



## AGRICULTURAL DEVELOPMENT BASED ON POLYPLOIDIZATION: A PERSPECTIVE CONTRIBUTION OF MINOR CROPS

P.V. HIEU

Biotechnology Center of Ho Chi Minh, Ho Chi Minh City, Vietnam  
 Corresponding author's e-mail: hieupvbio@gmail.com

### SUMMARY

Polyploidization is commonly known to become a vital process to succeed in developing potential crops. In the plant kingdom, the polyploids, i.e., aneuploidy and polyploidy, are generally developed through sexual and asexual pathways, resulting in totally increasing biomass, phytochemical compounds, and adaptation to detrimental environment. For more precision, thousands of polyploidy plant species adapted to various climatic and topographic conditions through genomic evolution. Autopolyploid, allopolyploid, and aneuploidy, as well as, different levels of ploidy are simply found in vegetables, such as, potatoes, and among fruits, i.e., bananas, watermelon, and so on. Contrastingly, in mammals, polyploidization causes congenital diseases and pregnancy loss, especially in human beings. This review article will first describe polyploidization in plants and then enumerate the advantages of its beneficial effects that are more valuable. The paper also intends to introduce new knowledge on polyploidization in crop breeding. Thus, it has further mentioned the polyploid like aneuploidy and polyploidy in a perspective contribution of minor crops in plant kingdoms and their beneficial and detrimental effects in the development of crop strategies.

**Keywords:** polyploidization, minor crops, evolution, agriculture, climate change

**Key findings:** This review sheds light on 1) discussing polyploidization in plants and then mentioning the benefits of its effects that are more valuable; 2) it further proves the perspectives of the polyploid like aneuploidy and polyploidy plant kingdoms and their beneficial and detrimental effects that are also informative to introduce new knowledge on polyploidization in crop breeding, and 3) enumeration of minor crops from polyploidization of wild plant species.

Communicating Editor: Dr. Quaid Hussain

Manuscript received: September 12, 2022; Accepted: October 29, 2022.

© Society for the Advancement of Breeding Research in Asia and Oceania (SABRAO) 2022

### INTRODUCTION

Addressing the need to increase food production demands under the effects of climate change that presents potential challenges can utilize the accelerated application of polyploidization. It includes modifying selection standards focusing on the effectiveness of adaptation and/or tolerance to stress/es in addition to total yield; determining

the efficiency and stress-tolerance alleles are still present and exploitable in elite plants and wider breeding germplasm; and developing novel and expanding the use of current minor and principal crops, especially for better nutrition, environmental sustainability, and resilience while requiring fewer inputs than traditional major crop species. The changed agricultural model, alongside reducing inputs,

**To cite this manuscript:** Hieu PV (2022). Agricultural development based on polyploidization: a perspective contribution of minor crops. *SABRAO J. Breed. Genet.* 54(5): 1125-1140. <http://doi.org/10.54910/sabrao2022.54.5.14>.

away from high inputs toward stability and environmental resilience of yields is a daunting challenge (Abberton *et al.*, 2016; Poerba *et al.*, 2019a). The scientific view is that polyploidization contributes to better adaptation in terms of sustainability for certain crops and other benefits of physiologically responding to the harsh environment. As far as the ecological perspectives are concerned, efficiency or adaptation to and tolerance to stresses are appropriate for some novel crops the best example are those involving adaptation, such as, abiotic tolerance and biotic resistance. Another reason states that although some hybrid crops integrate physiological features, this integration is limited. Farmers can immensely benefit since it improves good quality and high yield as a whole, thus, necessary for successful potential crops.

With the advances in biotechnology, various plant species can now gain natural and artificial polyploidization capabilities. While it is acceptable that the natural polyploid process can sometimes have positive benefits for the population, the other view indicates that artificial polyploidization show more important and worth exploring. Using the artificial polyploidization process through several chemicals, such as, spindle inhibitors and phytohormone induction can be advantageous for reasons related to time-saving, cost-effectiveness, and lots of choices. Concerning the former, chemical induction of polyploidization can perform faster than the randomly natural polyploidization process, and as a result, utilizing this method enables saving an amount of time and successfully being applied in several horticultural plants (Eng and Ho, 2019). Moreover, several polyploidy plants resulted from natural and artificial polyploidization recorded from the last centuries. More specifically, a number of these polyploidy plants have been contributing to primary and minor crops with several potential traits involving outstanding advantages, as listed in Table 1. A typical example of these involves practical proofs, such as, wheat and watermelon polyploid (Matsuoka, 2011; Feldman and Levy, 2012; Saminathan *et al.*, 2015; Zhang *et al.*, 2019; Verhage, 2021). As far as economic perspectives are concerned, artificial polyploidization processes consist of comparatively smaller colonies than the population in nature in the experimental phases, but the commercial farming of artificial polyploidization cultivars has occurred on an extremely large scale, such as, potatoes and wheat. Artificial polyploidization underwent first

research in laboratories and then undertook a small-scale field trial. Finally, several chemicals can induce artificial methods of polyploidization, adequately providing scientists and breeders with a wide range of options when needed. However, some argued that these mentioned benefits are eclipsed by the drawbacks in terms of aneuploid. It means aneuploid plants cannot overcome the unproductiveness due to gamete abnormalities. In addition, polyploidization in nature does not offer a need in humanity because this natural process can randomly occur daily. As such, natural polyploidization cannot exist in the adverse environment, especially with competition against diploids. Another way to explain this problem comes from natural polyploidization not easily discovered in a large population dispersed across the globe. In brief, scientists and breeders seemingly see the drawbacks of the technological process, which allow humanity to perform artificial polyploidization via chemicals or physical factors, outweighing the benefits involved.

With climate change's ever-increasing adverse effects, polyploidization occurs like popular natural events that redress the problem to ensure the world's food security demands through developing crops that humanity expands in breeding strategies to introduce seedless triploid plants, enrich ornamental characteristics, enhance environmental-stress tolerance, and more (Aziz *et al.*, 2016; Akbar *et al.*, 2018; Pham, 2021). Polyploidization supposedly expands to a new ecology for several reasons. One explanation comes up with polyploid plant species can be doing that because the new individual translocated in an area with a more suitable condition, which makes its life more adaptable. For instance, if tetraploid plant species expand from one ecological area to another, they will adapt to new places with a better climate and more nutrition. They will have easy access to a water source and avoid predators. They will have more chances of adaptable capacity as a result.

In the plant kingdom, thousands of polyploidy plant species underwent several studies, revealing that these higher levels are more adaptive to various ecological conditions and topography due to genomic evolution. Several modes of ploidy, such as, autopolyploid, allopolyploid, and aneuploidy, combined with different levels of ploidy, exist in a large number of vegetables (potatoes) and fruits (bananas and strawberries) (Machida-Hirano, 2015; Edger *et al.*, 2019; Hardigan *et al.*, 2019; Poerba *et al.*, 2019b; Whitaker *et*

**Table 1.** Some polyploidy plant species being developed as minor and major crops.

No.	Latin name	Mode of ploidy	Chromosome	Benefits	Reference
1	<i>Lonicera japonica</i> Thunb	Diploid & autotetraploid	2n = 2x = 18, 2n = 4x = 36	Salt stress	Yan <i>et al.</i> , 2015
2	<i>Oryza sativa</i> Nipponbare	Diploid & autotetraploid	2n = 2x = 24, 2n = 4x = 48	Salt stress	Tu <i>et al.</i> , 2014
3	<i>Brassica rapa</i> L	Diploid & autotetraploid	2n = 2x = 20, 2n = 4x = 40	Salt stress	Meng <i>et al.</i> , 2011; Gu <i>et al.</i> , 2016.
4	<i>Paulownia fortunei</i>	Diploid & autotetraploid	2n = 2x = 40, 2n = 4x = 80	Salt stress	Fan <i>et al.</i> , 2007; Fan <i>et al.</i> , 2016; Deng <i>et al.</i> , 2017.
5	<i>P. australis</i> ; <i>P. fortunei</i> ; <i>P. tomentosa</i>	Diploid & autotetraploid	2n = 2x = 40, 2n = 4x = 80;	Drought stress	Niu <i>et al.</i> , 2016; Cao <i>et al.</i> , 2017; Zhao <i>et al.</i> , 2018.
6	<i>Dioscorea</i> <i>zingiberensis</i>	Diploid & autotetraploid	2n = 2x = 20, 2n = 4x = 40	Heat stress	Zhang <i>et al.</i> , 2010
7	<i>Ranunculus kuepferi</i>	Diploid & autotetraploid	2n = 2x = 16, 2n = 4x = 32	Cold stress	Syngelaki <i>et al.</i> , 2021
8	<i>Nicotiana</i> <i>benthamiana</i>	Tetraploid & octaploid	2n = 4x = 38, 2n = 8x = 76	Cold stress	Bombarely <i>et al.</i> , 2012; Deng <i>et al.</i> , 2012;
9	<i>Arabidopsis thaliana</i>	Diploid & autotetraploid	2n = 2x = 10, 2n = 4x = 20	Copper stress	Li <i>et al.</i> , 2017
10	<i>Citrus sinensis</i> L. <i>Poncirus trifoliata</i> L	Diploid & autotetraploid	2n = 2x = 18, 2n = 4x = 36	Boron stress	Ruiz <i>et al.</i> , 2016
11	<i>Betula platyphylla</i>	Diploid & autotetraploid	2n = 2x = 28, 2n = 4x = 56	NaHCO <sub>3</sub> stress	Mu <i>et al.</i> , 2016
12	<i>Malus × domestica</i> Borkh	Diploid & autotetraploid	2n = 2x = 34, 2n = 4x = 68	Resistance of Venturia	Xue <i>et al.</i> , 2015; Hias <i>et al.</i> , 2018;
13	<i>Solanum chacoense</i>	Diploid & autotetraploid	2n = 2x = 24, 2n = 4x = 48	Common scab resistance	Jansky <i>et al.</i> , 2019
14	<i>Papaver somniferum</i> L.	Diploid and autotetraploid	2n = 2x = 22, 2n = 4x = 44	Increase in morphine 25% - 50%	Mishra <i>et al.</i> , 2010
15	<i>Catharanthus</i> <i>roseus</i>	Diploid and autotetraploid	2n = 2x = 16, 2n = 4x = 32	Increase in vincristine	Begum, 2011
16	<i>Catharanthus</i> <i>roseus</i> Don	Diploid and autotetraploid	2n = 2x = 16, 2n = 4x = 32	Increase in terpenoid indole alkaloids	Xing <i>et al.</i> , 2011
17	<i>Echinacea</i> <i>purpurea</i> (L.)	Diploid and autotetraploid	2n = 2x = 22, 2n = 4x = 44	Increase in cichoric acid (45%) and chlorogenic acid (71%)	Abdoli <i>et al.</i> , 2013
18	<i>Rosa hybrida</i> cv Iceberg	Triploid and autohexaploid	2n = 3x = 21, 2n = 6x = 42	Increase in phenolic	Ahmadi <i>et al.</i> , 2013
19	<i>Allium sativum</i> L.	Diploid and autotetraploid	2n = 2x = 16, 2n = 4x = 32	Increase in allicin, diallyl disulfide, allyl methyl trisulfide and diallyl trisulfide	Dixit <i>et al.</i> , 2014; Yousef <i>et al.</i> , 2020
20	<i>Centella asiatica</i> (L.)	Diploid and autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increase in total triterpenoid	Thong-on <i>et al.</i> , 2014
21	<i>Cichorium</i> <i>intybus</i> L	Diploid and autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increase in total phenolic; chlorogenic acid	Ghotbi <i>et al.</i> , 2013
22	<i>Dracocephalum</i> <i>kotschy</i> Boiss	Diploid and autotetraploid	2n = 2x = 20, 2n = 4x = 40	Increase in methoxylated hydroxyflavones	Zahedi <i>et al.</i> , 2014
23	<i>Citrullus lanatus</i>	Diploid, autotriploid and autotetraploid	2n = 2x = 22, 2n = 3x = 33 2n = 4x = 44	Increase in lycopene contents	Nasr <i>et al.</i> , 2004; Saminathan <i>et al.</i> , 2015; Dou <i>et al.</i> , 2017.
24	<i>Linum album</i>	Diploid and autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increase in podophyllotoxin (PTOX)	Javadian <i>et al.</i> , 2017

