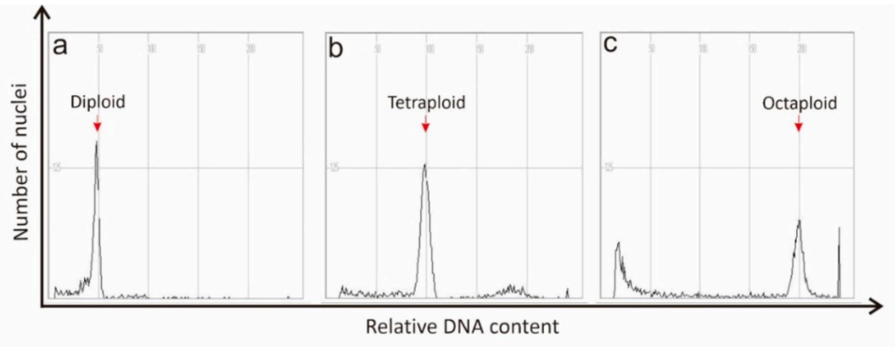

Figure 2. Histograms show the flow cytometry analysis of comparative changes in ploidy levels in watermelon. (**a**) Diploid ($2n = 2x = 24$), (**b**) tetraploid ($2n = 4x = 48$), and (**c**) octaploid ($2n = 8x = 96$). Red arrows indicate ploidy levels of diploid, tetraploid and octaploid.

4.2. In Situ Hybridization

Molecular cytogenetic research approaches such as FISH and GISH are commonly used and well-respected tools to investigate plant genetics. FISH and GISH have often been used to identify information surrounding chromosomal mutations, structure, and genomic evolution [99,100]. Oligos specific to a repetitive sequence or a particular genomic region can be visualized using fluorescence in situ hybridization [8,101–103]. For example, different ribosomal DNA (rDNA) signals are doubled in a tetraploid compared to those in a diploid. A study of 5S rDNA in cotton plants revealed that most diploids have two 5S rDNA signals and all allotetraploid species have four 5S rDNA signals [104]. The same result was found in a woody species of the genus *Rubus* [105]. The 45S, 18S, 25S, and

5S rDNA are commonly used as FISH markers for cytogenetic study. This method has been used intensely in gene duplication methods and amplification in intraspecific and interspecific polyploids. A brief working directory of FISH and GISH is shown in Figure 3.

