

Evolutionary Fixed Potential Agronomic Traits in Polysomic Polyploidy Plants with Special Reference to Potato

Pham Van Hieu

Biotechnology Center of Ho Chi Minh, Ho Chi Minh City, Vietnam

Email: hieupvbio@gmail.com

How to cite this paper: Hieu, P.V. (2023) Evolutionary Fixed Potential Agronomic Traits in Polysomic Polyploidy Plants with Special Reference to Potato. *American Journal of Plant Sciences*, 14, 793-811. <https://doi.org/10.4236/ajps.2023.147053>

Received: January 21, 2023

Accepted: July 22, 2023

Published: July 25, 2023

Copyright © 2023 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

It is commonly known that polyploidization has become one of major forces for a speciation and evolution, especially with evolutionary fixed potential agronomic traits in plants. Although several studies demonstrate that allopolyploid plants were successful in developing novel crops, autopolyploid ones are also more substantial and worth exploring. Obviously, autopolyploid development via sexual or asexual pathways can lead to advantages in biomass, changing process of development, and lots of benefits on coping with climate changes do not comprehend as a whole. This review shed light on 1) gaining gigantic effect and increasing phytochemical content; 2) enhancing biotic and abiotic tolerance to adapt to climate change; 3) changing in process of development; 4) adapting ecology. Based on these benefits, this review provides breeders with several choices when they need in the breeding strategies. Also further review on prospects of polyploidy potato in food security is concerned.

Keywords

Polyploidisation, Evolution, Agronomic Trait, Potato

1. Introduction

To start with, polyploidy is really vital for human beings mainly because it can open doors of opportunities for success in gaining newly potential crops. Over a century from finding an event that had a set of doubled chromosomes in some plants which was suggested as a polyploid hypothesis by Wing 1917, polyploids have actually undergone an ample history and numerous approaches [1] [2]. Based on origin of parental chromosome resulting polyploidization, two types of

polyploids could be classified, namely, paleopolyploids and neopolyploids. Paleopolyploid flora originated from polyploidy progenitor evolved and went through the milestones of genome doubling, but they existed as diploid due to its re-diploidization via reorganization of various chromosomal sets derived from their ancestors. Neopolyploid plants owned numerous sets of chromosomes which occurred on the periodic polyploidization after combining the parental chromosomes existing independence of each other [3]. According to homologous genomes originated from progenitors, polyploidy plants are also divided into allopolyploid and autopolyploid. With regard to the former, it is combined from parents being different species which forms heterozygous genomes. Autotetraploid results in the same genetic background of their parents having homogeneous genomes [4]. Polyploidization was formed by either sexual pathway or somatic chromosome doubling. Concerning the first pathway, the form comprising of the somatic number of chromosomes in diploid pollen and eggs created in meiosis barring the gametophytic number was so-called unreduced gametes or $2n$ gametes to make polyploidy progenitors and the basic component was for polyploidy development in flora. While, a somatic chromosome doubling was established as chromosomal doubling in somatic cells through mitosis pathway [5] [6].

With polyploidisation in plant species becoming more prevalent and recurrent than ever, as well as being one of the most essential evolutionary phenomena, resulting in extensively investigating the research field is concerned. Moreover, polyploidy plants become such attention, several favorable agronomic traits are observed that refer to large organ size, vigor, lasting flowers period etc. [7]. When polyploidization occurred, several changes affected by allele dosage related to gene expression and regulation would lead to sequence elimination, methylation, transposon activation, up- and downregulation, subfunctionalisation and neofunctionalisation to form potential agronomic traits [8] [9]. Regarding the former, loss and gain DNA sequences occurred in autotetraploid *C. lavandulifolium*, *A. thaliana*, *B. rapa* [10] [11] [12] [13] and changed in polymorphism at difference of generation of *Phlox drummondii* Hooker [14]; gene interaction in *A. arenosa* [15]. Alteration on gene expression in polysomic polyploid was not high such as *Paspalum notatum* in 10,000 genes showed 42 homologous genes to 26 divergent genes having function and 22 novel sequences [16], 4.3% divergent expression in *Isatis indigotica* [17], 10% genes changed expression in potato [18], 6.09% pivotal differential expression in *P. fortunei* [19], 2.87% changed level of gene expression in Mulberry (*Morus alba* L.) [20], 11.5% of transcriptome and proteome correlation between diploid and tetraploid *P. tomentosa* [21], 17% differential gene expression in *Tolmiea (Saxifragaceae)* [22], 2677 unigenes were significantly divergently expressed in tetraploid *P. tomentosa* [23], 22 genes that happened alternative splicing, showing abilities of making the difference of isoforms of protein in watermelon [24]. Methylation occurred in polysomic polyploid in rice, *Malus × domestica* Borkh, *B. rapa* [13] [25] [26]. Translocation appeared in rice and methylated class II of transposable elements

shown in *A. thaliana* [27] [28]. Change in miRNA in *C. nankingense* [29] [30]. Neofunctionalization was discovered in autotetraploid [16] [31] [32] [33] [34]. Subfunctionalization which is couples of genes exercise a subset of their original genetic functions revealed in maize, *Arabidopsis* [35] [36] [37]. Autotetraploid *Lycopersicon esculentum* changed the level of gene expression of the gene dosage such as malate dehydrogenase, acid invertase, glutamate dehydrogenase, and nitrate reductase [38]. Cis-regulatory elements showed extensive difference in regulatory elements and networks in ploidy *Arabidopsis*. Further, after polyploidisation, dominance effects of allele interaction can occur and be heritable [39]. Another way to contribute to elite polyploidy rice is concerned, heterosis analysis and molecular regulation support long rice panicles [40]. The resurgence of interest in polyploid in recent decades has changed the previous hypothesis which was evolutionary dead-ends in polysomic polyploids by major players in evolution [41] is pointed in **Figure 1**. This work provides insight into the features of naturally typed and resynthesized polysomic polyploid plants aimed to study evolutionary fixed potential agronomic traits including in extending size of organs and gaining more phytochemicals; reducing the effects of climate change by increasing biotic and abiotic tolerance; altering the developmental process; and widening environmental living and having been typically summarized in **Table 1**, with special references in potato.

2. Gigantic Effects and Enhance Phytochemical

That polysomic polyploidy outrank diploid one in terms of organ size and biomass typically asserts that up-regulation of genes related to cell division and cell expansion such as ARGOS, *ANT* (*AITEGUMENTA*), *CYCD3;1*, *Growth Regulating Factor 1* (*AtGRF1*) and *EXPASIN 10* (*AtEXPA10*) [42] [43] [44], *EXPB3*

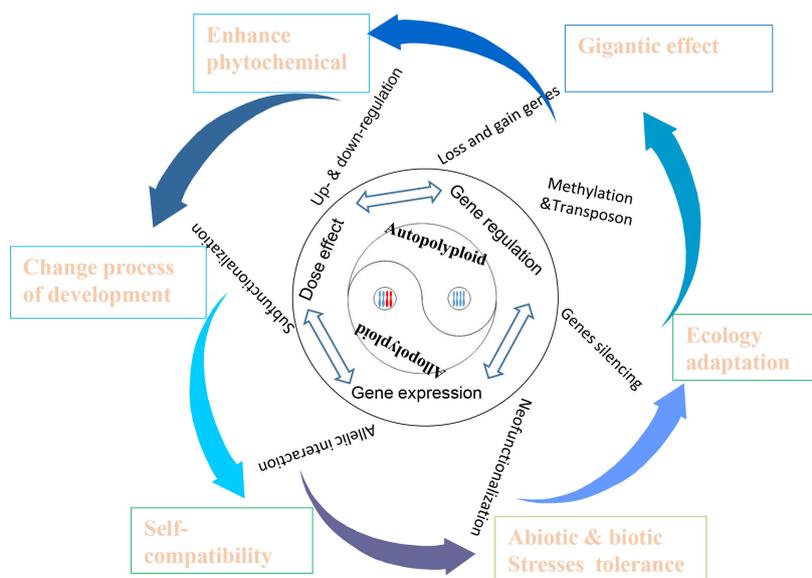


Figure 1. Diagram of evolutionary fixed potential traits in polyploidisation modified from Van Hieu, 2019.

Table 1. Some polysomic polyploidy lead to evolutionary fixed potentially agronomic traits.

