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REVIEW ARTICLE

Utilizing method of plant growth regulators induction in processing of polyploidization—A perspective crop development

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ABSTRACT

Nowadays, it seems like human beings are worried about how the world will meet its food security demand urgently when they have faced on rapidly increasing population and combat climate change. Scientists and researchers are indispensably investigating to enhance food sources such developing novel cops with high yield and good quality and even coping with the adverse environment in terms of biotic and abiotic stresses. Thus, there is one valuable method it is believed that should be developed further. In fact, it is believed that human beings should continue using it as soon as possible because it can provide the world with a source of food. Polyploidization introduced by plant growth regulator induction is a good method because it is safety and easy to develop new crops with potential agronomic traits, these polyploidy plants are rare aneuploid and it contains intriguing characteristics of polyploidy plants in adapting to ecological variability. This review sheds light on 1) summarizing molecular mechanism of plant growth regulator induction for plant ploidy manipulation; 2) achieving of polyploidization through plant growth regulator induction; 3) enumerating the perspectives of polyploidization in crop development to cope with climate change. Although the role of phytohormones is underestimated, the effectiveness on physiological level of plants to make polyploidy plants is worth considering and the effects and bio-safety of that on human are also concerned.

Keywords: polyploidization; plant growth regulator; cell cycle; food security; climate change

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1. Introduction

To start with, cell proliferation, cell elongation, and cell differentiation are three major combining processes of cellular level to support growth and development in plants that are apparently proved. Regarding mitosis, cell division, that initiates when chromosomal sets duplicate and then separate. This is a process that a cell's genetic materials go through transcribing and translating pathways to form the final cell shape via cell elongating and differentiating processes. It is commonly known that the eukaryotic cell cycle goes through four consecutive phases starting with mitosis (M phase), finishing with genetic material synthesis (S phase), and gap phases G1 and G2 separating the two phases mentioned above. To complete the cell cycle, the complex transitions have to overcome two important check-points consisting of from G1 to S and G2 to M phase which is actually required mitogenic signals. The M phase mistaking in the cell cycle results in endoreduplication and ploidy formation in some rare cases[1].

There were several main artificial processes to develop tetraploid plants from diploid counterpart. Each process consists of pros and cons. Here were some of them. Using 2n gametes by hybridizing different ploidy 4x-2x or 2x-2x can make tetraploid plants[2–4]. A typical

example was that 2n gametes had the prospect to become an remarkable method for potato germplasm application, yet elite potatoes do not always to be successful[2–5]. The next method could be applied to make polyploidy plant was the fusion of 2 protoplasts, but it is a complex technique[6,7]. Another method was using anti-spindle formation chemicals such as colchicine, oryzalin, trifluralin etc.[8,9]. However, using antimitotic chemicals might make a high ratio of chimera plants which reached 50%–100% by treating oryzalin[8,10]. In contrast, the method of phytohormone induction that can make euploidy plants with chromosomes doubling by phytohormone-based induction to be substantially successful[11,12] will be deeply discussed here. Although studies showed that residues of phytohormones when using in production or in the field can affect environmental pollution, the development of animal, human health problems, and food poisoning if using them was not corrected the producer's instruction[13,14]. Thus, the high residue of phytohormones in food can lead to toxicity to organs such as liver, kidney, neurosystem, fluctuate antioxidant defense system or even induce cancers[15–17]. Therefore, maximum residues limits of phytohormones have been controlled by international and national laws not only to monitor and regulate phytohormone residues in food but also to ensure the food safety. However, when comparing with using anti-mitotic chemicals (colchicine, oryzalin, trifluralin etc.) in polyploidization, phytohormones are safer to human beings and environments, especially polyploidisation only using in laboratory scale where biosafe was strictly protected.

This review provides insights into polyploidization by plant growth regulator induction and then think that the advantages of polyploid plant are more valuable as well as discussing the application for ploidy manipulation for plant breeding and crop improvement strategies. This review will first introduce the molecular mechanisms of polyploidy plant development by plant growth regulator induction is a valuable method because of the fact that it is easy to develop new crops with potential agronomic traits, but rare aneuploid and then discuss that polyploidy plants contain intriguing characteristics of polyploidy plants in adapting to ecological variability and climate change.

2. Molecular mechanisms of plant growth regulator induction for ploidy manipulation

2.1. Signaling auxin in cell cycle

It is proved that auxin, a class of key plant growth regulator regulating many aspects of plant development, has been illustrating its essential function in overcoming checkpoint of preparing DNA replication or transiting from G1 to S. To be more precise, several *in-vitro* plant propagations reveal the molecular mechanisms provided insights into the auxin function in regulating cell cycle[18]. The intriguing crosstalks showing this process are specifically described. Auxin-based induction occurred on the expression of genes related to the cell cycle involving cycD3:1, and CDKA:1 standing for a cyclin D gene and cyclin-dependent kinase gene, respectively. To be more accurate, the auxin receptor called an F-box protein TRANSPORT INHIBITOR RESPONSE1 (TIR1) binding auxin is pointed in **Figure 1A**. However, in other studies, it was mentioned that there was the second auxin receptor: AUXIN-BINDING PROTEIN 1 (ABP1) existing is also described in **Figure 1B**[19]. When auxin is presented, it combines with TIR1. This complex is a bridge between Aux/IAA and SCF to activate the degradation of Aux/IAA by the proteasome. Meanwhile, ARFs are free from Aux/IAA repressor and ARFs activate the transcription process[20]. These genes were key functions in forming CDKA/CYCD complex assembling (CYCD- D type cyclins). At the same time, two isoforms Kinesin-related Proteins including KRP1 and KRP2 encoded respective two CDK inhibitors reducing expression under auxin exposure and preserving the activated CDKA/CYCD complex. This phosphorylated complex could then phosphorylate a protein called transcriptional repressor retinoblastoma-related (RBR). This led to the release of its target complex consisting of Adenovirus E2 promoter-binding factor A/B (E2FA/B) and dimerization partner A (DPA). Stabilizing the E2FA/B and DPA by auxin through post-transcriptional regulation which

associated the expression's essential genes initiated the S phase. After S phase completion, auxin enhanced the degradation of F-box S phase kinase-associated protein 2A (SKP2A) via E3 ubiquitin ligase complex SCF (standing for Skp, Cullin, F-box) containing complex preserving E2FC and DPB complex. This complex repressed S phase genes to express. Many studies proved that auxin is not only a significant signal for transiting checkpoint G1/S or entering DNA synthesis but also the requirement of G2/M transition in completing the mitotic process[21].