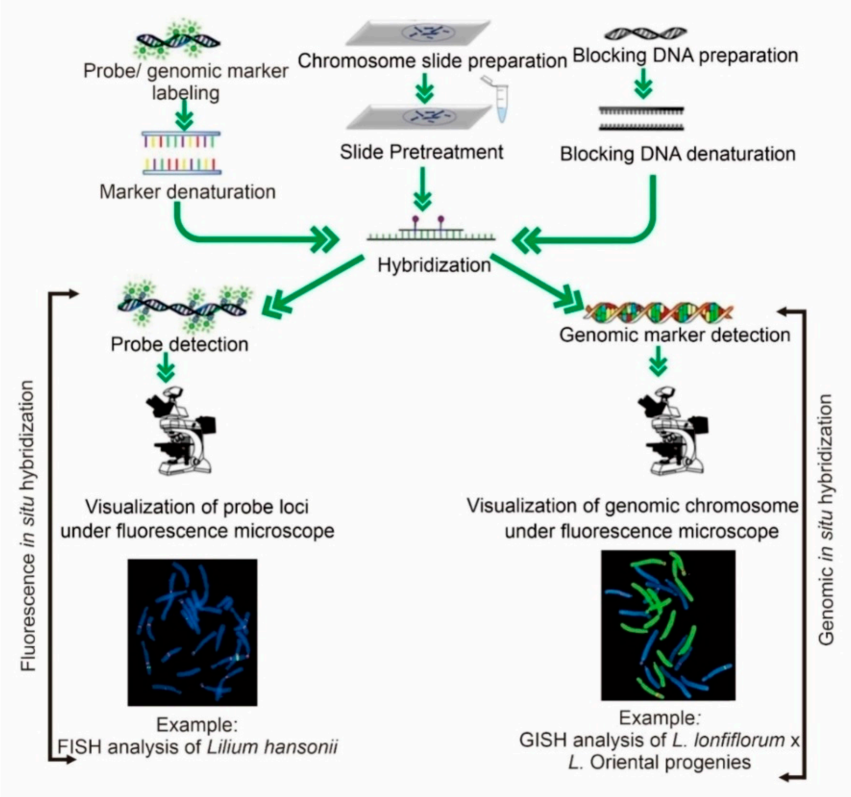

Figure 3. Working steps for fluorescent and genomic in situ hybridization were used for the cytogenetic study of horticultural modified crops. Different methods, such as nick translation, random primed labeling, and PCR, are used to label the probe during marker labeling. Various methods, such as autoclaving, shearing the DNA with a tiny needle in a syringe, or sonicating, are used to prepare to block DNA. Chromosome slide preparation is the selection of well-spread chromosomes prepared from a young root tip using an enzyme mixture at 37 °C. Slide pretreatment is the enzymatic digestion of the chromosomes in order to unmask the DNA prior to hybridization. Hybridization involves the attachment of blocking and probe/genomic markers with chromosomes to identify the specific loci/origin of the genome of the respective chromosome. During detection, attachment of the designed antibody against the target marker along with blocking buffer to detect the specific fluorochrome.

GISH is also useful for studying cytogenetics and determining hybridity status, particularly in the case of interspecific plant hybridization [22,106–109]. Within an interspecific polyploid, GISH distinguishes the genomic structure, chromosomal constituents, crossing over, aneuploidy, and alien genes introgression. For example, in diploid interspecific Lilium (*L. longiflorum* × Asiatic lily; $2n = 2x = 24$), 12 *L. longiflorum* and 12 Asiatic chromosomes can be identified using GISH (Figure 4). The number of *L. longiflorum* and Asiatic chromosomes are doubled in the induced tetraploids and can be visualized through GISH. Therefore, GISH is an advanced multicolor detection technique that plays a gratuitous role in the chromosomal and genomic investigation of induced polyploids.

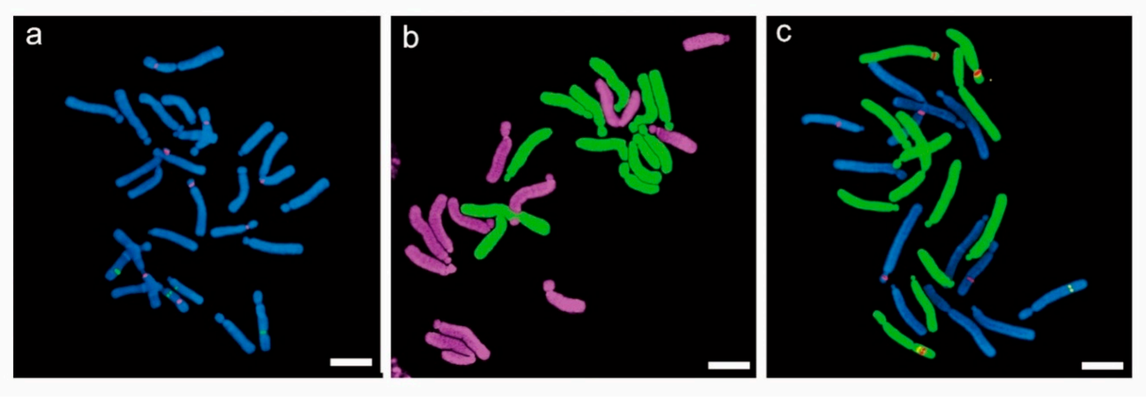

Figure 4. In situ hybridization of diploid ($2n = 2x = 24$) Lilium. (**a**). FISH analysis of intraspecific F1 using 5S and 45S ribosomal DNA; (**b**). GISH analysis of interspecific (*L. longiflorum* × *L. hansonii*) F1 using genomic DNA; and (**c**). FISH and GISH combined analysis of interspecific (*L. longiflorum* × *L.* Oriental hybrid) F_1 using 5S, 45S rDNA, and genomic DNA.

5. Effect of Polyploidization at the Morphological and Molecular Level

Polyploidization results in morphological changes in plants due to whole genome duplication, changes in chromosomal structure, nuclear enlargement along with gene dosage and epigenetic consequences, as well as an increased number of larger cells [18,110–114]. Further, due to the changes in different levels, several morphological traits such as plant height, root length and number, leaf number, area and size, pollen size and number, stomata number and size, and flowers and fruits number and size as summarized in Table 2.

Table 2. Effect of polyploidization on plant morphology and yield attributes.