Scientific name	Ploidy	Chromosome	The alternation after polyploidisation	Agronomic traits	Ref.
<i>Lonicera japonica</i> Thunb	Diploid & autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increasing Na ⁺ extrusion in root and supporting Na ⁺ transport to leaf, enhancing photosynthesis	Salt stress	[73]
<i>Oryza sativa</i> <i>Nipponbare</i>	Diploid & autotetraploid	2n = 2x = 24, 2n = 4x = 48	Increasing proline and proton transport; deducing MDA, and Na ⁺ influx into the root	Salt stress	[71]
<i>Brassica rapa</i> L.	Diploid & autotetraploid	2n = 2x = 20, 2n = 4x = 40	Up-regulation of antioxidant APX, CAT, POD, SOD, and GR; mitigating ROS	Salt stress	[70]
<i>Paulownia tomentosa</i>	Diploid & autotetraploid	2n = 2x = 40, 2n = 4x = 80	RNA transporter, phytohormone transduction and photosynthesis signal, protein processing, AP2/EREBP, MYB, NAC, and bHLH	Salt stress	[75] [79]
<i>Medicago sativa</i> L.	Diploid & autotetraploid	2n = 2x = 16, 2n = 4x = 32	SNP markers associated to salinity stress, genes functionalized to abiotic stress linked to markers supporting salt tolerance	Salt stress	[76]
<i>Malus domestica</i>	Diploid & autotetraploid	2n = 2x = 34, 2n = 4x = 68	Up-regulation of aquaporin gene (MdPIP1;1 and MdTIP1;1)	Salt stress	[72]
<i>Hordeum bulbosum</i>	Diploid & autotetraploid	2n = 2x = 14, 2n = 4x = 28	miRNAs pitfall salinity stress	Salt stress	[78]
<i>Paulownia fortunei</i>	Diploid & autotetraploid	2n = 2x = 40, 2n = 4x = 80	Rising of soluble sugars, up-regulated ATP synthase to increase ion transport changing proton 8 miRNAs more enhanced and new miRNAs	Salt stress	[74] [77]
<i>P. australis</i> , <i>P. fortunei</i> , <i>P. tomentosa</i> ,	Diploid & autotetraploid	2n = 2x = 40, 2n = 4x = 80	miRNAs and target genes associated to transcriptional regulation, hormone metabolism, and plant defense	Drought stress	[81] [82] [83]
<i>Dioscorea zingiberensis</i>	Diploid & autotetraploid	2n = 2x = 20, 2n = 4x = 40	Initiation of the antioxidant defense system and increased heat tolerance	Heat stress	[85]
<i>Nicotiana benthamiana</i>	Tetraploid & &octaploid	2n = 4x = 38, 2n = 8x = 76	Rising antioxidant (SOD, CAT, APX...)	Cold stress	[86]
<i>Arabidopsis thaliana</i>	Diploid & autotetraploid	2n = 2x = 10, 2n = 4x = 20	Genes related to Cu transported, AtHMA5, AtCOX17, and AtMT2b, activation of antioxidative defense, positive regulation of expression ABA-responsive genes	Copper stress	[89]
<i>Citrus sinensis</i> L. <i>Poncirus trifoliata</i> L.	Diploid & autotetraploid	2n = 2x = 22, 2n = 4x = 44	Alternation of root anatomical characters	Boron stress	[88]
<i>Betula platyphylla</i>	Diploid & autotetraploid	2n = 2x = 28, 2n = 4x = 56	Up-regulated genes associated to proline biosynthesis	NaHCO ₃ stress	[90]
<i>Malus</i> × <i>domestica</i> Borkh	Diploid & autotetraploid	2n = 2x = 34, 2n = 4x = 68	Significantly increased <i>Rvi6</i> resistance gene-locus	Resistance of <i>Venturia</i>	[91]
<i>Solanum chacoense</i>	Diploid & autotetraploid	2n = 2x = 24, 2n = 4x = 48	Scab resistance originated from <i>Solanum chacoense</i> has introgressed into tetraploid	Scab resistance	[92] [114]
<i>Papaver somniferum</i> L.	Diploid & autotetraploid	2n = 2x = 22, 2n = 4x = 44	Up-regulated alkaloid biosynthesis pathway through gene expression	Increase morphine 25% - 50%.	[56]
<i>Citrullus lanatus</i>	Diploid, autotriploid and autotetraploid	2n = 2x = 22, 2n = 3x = 33, 2n = 4x = 44	Enhancing lycopene biosynthesis pathway via up-regulation genes related	Increase lycopene contents	[58]
<i>Linum album</i>	Diploid and autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increasing the pathway of PTOX biosynthesis by upregulated genes related	Increase podophyllotoxin (PTOX)	[59]

and *TCP* [45], the expression of lipid transport genes, *wbc11-2* and *cer5-2* [46] [47] [48] and by proteins related to cell proliferation, glutathione metabolic pathways and cellulose, chlorophyll, pectin, lignin synthesis [49] [50]. Cytosine methylation genome-wide was as a way to make large body size autotetraploid [51]. Enlarged organ size in polysomic polyploid plants usually leads to increased yield and production crops [52]. These aforementioned benefits, polysomic polyploid enlarged size of plants, but in the case of autotetraploid Birch plant (*Betula platyphylla*) and apple plants (*Malus domestica*) were a dwarf morphology that affects by reduced phytohormone cues [53] [54].

Likewise, polysomic polyploid also increased phytochemical in several plants [55], the best example of which are those which involve natural compounds such as tetrasomic tetraploid opium poppy (*Papaver somniferum* L.) enhanced many genes expression related to alkaloid biosynthesis pathway lead to increased morphine content 25% - 50% [56]. Cytosine methylation of genome-wide enhanced phytochemical in autotetraploid *Cymbopogon* [51]. Investigation on autotetraploids *A. thaliana* Col-0 showed that metabolites and genes related to TCA (tricarboxylic acid cycle) and GABA (γ -amino butyric acid) changed compare with its diploid [57]. Lycopene in autotriploid watermelons increased due to a regulation of phytohormone on metabolic pathways and upregulation of genes related to biosynthetic lycopene [58]. Autotetraploid *Linum album* increased concentration of podophyllotoxin (PTOX) caused by upregulated genes related to pathway of PTOX biosynthesis [59]. Autotetraploid *Anoectochilus formosanus* Hayata produced significantly more contents of total flavonoid and gastrodin [60]. Tetraploid cytotypes of *Physalis angutala* Linn. from Rajasthan increased palmitic acid, linoleic acid and linolenic acid [61]. In the last century, many plant breeders have given objects based on the outstanding advantages of polyploids. Those breeders have utilized natural and artificial polyploidy as a way to gain elite plant cultivars due to the fact that the increment in plant organs size derived from some of the most significant consequence of polyploidisation [62].

3. Changing Process of Development

Polyploidy plants offer myriad benefits from enlarged flowers to more extensive the blooming period. A case in point is that whole genome duplication shifted the flowering time and tolerance to new environments in tetraploid *Anacamptis pyramidalis* [63]. Thus, based on study *Brassica rapa* (Chinese cabbage) by RNA-seq and sRNA-seq, it was revealed that autotetraploid one prolonged flowering time due to an increase of phyto-hormone levels including the jasmonic acid and indole-3-acetic acid, while a decrease of the abscisic acid as well as regulating of miRNA-target mRNA related to flowering period, petal growth, flowering blooming, and pollen development [64]. After polyploidisation, meiotic stability becomes important because this processing becomes complicated. In studying autotetraploid *Arabidopsis lyrata*, it is uncovered that novel alleles of

ASY1 and ASY3 supported greater stability in the meiotic process [65] [66]. Tetraploid *Centaurea phrygia* showed greater seed production [67]. Due to gigantic characteristics, autotetraploid rice is not only long and wide grains but also long panicle and seed setting that showed high heterosis and more potential agronomic traits [68]. Based on using CRISPR/cas9 to knock out two genes *TMD9-1* and *TMS5* in autotetraploid rice helped more pollen development which led to increasing rate of seeds [69].