**Table 1.** (cont'd.)

25	<i>Lycopersicum esculentum</i>	Diploid and autotetraploid	$2n = 2x = 24,$ $2n = 4x = 48$	Higher protein	Albuzio <i>et al.</i> , 1978; Gavrilenko <i>et al.</i> , 2001
26	<i>Musa balbisiana</i> Colla	Diploid, autotriploid and autotetraploid	$2n = 2x = 22$ $2n = 3x = 33$ $2n = 4x = 44$	Seedless triploid	Poerba <i>et al.</i> , 2019a
27	<i>Anoectochilus formosanus</i> Hayata	Diploid and autotetraploid	$2n = 2x = 24,$ $2n = 4x = 48$	Increase in total flavonoid and gastrodin	Chung <i>et al.</i> , 2017
28	<i>Panax ginseng</i> Mayer	Tetraploid and octaploid	$2n = 2x = 24,$ $2n = 4x = 48$	Increase in ginsenoside	Le <i>et al.</i> , 2020
29	<i>Artemisia cina</i>	Diploid and autotetraploid	$2n = 2x = 18,$ $2n = 4x = 36$	Increase in artemisinin, quercetin and kaempferol	Herawati <i>et al.</i> , 2020; Kasmiyati <i>et al.</i> , 2020
30	<i>Stevia rebaudiana</i>	Diploid and autotetraploid	$2n = 2x = 22,$ $2n = 4x = 44$	Increase in rebaudloside and stevioside	Yadav <i>et al.</i> , 2013; Hegde <i>et al.</i> , 2015; Rameshsing <i>et al.</i> , 2015; Mahdi <i>et al.</i> , 2018 Zhang <i>et al.</i> , 2018; Xiang <i>et al.</i> , 2019; Talei <i>et al.</i> , 2020
31	<i>Zingiber officinale</i> Roscoe cv. 'Fengtou' qingge	Diploid and autotetraploid	$2n = 2x = 22,$ $2n = 4x = 44$	Increase in carotenoids	Zhou <i>et al.</i> , 2020
32	<i>Lippia alba</i>	Diploid and autotetraploid	$2n = 2x = 30,$ $2n = 4x = 60$	Increase in linalool, citral	Julião <i>et al.</i> , 2020
33	<i>Melissa officinalis</i> L	Diploid and autotetraploid	$2n = 2x = 32,$ $2n = 4x = 64$	Increase in carotenoid and phenolic	Talei <i>et al.</i> , 2020
34	<i>Thymus vulgaris</i> L.	Diploid and autotetraploid	$2n = 2x = 30,$ $2n = 4x = 60$	Increase in thymol, carvocal and essential oil	Shmelt <i>et al.</i> , 2020
35	<i>Tetradenia riparia</i>	Diploid and autotetraploid	$2n = 2x = 24,$ $2n = 4x = 48$	Increase in essential oil	Hannweg <i>et al.</i> , 2016
36	<i>Echinacea purpurea</i> L.	Diploid, autotetraploid and autooctaploid	$2n = 2x = 22,$ $2n = 4x = 44$ $2n = 4x = 88$	Increase in cichoric acid	Li <i>et al.</i> , 2016
37	<i>Miscanthus × giganteus</i>	Triploid and hexaploid	$2n = 3x = 57,$ $2n = 6x = 114$	Increase in phenolic	Ghimire <i>et al.</i> , 2016
38	<i>Lippia integrifolia</i>	Diploid and autotetraploid	$2n = 2x = 36,$ $2n = 4x = 72$	Increase in total monoterpen	Iannicelli <i>et al.</i> , 2016
39	<i>Pogostemon cablin</i>	Tetraploid and autooctaploid	$2n = 4x = 64,$ $2n = 8x = 128$	Increase in patchoulic alcohol	Yan <i>et al.</i> , 2016
40	<i>Chamaemelum nobile</i> L.	Diploid and autotetraploid	$2n = 2x = 18,$ $2n = 4x = 36$	Increase in essential oil	Tsuro <i>et al.</i> , 2016
41	<i>Bacopa monnieri</i>	Diploid and autotetraploid	$2n = 2x = 18,$ $2n = 4x = 36$	Increase in bacoside	Kharde <i>et al.</i> , 2017
42	<i>Capsicum frutescens</i> L	Diploid and autotetraploid	$2n = 2x = 18,$ $2n = 4x = 36$	Increase in capsaicin	Pliankong <i>et al.</i> , 2017
43	<i>Aquilaria malaccensis</i> Lamarck	Diploid and autotetraploid	$2n = 2x = 14,$ $2n = 4x = 28$	Increase in sesquiterpene, a-gualene	Rahman, 2017
44	<i>Cannabis sativa</i> L	Diploid and autotetraploid	$2n = 2x = 20,$ $2n = 4x = 40$	Increase in cannabinoid	Mansouri <i>et al.</i> , 2017; Parsons <i>et al.</i> , 2019.
45	<i>Trachyspermum ammi</i> L	Diploid and autotetraploid	$2n = 2x = 18,$ $2n = 4x = 36$	Increase in thymol	Noori <i>et al.</i> , 2017

**Table 1.** (cont'd.)

46	<i>Dendrobium hybrids</i>	Diploid and autotetraploid	2n = 2x = 38, 2n = 4x = 76	Increase in shihundine and hircinol	Grosso <i>et al.</i> , 2018
47	<i>Sphagneticola calendulacea</i> (L.) Pruski	Diploid and autotetraploid	2n = 2x = 50, 2n = 4x = 100	Increase in wedelolactone	Kundu <i>et al.</i> , 2018
48	<i>Pfaffia glomerata</i> (Spreng.) Pedersen	Diploid and autotetraploid	2n = 2x = 34, 2n = 4x = 68	Increase in $\beta$ -ecdysone	Gomes <i>et al.</i> , 2014
49	<i>Echinacea purpurea</i> (L.) Moench	Diploid and autotetraploid	2n = 2x = 22, 2n = 4x = 44	Increase in caffeic acid and alkamides	Xu <i>et al.</i> , 2014
50	<i>Nigella sativa</i> L	Diploid and autotetraploid	2n = 2x = 12, 2n = 4x = 24	Increase in thymoquinone	Dixit <i>et al.</i> , 2015
51	<i>Thymus persicus</i>	Diploid and autotetraploid	2n = 2x = 28, 2n = 4x = 56	Increase in betulinic acid oleanolic acid ursolic acid	Tavan <i>et al.</i> , 2015; Navrátilová <i>et al.</i> , 2021
52	<i>Plantago ovata</i>	Diploid and autotetraploid	2n = 2x = 8, 2n = 4x = 16	Increase in carotenoid	Sabzehzari <i>et al.</i> , 2019b
53	<i>Plantago psyllium</i>	Diploid and autotetraploid	2n = 2x = 12, 2n = 4x = 24	Increase in carotenoid	Sabzehzari <i>et al.</i> , 2019a
54	<i>Eucalyptus polybractea</i> RT Baker	Diploid and autotetraploid	2n = 2x = 22, 2n = 4x = 44	Increase in essential oil	Fernando <i>et al.</i> , 2019
55	<i>Citrus limon</i> (L.) Osbeck	Diploid and autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increase in essential oil and limonene	Bhuvaneswari <i>et al.</i> , 2019
56	<i>Physalis peruviana</i> L	Diploid and autotetraploid	2n = 2x = 24, 2n = 4x = 48	Increase in total flavonoids, anthocyanin, and phenolic	Çömlekçioğlu & Özden, 2019
57	<i>Bacopa monnieri</i>	Diploid and autotetraploid	2n = 2x = 64, 2n = 4x = 128	Increase in bacoside	Inthima & Sujipuli, 2019
58	<i>Datura stramonium</i> L	Diploid and autotetraploid	2n = 2x = 24, 2n = 4x = 48	Increase in alkaloids	Al-Taweel <i>et al.</i> , 2019
59	<i>Salvia miltiorrhiza</i>	Diploid and autotetraploid	2n = 2x = 16, 2n = 4x = 32	Increase in dihydrotanshinone and total tanshinone	Chen <i>et al.</i> , 2018
60	<i>Andrographis paniculata</i>	Diploid and autotetraploid	2n = 2x = 50, 2n = 4x = 100	Increase in andrographolide	Li <i>et al.</i> , 2018
61	<i>Sophora tonkinensis</i> Gapnep	Diploid and autotetraploid	2n = 2x = 18, 2n = 4x = 36	Increase in matrine and oxymatrine	Wei <i>et al.</i> , 2018
62	<i>Eclipta alba</i> (L.) Hassk	Diploid and autotetraploid	2n = 2x = 22, 2n = 4x = 44	Increase in wedelolactone	Salma <i>et al.</i> , 2018