Induced Polyploid	Effect (Increased/Decreased)	References
Plant height	Increase	[52,54,115]
Root length and number	Increase	[86,116]
Number of leaves/plants	Increase/decrease	[117]
Leaf area	Increase/decrease	[17,118]
Leaf size	Increase	[17,112]
Stomata number/leaf	Decrease	[17,119,120]
Stomata size	Increase	[17,115,119]
Flower size, number	Increase	[52,112,117–125]
Pollen size	Increase	[123]
Fruit size, number	Increase	[98,116,124]
Seed size	Increase	[98,116]
Seeds/fruit	Decrease	[17,39]

With the increase of ploidy level, the plant height, width and length of flower, flower size, and the number of internodes in dendrobium increased [17,126–128]. Polyploidization affects the floral traits such as flowering time, flower diameter, shape, size, and color, as well as different parts of flowers in kiwifruit and salvia [9,129–137]. These shreds of evidence suggest that polyploidy can be applied in plant breeding by targeting the flower size, shape, color, modifications in size, and the number of floral parts. Fruit size and fruits number, along with other fruit characteristics such as fruit weight, fruit peel, flesh weight and seed number are affected by the increase of ploidy number [130,138–144]. Due to variations in cell size and chromosome size (Figure 5), polyploidy changes the characters of the leaf [145–153]. Stomata number, density, size, and area are the important traits of leaves that are affected by the change of ploidy number [154,155], and this effect (Figure 5) has been observed in citrus [120].

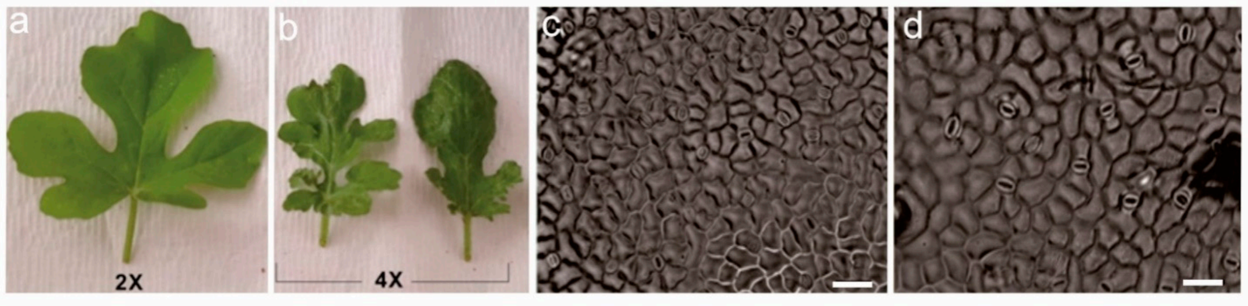

Figure 5. Leaf morphology and stomata size of watermelon induced by oryzalin. (**a**). diploid leaf, (**b**). tetraploid leaf, (**c**). stomata of diploid, and (**d**). stomata of a tetraploid leaf, respectively. Scale bar= 10 µm [17].

Changes in fruits, leaves, flowers, and color can be considered from the application point of view. Targeted traits can be achieved along with higher variation with the changes of ploidy level. A change in ploidy level also affects molecular and gene expression. Changing the ploidy level due to changes in nuclear DNA, chromosome number, and structure can manipulate genetic diversity, genome replication, gene expression, and heterosis [156]. Changes in ploidy level affect DNA content and the number of chromosomes [157–159]. During replication, polyploidization often induces epigenetic changes such as transposon simulation and chromatin modification, as well as the extension or loss of chromosomal fragments. The polyploidization effect at the plant morphology, physiology, and molecular levels needs extensive research to reveal the mechanisms that will help plant breeders for directed modification and crop improvement.

6. Effect of Polyploidization on Abiotic Stresses

6.1. Salinity Induced Stress Alleviation

H_2O_2 and malondialdehyde (MDA) concentrations increase in salinized tissues due to the generation of reactive oxygen species (ROS) [160,161]. Proline plays a pivotal role in alleviating salt-induced stress by maintaining cell turgor (i.e., as osmolyte) [162]. Polyploids reduce the H_2O_2 and MDA concentrations, increase proline concentration, and tolerate salinity stress. Higher proline concentration and lower H_2O_2 and MDA concentration (Table 3) in polyploid plants are reported in the studies [163,164]. Due to MDA's lower concentration in tetraploids-maintained cell membrane integrity, and Na+ hardly reached the cells. Conversely, higher H^+ transport through cells in tetraploid rice cultivars may be attributed to salt tolerance. Interestingly, Tu and coworkers [163] noticed that a defensive space between the pericycle and cortex contributes to more salt tolerance. Further, Jinag et al. [164] reported that the mortality rate of tetraploids in saline stress was 12.3–12.6% lower than that of diploid ones (Table 3). Meng et al. [165] reported that tetraploids show a stable K^+/Na^+ ratio (16:10 and 15:10, respectively, in roots and shoots), while K^+ decreased in diploid turnips (46:100, and 48:100, respectively, in roots and shoots). Diploid turnips also experienced a significant reduction in chlorophyll content (40.3% versus 11.9% in tetraploids). Furthermore, seed germination, root, and shoot growth were enhanced in polyploid during salt-induced stress (Table 3) [163,165–167]. Although salinity has a more extreme effect on diploids than on their corresponding tetraploids, the underlying mechanism in tetraploid plants is unclear. Besides, no study was conducted on actual saline containing different salt solution mixtures in different concentrations. Thus, tetraploid behavior in natural conditions is difficult to predict. Table 3 shows the salinity-inducing methods, test crop, polyploidy adaptation, and effect on test crop.