4. Enhancing Abiotic & Biotic Stress Tolerance

That polysomic polyploid plants increased abiotic stress tolerance and biotic resistance was clearly observed in coping with adversely environmental conditions. In case of salinity stress, polysomic polyploid flora used several processes to adapt to high salt concentration condition such as increasing Na⁺ extrusion in root, higher Na⁺ transport to leaf, adjust osmotic, enhanced of genes expression related to antioxidant, mitigating ROS, photosynthesis cues, phytohormone transduction cues, protein processing, regulated transcription factors, changing SNP marker related to salt stress, upregulation of aquaporin genes, up-regulated ATP synthase to enhance ion transport changing proton; using miRNAs [70]-[79]. To cope with drought stress, polysomic polyploid plants used miRNAs pathways and target genes related to transcriptional regulation, hormone metabolism and plant defense, an increase in ABA content [80] [81] [82] [83] [84]. Activation of antioxidant defense systems supported heat tolerance [85]. Polysomic polyploid plants enhanced cold stress tolerance by increasing antioxidant and epigenetic [86] [87]. Autotetraploid enhanced boron by changing root anatomical characters and copper tolerance by enhanced Cu transport gene, activation of antioxidative defense, positive regulation of expression ABA-responsive genes [88] [89]. Autopolyploid birch plant (*Betula platyphylla*) increased ability to NaHCO₃ stress tolerance by enhancing expression of some genes related to proline biosynthesis [90]. Autopolyploid enhanced to resistance of *Venturia* by significantly increased *Rv6* resistance gene-locus [91]. Likewise, Autotetraploid potato increased common scab resistance after crossing 2n gametes from diploid *Solanum chacoense* [92].

5. More Adaptation Ecology

Polyploidization is one of the major adaptation ecologies such by focusing on growth, morphological traits as well as ecology invasion, pollinators [93]. After polyploidisation, the cell size increased to lead to change physiological manners with their environmental condition as well as combining multiple novel alleles and altering regulatory processes can create new potentially advantageous morphological variation. These are to expand ecological space to polyploidy plants [94]. The adaptive potential from polyploidy *Arabidopsis thaliana* is caused by the increase resources of TE insertions in higher ploidy plant [95]. One of priorities in genotype development is to gain through combination of potential traits

which benefits in stress tolerance and nutritional aspects as a way to reduce the effects of climate change [96]. The view is that polyploidization contributes to better adapting environment in terms of suitability for growth and other benefits of cell size. Breeders can benefit immensely from more ecological adapting after polyploidisation since it improves potential traits as a whole.

6. Prospect of Polyploidy Potato Is a Main Non-Grain Staple Food

The statistics display the world's population will reach 9.7 billion people by 2050 so this leads to 70% increase in food demand [97]. Producing more food, however, in conditions having the same or less resources will become the huge challenges for human beings. The global food need can be met by the potato crop because of diversities of cultivation and environment which are gained by being adaptable, high yielding and nutrition-rich. Productivity improvement can be achieved by the way of increasing yield or expanding areas where potatoes grown. Nowadays, a potato staple food accounts for the production of 380 million metric tons according to Faostat 2019, and contributes for 1.3 billion people worldwide with popularly increasing the nutritious tubers [98]. Besides, the potato's adaptation with several soils and climates with being widely located from plain to high mountain regions of 4700 m compared with the sea level and also resist new drawbacks from biotic and abiotic are concerned [99]. Potato also impacts on society due to its having majority of nutrition and economy, especially with developing countries where potato output surpasses that in the other part of worldwide in ensuring food security [100] [101]. Being a source of employment and income also help to improve global food security from potato in developing countries due to the fact that potato can provide the major of vitamins, mineral, phytonutrients starch, protein as well as a source of energy and micronutrients [102] [103] [104]. Thus, potato utilizes water more efficiently than that for cereal crops that were up seven times (International Potato Center (CIP) 2018). With regard to the biodiversity, over 4000 native varieties including more than 180 wild relative potato were recorded [105]. In addition to being polyploidy, potato seems to be one of the most complex genetic modes with the various ploidy levels such as 76% were identified diploids, 3% triploids, 12% tetraploids, 2% pentaploids, and 7% hexaploids, among which tetraploid has the highest yield due to more level of genetic heterogeneity [106] [107] [108]. The practically empirical proofs shown that there were an existence of two groups of cultivated potato, one existed in high Andes of northern and central South America called the Andigenum group which consists of wide range of ploidy level, and the others are distributed in the lowlands southern Chile named the Chilotanum group which is tetraploid only [109].

In the history of potato development, the farmers have carefully selected potato to maintain the diversity of high landraces in the native field based on 1) giving that features of flavor, textures, color and shapes to enhance their diet; 2)

providing cultivars that are capable of abiotic tolerance and biotic tolerance (diseases, pests) to assure the survival and harvesting; 3) contributing in special consuming in food processing or ceremonial cultures [109]. To succeed in selecting the right traits after full testing and to create the number of seed tubers which supply to farmers, the breeders can take at least 15 years due to commercial potato being tetraploid contains four copies of each chromosome, hundreds of thousands of seedlings must be created and tested to select just one with the potential traits [99]. Moreover, with the biological features making hereditary improvement in potato was more complexity than in other staple crops, a powerful and effective approach conducted by potato breeders was the unique capacity of among ploidy and wild relative potato to cross as a way to introgress favorable agronomic traits derived from their genetic pools into the aim of the potato breeding strategies [110] [111]. For instance, the genetic diversity of Japanese potato cultivar was broadened by breeding with *Andigena* [112]. In another study, QTL associated with disease such Early Blight in tetraploid potato was identified in specific chromosomes [113]. The major QTL which is scab resistance originated from *Solanum chacoense* has introgressed into tetraploid offspring to exhibit stability in common scab resistance [92] [114]. The two traits of tuber starch and plant maturity were mapped by QTL to support the prospect of breeding potato programs [115]. A large number of elite traits in tetraploid potato linked to transcripts relating to development processes such as growth rate, high yield, tuber greening and early flowering ... as well as biotic resistance were investigated to elucidate the relationship between phenotype and gene expression [116]. In addition to the flavor and textural traits having identified genes and marker related to beneficial alleles may contribute to improve nutritional basis of novel potato cultivars [117]. Several traits correlation to abiotic and biotic stress have been investigated and utilized as an artificial selection marker in breeding programs, including both modern and conventional methods. However, that the adverse effects could be created by accumulating rapidly deleterious mutations during the polyploidisation of potato notes that in development novel crops [118]. Based on studying transcriptome of cultivated potato varieties, it is revealed that tetraploid potato confers the genetic diversity of the high heterozygous [119]. With the genomic era becoming more useful than ever, it is more efficient to introgress multi-genic traits which will make it possible to utilize recessive alleles and identify rare alleles. Potato cultivars containing favorable agronomic traits must be evaluated and planted in order to ensure high yield [120]. Using Next Generation genome sequence to study six polyploidy potato genomes revealed that valuable genetic resources relating to traits derived from native landraces have functioned in disease and pest resistances as well as nutrition and fiber using breeding strategies [121]. Advances in technology are successfully applied in developing new potato cultivar. For example, the CRISPR/cas 9 was also applied in tetraploid potato to successfully knockout *StPDS* gene or nucleotide transitions and transversions in the *StALS1*

gene by introduction of simultaneous nucleotides [122] [123]. This is essential for success to breeders for crop improvement goals [124].

7. Conclusion

In brief, due to advances in biotechnology, polyploidization is now capable of potentially making various crops containing favorable agronomic traits. While it is accepted that allopolyploid plants can often have positive effects on agriculture, other views of autopolyploid ones are significantly more important. Obviously, using autopolyploid developed by sexual or asexual method can be advantageous for reasons related to biomass, effectiveness on changing process of development, and lots of benefits on coping with climate changes. Concerning the former, whole genome doubling can perform better than (di)haploid counterparts, and as a result utilizing autopolyploid enables gaining not only gigantic effect but also increasing phytochemical content. As far as ecological prospects are concerned, autopolyploids are comparatively more effective than (di)haploid ones due to enhancing biotic and abiotic tolerance to adapt to climate change. Eventually, autopolyploid plants can also be more beneficial in the process of development that is adequate enough which provides breeders with a wide range of options when they need. It seems to human beings that the technological progress which allows us to perform autopolyploid development via unreduced gametes and somatic chromosome doubling does outweigh the benefits involved. With climate change becoming more serious than ever, we should create more elite crops as a way to address this problem assuring food security to those living on our planet. The polyploidy plants gained by sexual and asexual or somatic chromosomal doubling may affect how successful they are in their future crops development. It is unquestionable that polyploidy, whether sexual or somatically doubled chromosomes, is essential for success in gaining favorable agronomic traits.