*al.*, 2020; Hu *et al.*, 2021). In mammals, however, polyploidization causes congenital diseases and pregnancy loss, especially in human beings. Thus, it is also relevant to discuss that polyploidy, though scarcer in the animal kingdom, is observed in amphibia (African clawed frog) and distinct species of fish (Comai, 2005; Stenberg and Saura, 2013).

Minor crops existing in many regions showed as indigenous species collected from the wild, with the basic difference from major crops disclosing they lie in the level of knowledge and the scale of arable land. These

crops are considered endangered species, accentuate several benefits when cultivated and achieved plant breeding strategies. Such a highly effective way can save the plant population. It means minor crops benefit those living on the planet, such as, mitigating the threat of endangered species, increasing income for producers, and creating quality products. For example, a study in Pakistan from 1981–2018 revealed that the average income of major crops was less than minor crops when calculating the same acreage compared per hectare (Abro and Awan, 2020).

Another benefit states minor crops help to meet the ever-growing global nutrition demand to reach a high level of expertise because of improved resistance to pathogens, like plant diseases and pests, boosting yield, as well (Hias *et al.*, 2018, Janky *et al.*, 2019). Plant genetic diversity across the globe constantly has been expanding acknowledgment as a result of gaining more cultivation of novel species that becomes the case at the local level.

Minor crops also benefit genetic diversity by breeding and conserving these varieties, which contribute to adding unique features. With advances in technological methods used in major crops proving expensive, these cannot be applicable in minor crops over the last centuries. Concerning indigenous and even endemic species, one must have a deep knowledge of the agronomic characteristics of the species, as well as, the assessment of the genetic material. Humans could gain knowledge of genetic diversity, especially with the use of related species, with a point of breeding the desired features. As far as the breeding of local varieties is concerned, minor crops can help to maintain genetic diversity. Therefore, minor crops must keep a diverse gene pool regarding environmental adaptability. Minor crops play a critical role in the future because of climate variability, especially concerning abiotic and biotic tolerance. Numerous examples of local varieties exist that could adapt to the detrimental climate. This review article will discuss polyploidization in plants and then mention the benefits of its valued effects confirmed more advantageous. Further, the review proved the perspectives of polyploidy, e.g., aneuploidy and polyploidy plant kingdoms and their beneficial and detrimental effects. Lastly, it introduces essential knowledge on polyploidization in crop breeding, especially minor crops, from polyploidization of wild plant species also mentioned here.

### Adaptation and tolerance to stresses

Scientifically speaking, scientists and breeders seek to use several plant species as a subject of experimentation of polyploidization, having well-established methodological grounds. It could be due to polyploid plants' proven adaptation to detrimental environments by enhancing abiotic stress tolerance and biotic resistance. More precisely, several polyploidy plant species could cope with drought stress better than their diploid counterparts. The supposed reason reveals polyploid plants have

substantially changed miRNAs mechanisms and target genes regulating transcriptional regulation and plant defense to reduce the effect of water insufficiency. Likewise, hormone metabolism and a rise in ABA content also play a vital role in deciding how successful these polyploid plants tolerate drought stress. *Paulownia fortunei*, *Paulownia australis*, *Paulownia tomentosa*, *Lycium ruthenicum*, *Ziziphus jujuba* Mill. var. *Spinosa*, and *Arabidopsis* tetraploid play good examples here (del-Pozo and Ramirez-Parra, 2014; Niu *et al.*, 2016; Cao *et al.*, 2017; Zhao *et al.*, 2018; Rao *et al.*, 2020; Li *et al.*, 2021).

Polyploid plant species were known as more adaptive rather than diploid ones. More so, several polyploidy plants can respond to salinity stress due to higher levels of ploidy plants possessing several mechanisms, such as accumulating Na<sup>+</sup> extrusion under part of soil organs, intensifying Na<sup>+</sup> transfer to leaf, controlling osmosis, increasing the gene expression coupled with antioxidants, extenuating ROS, photosynthesis signaling, altering SNP marker associated to salt stress, up-regulating aquaporin genes, and growth regulator transduction cues. Additionally, protein synthesis, controlling transcription factors, enhancing ATP synthase to increase ion transport changing proton, and changing miRNAs can be seen (Meng *et al.*, 2011; Tu *et al.*, 2014; Xue *et al.*, 2015; Yan *et al.*, 2015; Fan *et al.*, 2016a, b; Yu *et al.*, 2016; Deng *et al.*, 2017; Liu *et al.*, 2017; Zhao *et al.*, 2017). Thus, the polyploid plant might also be capable of biotic resistance. Particularly, *Malus* × *Domestica* autotetraploid increased the resistance of *Venturia* by substantially increasing *Rvi6* a type of resistant gene locus (Hias *et al.*, 2018). Another example presented common scab resistance in autotetraploid potatoes was gained by crossing 2n gametes derived from diploid *S. chacoense* (Jansky *et al.*, 2019). Further, *Dioscorea* and *Arabidopsis* can have heat tolerance by sufficiently supporting antioxidant defense systems activated, a typical example (DeBolt, 2010; Zhang *et al.*, 2010). Polyploid plants can up-regulate antioxidants and epigenetics to become tolerant of cold stress (Deng *et al.*, 2012; Syngelaki *et al.*, 2020; 2021). Heavy metals like boron and copper may be toxic chemicals to plants. More accurately, changing root anatomical characters redressed the adaptation of a high concentration of boron in soil. Meanwhile, the Cu transport gene, activation of anti-oxidation defense, and up-regulation of expression of ABA-responsive genes mitigate for surviving in an environment

polluted by a high concentration of copper (Ruiz *et al.*, 2016; Li *et al.*, 2017). The autopolyploid birch plant (*B. platyphylla*) could cope with NaHCO<sub>3</sub> stress tolerance, as demonstrated by enhancing the expression genes regulating biosynthetic proline (Mu *et al.*, 2016).

### **Development of efficiency and stress-tolerance alleles to breeding germplasm**

With advances in genetic engineering and continual elucidation of alleles governing the life cycle and synthetic and reproductive processes, humanity is on the verge of making their dream a reality by partly changing and enhancing the expression of those alleles related to stress tolerance. A case in point is that scientists and breeders experienced in developing new crop strategies are more likely to find alleles conferring potential traits capable of efficiency and stress tolerance. Specifically, observing autotetraploid *Arabidopsis arenosa* showed that *two-pore channel 1*, exhibiting different evolution from independent new mutations at the identity, but preserving the site of the gate of the calcium channel selectivity, might adapt to an extreme environment associated with a pool of variants in all loci, both pre-existing variation and new polymorphisms (Konečná *et al.*, 2021). It is beyond whole-genome replication affecting subfunctionalization containing couples genes that exercise a subset of their original genetic function and neofunctionalization. The direct evidence associated with the relationship, along with gene doubling and adaptation to a harsh environment, explains this. Concerning the former, stress-tolerant alleles play a significant role in the expression of those transcripts. Take the ancestral AGAMOUS gene function in maize as an example. This gene existed in two paralogs with overlapping functions, but not an identical role. More precisely, ZAG1 and ZMM2 have functioned for male and female multiplicative organ development, respectively, especially with flower determinacy, belonging to the MADS-box family (Mena *et al.*, 1996). One can see this when investigating the evolution and function of mitochondrial GrpE (Mge) protein in modeling plant *Arabidopsis thaliana*. In particular, AtMge1 and AtMge2 were two alleles that originated from polyploidization, but ultraviolet B light-induced AtMge1; heat-induced AtMge2. The specific conversion of the *Arabidopsis* Mge transcript of the individual allele was a different type when duplication and subfunctionalization happened (Hu *et al.*,

2012). Another example presents the consequent subfunctionalization that happened in a wild potato, the line CMM1T belonging to wild *S. commersonii* and the commercial potato-like "Blondy," "Désirée," and "Double Fun," which identified that replication of R2R3 MYB genes, especially AN1 functioned on synthesizing anthocyanin while AN2 conserved the role in reacting to chili stress (D'Amelia *et al.*, 2018). A good illustration of neofunctionalization consists of a channel protein in *Arabidopsis*, which were the double copies of the OEP16 gene containing OEP16-L and OEP16-S, originating from a duplicative process. Concerning AtOEP16-S, its location rests in the promoter area of several G-box ABA-responsive elements (ABREs). The ABI3 and ABI5 regulate this allele, which is increasingly expressed during the maturing phase of seeds and pollen, both dehydrate adaptation in part of the plant. But AtOEP16-L does not have promoter ABREs mainly expressed in leaves, strongly cold stress induction, and is less responsive to osmotic pressure, salicylic acid, and exogenic abscisic acid (Drea *et al.*, 2006). The MADS protein domain, MIKC-type, significantly regulated flower growth in higher plants and altered in expression manner associated with a novel gene role in a short period. Thus the B-sister gene ABS (also known as TT16) in thale cress, *Arabidopsis thaliana*, regulated endothelium development and synthesized anthocyanidin. Similarly, GOA regulated fruit size via cell expansion (Erdmann *et al.*, 2010). It was an outstanding molecular level of neofunctionalization in polyploid plant species.