Table 3. Effect of polyploidy on abiotic stress management.

Stress	Inducing Method/Organism	Crop	Adaptation	Mechanism	References
Salinity	NaCl induced salinity in laboratory	Orange	Better adaptation	1. NPK, proline content was higher in tetraploid than diploid. 2. MDA and H_2O_2 content was lower in tetraploid than in diploid.	[167]
		Turnip	Better adaptation	1. 100% increase in seed germination in tetraploid in highest saline level 200 (m.mol L^{-1}). 2. Shoot and roots length reduced in diploid under salt stress condition compared to tetraploid. 3. At highest level of salinity, 74.7% diploid, and 64.4% tetraploid seedlings were injured. 4. Chlorophyll content reduced by 11.9% and 40.3% in tetraploid and diploid, respectively. 5. K^+ concentration was stable in tetraploid (16:10, 15:10 K^+/Na^+ but reduced in diploid (46:100, 48:100) in root and shoot, respectively.	[165]
		Rice	Better adaptation	1. Proline concentration was higher in tetraploid (23.3% higher than diploid). 2. MDA content was lower in tetraploid than in diploid.	[163]
		Lemon Seedling	Better adaptation	1. Malondialdehyde and hydrogen peroxide was greater in the leaves and roots of diploid seedlings. 2. Antioxidative enzymes (peroxidase, ascorbate peroxidase, glutathione reductase, and catalase) were higher in tetraploid.	[167]
		Rice	Better adaptation	1. Mortality rates of tetraploids were lower than diploid. 2. Proline content was increased in tetraploid.	[164]
	Hoagland solution in green house pot	Citrus	Better adaptation	Lower accumulations of chloride ions in leaves of the tetraploid plants as compared to diploid.	[166]

Table 3. *Cont.*

Stress	Inducing Method/Organism	Crop	Adaptation	Mechanism	References
Drought	Laboratory condition induced by polyethylene glycol	Apple	Better adaptation	1. Relative water content (RWC) was higher in tetraploid than diploid (after 3 h of treatment 81.76% and 63.84%, respectively, and after 6h of treatment 69.89% and 48.16%, respectively, in tetraploid and diploid cultivar). 2. Lower level of MDA content in tetraploid indicated membrane integrity under drought stress. 3. Less expression of aquaporin genes in drought stress was shown in tetraploid.	[168]
	Controlled environment, drought condition by limited water	A *solanaceous* plant	Better adaptation	1. Tetraploid plants grew normally, and leaves remained turgid where diploid plants died in drought stress. 2. Higher chlorophyll content and lower H_2O_2 synthesis were shown in tetraploid than diploid (less oxidative damage).	[169]
	Limited Water supply	*Arabidopsis*	Better adaptation	1. Tetraploid stomatal pore is 20% bigger than diploid due to the bigger size of the guard cells. 2. Higher survival rates in tetraploid. 3. ABA induced stomatal closure happened in tetraploid leaves. 4. ROS increased in cellular levels and affect stomatal aperture. 5. Polyploidy induced gene, which helps in stress adaptation.	[170]
	Limited Water supply	Rice	Better adaptation	1. MDA content was lower in tetraploid rice. 2. Phosphoenolpyruvate carboxylase (PEPC) alleviates photosynthesis inhibition. 3. Tetraploid showed more PEPC activities in drought stress. 4. Higher superoxide dismutase (SOD), POD (peroxidase), CAT (Catalase) was shown, ROS scavenging was more, and cell membrane damage was less in tetraploid rice.	[171]