Acknowledgements

Pham Van Hieu thanks the financial support from Ho Chi Minh City Government through HCMC Biotechnology center for his academic study and research in Japan

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

References

- [1] Lutz, A.M. (1907) A Preliminary Note on the Chromosomes of *Oenothera lamarckiana* and One of Its Mutants, *O. gigas*. *Science*, **26**, 151-152. <https://doi.org/10.1126/science.26.657.151>
- [2] Winge, O. (1917) The Chromosome. Their Numbers and General Importance. *Comptes rendus des travaux du Laboratoire Carlsberg*, **13**, 131-175.

- [3] Zhang, K., Wang, X. and Cheng, F. (2019) Plant Polyploidy: Origin, Evolution, and Its Influence on Crop Domestication. *Horticultural Plant Journal*, **5**, 231-239. <https://doi.org/10.1016/j.hpj.2019.11.003>
- [4] Barker, M.S., Arrigo, N., Baniaga, A.E., Li, Z., Levin, D.A. (2016) On the Relative Abundance of Autopolyploids and Allopolyploids. *New Phytologist*, **210**, 391-398. <https://doi.org/10.1111/nph.13698>
- [5] Storme, N.D. and Geelen, D. (2013) Sexual Polyploidization in Plants—Cytological Mechanisms and Molecular Regulation. *New Phytologist*, **198**, 670-684. <https://doi.org/10.1111/nph.12184>
- [6] Tel-Zur, N., Mouyal, J., Zurgil, U. and Mizrahi, Y. (2020) In Support of Winge's Theory of "Hybridization Followed by Chromosome Doubling". *Frontier of Plant Sciences*, **11**, 954. <https://doi.org/10.3389/fpls.2020.00954>
- [7] Manzoor, A., Ahmad, T., Bashir, M.A., Hafiz, I.A. and Silvestri, C. (2019) Studies on Colchicine Induced Chromosome Doubling for Enhancement of Quality Traits in Ornamental Plants. *Plants*, **8**, 194. <https://doi.org/10.3390/plants8070194>
- [8] Van Hieu, P. (2019) Polyploid Gene Expression and Regulation in Polysomic Polyploids. *American Journal of Plant Sciences*, **10**, 1409-1443. <https://doi.org/10.4236/ajps.2019.108101>
- [9] de C. Lara, L.A., Santos, M.F., Jank, L., Chiari, L., de M. Vilela, M., Amadeu, R.R., dos Santos, J.P.R., da S. Pereira, G., Zeng, Z.B. and Garcia, A.A.F. (2019) Genomic Selection with Allele Dosage in *Panicum maximum* Jacq. *G3: Genes, Genomes, Genetics*, **9**, 2463-2475. <https://doi.org/10.1534/g3.118.200986>
- [10] De Smet, R., Adams, K.L., Vandepoele, K., Van Montagu, M.C.E., Maere, S. and Van de Peer, Y. (2013) Convergent Gene Loss Following Gene and Genome Duplications Creates Single-Copy Families in Flowering Plants. *Proceedings of the National Academy of Sciences*, **110**, 2898-2903. <https://doi.org/10.1073/pnas.1300127110>
- [11] Gao, R., Wang, H., Dong, B., Yang, X., Chen, S., Jiang, J., Zhang, Z., Liu, C., Zhao, N. and Chen, F. (2016) Morphological, Genome and Gene Expression Changes in Newly Induced Autopolyploid *Chrysanthemum lavandulifolium* (Fisch. ex Trautv.) Makino. *International Journal of Molecular Sciences*, **17**, 1690. <https://doi.org/10.3390/ijms17101690>
- [12] Liu, S., Yang, Y., Wei, F., Duan, J., Braynen, J., Tian, B., Cao, G., Shi, G. and Yuan, J. (2017) Autopolyploidy Leads to Rapid Genomic Changes in *Arabidopsis thaliana*. *Theory in Biosciences*, **136**, 199-206. <https://doi.org/10.1007/s12064-017-0252-3>
- [13] Xu, Y., Zhang, W., Chen, G. and Wang, J. (2017) DNA Methylation Alteration Is a Major Consequence of Genome Doubling in Autotetraploid *Brassica rapa*. *Archives of Biological Sciences*, **69**, 689-697. <https://doi.org/10.2298/ABS170131015X>
- [14] Dar, T.H., Raina, S.N. and Goel, S. (2017) Cytogenetic and Molecular Evidences Revealing Genomic Changes after Autopolyploidization: A Case Study of Synthetic Autotetraploid *Phlox drummondii* Hook. *Physiology and Molecular Biology of Plants*, **23**, 641-650. <https://doi.org/10.1007/s12298-017-0445-8>
- [15] Hollister, J.D., Arnold, B.J., Svedin, E., Xue, K.S., Dilkes, B.P. and Bomblies, K. (2012) Genetic Adaptation Associated with Genome-Doubling in Autotetraploid *Arabidopsis arenosa*. *PLOS Genetics*, **8**, e1003093. <https://doi.org/10.1371/journal.pgen.1003093>
- [16] Martelotto, L., Ortiz, J.P.A., Juliana, S., Francisco, E., Quarin, C. and Silvina, C.P. (2005) A Comprehensive Analysis of Gene Expression Alterations in a Newly Synthesized *Paspalum notatum* Autotetraploid. *Plant Science*, **169**, 211-220.

- <https://doi.org/10.1016/j.plantsci.2005.03.015>
- [17] Lu, B., Pan, X., Zhang, L., Huang, B., Sun, L., Li, B., Yi, B., Zheng, S., Yu, X., Ding, R. and Chen, W. (2006) A Genome-Wide Comparison of Genes Responsive to Autopolyploidy in *Isatis indigotica* Using *Arabidopsis thaliana* Affymetrix Genechips. *Plant Molecular Biology Reporter*, **24**, 197-204. <https://doi.org/10.1007/BF02914058>
- [18] Stupar, R.M., Bhaskar, P.B., Yandell, B.S., Rensink, W.A., Hart, A.L., Ouyang, S., Veilleux, R.E., Busse, J.S., Erhardt, R.J., Buell, C.R. and Jiang, J. (2007) Phenotypic and Transcriptomic Changes Associated with Potato Autopolyploidization. *Genetics*, **176**, 2055-2067. <https://doi.org/10.1534/genetics.107.074286>
- [19] Zhang, X., Deng, M. and Fan, G. (2014) Differential Transcriptome Analysis between *Paulownia fortunei* and Its Synthesized Autopolyploid. *International Journal of Molecular Sciences*, **15**, 5079-5093. <https://doi.org/10.3390/ijms15035079>
- [20] Dai, F., Wang, Z., Luo, G. and Tang, C. (2015) Phenotypic and Transcriptomic Analyses of Autotetraploid and Diploid Mulberry (*Morus alba* L.). *International Journal of Molecular Sciences*, **16**, 22938-22956. <https://doi.org/10.3390/ijms160922938>
- [21] Yan, L., Fan, G., Deng, M., Zhao, Z., Dong, Y. and Li, Y. (2017) Comparative Proteomic Analysis of Autotetraploid and Diploid *Paulownia tomentosa* Reveals Proteins Associated with Superior Photosynthetic Characteristics and Stress Adaptability in Autotetraploid *Paulownia*. *Physiology and Molecular Biology of Plants*, **23**, 605-617. <https://doi.org/10.1007/s12298-017-0447-6>
- [22] Visger, C., Wong, G.K.S., Zhang, Y., Soltis, P.S. and Soltis, D.E. (2019) Divergent Gene Expression Levels between Diploid and Autotetraploid *Tolmiea* (Saxifragaceae) Relative to the Total Transcriptome, the Cell, and Biomass. *American Journal of Botany*, **106**, 280-291. <https://doi.org/10.1002/ajb2.1239>
- [23] Fan, G. (2015) Transcriptome Analysis of the Variations between Autotetraploid *Paulownia tomentosa* and Its Diploid Using High-Throughput Sequencing. *Molecular Genetics and Genomics*, **290**, 1627-1638. <https://doi.org/10.1007/s00438-015-1023-9>
- [24] Saminathan, T., Nimmakayala, P., Manohar, S., Malkaram, S., Almeida, A., Cantrell, R., Tomason, Y., Abburri, L., Rahman, M.A., Vajja, V.G., Khachane, A., Kumar, B., Rajasimha, H.K., Levi, A., Wehner, T. and Reddy, U.K. (2015) Differential Gene Expression and Alternative Splicing between Diploid and Tetraploid Watermelon. *Journal of Experimental Botany*, **66**, 1369-1385. <https://doi.org/10.1093/jxb/eru486>
- [25] Zhang, H., Zhao, H., Wu, S., Huang, F., Wu, K., Zeng, X., Chen, X., Xu, P. and Wu, X. (2016) Global Methylation Patterns and Their Relationship with Gene Expression and Small RNA in Rice Lines with Different Ploidy. *Frontiers in Plant Science*, **7**, 1002. <https://doi.org/10.3389/fpls.2016.01002>
- [26] He, P., Cheng, L., Li, H., Wang, H. and Li, L. (2017) A Comparative Analysis of DNA Methylation in Diploid and Tetraploid Apple (*Malus × domestica* Borkh.). *Current Opinion in Plant Biology*, **53**, 135-141. <https://doi.org/10.17221/55/2016-CJGPB>
- [27] Weiss, H. and Maluszynska, J. (2000) Chromosomal Rearrangement in Autotetraploid Plants of *Arabidopsis thaliana*. *Hereditas*, **133**, 255-261. <https://doi.org/10.1111/j.1601-5223.2000.00255.x>
- [28] Zhang, J., Liu, Y., Xia, E.H., Yao, Q.Y., Liu, X.D. and Gao, L.Z. (2015) Autotetraploid Rice Methylome Analysis Reveals Methylation Variation of Transposable Elements and Their Effects on Gene Expression. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, E7022-E7029.