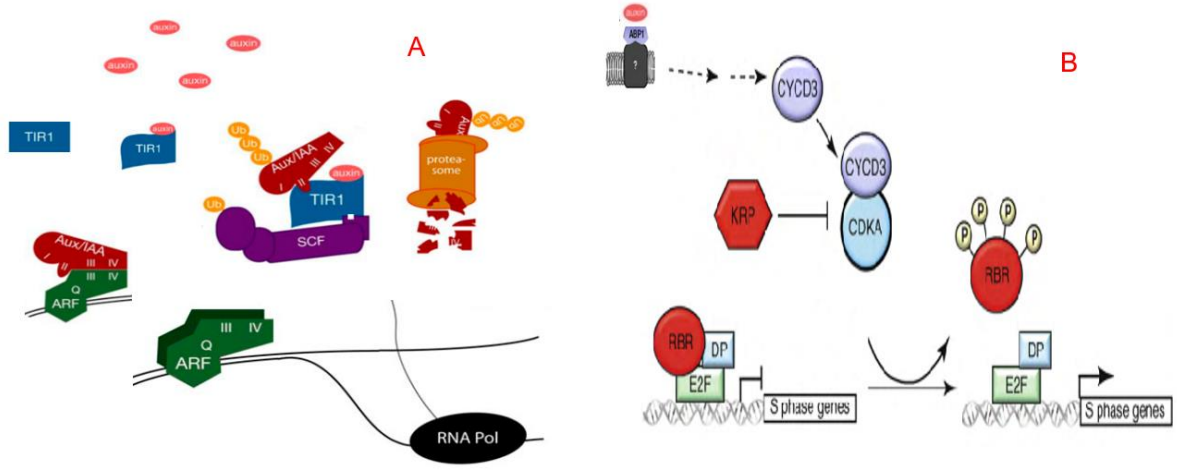

Figure 1. TIR1 and ABP1 receptors of auxin in signaling pathways. A. The auxin receptor called an F-box protein TRANSPORT INHIBITOR RESPONSE1 (TIR1) binding auxin, B. The auxin receptor named AUXIN-BINDING PROTEIN 1 (ABP1) binding auxin.

2.2. Sugar molecules in cell cycle

Sugar is a hugely vital function in distributing not only carbon structure and energy source but also the role of transmission of signaling molecules in controlling gene expression. To be more exact, there was a tight correlation among glucose and expression of genes related to cyclins such as cycD2;1, cycD3;2, cycA3;2 and cycB1;2[22,23] related to cell cycle is shown in **Figure 2**. Thus, it was also proved that the D-type cyclin was a function as sensors of outer condition and coupled with a kind of kinases named cyclin-dependent kinase as CDKA to modulate phases of cell while A3 and B1 could have a function in the change of G1/S and G2/M, in turn[24,25]. The transition of G2/M was an important step to assist the mitotic process that was regulated by several genes. A case in point is that glucose (Glc) signaling pathway in *Arabidopsis thaliana* meristematic tissue commences the G2/M shift via the inhibiting process of the transcriptional process of the negative regulator named TPR-DOMAIN (Tetratricopeptide repeat (TPR)- domains bind specific peptide ligands to mediate protein–protein interactions) SUPPRESSOR OF STIMPY(TSS). Crucial phases of cell genes like CYCB1;1 (B type cyclins) and CDKB1;1 (cyclin-dependent kinases)were activated to overcome G2/M transition. Although glucose inadequate led to initiate mitotic pathway, auxin-regulated to complete the process[26]. In shortly, auxin and glucose, a sugar synchronized role in regulating G2/M transition.