Table 3. *Cont.*

Stress	Inducing Method/Organism	Crop	Adaptation	Mechanism	References
Drought	Both controlled and field trial	Westerwolths rye grass	Better adaptation	1. 30–40% more phenolic content and higher antiradical activities, better stress adaptation found in tetraploid. 2. More biomass in tetraploid.	[172]
	Laboratory	Honeysuckle plant	Better adaptation	1. No photosynthesis in diploid, 80% reduction in tetraploid. 2. Higher MDA in diploid.	[173]
Temperature	Heat Stress (42 °C)	*Dioscorea zingiberensis*	Better adaptation	1. Relative electrolyte leakage (%) and MDA content was lower in tetraploid than diploid in heat stress condition. 2. ROS production rate was higher in diploid and antioxidant enzymes such SOD, CAT, and APX were higher in tetraploid. 3. Glutathione-ascorbate and AsA declined slowly in tetraploid were drastically in diploid.	[123]
	Drought and Heat Stress (52 °C), field condition	Keystone grass	Better adaptation	1. 20% heavier seeds in tetraploid under stress condition. 2. Genome duplication and reproductive flexibility jointly contributes to stress alleviation. 3. Homeostatic maintenance of reproductive output under increasing abiotic stress. 4. Fixed differences in seed size and morphology that increase propagule fitness and mobility.	[174]
	Laboratory condition	*Dendranthema nankingense*	Lower heat stress adaptability	1. Higher cold stress adaptability in tetraploid but lower heat stress adaptability. 2. Tetraploid did not show much morphological change with diploid.	[175]
	Laboratory condition (39 °C day/30 °C night	*Dioscorea zingiberensis*	Better adaptation	1. Activation transcriptomic response in tetraploid (19 bands silenced and 47 bands activated) where in diploid 32 silenced and 28 activated. 2. Activation transcriptomic responses may confer tolerance in heat stress in tetraploid.	[176]
	96 h long stress at 45 °C.	*Asparagus officinalis*	Better adaptation	1. During heat stress MDA decreased by 42% in tetraploid, SOD increased by 81%, POD increased by 119%, and PRO content increased by 63% compared to diploid.	[177]

6.2. Drought Stress Alleviation

Previous ploidy-level research has suggested that enhancing ploidy can successfully alleviate or help plants better adapt to drought stress, as depicted in Table 3. Due to osmotic stress effects, cell plants usually incur damage by producing MDA and other superoxide's that cause cell membrane disintegration. Tetraploid plants showed lower MDA concentrations for drought tolerance than diploid plants [168,171,173]. Although diploids and tetraploids experience increased ROS production due to drought stress, ROS scavenging and ROS homeostasis increased in tetraploids [171,172]. Moreover, Yang et al. [131] found more superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) in tetraploid ones during drought stress. Similarly, 30–40% more phenolic content and higher antiradical activity are found in tetraploid cultivars than in diploid cultivars, indicating ROS homeostasis and better tetraploid stress adaptation [172].

To mitigate drought stress, plants undergo stomatal leaf closure to reduce transpiration. Enhanced ABA in plants, especially in leaves, reduces leaf turgor, resulting in decreased stomatal pore aperture, which reduces the incidence of leaf water loss. Eventually, plants can conserve water within themselves. Polyploid plants show more ABA synthesis than diploids when under drought. Detailed work has been carried out by Rao et al. [169], establishing that polyploid plants show more drought stress synthesis than diploids. In addition, some ABA expresser enzymes such as 9-cis-epoxycarotenoid dioxygenase 1 (NCED1), NCED2, and gene expression ABRE binding factor 5-like (ABF5-like) were observed; such phenomena in tetraploids are responsible for increasing ABA synthesis and signaling pathways for stress adaptation. On the other hand, aquaporin genes such as MdPIP1;1 and MdTIP1;1, which are responsible for cell-to-cell water transportation, are expressed less in polyploid plants ([168] Table 3). Overall, morphological growth and chlorophyll content in tetraploids were higher than in diploids during drought stress [168–172] (Table 3). Nevertheless, consideration should be given to the relative fitness of different ploidy levels at different drought levels. In addition, to evaluate the efficacy of polyploidy in drought tolerance, other environmental factors associated with drought stress are also important.

6.3. Temperature Stress Alleviation

Extreme temperature escape by polyploidy has certain trade-offs. Chen et al. [177] experimented on the effects of heat stress on diploid and tetraploid *Asparagus officinalis* by putting both cultivars under extended stress. They placed both cultivars at 45 °C for 96 h and observed better adaptation of tetraploid plants than diploids (Table 3). The tetraploid cultivar also had higher photosynthetic pigments and lower stomatal densities than the diploid. Zhang et al. [53] worked on diploid and tetraploid *Dioscorea zingiberensis* and found similar results from tetraploids under temperature stress. Usually, in temperature stress, due to ROS production, plants experience decreases in the level of ascorbate (AsA) and glutathione (GSH). Polyploid *Dioscorea zingiberensis* showed a gradual instead of a drastic reduction in diploids in these antioxidant compounds [53]. This result is strong evidence of tetraploid heat-stress alleviation. However, Godfree et al. [174] proposed that polyploidy is not solely responsible for stress adaptation. They suggested that both polyploidy and reproductive homeostasis contribute to heat stress alleviation. They found distinct morphological differences, consistently heavier seeds, and decreased seed sizes in tetraploids than diploid, which they considered stressful reproductive production homeostatic maintenance. To understand how polyploidy affects transcriptomic responses to temperature stress, Yin et al. [178] experimented with a diploid and a tetraploid *Dioscorea zingiberensis*. They found "Activation Transcriptomic Reaction" in tetraploids, in which 19 bands were silenced and 47 bands were activated in diploids, 32 bands were silenced, and 28 bands were activated under temperature stress. They reported that enhanced transcriptomic responses to activation could confer tolerance in tetraploids during heat stress. Alternatively, Liu et al. [175] observed varied heat and cold stress responses from tetraploids. They calculated the LT_{50} (lethal time to 50% plant mortality under stress) and found that tetraploid LT_{50} was 2.40 times lower than that of diploids in cold conditions. Although in heat stress, diploid LT_{50} was 1.20 times higher than tetraploid, which suggests lower tetraploid heat stress tolerance. Such varied results and findings from various research indicate the need for further research on temperature stress. Information regarding polyploidy-induced abiotic stress alleviation is presented in Table 3.