- <https://doi.org/10.1073/pnas.1515170112>
- [29] Dong, B., Wang, H., Song, A., Liu, T., Chen, Y., Fang, W., Chen, S., Chen, F., Guan, Z. and Jiang, J. (2016) miRNAs Are Involved in Determining the Improved Vigor of Autotetraploid *Chrysanthemum nankingense*. *Frontiers in Plant Science*, **7**, 1412. <https://doi.org/10.3389/fpls.2016.01412>
- [30] Zhang, F., Zhao, J., Xu, S., Fang, W., Chen, F. and Teng, N. (2017) MicroRNA and Putative Target Discoveries in *Chrysanthemum* Polyploidy Breeding. *International Journal of Genomics*, **2017**, Article ID: 6790478. <https://doi.org/10.1155/2017/6790478>
- [31] Rastogi, S. and Liberles, D. (2005) Subfunctionalization of Duplicated Gene as a Transition State to Neofunctionalization. *BMC Evolutionary Biology*, **5**, 28. <https://doi.org/10.1186/1471-2148-5-28>
- [32] Conant, G.C. and Wolfe, K.H. (2008) Turning a Hobby into a Job: How Duplicated Genes Find New Functions. *Nature Reviews Genetics*, **9**, 938-950. <https://doi.org/10.1038/nrg2482>
- [33] Drea, S.C., Lao, N.T., Wolfe, K.H. and Kavanagh, T.A. (2006) Gene Duplication, Exon Gain and Neofunctionalization of *OEPI6*-Related Genes in Land Plants. *The Plant Journal*, **46**, 723-735. <https://doi.org/10.1111/j.1365-313X.2006.02741.x>
- [34] Erdmann, R., Gramzow, L., Melzer, R., Theissen, G. and Becker, A. (2010) *GORDITA* (*AGL63*) Is a Young Paralog of the *Arabidopsis thaliana* B (Sister) *MADS* Box Gene *ABS* (*TT16*) That Has Undergone Neofunctionalization. *The Plant Journal*, **63**, 914-924. <https://doi.org/10.1111/j.1365-313X.2010.04290.x>
- [35] Mena, M., Ambrose, B., Meeley, R., Briggs, S., Yanofsky, M. and Schmidt, R. (1996) Diversification of C-Function Activity in Maize Flower Development. *Science*, **274**, 1537. <https://doi.org/10.1126/science.274.5292.1537>
- [36] Hu, C., Lin, S., Chi, W. and Charng, Y. (2012) Recent Gene Duplication and Subfunctionalization Produced a Mitochondrial GrpE, the Nucleotide Exchange Factor of the Hsp70 Complex, Specialized in Thermotolerance to Chronic Heat Stress in *Arabidopsis*. *Plant Physiology*, **158**, 747-758. <https://doi.org/10.1104/pp.111.187674>
- [37] D'Amelia, V., Aversano, R., Ruggiero, A., Batelli, G., Appelhagen, I., Dinacci, C., Hill, L., Martin, C. and Carputo, D. (2018) Subfunctionalization of Duplicate *MYB* Genes in *Solanum commersonii* Generated the Cold-Induced *ScAN2* and the Anthocyanin Regulator *ScAN1*. *Plant, Cell & Environment*, **41**, 1038-1051. <https://doi.org/10.1111/pce.12966>
- [38] Albuzio, A., Spettoli, P. and Cacco, G. (1978) Changes in Gene Expression from Diploid to Autotetraploid Status of *Lycopersicon esculentum*. *Physiologia Plantarum*, **44**, 77-80. <https://doi.org/10.1111/j.1399-3054.1978.tb01617.x>
- [39] Amadeu, R.R., Ferrao, L.F., Oliveira, I.B., Benevenuto, J., Endelman, J. and Munoz, P.R. (2019) Impact of Dominance Effects on Autotetraploid Genomic Prediction. *Crop Science*, **60**, 656-665. <https://doi.org/10.1002/csc2.20075>
- [40] Ghaleb, M.A.A., Li, C., Shahid, M.Q., Yu, H., Liang, J., Chen, R., Wu, J. and Liu, X. (2020) Heterosis Analysis and Underlying Molecular Regulatory Mechanism in a Wide Compatible Neo-Tetraploid Rice Line with Long Panicles. *BMC Plant Biology*, **20**, 83. <https://doi.org/10.1186/s12870-020-2291-z>
- [41] Lavania, U.C. (2020) Plant Speciation and Polyploidy: In Habitat Divergence and Environmental Perspective. *Nucleus*, **63**, 1-5. <https://doi.org/10.1007/s13237-020-00311-6>
- [42] Wang, B., Sang, Y., Song, J., Gao, X.Q. and Zhang, X. (2009) Expression of a Rice *OsARGOS* Gene in *Arabidopsis* Promotes Cell Division and Expansion and In-