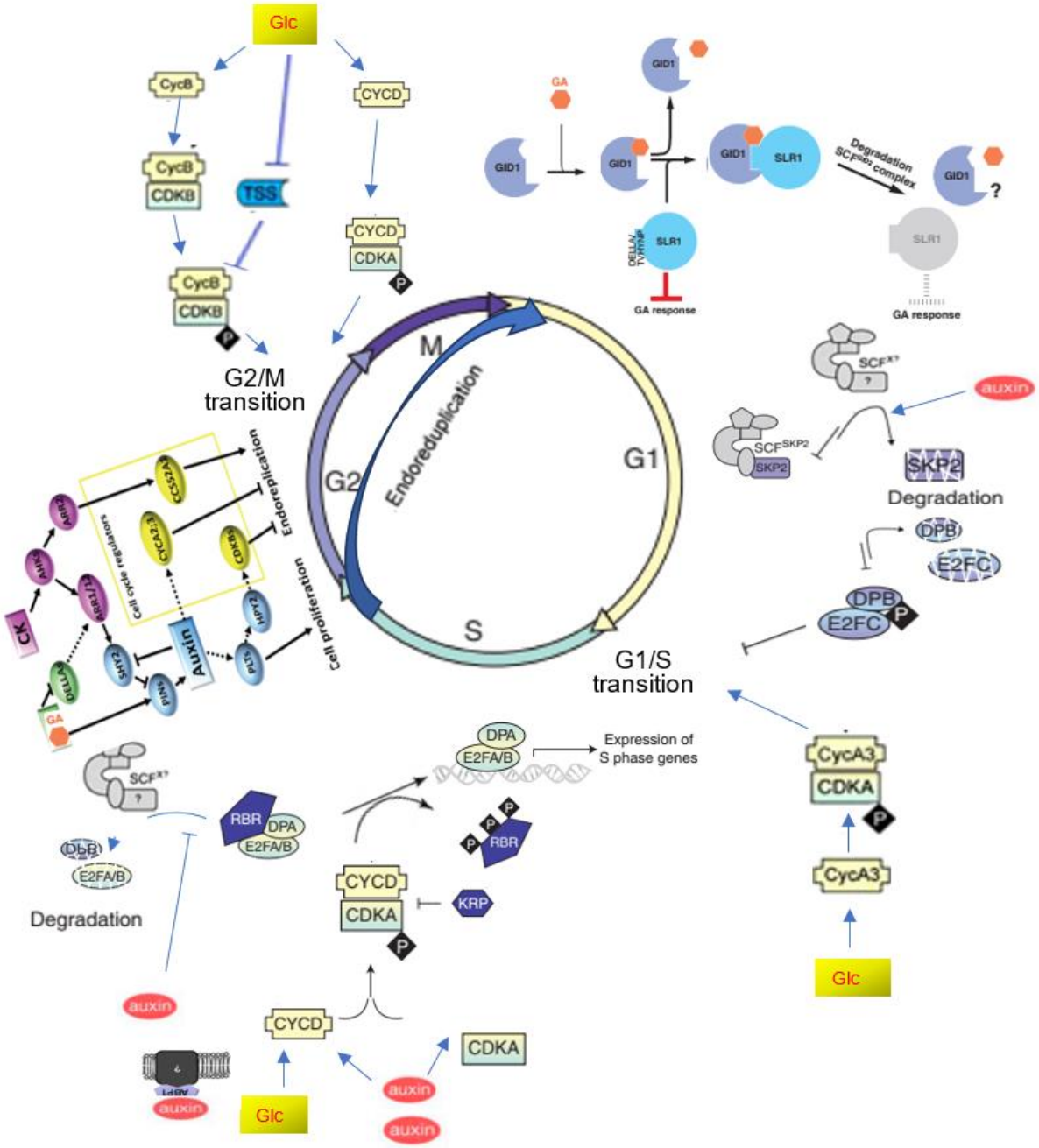

Figure 2. The signaling pathways of plant growth regulators and sugar on cell cycle and endoduplication that formates polyploid.

2.3. Gibberellin in regulating cell cycle

An essential plant growth regulator in controlling cell expansion, cell differentiation, and seed germination named gibberellin or gibberellic acid (GA) is related to the mitotic process. To be more accurate, the process regulating the cell cycle of gibberellin is very complex. This means GA elevates significant pathways of plant growth via cell expansion through promoting the reduction of DELLAs' nuclear factor that DELLA proteins get their name from five conserved amino acids (aspartic acid, glutamic acid, leucine, leucine, and alanine) is summarized in **Figure 2**[27,28]. To start with, GA binding with a kind of receptor named receptor GA-INSENSITIVE DWARF1 (GID1) enhanced interface of GID1 with growth-repressing DELLA proteins restraining cell production[29,30], following DELLAs polyubiquitinated through the E3 ubiquitin-ligase SCF^{SLY1} (SCF standing for Skp, Cullin, F-box and SLY1 standing for SLEEPY1) and DELLAs have finally destructed by a protein degraded construction as 26S proteasome[31,32] of which SCF complexes are the largest family of

E3 ubiquitin–protein ligases and mediate the ubiquitination. When the GA-deficient ga1-3 or the mutant of F box factor as sly1-10 lead to dwarf phenotype due to the lack of DELLA function[27,32,33]. Thus, it is observed that DELLAs detain cell production through increasing Kip-related protein 2 (KRP2) and SIAMESE (SIM), the cell cycle inhibitors. This means that DELLAs involve in plant growth inhibitory activity by reducing not only cell division and elongation rates leading to phenotypic plasticity[34].

3. Achievements of polyploidization through plant growth regulators induction

That polyploidization through phytohormone induction outranks other methods in terms of time-saving, rare aneuploid, and easy to conduct. In particular, several successful studies proved that exploitation of plant growth regulators induced polyploidization the typical of which are those which involve various plants such as crops, ornamental and medicinal plants. For instance, a medicinal plant obtaining polyploidy *Artemisia cina* by inducing plant growth regulators after treating with 2,4D combined with BA was observed that polyploid ones enhance biomass such as larger leaves, larger stomatal size, and higher chlorophyll content in comparison with diploid baring stomatal density. Likewise, observing polyploid *Artemisia cina* induced by one kind of spindle inhibitor, colchicine, combined with two plant growth regulators consisting of BA and 2,4D revealed that higher ploidy plant significantly increased not only biomass of leaves and root but also quercetin and kaempferol contents in comparison with lower ploidy one[35,36]. Another typical example is that tetraploid potato gained by plant growth regulators induction of zeatin riboside combining with indole acetic acid, gibberellin, and sugar as well. Particularly, the polyploidization has occurred in two consecutive phases. The first phase is that induction mitosis was conducted in Murashige Minimal Organic Medium added sucrose, zeatin riboside, indole acetic acids (IAA), and gibberellic acid (GA_3). Zeatin riboside and IAA have functioned to promote the S-phase of the cell cycle. While the high concentration of sugar with 50 g/L and a high concentration of GA_3 of 10 mg/L stimulate S-phase but inhibit mitosis. The explants were sub-cultured in the same medium after every two weeks and repeated up to three times to maintain the concentration of growth regulator and sugar. The second phase is that shoots form, the callus was changed into the MSA medium (CIP-Centro Internacional de la Papa- International Potato Center): Murashige Minimal Organic Medium with a low concentration of GA_3 and sucrose. Interestingly, these tetraploid potatoes are more likely to be resistant to potato tuber moths[12,37,38]. In micropropagation of tomato (*Solanum lycopersicum*) induced by IAA and zeatin, the frequency of polyploid found ranging 9%–14% is an apparent example[39]. Another example is that Gibberellin induces diploid pollen formation via interfering with meiotic cytokinesis is observed in *Arabidopsis*. The production of diploid (2n) pollen grains is related to repressor of ga1-3 (RGA) and Gibberellic acid insensitive (GAI), a member of the DELLA family, which functions as a suppressor of GA signaling[40]. Autopolyploid *A. platanoides* 'Crimson Sentry' was gained by pretreating for 7 days on MS medium adding 4 μM benzyl adenine (BA) alone or combined with 1 μM Indole-3-butyric acid (IBA), indole-3-acetic acid (IAA), or 1-naphthaleneacetic acid and then treating in liquid MS medium containing 15 μM oryzalin for 3 days[41]. Using growth regulators as Zeatin and IBA have successfully induced tetraploid eggplant is a typical protocol for polyploidization recently without having formed a chimeric plant[42]. It seems that the advantages of technological progress which allow people to perform polyploidization via growth regulators do outweigh the benefits involved.