7. Effect of Polyploidization on Plant Biotic Stresses

7.1. Polyploid-Insect Interaction

While plant polyploidy on insect abundance and dispersal is uncertain, two major events are observed in insect physiology, such as i. polyploidy caused novel insect defense (herbivores), and ii. co-opt counter-insect defense and extended host selection [178–180]. One example of a polyploidy-induced defense mechanism can be seen in Brassicales, in which genome duplication contributes to the development of glucosinolate compounds to establish protection against butterflies [180]. However, Edger et al. [180] also stated that, in some cases, herbivores are drawn to polyploids through coevolutionary mechanisms. Polyploidy shows different effects on herbivory, often divided into attraction and escape. Concerning attraction, Arvanitis et al.'s [178] findings provide adequate evidence. In a common garden where the corresponding tetraploid and octoploid Cardamine pratensis were grown, bud gall midge *Dasineura cardamine* preferred octoploid over tetraploid where tetraploid cardamines rarely struck. Does higher polyploidy attract insects? Herbivores are typically fond of polyploids. Their argument is backed by Thompson et al. [181], who recorded higher infestations of prodoxy moth *Greya politella* in *Heuchera grossulariifolia* tetraploids compared to its diploid ones. Similarly, in tetraploid *Arnica cordifolia* [182], tephritid fly *Campiglossa footeorum* displayed higher attack rates than triploid cultivars.

On the other hand, Nuismer and Thompson [183] recorded frequent attacks by a stem borer moth *Greya piperella* in *Heuchera grossulariifolia* diploids rather than in tetraploids. Likewise, diploid *Gymnadenia conopsea* orchids [184] were more frequently attacked by aphids than their corresponding tetraploids. These contrasting findings indicate that polyploidy does not inhibit the behavior of herbivores. However, it has been suggested that insect herbivory is not a cytotype-dependent habitat selection but plays a key role in host-seeking. In open fields and natural ecosystems, insects typically prefer the most common host in that habitat. Alternatively, in a typical garden (Figure 6) where all cytotypes are grown, insects forage the hosts equally [185]. Although the results show that polyploidy has various implications concerning insect attacks, it can provide some trade-offs. Generally, polyploids produce higher growth and reproductive ability. Therefore, polyploids can help avoid economic injury and an herbivory-induced economic threshold, which can be difficult in diploids.

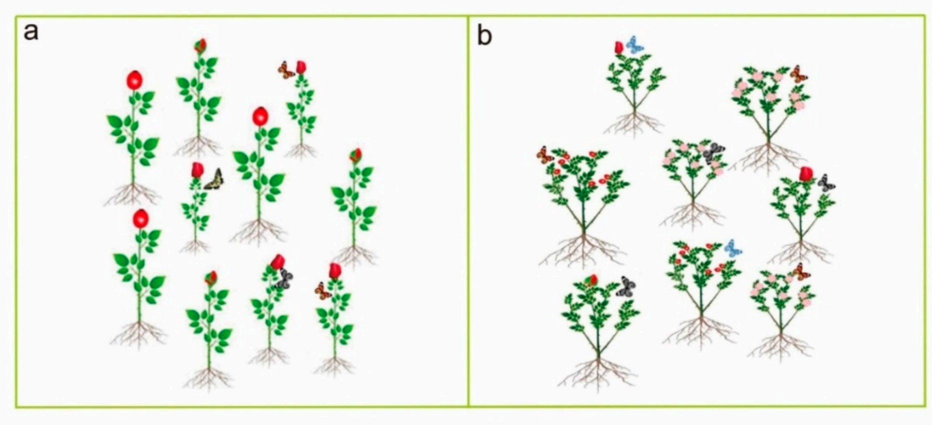

Figure 6. Can insects identify different ploidy level plants? According to Segraves and Anneberg [185], insects forage more on predominant cytotypes in a natural habitat where different ploidy plants coexist ((**a**); where we imagine that small plants are predominant here, insect will forage more on small plants

rather than flowers of bigger plants, i.e., irrespective of ploidy level). Contrarily, insects forage equally in a common garden where mixed cytotypes are grown ((**b**); imagine there are different ploidy levels flower in the common garden. Insects generally fail to detect different ploidy levels; thus, they forage equally in a common garden).