- creases Organ Size. *Journal of Genetics and Genomics*, **36**, 31-40.
[https://doi.org/10.1016/S1673-8527\(09\)60004-7](https://doi.org/10.1016/S1673-8527(09)60004-7)
- [43] Allario, T., Brumos, J., Colmenero-Flores, J.M., Tadeo, F., Froelicher, Y., Talon, M., Navarro, L., Ollitrault, P. and Morillon, R. (2011) Large Changes in Anatomy and Physiology between Diploid Rangpur Lime (*Citrus limonia*) and Its Autotetraploid Are Not Associated with Large Changes in Leaf Gene Expression. *Journal of Experimental Botany*, **62**, 2507-2519. <https://doi.org/10.1093/jxb/erq467>
- [44] Gu, A.X., Zhao, J.J., Li, L.M., Wang, Y.H., Zhao, Y.J., Hua, F., Xu, Y.C. and Shen, S.X. (2016) Analyses of Phenotype and ARGOS and ASY1 Expression in a Ploidy Chinese Cabbage Series Derived from One Haploid. *Breeding Science*, **66**, 161-168. <https://doi.org/10.1270/jsbbs.66.161>
- [45] Qiao, G., Liu, M., Song, K., Li, H., Yang, H., Yin, Y. and Zhuo, R. (2017) Phenotypic and Comparative Transcriptome Analysis of Different Ploidy Plants in *Dendrocalamus latiflorus* Munro. *Frontiers in Plant Science*, **8**, 1371. <https://doi.org/10.3389/fpls.2017.01371>
- [46] Bird, D., Beisson, F., Brigham, A., Shin, J., Greer, S., Jetter, R., Kunst, L., Wu, X., Yephremov, A. and Samuels, L. (2007) Characterization of *Arabidopsis* ABCG11/WBC11, an ATP Binding Cassette (ABC) Transporter That Is Required for Cuticular Lipid Secretion. *Plant Journal*, **52**, 485-498. <https://doi.org/10.1111/j.1365-313X.2007.03252.x>
- [47] Narukawa, H., Yokoyama, R., Komaki, S., Sugimoto, K. and Nishitani, K. (2015) Stimulation of Cell Elongation by Tetraploidy in Hypocotyls of Dark-Grown *Arabidopsis* Seedlings. *PLoS ONE*, **10**, e0134547. <https://doi.org/10.1371/journal.pone.0134547>
- [48] Narukawa, H., Yokoyama, R. and Nishitani, K. (2016) Possible Pathways Linking Ploidy Level to Cell Elongation and Cuticular Function in Hypocotyls of Dark-Grown *Arabidopsis* Seedlings. *Plant Signaling and Behavior*, **11**, e1118597. <https://doi.org/10.1080/15592324.2015.1118597>
- [49] Zhou, Y., Kang, L., Liao, S., Pan, Q., Ge, X. and Li, Z. (2015) Transcriptomic Analysis Reveals Differential Gene Expressions for Cell Growth and Functional Secondary Metabolites in Induced Autotetraploid of Chinese Woad (*Isatis indigotica* Fort.). *PLoS ONE*, **10**, e0116392. <https://doi.org/10.1371/journal.pone.0116392>
- [50] Wang, Z., Fan, G., Dong, Y., Zhai, X., Deng, M., Zhao, Z., Liu, W. and Cao, Y. (2017) Implications of Polyploidy Events on the Phenotype, Microstructure, and Proteome of *Paulownia australis*. *PLoS ONE*, **12**, e0172633. <https://doi.org/10.1371/journal.pone.0172633>
- [51] Lavania, U.C., Srivastava, S., Lavania, S., Basu, S., Misra, N.K. and Mukai, Y. (2012) Autopolyploidy Differentially Influences Body Size in Plants, But Facilitates Enhanced Accumulation of Secondary Metabolites, Causing Increased Cytosine Methylation. *The Plant Journal*, **71**, 539-549. <https://doi.org/10.1111/j.1365-313X.2012.05006.x>
- [52] Alam, H., Razaq, M. and Salahuddin (2015) Induced Polyploidy as a Tool for Increasing Tea (*Camellia sinensis* L.). *Production Journal of Northeast Agricultural University (English Edition)*, **22**, 43-47. [https://doi.org/10.1016/S1006-8104\(16\)30005-8](https://doi.org/10.1016/S1006-8104(16)30005-8)
- [53] Mu, H., Liu, Z., Lin, L., Li, H., Jiang, J. and Liu, G. (2012) Transcriptomic Analysis of Phenotypic Changes in Birch (*Betula platyphylla*) Autotetraploids. *International Journal of Molecular Sciences*, **13**, 13012-13029. <https://doi.org/10.3390/ijms131013012>

- [54] Ma, Y., Xue, H., Zhang, L., Zhang, F., Ou, C., Wang, F. and Zhang, Z. (2016) Involvement of Auxin and Brassinosteroid in Dwarfism of Autotetraploid Apple (*Malus × domestica*). *Scientific Reports*, **6**, Article No. 26719. <https://doi.org/10.1038/srep26719>
- [55] Gantait, S. and Mukherjee, E. (2021) Induced Autopolyploidy—A Promising Approach for Enhanced Biosynthesis of Plant Secondary Metabolites: An Insight. *Genetic Engineering and Biotechnology*, **19**, 4. <https://doi.org/10.1186/s43141-020-00109-8>
- [56] Mishra, B., Pathak, S., Sharma, A., Trivedi, P. and Shukla, S. (2010) Modulated Gene Expression in Newly Synthesized Auto-Tetraploid of *Papaver somniferum* L. *South African Journal of Botany*, **76**, 447-452. <https://doi.org/10.1016/j.sajb.2010.02.090>
- [57] Vergara, F., Kikuchi, J. and Breuer, C. (2016) Artificial Autopolyploidization Modifies the Tricarboxylic Acid Cycle and GABA Shunt in *Arabidopsis thaliana* Col-0. *Scientific Reports*, **6**, Article No. 26515. <https://doi.org/10.1038/srep26515>
- [58] Dou, J., Yuan, P., Zhao, S., He, N., Zhu, H., Gao, L., Ji, W., Lu, X. and Liu, W. (2017) Effect of Ploidy Level on Expression of Lycopene Biosynthesis Genes and Accumulation of Phytohormones during Watermelon (*Citrullus lanatus*) Fruit Development and Ripening. *Journal of Integrative Agriculture*, **16**, 1956-1967. [https://doi.org/10.1016/S2095-3119\(16\)61618-0](https://doi.org/10.1016/S2095-3119(16)61618-0)
- [59] Javadian, N., Karimzadeh, G., Sharifi, M., Moieni, A. and Behmanesh, M. (2017) *In Vitro* Polyploidy Induction: Changes in Morphology, Podophyllotoxin Biosynthesis, and Expression of the Related Genes in *Linum album* (*Linaceae*). *Planta*, **245**, 1165-1178. <https://doi.org/10.1007/s00425-017-2671-2>
- [60] Chung, H.H., Shi, S.K., Huang, B. and Chen, J.T. (2017) Enhanced Agronomic Traits and Medicinal Constituents of Autotetraploids in *Anoectochilus formosanus* Hayata, a Top-Grade Medicinal Orchid. *Molecules*, **22**, 1907. <https://doi.org/10.3390/molecules22111907>
- [61] Preet, R. and Gupta, R.C. (2017) Fatty Acid Profiling in Diploid (n = 12) and Tetraploid Cytotypes (n = 24) of *Physalis angulata* Linn. from Rajasthan by Gas Chromatography. *International Journal of Pharmaceutical Sciences and Research*, **8**, 3458-3462.
- [62] Sattler, M.C., Carvalho, C.R. and Clarindo, W.R. (2015) The Polyploidy and Its Key Role in Plant Breeding. *Planta*, **243**, 281-296. <https://doi.org/10.1007/s00425-015-2450-x>
- [63] Pegoraro, L., Cafasso, D., Rinaldi, R., Cozzolino, S. and Scopece, G. (2016) Habitat Preference and Flowering-Time Variation Contribute to Reproductive Isolation Between Diploid and Autotetraploid *Anacamptis pyramidalis*. *Journal of Evolutionary Biology*, **29**, 2070-2082. <https://doi.org/10.1111/jeb.12930>
- [64] Shi, F., Wang, Y., Huang, S., Dong, S., Liu, Z. and Feng, H. (2020) Investigation of Genes Associated with Petal Variations between Diploid and Autotetraploid in Chinese Cabbage (*Brassica rapa* L. ssp. *pekinensis*) by RNA-seq and sRNA-seq. *Molecular Genetics and Genomics*, **295**, 1459-1476. <https://doi.org/10.1007/s00438-020-01713-6>
- [65] Morgan, C., Zhang, H., Henry, C.E., Chris, F., Franklin, H. and Bomblies, K. (2020) Derived Alleles of Two Axis Proteins Affect Meiotic Traits in Autotetraploid *Arabidopsis arenosa*. *PNAS*, **117**, 8980-8988. <https://doi.org/10.1073/pnas.1919459117>
- [66] Seear, P.J., France, M.G., Gregory, C.L., Heavens, D., Schmickl, R., Yant, L. and Higgins, J.D. (2020) A Novel Allele of *ASY3* Is Associated with Greater Meiotic Sta-