4. Perspectives of polyploidization in crop development

Polyploidization provides insight into a potent means in support of novel crop advancement by facilitating breeding. This means induction of polyploidization is vital for human beings mainly because it can open the doors of breeding opportunities for success in emerging new crops. A case in point is that polyploidization through plant growth regulators induction is more likely to be successful in the future of crop development

strategies associated with developing seedless forms thanking triploid plants, increasing ornamental features, adapting to harsh environmental conditions, enhancing biomass, and restoring fertility were enumerated in several reviews[43,44]. To be more specific, whole-genome duplication may substantially affect crop breeding and development strategies due to the fact that they may cause noteworthy genetic changes in gene function and gene expression, and regulation[43–46]. The specific effects from polyploidization may be proved in various greatly along to species, especially with polyploid induction methods that have been mentioned above.

Concerning the increasing ornamental characteristics, many findings were proved that higher levels of ploidy plant species gained a number of intriguing traits. For example, the flower of tetraploid gerbera (*Gerbera hybrida*; Asteraceae) gained fascinating characteristics such as flower became larger, ray florets were wider, flower scapes were thicker, etc., in comparison with diploid counterpart[47]. Regarding seedless nursery crops, several triploid plant species have gained from the hybrid of diploid and tetraploid counterparts that were seedless. To be more precise, watermelon and banana triploid were typical, successful examples of triploid seedless and have been popularly exploited in commercial for several decades[48–50]. As far as enhancing biomass is concerned, whole-genome duplication benefits the biology of plant species. A case in point is that cell size increases substantially in polyploids that might affect the organism especially in guard cells, pollen tubes, xylem, and other organs[51–54]. With regard to guard cells, epidermal cells have flank stomata that are the pores in the leaf surface assisting gas change which is essential for energy production by the photosynthetic process. It is known that stomatal size and density relate to the rate of CO_2 uptake into the plant and transpiration rate of water as well[55,56]. To be more accurate, studying mutants in *Arabidopsis thaliana* revealed that more stomatal density leads to higher CO_2 assimilation under high light, but less stomatal density could reduce gas exchange and photosynthetic rates[57,58]. As well as this, restoring fertility is a vital characteristic of polyploidization. This provides a homolog for chromosomes to pair with during meiosis, then restore fertility. To be more precise, whole genome doubling has led to success in restoring fertility in the wide hybrids *Rhododendron* 'Fragrant Affinity'[59], × *Chitalpa tashkentensis*[60], and *Rudbeckia sp.*[61]. Furthermore, chromosome duplication restored fertility to *Miscanthus* × *giganteus*, the interspecific triploid bioenergy grass is a typical example[62].

In addition to this, polyploid has efficiently mitigated and adapted to detrimental environmental conditions[53]. Abiotic stress tolerance and biotic resistance were obviously witnessed in coping with a deleterious environment. Concerning salt stress, several investigations revealed that polyploid plants response to salinity stress to adapt to high salt concentration conditions consisting in not only physical processes such as cumulating Na^+ extrusion in the root, rising Na^+ transport to leaf, regulating osmotic but also genes expression related to antioxidant, mitigating reactive oxygen species (ROS)-functioning as signal transduction molecules that regulates different pathways during plant acclimation to stress, photosynthesize cues, changing single nuclotide polymorphism (SNP) marker related to salt stress, up-regulating aquaporin genes, phytohormone transduction cues, protein processing, regulating transcription factors, up-regulating ATP synthase, a catalyzing protein that functions the formation of the energy storage molecule adenosine triphosphate (ATP) using adenosine diphosphate (ADP) and inorganic phosphate (P_i), to enhance ion transport changing proton as well as using miRNAs[63–72]. Concerning drought stress, polyploidy plants have used miRNAs mechanisms and target genes controlling transcriptional regulation, hormone metabolism, and plant defense, a rise in abscisic acid (ABA) content, a plant hormone functions in plant developmental processes, consisting of seed and bud dormancy, the control of organ size and stomatal closure, especially important for plants in the response to environmental stresses, cope with water insufficiency in several polyploidy plants were witnessed in *Paulownia fortunei*, *P. australis, P. tomentosa*, *Lycium ruthenicum*[73–78]. Activating antioxidant defense systems were to sufficiently exist in heat stress in polyploidy *Dioscorea* and *Arabidopsis* are typical examples[79–82]. Polyploidy plants might increase antioxidant and epigenetic to adapt to cold

temperature[83,84]. A way to survive in an environment containing a high concentration of copper to higher ploidy plants is that they have enhanced Cu transport gene, activated anti-oxidation defense, positive regulated expression ABA-responsive genes, while autotetraploid have changed root anatomical characters to adapt to the high concentration of boron in environmental living[85,86]. The capacity of $NaHCO_3$ stress tolerance of autopolyploid birch plant (*B. platyphylla)* was illustrated by enhancing expression of target genes controlled proline biosynthetic process[87]. As far as biotic resistance is concerned, there were to witness autotetraploid plants such as *Malus* × *domestica* and *S. chacoense.* For instance, the capacity of common scab resistance of autotetraploid potato has been gained by hybridizing 2n gametes from diploid *S. chacoense*[88]. Further, a way to support autopolyploid to enhance the resistance of *Venturia* is that significantly increases Rvi6 resistance gene-locus[89]. This review is mentioned that polyploidization contributes better adapting to a harsh environmental condition in terms of suitability for cultivars due to the aforementioned benefits. Scientists and breeders can benefit immensely from polyploidization since it contributes potential agronomic traits being exploited efficiently to those desiring development of new cultivars.