### **Expansion of minor crops with better nutrition, environmental sustainability, and resilience**

Polyploidization is vital for humanity mainly because it can open doors of opportunities for success in expanding both minor and primary crops to more likely develop potential crops with better nutrition, environmental sustainability, and resilience than diploid counterparts. Table presents some polyploidy plant species being developed as minor and major crops. Concerning nutrition-rich, polyploid plants enhance secondary metabolites, including natural compounds beneficial for humanity, especially with medicinal plants currently studied (Gantait and Mukherjee, 2021). Data explained these medicinal plants contribute more varied characteristics consisting of the modified phytochemical profile, increased content of

desired pharma molecules, and fragrance after polyploidization occurred (Niazian and Nalouisi, 2020; Ghasemi *et al.*, 2021). Polyploidization not only changed the expression of several genes modulating the alkaloid biosynthesis process but also increased 25%–50% morphine content in tetraploid opium poppy (*P. somniferum* L.) as a clear example (Mishra *et al.*, 2010). Another example showed observing tetraploid *Linum album* revealed that the content of podophyllotoxin (PTOX) increased due to upregulating genes related to the biosynthesis pathway of PTOX in comparison with diploid counterpart (Javadian *et al.*, 2017). The increase in producing secondary metabolites, especially with medicinal plants, proves a promising approach to gaining substantial value addition from polyploidization. Moreover, polyploidy plants also have worth in ornament subjects for the changes in plant form, flower color, size and style, fragrance, vase life, and prolonged flowering period. In particular, *Phalaenopsis* orchid tetraploid gained from the protocorm-like body of diploid introduced favorable characteristics, i.e., large flower size than those of the diploids as a typical example (Chen *et al.*, 2009). Likewise, several studies found that polyploid plants gained large flower sizes boosting ornamental application (Urwin, 2014; Kushwah *et al.*, 2018; Tu *et al.*, 2018; Khalili *et al.*, 2019). Interestingly, a recent study revealed that triploid and tetraploid *Averrhoa carambola* L. increased fruit size substantially and the shelf life of fruits, which became much longer than that in its diploid. Polyploidization in ornamental and medicinal plants leads to substantial economic consequences received validation in current modern agriculture. Concerning environmental sustainability and resilience, plenty of plant species are widely available on earth and acclimatize in innumerable topographies and climates, which means plant species increase both abundantly genetically and in the capability of adapting to the improvement of evolution in detrimentally environmental conditions (Storme and Mason, 2014; Bohutinska *et al.*, 2021). The best example of this shows those involved in several modes of polyploid, such as autopolyploid, allopolyploid, and aneuploidy. A typical witness indicates potato, which contains over 4,000 native varieties compared with only 180 wild potato relatives (Machida-Hirano, 2015). In particular, potato, one of the most modes of polyploidy plants involving 76% documented diploids, 3% triploids, 12% tetraploids, 2% pentaploid, and 7% hexaploids, especially with an increased

level of genetic heterogeneity makes tetraploid the highest yield (Hawkes, 1990; Muthoni *et al.*, 2015; Watanabe, 2015). The practically empirical proofs gained observation and got categorized into two distinctive groups of cultured potatoes, one located in the high Andes of northern and central South America, consisting of a wide range of ploidy levels named the Andigenum group, and the lowlands southern Chile called the Chilotanum group, with tetraploid as the only others existing (Jansky and Spooner, 2018).

Polyploidization might sound like a really difficult task, but it is also a very rewarding tool. From helping scientists and researchers to see what desired traits people enjoyed and what new crops they found to be the most interesting and/or useful to making new opportunities in developing crops, polyploidization can open new doors for humanity. Convincing scientists and breeders need to know just why polyploidization will change agriculture based on molecular mechanisms, including the control of the flowering process, fruit formation and development, fruit quality, and interactions of plant pathogens (Van Hieu, 2019). How to ensure food security for nine billion people in 2050 remains a topic of debate. While some propose investing time and money to improve inputs, such as fertilizers and soil, one can argue that it is wiser to spend sources on new developmental crops obtaining desired agronomic traits. On the one hand, some justifications prevail for making novel crops and exerting efforts just to ensure human food demand. Facts show that wild species play an integral part in ecological balance. As wild plants ensure biodiversity, these also contribute to human well-being having people still rely on plants for food and medicine. If wild plants are on the verge of extinction, humans will encounter hardships, and Mother Nature will lose its diversity. However, the role of wild plant species still needs further exaggeration. There have been witnesses to the extinction of several species from the past centuries that posed immense threats to ecosystems, human food development, and gene resources. Thus, human beings should place too much emphasis on protecting wild species at the expense of people's lives. Furthermore, it is imperative to save wild plant species which can be used as crops. These plants often suffer from natural disasters causing lack of accessibility and unavailability of food and medicine while most fail to make ends meet. Human beings will have difficulty to meet food demands if they do nothing keeping



their fingers crossed to overcome starvation and have living conditions fully ameliorated. Since humanity is desperate to meet food strategies, wild species need no marginalization, lessening exerted efforts to protect primary crops. In brief, while admittedly wild plant species proved crucial and need conserving, these also deserve much attention from scientists and breeders. Indeed, scientists and researchers need to focus on helping minor crops reach their maximum potential.

Recently, another aspect concerns molecular breeding significantly contributing to the strategies of developmental crops based on modern techniques, such as, next-generation sequencing (NGS), genome-wide association study (GWAS), high throughput single nucleotide polymorphisms (SNP) sequencing, and CRISPR/cas9, that help breeders save time, labor, and more. An explanation states these techniques promote the development of crops with complex genomes, like polyploidy crops. A case in point is that next-generation sequencing provides the genome sequences and transcriptomes of various plants that have accelerated plant breeding (Ashraf *et al.*, 2022). More precisely, with next-generation sequencing rapidly advancing than ever, the complex genomes of several important polyploidy crop species, such as, potato and wheat, have been sequenced to supply reliable platforms for breeding by providing the opportunity for enhanced resolution of QTLs and identification of genetic variation. Most importantly, GWAS offers potential marker-assisted breeding that unravels the mechanisms leading to high-resolution mapping in a larger population via offering the detection of statistically significant phenotype-genotype association with linkage disequilibrium (Yasir *et al.*, 2022). Besides, high throughput SNP sequencing is also made available decode nucleotide offering to identify candidate genes to exploit better crop yield and quality (Naqvi *et al.*, 2022). On top of that, a technique called CRISPR-Cas9, the most widely used genome editing tool today serves to fast design and accurate in the ability to target any sequence in the genome and multiple sites at once. The gene-editing potato tetraploid illustrates the best example, which is more effective to introgress multi-genic traits making it possible to utilize recessive alleles and identify rare alleles. Polyploidy potato cultivars containing favorable agronomic traits must be evaluated and planted to ensure a high yield (Bethke *et al.*, 2019). A typical example presented applying next-generation

genome sequence to research six polyploidy potato genomes discovered that valuable genetic resources relating to traits derived from native landraces have functioned well in disease and pest resistance and nutrition and fiber, using breeding strategies (Kyriakidou *et al.*, 2020). Magnificent application of advances in technology in developing new potato cultivars, the best example presents those which involve the CRISPR/Cas 9, also applied in tetraploid potatoes, to successfully knock out *StPDS* gene or nucleotide transitions and transversions in the *StALS1* gene by the introduction of simultaneous nucleotides (Ma *et al.*, 2019; Veillet *et al.*, 2020). It proves essential for the success of breeders to crop improvement goals in the future (Dar *et al.*, 2017). Notably, polyploidy breeding is a vital decision-making process because all the phases of the breeding program consist of testing, mapping, and introgression of traits. It means breeders select the individual plants from huge segregating populations harboring the best traits. In short, biotechnological interventions play a critical role in crop development having desirable traits via molecular breeding.

## CONCLUSIONS

Unquestionably, polyploidization, whether sexual or asexual formation, is essential for humans chiefly because it can open doors of opportunities for success in developing potential crops. A case in point is scientists and breeders who have experience in breeding strategy are more likely to select criteria focusing on effectiveness or stress tolerance rather than a minimum benefit. More importantly, several researchers, today need to find efficiency and stress-tolerance alleles to breed germplasm before considering an application in production. Finally, the farmers also desire to expand minor and major crops with nutrition-rich, environmentally sustainable, and resilient derived from polyploidization. It means that having credentials provide ample opportunity for securing a crop for those living on earth. Those who think scientists and breeders should be encouraged to evaluate and criticize their crops studied may have a cogent reason. They may well argue that it is valuable feedback the farmers provide that may help the scientists to see what polyploidization methods farmers enjoyed and what desired traits they found to be the most distinctive and/or suitable. This information is beneficial for breeders in

preparing development strategies for future crops.

## ACKNOWLEDGMENTS

The author thanks the financial support and the kind assistance received from the HCMC Biotechnology Center.