7.2. Polyploidy and Pathogen Resistance

Pathogens, including fungi, bacteria, and viruses, are the most daunting factor for crop cultivation worldwide. The grower must account for high economic losses incurred by yield loss and the application of pesticides to combat diseases [186]. Developing pathogen-resistant crop varieties through selective breeding is crucial to address this problem. The induction of polyploidy may be a promising solution [149]. Naturally occurring varieties of different crop species, including banana, strawberry, and watermelon, have been reported to resist a broad range of pathogens [186,187]. Allotriploid cultivars of banana (AAB) and polyploid watermelon germplasm are fusarium-resistant [187]. Many cultivars of octoploid *Fragaria* × *ananassa* Duchesne are resistant to anthracnose, fusarium wilt, crown rot, red core, verticillium wilt, and angular leaf spot [186]. Polyploid strawberries (US4808 and US4809) reported resistance to four *Xanthomonas fragariae* groups [186].

Several studies have reported that pathogen resistance in the polyploid genotype is higher than its diploid generation [187,188]). Autotetraploid and autotriploid watermelon demonstrated higher fusarium resistance than diploid watermelon [187]. Diploid apple cultivars are more susceptible to *Alternaria alternata*, and *Colletotrichum gloeosporioides* than autotetraploid apple cultivars Hanfu and Gala [188]. Allopolyploid tobacco prevents plant viruses better than diploid tobacco [189]. Tetraploid wheat avoids more powdery mildew and leaf rust than diploid wheat [190,191]. Allelic diversity, gene expression (over), and physiological state are the key factors determining a host plant's ability to withstand various pathogens.

Polyploidy may influence plant species' allelic diversity, gene expression (over), and physiological condition (Figure 7). The extra alleles at a given locus in polyploids increase allelic diversity due to the high probability of heterozygosity and enhance resistance. Multiple polyploid chromosome sets increase gene expression [192,193]. In contrast, it has been proposed that gene expression is downregulated (in certain loci or in the whole genome and sometimes even silenced) with increased ploidy level [10]. Polyploid plants can adapt to a wide range of environmental conditions by developing stress tolerance [194]. Invasive plant species are more tolerant of diseases than individuals suffering from environmental stressors [195]. Therefore, the polyploid with higher allelic diversity at resistance genes, higher expression levels of immune genes should select for cultivar development. The positive relationship between the disease resistance of the plant and environmental stressors also needs to be considered.

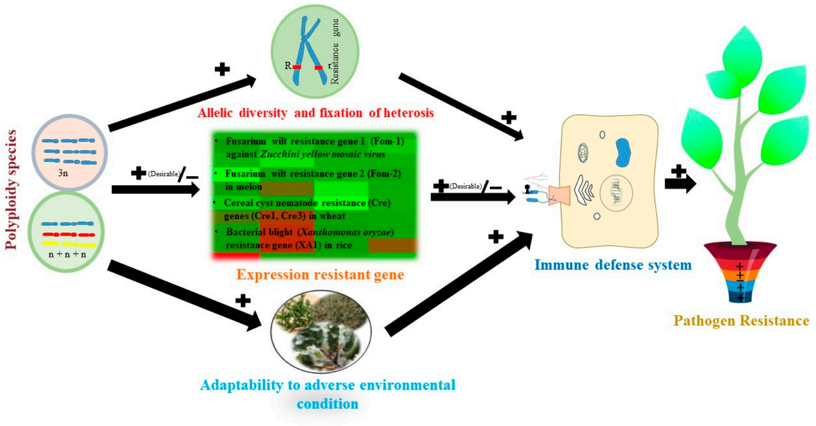

Figure 7. Effect of polyploidy on pathogen resistance. The sign next to the arrow gives the direction of the effect. The sign "+" means the higher ploidy level increases the probability of effects, while "−" means the higher ploidy level decreases the probability of effects. Pot represents the combined effect

of the polyploidy plant. The gene-for-gene model is the general mechanism of pathogen resistance. In the polyploidy host, high allelic diversity with dominant allele, fixed heterosis, and high expression (desirable) of resistance gene directly influence the pathogen resistance. The validated disease resistance genes and their target pathogens are given as examples [54]. The effects of ploidy-level variation on host adaptability under diverse environmental conditions (biotic and abiotic stress) could indirectly influence parasite resistance.