5. Conclusion

In brief, it is true that current crops cannot supply all of the world's food security needs much longer. However, human beings can develop novel potential crops that contain good quality and high yield from the initiated development in the laboratories to field trials through developing polyploidization. Polyploids developed through plant hormone induction do outweigh the benefits involved, especially polyploidy induction process only being applied in laboratory scale to make plant parents where biosafe was strictly protected to avoid effects and bio-safety of that on human. It is undeniable that polyploidization nowadays plays an important role in breeding strategies which scientists and breeders may benefit immensely from gaining higher ploidy level plants after polyploidization since it contributes to desired agronomic traits being exploited for breeding as a whole. Polyploidy plants not only are food supplies, ornaments, and medicinal materials but also are void of the detrimental environment by enhancing abiotic and biotic tolerance. Unquestionably, new crops whether the artificial or natural polyploid formation is essential for success to ensure source's food security to those living on this planet to cope with climate change in the future.

Conflict of interest

The author declares no conflict of interest.

References

1. Joubés J, Chevalier C. Endoreduplication in higher plants. *Plant Molecular Biology* 2000; 43: 735–745. doi: 10.1023/A:1006446417196
2. Iwanaga M, Peloquin SJ. Origin and evolution of cultivated tetraploid potatoes via 2n gametes. *Theoretical and applied genetics* 1982; 61: 161–169. doi: 10.1007/bf00273885
3. Carputo D, Barone A, Frusciante L. 2n gametes in the potato: Essential ingredients for breeding and germplasm transfer. *Theoretical and Applied Genetics* 2000; 101: 805–813. doi: 10.1007/s001220051547
4. Carputo D, Barone A. Ploidy level manipulations in potato through sexual hybridisation. *Annals of Applied Biology* 2005; 146: 71–79. doi: 10.1111/j.1744-7348.2005.04070.x
5. Spooner D, Hijmans R. Potato Systematics and Germplasm Collecting, 1989–2000. *American Journal of Potato Research* 2001; 78: 237–268. doi: 10.1007/BF02875691
6. Wenzel G, Schieder O, Przewozny T, et al. Comparison of single cell culture derived *Solanum tuberosum* L. plants and a model for their application in breeding programs. *Theoretical and applied genetics* 1979; 55: 49–55. doi: 10.1007/bf00285189
7. Karp A, Nelson Thomas RE, Bright SWJ. Chromosome variation in protoplast-derived potato plants. *Theoretical and Applied Genetics* 1982; 63: 265–272. doi: 10.1007/BF00304006
8. Chauvin JE, Souchet C, Dantec JP, Ellissèche D. Chromosome doubling of 2x *Solanum* species by oryzalin: Method development and comparison with spontaneous chromosome doubling in vitro. *Plant Cell Tissue and Organ Culture* 2003; 73: 65–73. doi: 10.1023/A:1022663816052