## REFERENCES

- Abberton M, Batley J, Bentley A, Bryant J, Cai H, Cockram J (2016). Global agricultural intensification during climate change: A role for genomics. *Plant Biotechnol. J.* 14: 1095-1098. <https://doi.org/10.1111/pbi.12467>.
- Abdoli M, Moieni A, Badi HN (2013). Morphological, physiological, cytological, and phytochemical studies in diploid and colchicine-induced tetraploid plants of *Echinacea purpurea* (L.). *Acta Physiol. Plant.* 35(7):2075-2083. <https://doi.org/10.1007/s11738-013-1242-9>.
- Abro AA, Awan NW (2020). Comparative analysis of the profitability of major and minor crops in Pakistan. *J. Saudi Soc. Agri. Sci.* 19: 476-481. <https://doi.org/10.1016/j.jssas.2020.09.001>.
- Ahmadi T, Jafarkhani Kermani M, Mashayekhi K, Hasanloo T, Shariatpanahi ME (2013). Comparing plant morphology, fertility, and secondary metabolites in *Rosa hybrida* cv. Iceberg and its chromosome-doubled progenies. *Int. Res. J. Appl. Basic Sci.* 4: 3840-3849.
- Akbar MR, Purwoko BS, Dewi IS, Suwarno WB, Sugiyanta (2018). Agronomic and drought tolerance evaluation of doubled haploid rice breeding lines derived from anther culture. *SABRAO J. Breed. Genet.* 50(2): 115-128.
- Albuzio A, Spettoli P, Cacco G (1978). Changes in gene expression from diploid to autotetraploid status of *Lycopersicon esculentum*. *Physiol. Plant.* 44: 77-80. <https://doi.org/10.1111/j.1399-3054.1978.tb01617.x>.
- Al-Taweel SK, Al-Amrani HA, Al-Rawi TK (2019). Induction and flow cytometry, GC-MS identification of tetraploids through colchicine treatments in *Datura stramonium* L. *Plant Arch.* 19(1): 241-250.
- Ashraf MF, Hou D, Hussain Q, Imran M, Pei J, Ali M, Shehzad A, Anwar M, Noman A, Waseem M, Lin X (2022). Entailing the next-generation sequencing and metabolome for sustainable agriculture by improving plant tolerance. *Int. J. Mol. Sci.* 23: 651. <https://doi.org/10.3390/ijms23020651>.
- Aziz SA, Azmi TKK, Sukma D, Qonitah FZ (2016). Morphological characters of triploids and tetraploids produced by colchicine on buds and flowers of *Phalaenopsis amabilis*. *SABRAO J. Breed. Genet.* 48(3): 352-358.
- Begum F (2011). Augmented production of vincristine in induced tetraploids of *Agrobacterium* transformed shooty teratomas of *Catharanthus roseus*. *Med. Plant* 3: 59-64. doi: 10.5958/j.0975-4261.3.1.007.
- Bethke PC, Halterman DA, Jansky SH (2019). Potato germplasm enhancement enters the genomics era. *Agronomy* 9: 575. doi: 10.3390/agronomy9100575.
- Bhuvanewari G, Thirugnanasampandan R, Gogulramnath M (2019). Effect of colchicine-induced tetraploidy on morphology, cytology, essential oil composition, gene expression and antioxidant activity of *Citrus limon* (L.) Osbeck. *Physiol. Mol. Biol. Plants* 26(2): 271-279. doi: 10.1007/s12298-019-00718-9.
- Bohutinska M, Alston M, Monnahan P, Mandakova T, Bray S, Paajanen P, Kolař F, Yant L (2021). Novelty and convergence in adaptation to whole-genome duplication. *Mol. Biol. Evol.* doi:10.1093/molbev/msab096.
- Bombarely A, Rosli H, Vrebalov J, Moffett P, Mueller L, Martin G (2012). A draft genome sequence of *Nicotiana benthamiana* to enhance molecular plant-microbe biology research. *Mol. Plant-Microbe Interact.* 25: 1523-1530. <https://doi.org/10.1094/MPMI-06-12-0148-TA>.
- Cao X, Fan G, Cao L, Deng M, Zhao Z, Niu S, Wang Z, Wang Y (2017). Drought stress-induced changes of microRNAs in diploid and autotetraploid *Paulownia tomentosa*. *Genes Genomics* 39(1): 77-86. DOI: 10.1007/s13258-016-0473-8.
- Chen EG, Tsai KL, Chung HH, Chen JT (2018). Chromosome doubling enhanced biomass and dihydrotanshinone I production in *Salvia miltiorrhiza*, a traditional Chinese medicinal plant. *Molecules* 23(12): 3106. <https://doi.org/10.3390/molecules23123106>.
- Chen WH, Tang CY, Kao YL (2009). Ploidy doubling by *in vitro* culture of excised protocorms or protocorm-like bodies in *Phalaenopsis* species. *Plant Cell Tissue Organ Cult. (PCTOC)* 98:229-238. doi: 10.1007/s11240-009-9557-3.
- Chung HH, Shi SK, Huang B, Chen JT (2017). Enhanced agronomic traits and medicinal constituents of autotetraploids in *Anoetochilus formosanus* Hayata, a top-grade medicinal orchid. *Molecules* 22: 1907. <https://doi.org/10.3390/molecules22111907>.
- Comai L (2005). The advantages and disadvantages of being polyploid. *Nature* 6: 836-846. doi: 10.1038/nrg1711.
- Çömlekçioğlu N, Özden M (2019). Effects of colchicine application and ploidy level on fruit secondary metabolite profiles of goldenberry (*Physalis peruviana* L.). *Appl. Ecol. Environ. Res.* 18(1): 289-302. doi: 10.15666/aer/1801\_289302.

- D'Amelia V, Aversano R, Ruggiero A, Batelli G, Appelhagen I, Dinacci C, Hill L, Martin C, Carputo D (2018). Subfunctionalization of duplicate MYB genes in *Solanum commersonii* generated the cold-induced ScAN2 and the anthocyanin regulator ScAN1. *Plant Cell Environ.* 41: 1038-1051. <https://doi.org/10.1111/pce.12966>
- Dar J, Beigh Z, Wani AA (2017). Polyploidy: Evolution and crop improvement. *Asynapsis and Desynapsis in Plants*: 201-218.
- DeBolt S (2010). Copy number variation shapes genome diversity in *Arabidopsis* over immediate family generational scales. *Genome Biol. Evol.* 2: 441-453. <https://doi.org/10.1093/gbe/evq033>.
- del-Pozo JC, Ramirez-Parra E (2014). Deciphering the molecular bases for drought tolerance in *Arabidopsis* autotetraploid. *Plant Cell Environ.* 37(12): 2722-2737. doi:10.1111/pce.12344.
- Deng B, Du W, Changlai L, Sun W, Tian S, 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 Regul.* 66(1): 37-47. doi: 10.1007/s10725-011-9626-6.
- Deng M, Dong Y, Zhao Z, Li Y, 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(7): e0181937 doi: 10.1371/journal.pone.0181937.
- Dixit V, Chaudhary BR (2014). Colchicine-induced tetraploidy in garlic (*Allium sativum* L.) and its effect on allicin concentration. *J. Hortic. Sci. Biotechnol.* 89: 585-591. <https://doi.org/10.1080/14620316.2014.11513124>.
- Dixit V, Verma S, Chaudhary BR (2015). Changes in ploidy and its effect on thymoquinone concentrations in *Nigella sativa* L. seeds. *J. Hortic. Sci. Biotechnol.* 90: 537-542. <https://doi.org/10.1080/14620316.2015.11668711>.
- Dou J, Yuan P-L, Zhao S, He N, Zhu H, Gao L, Ji W, Lu X, Liu W (2017). Effect of ploidy level on the expression of lycopene biosynthesis genes and accumulation of phytohormones during watermelon (*Citrullus lanatus*) fruit development and ripening. *J. Integr. Agric.* 16: 1956-1967. [https://doi.org/10.1016/S2095-3119\(16\)61618-0](https://doi.org/10.1016/S2095-3119(16)61618-0).
- Drea SC, Lao NT, Wolfe KH, Kavanagh TA (2006). Gene duplication, exon gain, and neofunctionalization of OE16-related genes in land plants. *Plant J.* 46: 723-735. <https://doi.org/10.1111/j.1365-313X.2006.02741.x>.
- Edger PP, Poorten TJ, VanBuren R, Hardigan MA, Colle M, McKain MR, Smith RD, Teresi SJ, Nelson ADL, Wai CM, Alger EI, Bird KA, Yocca AE, Pumphlin N, Ou S, Ben-Zvi G, Brodt A, Baruch K, Swale T, Shiue L, Acharya CB, Cole GS, Mower JP, Childs KL, Jiang N, Lyons E, Freeling M, Puzey JR, Knap SJ (2019). Origin and evolution of the octoploid strawberry genome. *Nat. Genet.* 51: 541-547. <https://doi.org/10.1038/s41588-019-0356-4>.
- Eng WH, Ho WS (2019). Polyploidization using colchicine in horticultural plants: A review. *Sci. Hortic.* 246: 604-617. <https://doi.org/10.1016/j.scienta.2018.11.010>.
- Erdmann R, Gramzow L, Melzer R, Theissen G, Becker A (2010). GORDITA (AGL63) Is a young paralog of the *Arabidopsis thaliana* Bsister MADS Box gene ABS (TT16) that has undergone neofunctionalization. *Plant J.* 63: 914-924. <https://doi.org/10.1111/j.1365-313X.2010.04290.x>.
- Fan G, Li X, Deng M, Zhao Z, Yang L (2016a). Comparative analysis and identification of miRNAs and their target genes responsive to salt stress in diploid and tetraploid *Paulownia fortunei* seedlings. *PLoS one* 11(2): e0149617. doi:10.1371/journal.pone.0149617.
- Fan G, Wang L, Deng M, Zhao Z, Dong Y, Zhang X, Li Y (2016b). Changes in transcript related to osmosis and intracellular ion homeostasis in *Paulownia tomentosa* under salt stress. *Front. Plant Sci.* 7: 384. doi:10.3389/fpls.2016.00384.
- Fan GQ, Cao YC, Zhao ZL, Yang ZQ (2007). Induction of autotetraploid of *Paulownia fortunei*. *Sci Silvae Sin.* 43: 31-35.
- Feldman M, Levy AA (2012). Genome evolution due to allopolyploidization in wheat. *Genetics* 192: 763-774 doi: 10.1534/genetics.112.146316.
- Fernando SC, Goodger JQ, Chew BL, Cohen TJ, Woodrow IE (2019). Induction and characterization of tetraploidy in *Eucalyptus polybractea* RT baker. *Ind. Crops and Prod.* 140: 111633. <https://doi.org/10.1016/j.indcrop.2019.111633>.
- Gantait S, Mukherjee E (2021). Induced autopolyploidy a promising approach for enhanced biosynthesis of plant secondary metabolites: An insight. *J. Genet. Eng. Biotechnol.* 19(4): <https://doi.org/10.1186/s43141-020-00109-8>.
- Gavrilenko T, Thieme R, Rokka VM (2001). Cytogenetic analysis of *Lycopersicon esculentum* (+) *Solanum tuberosum* somatic hybrids and their androgenetic regenerants. *Theor. Appl. Genet.* 103: 231-239. doi: 10.1007/s001220100626.
- Ghasemi M, Aelaei M, Akbari-Soltankohi F, Minaei Chenar H, Bahrami-Rad E (2021). Studies on polyploidy induction for improvement of quality traits in ornamental and medicinal plants. *Central Asian J. Plant Sci. Innov.* 2: 76-90. doi: 10.22034/CAJPSI.2021.02.03.
- Ghimire BK, Seong ES, Nguyen TX, Yoo JH, Yu CY, Kim SH, Chung IM (2016). Assessment of morphological and phytochemical attributes in triploid and hexaploid plants of the bioenergy crop *Miscanthus × giganteus*. *Ind.*