- bility in Autotetraploid *Arabidopsis lyrata*. *PLOS Genetics*, **16**, e1008900. <https://doi.org/10.1371/journal.pgen.1008900>
- [67] Münzbergová, Z. and Skuhrovec, J. (2017) Contrasting Effects of Ploidy Level on Seed Production in a Diploid-Tetraploid System. *AoB Plants*, **9**, plw077. <https://doi.org/10.1093/aobpla/plw077>
- [68] Guo, H., Shahid, M.Q., Zhao, J., Li, Y., Wang, L. and Liu, X. (2016) Agronomic Traits and Cytogenetic Evaluation of Newly Developed Autotetraploid Rice Line. *Pakistan Journal of Agricultural Sciences*, **53**, 291-301. <https://doi.org/10.21162/PAKJAS/16.3143>
- [69] Wu, J., Chen, Y., Lin, H., Chen, Y., Yu, H., Lu, Z., Li, X., Zhou, H., Chen, Z. and Liu, X. (2020) Comparative Cytological and Transcriptome Analysis Revealed the Normal Pollen Development Process and Up-Regulation of Fertility-Related Genes in Newly Developed Tetraploid Rice. *International Journal of Molecular Sciences*, **21**, 7046. <https://doi.org/10.3390/ijms21197046>
- [70] Meng, H., Jiang, S., Hua, S., Lin, X., Li, Y., Guo, W. and Jiang, L. (2013) Comparison between a Tetraploid Turnip and Its Diploid Progenitor (*Brassica rapa* L.): The Adaptation to Salinity Stress. *Agricultural Sciences in China*, **10**, 363-375. [https://doi.org/10.1016/S1671-2927\(11\)60015-1](https://doi.org/10.1016/S1671-2927(11)60015-1)
- [71] Tu, Y., Jiang, A., Gan, L., Hossain, M., Zhang, J., Peng, B., Xiong, Y., Song, Z., Cai, D., Xu, W., Zhang, J. and He, Y. (2014) Genome Duplication Improves Rice Root Resistance to Salt Stress. *Rice*, **7**, 15. <https://doi.org/10.1186/s12284-014-0015-4>
- [72] Xue, H., Zhang, F., Zhang, Z., Fu, J., Wang, F., Zhang, B. and Ma, Y. (2015) Differences in Salt Tolerance between Diploid and Autotetraploid Apple Seedlings Exposed to Salt Stress. *Scientia Horticulturae*, **190**, 24-30. <https://doi.org/10.1016/j.scienta.2015.04.009>
- [73] Yan, K., Wu, C., Zhang, L. and Chen, X. (2015) Contrasting Photosynthesis and Photoinhibition in Tetraploid and Its Autodiploid Honeysuckle (*Lonicera japonica* Thunb.) under Salt Stress. *Frontiers of Plant Science*, **6**, 227. <https://doi.org/10.3389/fpls.2015.00227>
- [74] Fan, G., Li, X., Deng, M., Zhao, Z. and Yang, L. (2016) Comparative Analysis and Identification of miRNAs and Their Target Genes Responsive to Salt Stress in Diploid and Tetraploid *Paulownia fortunei* Seedlings. *PLoS ONE*, **11**, e0149617. <https://doi.org/10.1371/journal.pone.0149617>
- [75] Fan, G., Wang, L., Deng, M., Zhao, Z., Dong, Y., Zhang, X. and Li, Y. (2016) Changes in Transcript Related to Osmosis and Intracellular Ion Homeostasis in *Paulownia tomentosa* under Salt Stress. *Frontiers in Plant Science*, **7**, 384. <https://doi.org/10.3389/fpls.2016.00384>
- [76] Yu, L., Liu, X., Boge, W. and Liu, X. (2016) Genome-Wide Association Study Identifies Loci for Salt Tolerance during Germination in Autotetraploid Alfalfa (*Medicago sativa* L.) Using Genotyping-by-Sequencing. *Frontiers in Plant Science*, **7**, 956. <https://doi.org/10.3389/fpls.2016.00956>
- [77] Deng, M., Dong, Y., Zhao, Z., Li, Y. and Fan, G. (2017) Dissecting the Proteome Dynamics of the Salt Stress Induced Changes in the Leaf of Diploid and Autotetraploid *Paulownia fortunei*. *PLoS ONE*, **12**, e0181937. <https://doi.org/10.1371/journal.pone.0181937>
- [78] Liu, B. and Sun, G. (2017) microRNAs Contribute to Enhanced Salt Adaptation of the Autopolyploid *Hordeum bulbosum* Compared with Its Diploid Ancestor. *Plant Journal*, **91**, 57-69. <https://doi.org/10.1111/tpj.13546>
- [79] Zhao, Z., Li, Y., Liu, H., Zhai, X., Deng, M., Dong, Y. and Fan, G. (2017) Ge-

- nome-Wide Expression Analysis of Salt-Stressed Diploid and Autotetraploid *Paulownia tomentosa*. *PLoS ONE*, **12**, e0185455. <https://doi.org/10.1371/journal.pone.0185455>
- [80] del Pozo, J.C. and Ramirez-Parra, E. (2014) Deciphering the Molecular Bases for Drought Tolerance in *Arabidopsis* Autotetraploids. *Plant, Cell and Environment*, **37**, 2722-2737. <https://doi.org/10.1111/pce.12344>
- [81] Niu, S., Wang, Y., Zhao, Z., Deng, M., Cao, L., Yang, L. and Fan, G. (2016) 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*, **11**, e0158750. <https://doi.org/10.1371/journal.pone.0158750>
- [82] Cao, X., Fan, G., Cao, L., Deng, M., Zhao, Z., Niu, S., Wang, Z. and Wang, Y. (2017) Drought Stress-Induced Changes of microRNAs in Diploid and Autotetraploid *Paulownia tomentosa*. *Genes and Genomics*, **39**, 77-86. <https://doi.org/10.1007/s13258-016-0473-8>
- [83] Zhao, Z., Niu, S., Fan, G., Deng, M. and Wang, Y. (2018) 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*, **9**, 88. <https://doi.org/10.3390/f9020088>
- [84] Rao, S., Tian, Y., Xia, X., Li, Y. and Chen, J. (2020) Chromosome Doubling Mediates Superior Drought Tolerance in *Lycium ruthenicum* via Abscisic Acid Signaling. *Horticulture Research*, **7**, 40. <https://doi.org/10.1038/s41438-020-0260-1>
- [85] Zhang, X.Y., Hu, C.G. and Yao, J.L. (2010) Tetraploidization of Diploid *Dioscorea* Results in Activation of the Antioxidant Defense System and Increased Heat Tolerance. *Journal of Plant Physiology*, **167**, 88-94. <https://doi.org/10.1016/j.jplph.2009.07.006>
- [86] Deng, B., Du, W., Liu, C.L., Sun, W., Tian, S. and Dong, H. (2012) 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*, **66**, 37-47. <https://doi.org/10.1007/s10725-011-9626-6>
- [87] Syngelaki, E., Daubert, M., Klatt, S. and Hörandl, E. (2020) Phenotypic Responses, Reproduction Mode and Epigenetic Patterns under Temperature Treatments in the Alpine Plant Species *Ranunculus kuepferi* (*Ranunculaceae*). *Biology*, **9**, 315. <https://doi.org/10.3390/biology9100315>
- [88] Ruiz, M., Quiñones, A., Martínez-Alcántara, B., Aleza, P., Morillon, R., Navarro, L., Primo-Millo, E. and Martínez-Cuenca, M. (2016) Tetraploidy Enhances Boron-Excess Tolerance in Carrizo Citrange (*Citrus sinensis* L. Osb. × *Poncirus trifoliata* L. Raf.). *Frontiers in Plant Science*, **7**, 701. <https://doi.org/10.3389/fpls.2016.00701>
- [89] Li, M., Xu, G., Xia, X., Wang, M., Yin, X., Zhang, B., Zhang, X. and Cui, Y. (2017) Deciphering the Physiological and Molecular Mechanisms for Copper Tolerance in Autotetraploid *Arabidopsis*. *Plant Cell Reports*, **36**, 1585-1597. <https://doi.org/10.1007/s00299-017-2176-2>
- [90] Mu, H., Lin, L., Zhang, Q., Tang, X., Zhang, X. and Cheng, G. (2016) Growth, Proline Content and Proline-Associated Gene Expression of Autotetraploid *Betula platyphylla* Responding to NaHCO₃ Stress. *Dendrobiology*, **75**, 123-129. <https://doi.org/10.12657/denbio.075.012>
- [91] Hias, N., Svava, A. and Wannes Keulemans, J. (2018) Effect of Polyploidisation on the Response of Apple (*Malus* × *domestica* Borkh.) to *Venturia inaequalis* Infection. *European Journal of Plant Pathology*, **151**, 515-526. <https://doi.org/10.1007/s10658-017-1395-2>