9. Tamayo Ordoñez MC, Espinosa L, De Jesús Y, et al. Advances and perspectives in the generation of polyploid plant species. *Euphytica* 2006; 209: 1–22. doi: 10.1007/s10681-016-1646-x
10. Tomé LGO, Silva AB, Pinto CABP, et al. Colchicine and oryzalin effects on tetraploid induction and leaf anatomy of *Solanum commersonii* ssp. *Ciência Rural* 2016; 46: 1973–1979.
11. Hermsen JGT, Ramanna MS, Roest S, Bokelmann GS. Chromosome doubling through adventitious shoot formation on in vitro cultivated leaf explants from diploid interspecific potato hybrids. *Euphytica* 1981; 30: 239–246. doi: 10.1007/BF00033983
12. Watanabe J, Orrillo M, Watanabe KN. Evaluation of In Vitro Chromosome-doubled Regenerates with Resistance to Potato Tuber Moth [*Phthorimaea operculella* (Zeller)]. *Plant Biotechnology* 1999; 16: 225–230. doi: 10.5511/plantbiotechnology.16.225
13. Ismail C, Yasin T, Ismail I. Evalution of toxicity of abcisic acid and gibberellic acid in rats: 50 days drinking water study. *Journal of Enzyme Inhibition and Medicinal Chemistry* 2007; 22: 219–226.
14. Liu S, Huang X, He H, et al. Evaluation of selected plant growth regulators and fungicide residues in fruits for dietary risk assessment. *Human and Ecological Risk Assessment*: *An International Journal* 2016; 22: 1386–1395.
15. Celik I, Turker M, Tuluce Y. Abcisic acid and gibberellic acid cause increased lipid peroxidation and fluctuated antioxidant defense systems of various tissues in rats. *Journal of Hazardous Materials* 2007; 148: 623–629
16. Isik I, Celik I. Investigation of neurotoxic and immunotoxic effects of some plant growth regulators at subacute and subchronic applications on rats. *Toxicology and Industrial Health* 2015; 31: 1095–1105.
17. Kocaman AY, Guven B. In vitro genotoxicity assessment of the synthetic plant growth regulator, 1-naphthaleneacetamide. *Cytotechnology* 2016; 68: 947–956.
18. Perrot-Rechenmann C. Cellular responses to auxin: Division versus expansion. *Cold Spring Harbor Perspective Biology* 2010; 2: a001446. doi: 10.1101/cshperspect.a001446
19. Scherer FEG. AUXIN-BINDING-PROTEIN1, the second auxin receptor: What is the significance of a two-receptor concept in plant signal transduction? *Journal of Experimental Botany* 2011; 62(10): 3339–3357. doi: 10.1093/jxb/err033
20. Woodward AW, Bartel D. A receptor for auxin. *The plant cell* 2005; 17: 2425–2429.
21. Urano D, Phan N, Jones JC, et al. Endocytosis of the seven-transmembrane RGS1 protein activates G-protein coupled signaling in *Arabidopsis*. *Nature Cell Biology* 2012; 14: 1079–1088. doi: 10.1038/ncb2568
22. Hartig K, Beck E. Crosstalk between auxin, cytokinins, and sugars in the plant cell cycle. *Plant Biology* 2006; 8: 389–396. doi: 10.1055/s-2006-923797
23. Riou-Khamlichi C, Menges M, Healy JM, Murray JA. Sugar control of the plant cell cycle: Differential regulation of *Arabidopsis* D-type cyclin gene expression. *Molecular Cell Biology* 2000; 20: 4513–4521. doi: 10.1128/MCB.20.13.4513-4521.2000
24. Menges M, deJager SM, Gruissem W, Murray JA. Global analysis of the core cell cycle regulators of *Arabidopsis* identifies novel genes, reveals multiple and highly specific profiles of expression and provides a coherent model for plant cell cycle control. *Plant Journal* 2005; 41: 546–566. doi: 10.1111/j.1365- 313X.2004.02319.x
25. Nieuwland J, Menges M, Murray JAH. The plant cyclins. In: *Cell Cycle Control and Plant Development*. BlackwellPublishing; 2007. pp. 31–61. doi: 10.1002/9780470988923.ch2
26. Skylar A, Sung F, Hong F, et al. Metabolic sugar signal promotes *Arabidopsis* meristematic proliferation via G2. *Development Biology* 2011; 351: 82–89. doi: 10.1016/j.ydbio.2010.12.019
27. Silverstone AL, Jung HS, Dill A, et al. Repressing a repressor: Gibberellin-induced rapid reduction of the RGA protein in *Arabidopsis*. *Plant Cell* 2001; 13: 1555–1566.
28. Olszewski N, Sun T, Gubler F. Gibberellin signaling: Biosynthesis, catabolism, and response pathways. *Plant Cell* 2002; 14: S61–S80
29. Ueguchi-Tanaka M, Ashikari M, Nakajima M, et al. GIBBERELLIN INSENSITIVE DWARF1 encodes a soluble receptor for gibberellin. *Nature* 2005; 437: 693–698.
30. Willige BC, Ghosh S, Nill C, et al. The DELLA domain of GA INSENSITIVE mediates the interaction with the GA INSENSITIVE DWARF1A gibberellin receptor of *Arabidopsis. Plant Cell* 2007; 19: 1209–1220.
31. McGinnis KM, Thomas SG, Soule JD, et al. The *Arabidopsis* SLEEPY1 gene encodes a putative F-box subunit of an SCF E3 ubiquitin ligase. *Plant Cell* 2003; 15: 1120–1130.
32. Fu X, Richards DE, Fleck B, et al. The *Arabidopsis* mutant sleepy1gar2–1 protein promotes plant growth by increasing the affinity of the SCFSLY1 E3 ubiquitin ligase for DELLA protein substrates. *Plant Cell* 2004; 16: 1406–1418.
33. Dill A, Thomas SG, Hu J, et al. The *Arabidopsis* F-box protein SLEEPY1 targets gibberellin signaling repressors for gibberellin-induced degradation. *Plant Cell* 2004; 16: 1392–1405.
34. Achard P, Gusti A, Cheminant S, et al. Gibberellin signaling controls cell proliferation rate in *Arabidopsis*. *Current Biology* 2009; 19: 1188–1193. doi: 10.1016/j.cub.2009.05.059
35. Herawati MM, Pudjihartati E, Pramono S, et al. Obtaining *Artemisia cina* polyploidy through plant growth regulator treatment in shoot culture. *Agrivita* 2015; 37(2): 178–184. doi: 10.17503/agrivita.v37i2.490