- Crops Prod.* 89: 231-243. doi: 10.1016/j.indcrop.2016.04.051.
- Ghotbi Ravandi E, Rezanejad F, Zolala J, Dehghan E (2013). The effects of chromosome-doubling on selected morphological and phytochemical characteristics of *Cichorium intybus* L. *J. Hortic. Sci. Biotechnol.* 88(6): 701-709. doi: 10.1080/14620316.2013.11513027.
- Gomes SSL, Saldanha CW, Neves CS, Trevizani M, Raposo NRB, Notini MM, de Oliveira Santos M, Campos JMS, Otoni WC, Viccini LF (2014). Karyotype, genome size, and *in vitro* chromosome doubling of *Pfaffia glomerata* (Spreng.) Pedersen. *Plant Cell Tissue Organ Cult.* (PCTOC) 118(1): 45-56. doi: 10.1007/s11240-014-0460-1.
- Grosso V, Farina A, Giorgi D, Nardi L, Diretto G, Lucretti S (2018). A high-throughput flow cytometry system for early screening of *in vitro* made polyploids in *Dendrobium hybrids*. *Plant Cell Tissue Organ Cult.* (PCTOC) 132: 57-70. <https://doi.org/10.1007/s11240-017-1310-8>.
- Gu AX, Zhao JJ, Li LM, Wang YH, Zhao YJ, Hua F, Xu YC, Shen SX (2016). Analyses of phenotype and ARGOS and ASY1 expression in a ploidy Chinese cabbage series derived from one haploid. *Breed. Sci.* 66: 161-168. doi: 10.1270/jsbbs.66.161.
- Hannweg K, Visser G, de Jager K, Bertling I (2016). *In vitro*-induced polyploidy and its effect on horticultural characteristics, essential oil composition and bioactivity of *Tetradenia riparia*. *South African J. Bot.* 106: 186-191. <https://doi.org/10.1016/j.sajb.2016.07.013>.
- Hardigan MA, Feldmann MJ, Lorant A, Famula R, Acharya C, Cole G, Edger PP, Knapp SJ (2019). Chromosome evolution of octoploid strawberry DOI: <https://doi.org/10.1101/861526>.
- Hawkes JG (1990). The potato: Evolution, biodiversity and genetic resources. *Am. Potato J.* 67: 733-735. doi: 10.1007/BF03044023.
- Hegde SN, Rameshsing CN, Vasundhara M (2015). Characterization of *Stevia rebaudiana* Bertoni polyploids for growth and quality. *Med. Plant* 7: 188-195. doi: 10.5958/0975-6892.2015.00027.1.
- Herawati MM, Pudjihartati E, Kurnia TD, Setiawan AW (2020). The agronomic performance and artemisinin content of colchicine-induced polyploid genotypes *Artemisia cina*. *IOP Conference Series Materials Science and Engineering, 15th Joint Conference on Chemistry, Indonesia* 959(1): 012032. doi: 10.1088/1757-899X/959/1/012032.
- Hias N, Svava A, Wannas Keulemans J (2018). Effect of polyploidization on the response of apple (*Malus × domestica* Borkh.) to *Venturia inaequalis* infection. *Eur. J. Plant Pathol.* 151(2): 515-526. doi: 10.1007/s10658-017-1395-2.
- Hu C, Lin S, Chi W, 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 Physiol.* 158: 747-758. <https://doi.org/10.1104/pp.111.187674>.
- Hu Y, Sun D, Hu H, Zuo X, Xia T, Xie J (2021). A comparative study on morphological and fruit quality traits of diploid and polyploid carambola (*Averrhoa carambola* L.) genotypes. *Sci. Hortic.* 277: 109843 <https://doi.org/10.1016/j.scienta.2020.109843>.
- Iannicelli J, Elechosa MA, Juarez MA, Martinez A, Bugallo V, Bandoni AL, Escandon AS, Van Bare CM (2016). Effect of polyploidization in the production of essential oils in *Lippia integrifolia*. *Ind. Crops Prod.* 81: 20-29. <https://doi.org/10.1016/j.indcrop.2015.11.053>.
- Inthima P, Sujipuli K (2019). Improvement of growth and bacoside production in *Bacopa monnieri* through induced autotetraploidy with colchicine. *Peer J.* 7: e7966. <https://doi.org/10.7717/peerj.7966>.
- Jansky S, Haynes K, Douches D (2019). Comparison of two strategies to introgress genes for resistance to common Scab from diploid *Solanum chacoense* into tetraploid cultivated potato. *Am. J. Potato Res.* 96: 255-261. <https://doi.org/10.1007/s12230-018-09711-6>.
- Jansky SH, Spooner DM (2018). The evolution of potato breeding. *Plant Breed. Rev.* 41: 169-214. doi: 10.1002/9781119414735.
- Javadian N, Karimzadeh G, Sharifi M, Moieni A, Behmanesh M (2017). *In vitro* polyploidy induction: changes in morphology, podophyllotoxin biosynthesis, and expression of the related genes in *Linum album* (Linaceae). *Planta* 245(6): 1165-1178. doi: 10.1007/s00425-017-2671-2.
- Julião SA, Ribiero CDV, Lopes JML, Matos EMD, Reis AC, Peixoto PHP, Machado MA, Azevedo ALS, Grazul RM, Campos JMDS, Viccini LF (2020). Induction of synthetic polyploids and assessment of genomic stability in *Lippia alba*. *Front. Plant Sci.* 11: 292. <https://doi.org/10.3389/fpls.2020.00292>.
- Kasmiyati S, Kristiani EBE, Herawati MM (2020). Effect of induced polyploidy on plant growth, chlorophyll, and flavonoid content of *Artemisia cina*. *Biosaintifika: J. Biol. Biol. Edu.* 12(1): 90-96. doi: <http://dx.doi.org/10.15294/biosaintifika.v12i1.22548>.
- Khalili S, Niazian M, Arab M, Norouzi M (2019). *In vitro* chromosome doubling of African daisy, *Gerbera jamesonii* Bolus cv. Mini Red. *Nucleus* 63: 59-65. <https://doi.org/10.1007/s13237-019-00282-3>.
- Kharde AV, Chavan NS, Chandre MA, Autade RH, Khetmalas MB (2017). *In vitro* enhancement of bacoside in brahmi (*Bacopa monnieri*) using colchicine. *J. Plant Biochem. Physiol* 5: 1-6. doi: 10.4172/2329-9029.1000172.