8. Challenges of Polyploidization

8.1. Changes in Cellular Architecture

Due to an increase in an organism's genomic content, cell volume usually increases. It has the consequent change in the relationship between the cell's tridimensional and bidimensional components [196,197]. Doubling the genome is expected to double the amount of chromatin, but only causes a 1.6-fold increase in the nuclear envelope surface. Cell size expansion can contribute to anatomical imbalances and deleterious effects, such as gene redundancy shields polyploids from the mutations' prejudicial effect, infertility, brittle wood, and watery fruits [198]. Moreover, polyploidization can cause albinism [199].

8.2. Mitotic and Meiotic Abnormalities

Normal mitosis and meiosis are frequently disrupted in polyploids. Due to additional sets of chromosomes present in an induced polyploid, faces various challenges during mitotic chromosome segregation. As we observed that the homozygosity or heterozygosity level significantly differs in polyploids. It depends on the formation pathway like autopolyploid or allopolyploid that affect the performance of the polyploids in fertility, growth and even yield [200,201]. Autotetraploid yeast demonstrates increased mitotic loss of chromosomes, producing aneuploidy cells [202]. Spindle abnormalities usually cause difficulties in mitosis. Chaotic mitotic chromosomal segregation also occurs in wild yeast [203]. However, there is little knowledge regarding the mitotic stability of polyploid plant cells. Meiosis requires three or more chromosome sets in which the frequency and manner of development of aneuploidy depend on the type of polyploidy. Triploidy and aneuploidy, which may arise from meiotically unpaired DNA, are more unstable states than tetraploidy. These frequently lead to or result from the more stable polyploidy states. Both conditions may have potentially detrimental effects on genome regulation [52]. Several experiments resulted in 30–40% aneuploidy of autotetraploid maize [204,205]. Another problem occurs in triploids and pentaploids; trivalent cannot be solved into balanced products in triploids, and a spontaneous division of multiple forms of chromosomes produces mainly aneuploid gametes. In addition, normal chromosomal segregation is another challenge in auto and allopolyploid where the multivalent complex structure is often associated. Our study found that the multivalent has an important role in abnormal chromosomal segregation reducing fertility [200,206].

8.3. Epigenetic Instability

Aneuploidy can cause epigenetic and genomic instability [207,208]. In autopolyploids, instability can directly or indirectly contribute to genome duplication. The proof was demonstrated when diploid and tetraploid Arabidopsis thaliana compared epigenetic effects at a transgenic locus [158,209,210]. Epigenetic changes in the gene have also been found in allopolyploids. Theoretically, *A. thaliana* has also demonstrated regulatory improvements in autopolyploid strains in parents. Such changes involved silencing or activating genes, including activating a Spa-CACTA family DNA transposon [201,210]. Therefore, mismatches in gene expression and gene product regulatory controls can decrease fitness.

9. Conclusions and Future Perspective

In plant breeding, polyploidization is a successful technique for developing novel traits. Polyploidy causes significant transcriptomic and regulatory changes that bring physiological and morphological changes. Disrupted regulatory factor stoichiometries, small RNAs, and other genome interactions could potentially set these in motion, cascading through entire networks of transformed regulatory modules from single-gene expression modification. Plants with duplicate whole chromosome sets have more distinctive features, such as a different phytochemical profile, higher content of desired pharmaceutical molecules, plant shape, flower color, size and style, fragrance, vase life, and extended flowering time. However, they do not always act in the same way. Furthermore, polyploid clones of *Eucalyptus grandis*, *E. urophylla* recently produced a fiber with higher length and thickness, resulting in improved paper formation and strength, suggesting that polyploids could be used in pulp and paper production. Stable C35 citrange tetraploids are becoming popular in high-density orchards.

The latest polyploidization trend involves polyploid characterization in their protocol regarding polyploid ultrastructure, bioactive compounds, photosynthetic capabilities, and metabolomics studies. Despite progress, we still lack a thorough understanding of polyploidization. Conflicting results have been reported for different polyploid species, and a single hypothesis cannot be proposed to explain plant polyploid evolution. Nevertheless, advances in sequencing technology, improved experimental analysis, multi-omics data quality, and more efficient analytical methods are likely to enhance our understanding of polyploidization in the near future significantly. In abiotic and biotic stress management cases, revealing the underlying mechanism is the most important research prospect of polyploidy. Polyploidy-based breeding combines the advantages of heterosis and apomixes, which can be a viable option for crop improvement in the future. A molecular approach to understanding the effects of polyploid plants on insects is necessary concerning polyploid-insect interaction.

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