36. Kasmiyati S, Kristiani EBE, Herawati MM. Effect of induced polyploidy on plant growth, chlorophyll and flavonoid content of *Artemisia cina*. *Biosaintifika: Journal of Biology & Biology Education* 2020; 12(1): 90–96. doi: 10.15294/biosaintifika.v12i1.22548
37. Watanabe KM, Orrillo M, Iwanaga R, et al. Diploid potato germplasm derived from wild and landrace genetic resources. *American Potato Journal* 1994; 71: 599–604.
38. Watanabe KN. Potato genetics, genomics, and applications. *Breeding Science* 2015; 65: 53–68. doi: 10.1270/jsbbs.65.53
39. Soressia GP, Cammareri G, Picarella ME. Improvement of in vitro vegetative propagation technique in tomato (*Solanum lycopersicum*). *Acta Horticulturae* 2009; 812(812): 283–288. doi: 10.17660/ActaHortic.2009.812.38
40. Liu B, Storme ND, Geelen D. Gibberellin Induce Diploid Pollen Formation by Interfering with Meiotic Cytokinesis. *Plant Physiology* 2017; 173: 338–353. doi: 10.1104/pp.16.00480
41. Lattier JD, Touchell DH, Ranney TG, Smith JC. Micropropagation and Polyploid Induction of Acer platanoides 'Crimson Sentry. *Journal of Environmental Horticultures* 2013; 31(4): 246–252.
42. García-Fortea E, Garcı´a-Pe´rez A, Gimeno-Paez E, et al. Ploidy modification for plant breeding using in vitro Organogenesis: A case in Eggplant Pasquale Tripodi (2021), Crop Breeding: Genetic Improvement Methods. *Methods in Molecular Biology* 2021; 2264. doi: 10.1007/978-1-0716-1201-914
43. Hieu PV. Polyploid gene expression and regulation in polysomic polyploids. *American Journal of Plant Sciences* 2019; 10: 1409–1443. doi: 10.4236/ajps.2019.108101
44. Hieu P. Evolutionary Fixed Potential Agronomic Traits in Polysomic Polyploidy Plants with Special Reference to Potato. *American Journal of Plant Sciences* 2023; 14: 793–811. doi: 10.4236/ajps.2023.147053
45. Hieu PV. The Unique Existence of Chromosomal Abnormalities in Polyploidy Plants. In: *Down Syndrome and Other Chromosome Abnormalities*. IntechOpen; 2021. doi: 10.5772/intechopen.99821
46. Touchell DH, Palmer IE, Ranney TG. *In vitro* Ploidy Manipulation for Crop Improvement. *Frontier in Plant Sciences* 2020; 11: 722. doi: 10.3389/fpls.2020.00722
47. Bhattarai K, Kareem A, Deng Z. In vivo induction and characterization of polyploids in gerbera daisy. *Scientia Horticulturae* 2021; 282: e110054. doi: 10.1016/j.scienta.2021.110054
48. Saminathan T, Nimmakayala Manohar S, Malkaram S, et al. Differential Gene Expression and Alternative Splicing between Diploid and Tetraploid Watermelon. *Journal of Experimental Botany* 2015; 66: 1369–1385. doi: 10.1093/jxb/eru486
49. Zhang N, Bao Y, Xie Z, et al. Efficient Characterization of Tetraploid Watermelon. *Plants* 2019; 8: 419. doi: 10.3390/plants8100419
50. Raboin LM, Carreel F, Noyer JL, et al. Diploid ancestors of triploid export banana cultivars: Molecular identification of 2n restitution gamete donors and n gamete donors. *Molecular Breeding* 2005; 16: 333–341. doi: 10.1007/s11032-005-2452-7
51. Marshall WF, Young KD, Swaffer M, et al. What determines cell size? *BMC Biology* 2012; 10: 101. doi: 10.1186/1741-7007-10-101
52. Doyle J, Coate J. Polyploidy, the nucleotype, and novelty: The impact of genome doubling on the biology of the cell. *International Journal Plant Sciences* 2019; 180: 1–52. doi: 10.1086/700636
53. Bomblies K. When everything changes at once: Finding a new normal after genome duplication. *Proceeding of the royal society B* 2020; 287: 20202154. doi: 10.1098/rspb.2020.2154
54. Roddy AB, Théroux-Rancourt G, Abbo T, et al. The scaling of genome size and cell size limits maximum rates of photosynthesis with implications for ecological strategies. *International Journal Plant Sciences* 2020; 181: 75–87. doi: 10.1086/706186
55. Bergmann DC, Sack FD. Stomatal development. *Annual Review Plant Biology* 2007; 58: 163–181. doi: 10.1146/annurev.arplant.58.032806.104023
56. Brodribb TJ, Sussmilch F, McAdam SAM. From reproduction to production, stomata are the master regulators. *Plant Journal* 2020; 101: 756–767. doi: 10.1111/tpj.14561
57. Schlüter U, Muschak M, Berger D, Altmann T. Photosynthetic performance of an *Arabidopsis* mutant with elevated stomatal density (sdd1–1) under different light regimes. *Journal Experienced Botany* 2003; 54: 867–874. doi: 10.1093/jxb/erg087
58. Büssis D, von Groll U, Fisahn J, Altmann T. Stomatal aperture can compensate altered stomatal density in *Arabidopsis thaliana* at growth light conditions. *Functional Plant Biology* 2006; 33: 1037–1043. doi: 10.1071/FP06078
59. Contreras RN, Ranney TG, Tallury SP. Reproductive behavior of diploid and allotetraploid *Rhododendron* L. *'Fragrant Affinity'*. *Hortscience* 2007; 42: 31–34. doi: 10.21273/hortsci.42.1.31
60. Olsen RT, Ranney TG, Viloria Z. Reproductive behavior of induced allotetraploid x *Chitalpa* and in vitro embryo culture of polyploidy progeny. *Journal American Society Horicticultural Sciences* 2006; 131: 716–724. doi: 10.21273/jashs.131.6.716
61. Oates KM, Ranney TG, Touchell DH. Influence of Induced Polyploidy on Fertility and Morphology of *Rudbeckia* Species and Hybrids. *Hortscience* 2012; 47: 1217–1221. doi: 10.21273/hortsci.47.9.1217