- Konečná V, Bray S, Vlček J, Bohutínská M, Požárová D, Choudhury RR, Bollmann-Giolai A, Flis P, Salt DE, Parisod C, Yant L, Kolář F (2021). Parallel adaptation in autopolyploid *Arabidopsis arenosa* is dominated by repeated recruitment of shared alleles. *Nat. Commun.* 12: 4979. <https://doi.org/10.1038/s41467-021-25256-5>.
- Kundu S, Salma U, Ali MN, Mandal N (2018). *In vitro* tetraploidization for the augmentation of wedelolactone in *Sphagneticola calendulacea* (L.) Pruski. *Acta Physiol. Plant* 40: 215. <https://doi.org/10.1007/s11738-018-2786-5>.
- Kushwah KS, Verma RC, Patel S, Jain NK (2018). Colchicine induced polyploidy in *Chrysanthemum carinatum* L. *J. Phylogenetics Evol. Biol.* 6(193): 2. <https://doi.org/10.4172/2329-9002.1000193>.
- Kyriakidou M, Anglin NL, Ellis D, Tai HH, Strömviik MV (2020). Genome assembly of six polyploidy potato genomes. *Sci. Data* 7: 88. <https://doi.org/10.1038/s41597-020-0428-4>.
- Le KC, Ho TT, Lee JD, Paek KY, Park SY (2020). Colchicine mutagenesis from long-term cultured adventitious roots increases biomass and ginsenoside production in wild ginseng (*Panax ginseng* Mayer). *Agronomy* 10(6): 785. <https://doi.org/10.3390/agronomy10060785>.
- Li M, Xu G, Xia X, Wang M, Yin X, Zhang B, Zhang X, Cui Y (2017). Deciphering the physiological and molecular mechanisms for copper tolerance in autotetraploid *Arabidopsis*. *Plant Cell Rep.* 36(10): 1585-1597. doi: 10.1007/s00299-017-2176-2.
- Li M, Zhang C, Hou L, Yang W, Liu S, Pang X, Li Y (2021). Multiple responses contribute to the enhanced drought tolerance of the autotetraploid *Ziziphus jujuba* Mill. var. *spinosa*. *Cell Biosci.* 11: 119 <https://doi.org/10.1186/s13578-021-00633-1>.
- Li Q, Yang Y, Wu H (2016). *In vitro* segregation of tetraploid and octoploid plantlets from colchicine-induced ploidy chimeras in *Echinacea purpurea* L. *Hortic. Sci.* 51: 549-557. <https://doi.org/10.21273/HORTSCI.51.5.549>.
- Li QQ, Zhang J, Liu JH, Yu BY (2018). Morphological and chemical studies of artificial *Andrographis paniculata* polyploids. *Chinese J. Nat. Med.* 16(2): 81-89. [https://doi.org/10.1016/S1875-5364\(18\)30033-5](https://doi.org/10.1016/S1875-5364(18)30033-5).
- Liu B, Sun G (2017). microRNAs contribute to enhanced salt adaptation of the autopolyploid *Hordeum bulbosum* compared with its diploid ancestor. *Plant J.* 91(1): 57-69. doi: 10.1111/tpj.13546.
- Ma J, Zheng A, Zhou P, Yuan Q, Wu R, Chen C, Wu X, Zhang F, Sun B (2019). Targeted editing of the *StPDS* gene using the CRISPR/Cas9 system in tetraploid potato. *Emir. J. Food Agric.* 31(7): 482-490. doi: 10.9755/efja.2019.v31.i7.1974.
- Machida-Hirano R (2015). Diversity of potato genetic resources. *Breed. Sci.* 65: 26-40. <https://doi.org/10.1270/jsbbs.65.26>.
- Mahdi SA, Meena CM, Tholakabavi A (2018). Induction of genetic variability by colchicine treatment in *Stevia rebaudiana* Bertoni. *Al-Qadisiyah J. Pure Sci.* 23(3): 161-173. <https://doi.org/10.29350/jops.2018.23.3.903>.
- Mansouri H, Bagheri M (2017). Induction of polyploidy and its effect on *Cannabis sativa* L. In: *Cannabis sativa* L. *Bot. Biotechnol. Springer, Cham*, 365-383. doi: 10.1007/978-3-319-54564-6\_17.
- Matsuoka Y (2011). Evolution of polyploid triticum wheats under cultivation: The role of domestication, natural hybridization and allopolyploid speciation in their diversification. *Plant Cell Physiol.* 52(5): 750-764. doi:10.1093/pcp/pcr018.
- Mena M, Ambrose B, Meeley R, Briggs S, Yanofsky M, Schmidt R (1996). Diversification of C-function activity in maize flower development. *Sciences* 274: 1537-1540. <https://doi.org/10.1126/science.274.5292.1537>.
- Meng H, Jiang S, Hua S, Lin X, Li Y, Guo W, Jiang L (2011). Comparison between a tetraploid turnip and its diploid progenitor (*Brassica rapa* L.): The adaptation to salinity stress. *Agric. Sci. China* 10(3): 363-375. doi: 10.1016/S1671-2927(11)60015-1.
- Mishra B, Pathak S, Sharma A, Trivedi P, Shukla S (2010). Modulated gene expression in newly synthesized auto-tetraploid of *Papaver somniferum* L. *S. Afr. J. Bot.* 76(3): 447-452. doi: 10.1016/j.sajb.2010.02.090.
- Mu H, Lin L, Zhang Q, Tang X, Zhang X, Cheng G (2016). Growth, proline content and proline-associated gene expression of autotetraploid *Betula platyphylla* responding to NaHCO<sub>3</sub> stress. *Dendrobiology* 75: 123-129. doi: 10.12657/denbio.075.012.
- Muthoni J, Kabira J, Shimelis H, Melis R (2015). Tetrasomic inheritance in cultivated potato and implications in conventional breeding. *Aust. J. Crop Sci.* 9: 185-190.
- Naqvi RZ, Siddiqui HA, Mahmood MA, Najeebullah S, Ehsan A, Azhar M, Farooq M, Amin I, Asad S, Mukhtar Z, Mansoor S, Asif M (2022). Smart breeding approaches in post-genomics era for developing climate-resilient food crops. *Front. Plant Sci.* 13:972164. doi: 10.3389/fpls.2022.972164.
- Nasr M, Habib HM, Ibrahim IA, Kapiel T (2004). *In vitro* induction of autotetraploid watermelons using colchicine and four dinitroaniline compounds. *Pro. Int. Conf. Genet. Eng. Appl. Sharm Elsheik, Egypt*, 8-11 April 2004, 1-20. doi: 10.13140/2.1.3144.3840.
- Navrátilová B, Švécárová M, Bednář J, Ondřej V (2021). *In vitro* polyploidization of *Thymus vulgaris* L. and its effect on the composition

- of essential oils. *Agronomy* 11: 596. <https://doi.org/10.3390/agronomy11030596>.
- Niazian M, Nalouisi AM (2020). Artificial polyploidy induction for improvement of ornamental and medicinal plants. *Plant Cell Tissue Organ Cult. (PCTOC)* <https://doi.org/10.1007/s11240-020-01888-1>.
- Niu S, Wang Y, Zhao Z, Deng M, Cao L, Yang L, 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(7): p. e0158750. <https://doi.org/10.1371/journal.pone.0158750>.
- Noori SAS, Norouzi M, Karimzadeh G, Shirkooll K, Niazian M (2017). Effect of colchicine-induced polyploidy on morphological characteristics and the essential oil composition of ajowan (*Trachyspermum ammi* L.). *Plant Cell Tissue Organ Cult. (PCTOC)* 130: 543-551. doi: 10.1007/s12298-019-00718-9.
- Parsons JL, Martin SL, James T, Golenia G, Boudko EA, Hepworth SR (2019). Polyploidization for the genetic improvement of *Cannabis sativa*. *Front. Plant Sci.* 10: 476. <https://doi.org/10.3389/fpls.2019.00476>.
- Pham VH (2021). The unique existence of chromosomal abnormality in polyploidy plants, in Down syndrome and other chromosome abnormalities. *Intechopen* 1-13. doi: <http://dx.doi.org/10.5772/intechopen.99821>.
- Pliankong P, Suksa-Ard P, Wannakrairoj S (2017). Effects of colchicine and oryzalin on polyploidy induction and production of capsaicin in *Capsicum frutescens* L. *Thai J. Agric. Sci.* 50: 108-120.
- Poerba YS, Martanti D, Handayani T, Witjaksono (2019a). Induction of banana autotetraploid "Klutuk Sukun" and their reproductive function for producing triploid hybrids. *Asian J. Plant Sci.* 18(2): 91-100. doi: 10.3923/ajps.2019.91.100.
- Poerba YS, Martanti D, Handayani T, Witjaksono (2019b). Morphology and reproductive function of induced autotetraploid banana by chromosome doubling. *SABRAO J. Breed. Genet.* 51(2): 175-190.
- Rahman SSBA (2017). Enhancement of key chemical constituents in *Aquilaria malaccensis* Lamarck (Karas) through *in vitro* polyploidization. PhD Thesis, University Putra Malaysia.
- Rameshsing CN, Hegde SN, Vasundhara M (2015). Enhancement of steviol glycosides in stevia (*Stevia rebaudiana* Bertoni) through induction of polyploidy. *Curr. Trend. Biotechnol. Pharma.* 9: 141-146.
- Rao S, Tian Y, Xia X, Li Y, Chen J (2020). Chromosome doubling mediates superior drought tolerance in *Lycium ruthenicum* via abscisic acid signaling. *Hortic. Res.* 7: 40 <https://doi.org/10.1038/s41438-020-0260-1>.
- Ruiz M, Quiñones A, Martínez-Alcántara B, Aleza P, Morillon R, Navarro L, Primo-Millo E, Martínez-Cuenca M (2016). Tetraploidy enhances boron-excess tolerance in Carrizo Citrange (*Citrus sinensis* L. Osb. × *Poncirus trifoliata* L. Raf.). *Front. Plant Sci.* 7: 701. doi: 10.3389/fpls.2016.00701.
- Sabzehzari M, Hoveidamanesh S, Modarresi M, Mohammadi V (2019a). Morphological, anatomical, physiological, and cytological studies in diploid and tetraploid plants of *Plantago psyllium*. *Plant Cell Tissue Organ Cult.* 139: 131-137. <https://doi.org/10.1007/s11240-019-01670-y>.
- Sabzehzari M, Hoveidamanesh S, Modarresi M, Mohammadi V (2019b). Morphological, anatomical, physiological, and cytological studies in diploid and tetraploid plants of Ispaghul (*Plantago ovata* Forsk.). *Genet. Resour. Crop Evol.* 67(1): 129-137. [https://doi.org/10.1007/s10722-019-00846-x\(0123456789\)](https://doi.org/10.1007/s10722-019-00846-x(0123456789)).
- Salma U, Kundu S, Hazra AK, Ali MN, Mandal N (2018). Augmentation of wedelolactone through *in vitro* tetraploid induction in *Eclipta alba* (L.) Hassk. *Plant Cell Tissue Organ Cult. (PCTOC)* 133: 289-298. <https://doi.org/10.1007/s11240-018-1381-1>.
- Saminathan T, Nimmakayala, Manohar S, Malkaram S, Almeida A, Cantrell R, Tomason Y, Abburi L, Rahman MA, Vajja VG, Khachane A, Kumar B, Rajasimha HK, Levi A, Wehner T, Reddy UK (2015). Differential gene expression and alternative splicing between diploid and tetraploid watermelon. *J. Exp. Bot.* 66: 1369-1385. <https://doi.org/10.1093/jxb/eru486>.
- Shmeit YH, Fernandez E, Novy P, Kloucek P, Orosz M, Kokoska L (2020). Autopolyploidy effect on morphological variation and essential oil content in *Thymus vulgaris* L. *Sci. Hortic.* 263: 109095, <https://doi.org/10.1016/j.scienta.2019.109095>.
- Stenberg P, Saura A (2013). Meiosis and its deviations in polyploid animals. *Cytogenet. Genome Res.* 140: 185-203. doi: 10.1159/000351731.
- Storme ND, Mason A (2014). Plant speciation through chromosome instability and ploidy change: Cellular mechanisms, molecular factors, and evolutionary relevance. *Curr. Plant Biol.* 1: 10-33. <https://doi.org/10.1016/j.cpb.2014.09.002>.
- Syngelaki E, Daubert M, Klatt S, Hörandl E (2020). Phenotypic responses, reproduction mode and epigenetic patterns under temperature treatments in the alpine plant species *Ranunculus kuepferi* (*Ranunculaceae*). *Biology* 9: 315. doi: 10.3390/biology9100315.
- Syngelaki E, Paetzold C, Hörandl E (2021). Gene expression profiles suggest a better cold