- [92] Jansky, S., Haynes, K. and Douches, D. (2019) 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*, **96**, 255-261. <https://doi.org/10.1007/s12230-018-09711-6>
- [93] Ramsey, J. and Ramsey, T.S. (2014) Ecological Studies of Polyploidy in the 100 Years Following Its Discovery. *Philosophical Transaction of the Royal Society B*, **369**, Article ID: 20130352. <https://doi.org/10.1098/rstb.2013.0352>
- [94] Spoelhof, J.P., Soltis, P.S. and Soltis, D.E. (2017) Pure Polyploidy: Closing the Gaps in Autopolyploid Research. *Journal of Systematics and Evolution*, **55**, 340-352. <https://doi.org/10.1111/jse.12253>
- [95] Baduel, P., Quadrana, L., Hunter, B., Bomblies, K. and Colot, V. (2019) Relaxed Purifying Selection in Autopolyploids Drives Transposable Element Over-Accumulation Which Provides Variants for Local Adaptation. *Nature Communications*, **10**, 5818. <https://doi.org/10.1038/s41467-019-13730-0>
- [96] Campos, H. and Ortiz (2020) The Potato Crop. Its Agricultural, Nutritional and Social Contribution to Humankind. Springer, Berlin. <https://doi.org/10.1007/978-3-030-28683-5>
- [97] FAO, IFAD, UNICEF, WFP and WHO (2018) The State of Food Security and Nutrition in the World 2018. Building Climate Resilience for Food Security and Nutrition. FAO, Rome.
- [98] Devaux, A., Goffart, J.P., Petsakos, A., Kromann, P., Gatto, M., Okello, J., Suarez, V. and Hareau, G. (2020) Global Food Security, Contributions from Sustainable Potato Agri-Food Systems. In: Campos, H. and Ortiz, O., Eds., *The Potato Crop*, Springer, Berlin, 3-35, Chapter 1. https://doi.org/10.1007/978-3-030-28683-5_1
- [99] Stokstad, E. (2019) The New Potato, Breeders Seek a Breakthrough to Help Farmers Facing an Uncertain Future. *Science*, **363**, 574-577. <https://doi.org/10.1126/science.363.6427.574>
- [100] Bamberg, J. and Greenway, G. (2019) Nutritional and Economic Prospects for Expanded Potato Outlets. *American Journal of Potato Research*, **96**, 206-215. <https://doi.org/10.1007/s12230-018-09698-0>
- [101] Wijesinha-Bettoni, R. and Mouillé, B. (2019) The Contribution of Potatoes to Global Food Security, Nutrition and Healthy Diets. *American Journal of Potato Research*, **96**, 139-149. <https://doi.org/10.1007/s12230-018-09697-1>
- [102] Kanter, R., Walls, H.L., Tak, M., Roberts, F. and Waage, J. (2015) A Conceptual Framework for Understanding the Impacts of Agriculture and Food System Policies on Nutrition and Health. *Food Security*, **7**, 767-777. <https://doi.org/10.1007/s12571-015-0473-6>
- [103] Navarre, D.A., Brown, C.R. and Sathuvalli, V.R. (2019) Potato Vitamins, Minerals and Phytonutrients from a Plant Biology Perspective. *American Journal of Potato Research*, **96**, 111-126. <https://doi.org/10.1007/s12230-018-09703-6>
- [104] Jansky, S., Navarre, R. and Bamberg, J. (2019) Introduction to the Special Issue on the Nutritional Value of Potato. *American Journal of Potato Research*, **96**, 95-97. <https://doi.org/10.1007/s12230-018-09708-1>
- [105] Machida-Hirano, R. (2015) Diversity of Potato Genetic Resources. *Breeding Science*, **65**, 26-40. <https://doi.org/10.1270/jsbbs.65.26>
- [106] Hawkes, J.G. (1990) The Potato: Evolution, Biodiversity and Genetic Resources. *American Potato Journal*, **67**, 733-735. <https://doi.org/10.1007/BF03044023>
- [107] Watanabe, K.N. (2015) Potato Genetics, Genomics, and Applications. *Breeding*

- Science*, **65**, 53-68. <https://doi.org/10.1270/jsbbs.65.53>
- [108] Muthoni, J., Kabira, J., Shimelis, H. and Melis, R. (2015) Tetrasomic Inheritance in Cultivated Potato and Implications in Conventional Breeding. *Australian Journal of Crop Science*, **9**, 185-190.
- [109] Jansky, S.H. and Spooner, D.M. (2018) The Evolution of Potato Breeding. *Plant Breeding Review*, **41**, 169-214. <https://doi.org/10.1002/9781119414735.ch4>
- [110] Ortiz, R. and Mihovilovich, E. (2020) Genetics and Cytogenetics of the Potato. In: Campos, H. and Ortiz, O., Eds., *The Potato Crop*, Springer, Berlin, Chapter 7, 219-247. https://doi.org/10.1007/978-3-030-28683-5_7
- [111] Ortiz, R. (2020) Genomic-Led Potato Breeding for Increasing Genetic Gains: Achievements and Outlook. *Crop Breeding Genetics and Genomics*, **2**, e200010.
- [112] Hosaka, K. and Sanetomo, R. (2020) Broadening Genetic Diversity of the Japanese Potato Gene Pool. *American Journal of Potato Research*, **97**, 127-142. <https://doi.org/10.1007/s12230-020-09762-8>
- [113] Odilbekov, F., Selga, C., Ortiz, R., Chawade, A. and Liljeroth, E. (2020) QTL Mapping for Resistance to Early Blight in a Tetraploid Potato Population. *Agronomy*, **10**, 728. <https://doi.org/10.3390/agronomy10050728>
- [114] Jansky, S., Douches, D. and Haynes, K. (2018) Transmission of Scab Resistance to Tetraploid Potato via Unilateral Sexual Polyploidization. *American Journal of Potato Research*, **95**, 272-277. <https://doi.org/10.1007/s12230-017-9628-7>
- [115] Li, J., Wang, Y., Wen, G., Li, G., Li, Z., Zhang, R., Ma, S., Zhou, J. and Xie, C. (2019) Mapping QTL Underlying Tuber Starch Content and Plant Maturity in Tetraploid Potato. *The Crop Journal*, **7**, 261-272. <https://doi.org/10.1016/j.cj.2018.12.003>
- [116] Alexandersson, E., Kushwaha, S., Subedi, A., Weighill, D., Climer, S., Jacobson, D. and Andreasson, E. (2020) Linking Crop Traits to Transcriptome Differences in a Progeny Population of Tetraploid Potato. *BMC Plant Biology*, **20**, 120. <https://doi.org/10.1186/s12870-020-2305-x>
- [117] Morris, W.L. and Taylor, M.A. (2019) Improving Flavor to Increase Consumption. *American Journal of Potato Research*, **96**, 195-200. <https://doi.org/10.1007/s12230-018-09702-7>
- [118] Lian, Q., Tang, D., Bai, Z., Qi, J., Lu, F., Huang, S. and Zhang, C. (2019) Acquisition of Deleterious Mutations during Potato Polyploidization. *Journal of Integrative Plant Biology*, **61**, 7-11. <https://doi.org/10.1111/jipb.12748>
- [119] Petek, M., Zagorščak, M., Ramšak, Ž., Sanders, S., Tomaž, Š., Tseng, E., Zouine, M., Coll, A. and Gruden, K. (2020) Cultivar-Specific Transcriptome and Pan-Transcriptome Reconstruction of Tetraploid Potato. *Scientific Data*, **7**, 249. <https://doi.org/10.1038/s41597-020-00581-4>
- [120] Bethke, P.C., Halterman, D.A. and Jansky, S.H. (2019) Potato Germplasm Enhancement Enters the Genomics Era. *Agronomy*, **9**, 575. <https://doi.org/10.3390/agronomy9100575>
- [121] Kyriakidou, M., Anglin, N.L., Ellis, D., Tai, H.H. and Strömviik, M.V. (2020) Genome Assembly of Six Polyploidy Potato Genomes. *Scientific Data*, **7**, 88. <https://doi.org/10.1038/s41597-020-0428-4>
- [122] Ma, J., Zheng, A., Zhou, P., Yuan, Q., Wu, R., Chen, C., Wu, X., Zhang, F. and Sun, B. (2019) Targeted Editing of the *StPDS* Gene Using the CRISPR/Cas9 System in Tetraploid Potato. *Emirates Journal of Food and Agriculture*, **31**, 482-490. <https://doi.org/10.9755/ejfa.2019.v31.i7.1974>
- [123] Veillet, F., Kermarrec, M.-P., Chauvin, L., Guyon-Debast, A., Chauvin, J.-E., Gal-

- lois, J.L. and Nogue, F. (2020) Prime Editing Is Achievable in the Tetraploid Potato, But Needs Improvement. <https://doi.org/10.1101/2020.06.18.159111>
- [124] Dar, J., Beigh, Z. and Wani, A.A. (2017) Polyploidy: Evolution and Crop Improvement. In: Bhat, T.A. and Wani, A.A., Eds., *Chromosome Structure and Aberrations*, Springer, Berlin, 201-218. https://doi.org/10.1007/978-81-322-3673-3_10