62. Touchell DH, Ranney TG. Chromosome doubling and fertility restoration in *Miscanthus* × *giganteus*. *HortScience* 2012; 47: S334. doi: 10.1139/g97-072
63. Meng H, Jiang S, Hua S, et al. Comparison between a tetraploid turnip and its diploid progenitor (*Brassica rapa* L.): The adaptation to salinity stress. *Agricultural Sciences in China* 2013; 10(3): 363–375. doi: 10.1016/S1671-2927(11)60015-1
64. Tu Y, Jiang A, Gan L, et al. Genome duplication improves rice root resistance to salt stress. *Rice* 2014; 7(1): 15. doi: 10.1186/s12284-014-0015-4
65. Xue H, Zhang F, Zhang Z, et al. Differences in salt tolerance between diploid and autotetraploid apple seedlings exposed to salt stress. *Scientia Horticulturae* 2015; 190: 24–30. doi: 10.1016/j. scienta.2015.04.009
66. Yan K, Wu C, Zhang L, Chen X. Contrasting photosynthesis and photoinhibition in tetraploid and its autodiploid honeysuckle (*Lonicera japonica* Thunb.) under salt stress. *Frontiers of Plant Science* 2015; 6: 227. doi: 10.3389/fpls.2015.00227
67. Fan G, Li X, Deng M, et al. Comparative analysis and identification of miRNAs and their target genes responsive to salt stress in diploid and tetraploid *Paulownia fortunei* seedlings. *PLOS One* 2016; 11(2): e0149617. doi: 10.1371/journal. pone.0149617
68. Fan G, Wang L, Deng M, et al. Changes in transcript related to osmosis and intracellular ion homeostasis in *Paulownia tomentosa* under salt stress. *Frontiers in Plant Science* 2016; 7: 384. doi: 10.3389/fpls.2016.00384
69. Yu L, Liu X, Boge W, Liu X. Genome-wide association study identifies loci for salt tolerance during germination in autotetraploid alfalfa (*Medicago sativa* L.) using genotypingby-sequencing. *Frontiers in Plant Science* 2016; 7: 956. doi: 10.3389/fpls.2016. 0956
70. Deng M, Dong Y, Zhao Z, et al. Dissecting the proteome dynamics of the salt stress induced changes in the leaf of diploid and autotetraploid *Paulownia fortunei*. *PLOS One* 2017; 12(7): e0181937. doi: 10.1371/journal.pone.0181937
71. Liu B, Sun G. microRNAs contribute to enhanced salt adaptation of the autopolyploid *Hordeum bulbosum* compared with its diploid ancestor. *Plant Journal* 2017; 91(1): 57–69. doi: 10.1111/tpj.13546
72. Zhao Z, Li Y, Liu H, et al. Genome-wide expression analysis of salt-stressed diploid and autotetraploid *Paulownia tomentosa*. *PLOS One* 2017; 12(10): e0185455. doi: 10.1371/journal. pone.0185455
73. del Pozo JC, Ramirez-Parra E. Deciphering the molecular bases for drought tolerance in *Arabidopsis* autotetraploids. *Plant, Cell and Environment* 2014; 37(12): 2722–2737. doi: 10.1111/pce.12344
74. Niu SY, Wang Z, Zhao M, et al. Transcriptome and Degradome of microRNAs and Their Targets in Response to Drought Stress in the Plants of a Diploid and Its Autotetraploid *Paulownia australis*. *PLOS One* 2016; 11(7): e0158750. doi: 10.1371/journal.pone.0158750
75. Cao X, Fan G, Cao L, et al. Drought stress-induced changes of microRNAs in diploid and autotetraploid *Paulownia tomentosa*. *Genes and Genomics* 2017; 39(1): 77–86. doi: 10.1007/s13258-016-0473-8
76. Zhao Z, Niu S, Fan G, et al. Genome-wide analysis of gene and microRNA expression in diploid and autotetraploid *Paulownia fortunei* (Seem) Hemsl. under drought stress by transcriptome, microRNA, and degradome sequencing. *Forests* 2018; 9(2): 88. doi: 10.3390/f9020088
77. Rao S, Tian Y, Xia X, et al. Chromosome doubling mediates superior drought tolerance in *Lycium ruthenicum* via abscisic acid signaling. *Horticulture Research* 2020; 7: 40. doi: 10.1038/s41438-020-0260-1
78. Li M, Zhang C, Hou L, et al. Multiple responses contribute to the enhanced drought tolerance of the autotetraploid *Ziziphus jujuba* Mill. var. *spinosa*. *Cell Bioscience* 2021; 11: 119. doi: 10.1186/s13578-021-00633-1
79. Zhang XY, Hu CG, Yao JL. Tetraploidization of diploid *Dioscorea* results in activation of the antioxidant defense system and increased heat tolerance. *Journal of Plant Physiology* 2010; 167(2): 88–94. doi: 10.1016/j.jplph.2009.07.006
80. DeBolt S. Copy number variation shapes genome diversity in *Arabidopsis* over immediate family generational scales. *Genome Biology and Evolution* 2010; 2: 441–453. doi: 10.1093/gbe/evq033
81. Caruso I, Lepore L, De Tommasi N, et al. Secondary metabolite profile in induced tetraploids of wild *Solanum commersonii* dun. *Chemistry & Biodiversity* 2011; 8: 2226–2237
82. Caruso I, Dal Piaz F, Malafronte N, et al. Impact of ploidy change on secondary metabolites and photochemical efficiency in *Solanum bulbocastanum*. *Natural Product Communications* 2013; 8: 1934578X1300801011.
83. Deng B, Du W, Changlai L, et al. Antioxidant response to drought, cold and nutrient stress in two ploidy levels of tobacco plants: Low resource requirement confers polytolerance in polyploids. *Plant Growth Regulation* 2012; 66(1): 37–47. doi: 10.1007/s10725-011-9626-6
84. Syngelaki E, Daubert M, Klatt S, Hörandl E. Phenotypic Responses, Reproduction Mode and Epigenetic Patterns under Temperature Treatments in the Alpine Plant Species *Ranunculus kuepferi* (*Ranunculaceae*). *Biology* 2020; 9: 315. doi: 10.3390/biology9100315
85. Ruiz M, Quiñones A, MartínezAlcántara B, et al. Tetraploidy Enhances Boron-Excess Tolerance in Carrizo Citrange (*Citrus sinensis* L. Osb. × *Poncirus trifoliata* L. Raf.). *Frontiers in Plant Science* 2016; 7: 701. doi: 10.3389/fpls.2016.00701
86. Li M, Xu G, Xia X, et al. Deciphering the physiological and molecular mechanisms for copper tolerance in autotetraploid *Arabidopsis*. *Plant Cell Reports* 2017; 36(10): 1585–1597. doi: 10.1007/s00299-017-2176-2

87. Mu H, Lin L, Zhang Q, et al. Growth, proline content and proline-associated gene expression of autotetraploid *Betula platyphylla* responding to $NaHCO_3$ stress. *Dendrobiology* 2016; 75: 123–129. doi: 10.12657/denbio.075.012
88. Jansky S, Haynes K, Douches D. Comparison of Two Strategies to Introgress Genes for Resistance to Common Scab from Diploid *Solanum chacoense* into Tetraploid Cultivated Potato. *American Journal of Potato Research* 2019; 96: 255–261. doi: 10.1007/s12230-018-09711-6
89. Hias N, Svara A, Wannes Keulemans J. Effect of polyploidisation on the response of apple (*Malus* × *domestica* Borkh.) to *Venturia inaequalis* infection. *European Journal of Plant Pathology* 2018; 151(2): 515–526. doi: 10.1007/s10658-017-1395-2