- acclimation of polyploids in the alpine species *Ranunculus kuepferi* (Ranunculaceae). *Genes* 12: 1818. <https://doi.org/10.3390/genes12111818>.
- Talei D, Fotokian MH (2020). Improving growth indices and productivity of phytochemical compounds in lemon balm (*Melissa officinalis* L.) through induced polyploidy. *Bio Technologia* 101(3): 215-226. <https://doi.org/10.5114/bta.2020.97880>.
- Talei D, Nekouei MN, Mardi M, Kadkhodaei S (2020). Improving productivity of steviol glycosides in *Stevia rebaudiana* via induced polyploidy. *J. Crop Sci. Biotechnol.* 23: 301, <https://doi.org/10.1007/s12892-020-00038-5>.
- Tavan M, Mirjalili MH, Karimzadeh G (2015). *In vitro* polyploidy induction: Changes in morphological, anatomical and phytochemical characteristics of *Thymus persicus* (Lamiaceae). *Plant Cell Tissue Organ Cult. (PCTOC)* 122: 573-583.
- Thong-on W, Arimatsu P, Pitiporn S, Soonthornchareonnon N, Prathanturug S (2014). Field evaluation of *in vitro*-induced tetraploid and diploid *Centella asiatica* (L.) urban. *J. Nat. Med.* 68: 267-273. doi: 10.1007/s11418-013-0761-4.
- Tsuro M, Kondo N, Noda M, Ota K, Nakao Y, Asada S (2016). *In vitro* induction of autotetraploid of Roman chamomile (*Chamaemelum nobile* L.) by colchicine treatment and essential oil productivity of its capitulum. *In Vitro Cell. Dev. Biol. Plant.* 52(5): 479-483. doi: 10.1007/s11627-016-9779-0.
- Tu HY, Zhang AL, Xiao W, Lin YR, Shi JH, Wu YW, Wu ST, Zhong CH, Mo SX (2018). Induction and identification of tetraploid *Hedychium coronarium* through thin cell layer culture. *Plant Cell Tissue Organ Cult. (PCTOC)* 135(3): 395-406. <https://doi.org/10.1007/s11240-018-1472-z>.
- Tu Y, Jiang A, Gan L, Hossain M, Zhang J, Peng B, Xiong Y, Song Z, Cai D, Xu W, Zhang J, He Y (2014). Genome duplication improves rice root resistance to salt stress. *Rice* 7(1): 15-15. doi: 10.1186/s12284-014-0015-4.
- Urwin NA (2014). Generation and characterization of colchicine-induced polyploid *Lavandula x intermedia*. *Euphytica* 197(3): 331-339. <https://doi.org/10.1007/s10681-014-1069-5>.
- Van Hieu P (2019). Polyploid gene expression and regulation in polysomic polyploids. *Am. J. Plant Sci.* 10(8): 1409-1443. doi:10.4236/ajps.2019.108101.
- Veillet F, Kermarrec M-P, Chauvin L, Guyon-Debast A, Chauvin J-E, Gallois JL, Nogue F (2020). Prime editing is achievable in the tetraploid potato, but needs improvement. doi: <https://doi.org/10.1101/2020.06.18.159111>.
- Verhage L (2021). Diploid, triploid, tetraploid – chromatin organization in polyploid watermelon. *Plant J.* 106: 586-587. <https://doi.org/10.1111/tpj.15256>.
- Watanabe K (2015). Potato genetics, genomics, and applications. *Breed. Sci.* 65: 53-68. <https://doi.org/10.1270/jsbbs.65.53>.
- Wei KH, Xu JP, Li LX, Cai JY, Miao JH, Li MH (2018). *In vitro* induction and generation of tetraploid plants of *Sophora tonkinensis* Gapnep. *Pharmacogn. Mag.* 14(54): 149-154. doi: 10.4103/pm.pm\_170\_17.
- Whitaker VM, Knapp SJ, Hardigan MA, Edger PP, Slovin JP, Bassil NV, Hytönen T, Mackenzie K, Lee S, Jung S, Main D, Barbey CR, Verma S (2020). A roadmap for research in octoploid strawberry. *Hortic. Res.* 7: 33 <https://doi.org/10.1038/s41438-020-0252-1>.
- Xiang ZX, Tang XL, Liu WH, Song CN (2019). A comparative morphological and transcriptomic study on autotetraploid *Stevia rebaudiana* (Bertoni) and its diploid. *Plant Physiol. Biochem.* 143: 154-164. doi: 10.1016/j.plaphy.2019.09.003.
- Xing SH, Guo XB, Wang Q, Pan QF, Tian YS, Liu P, Zhao JY, Wang GF, Sun XF, Tang KX (2011). Induction and flow cytometry identification of tetraploids from seed-derived explants through colchicine treatments in *Catharanthus roseus* (L.) G. Don. *J. Biomed. and Biotechnol.* Res Int 2011:793198. doi:10.1155/2011/793198.
- Xu CG, Tang TX, Chen R, Liang CH, Liu XY, Wu CL, Yang YS, Yang DP, Wu H (2014). A comparative study of bioactive secondary metabolite production in diploid and tetraploid *Echinacea purpurea* (L.) Moench. *Plant Cell Tissue Organ Cult.* 116: 323-332. <https://doi.org/10.1080/13102818.2015.1086281>.
- Xue H, Zhang F, Zhang Z, Fu J, Wang F, Zhang B, Ma Y (2015). Differences in salt tolerance between diploid and autotetraploid apple seedlings exposed to salt stress. *Sci. Hortic.* 190: 24-30. doi:10.1016/j.scienta.2015.04.009.
- Yadav AK, Singh S, Yadav SC, Dhyani D, Bhardwaj G, Sharma A, Singh B (2013). Induction and morpho-chemical characterization of *Stevia rebaudiana* colchiploids. *Indian J. Agric. Sci.* 83: 159-165.
- Yan HJ, Xiong Y, Zhang HY, He ML (2016). *In vitro* induction and morphological characteristics of octoploid plants in *Pogostemon cablin*. *Breed. Sci.* 66: 169-174. doi: 10.1270/jsbbs.66.169.
- Yan K, Wu C, Zhang L, Chen X (2015). Contrasting photosynthesis and photoinhibition in tetraploid and its autopolyploid honeysuckle (*Lonicera japonica* Thunb.) under salt stress. *Front. Plant Sci.* 6: 227.
- Yasir M, Kanwal HH, Hussain Q, Riaz MW, Sajjad M, Rong J, Jiang Y (2022). Status and prospects of genome-wide association studies in cotton. *Front. Plant Sci.* 13: 1019347. doi: 10.3389/fpls.2022.1019347.
- Yousef EAH, Elsadek MA (2020). A comparative study of morphological and volatile oil composition characteristics in diploid and

- tetraploid garlic plants. *Egyptian J. Hortic.* 47: 295-308 doi:10.21608/ejoh.2019.18311.1118.
- Yu L, Liu X, Boge W, Liu X (2016). Genome-wide association study identifies loci for salt tolerance during germination in autotetraploid alfalfa (*Medicago sativa* L.) using genotyping-by-sequencing. *Front. Plant Sci.* 7: 956. DOI: 10.3389/fpls.2016.00956.
- Zahedi AA, Hosseini B, Fattahi M, Dehghan E, Parastar H, Madani H (2014). Overproduction of valuable methoxylated flavones in induced tetraploid plants of *Dracocephalum kotschyi* Boiss. *Bot. Stud.* 55: 22 <https://doi.org/10.1186/1999-3110-55-22>.
- Zhang H, An S, Hu J, Lin Z, Liu X, Bao H, Chen R (2018). Induction, identification and characterization of polyploidy in *Stevia rebaudiana* Bertoni. *Plant Biotechnol.* 35: 81-86. doi: 10.5511/plantbiotechnology.17.1227a.
- Zhang N, Bao Y, Xie Z, Huang X, Sun Y, Feng G, Zeng H, Ren J, Li Y, Xiong J, Chen W, Yan C, Tang M (2019). Efficient characterization of tetraploid watermelon. *Plants* 8(10), 419. <https://doi.org/10.3390/plants8100419>.
- Zhang XY, Hu CG, Yao JL (2010). Tetraploidization of diploid *Dioscorea* results in activation of the antioxidant defense system and increased heat tolerance. *J. Plant Physiol.* 167(2): 88-94. doi: 10.1016/j.jplph.2009.07.006.
- Zhao Z, Li Y, Liu H, Zhai X, Deng M, Dong Y, Fan G (2017). Genome-wide expression analysis of salt-stressed diploid and autotetraploid *Paulownia tomentosa*. *PLoS one* 12(10): e0185455. doi: 10.1371/journal.pone.0185455.
- Zhao Z, Niu S, Fan G, Deng M, 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(2): 88. DOI: 10.3390/f9020088.
- Zhou J, Guo F, Fu J, Xiao Y, Wu J (2020). *In vitro* polyploid induction using colchicine for *Zingiber officinale* roscoe cv. 'Fengtou' ginger. *Plant Cell Tissue Organ Cult.* (PCTOC) 142(1): 87-94, <https://doi.org/10.1007/s11240-020-01842-1>.