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REVIEW

The polyploidy and its key role in plant breeding

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Abstract
Main conclusion **This article provides an up-to-date review concerning from basic issues of polyploidy to aspects regarding the relevance and role of both natural and artificial polyploids in plant breeding programs.** Polyploidy is a major force in the evolution of both wild and cultivated plants. Polyploid organisms often exhibit increased vigor and, in some cases, outperform their diploid relatives in several aspects. This remarkable superiority of polyploids has been the target of many plant breeders in the last century, who have induced polyploidy and/or used natural polyploids in many ways to obtain increasingly improved plant cultivars. Some of the most important consequences of polyploidy for plant breeding are the increment in plant organs ("gigas" effect), buffering of deleterious mutations, increased heterozygosity, and heterosis (hybrid vigor). Regarding such features as tools, cultivars have been generated with higher yield levels, improving the product quality and increasing the tolerance to both biotic and abiotic stresses. In some cases, when the crossing between two species is not possible because of differences in ploidy level, polyploids can be used as a bridge for gene transferring between them. In addition, polyploidy often results in reduced fertility due to meiotic errors, allowing the production of seedless varieties. On the other hand, the genome doubling in a newly formed sterile hybrid allows the restoration of its fertility. Based on these aspects, the present review initially concerns the origin, frequency and classification of the polyploids, progressing to show the revolution promoted by the discovery of natural polyploids and polyploidization induction in the breeding program status of distinct crops.

Keywords Autopolyploidy · Allopolyploidy · Hybridization · Plant breeding · Heterosis · Hybrid bridge · "Gigas" effect

Introduction

Polyploidy refers to the presence of more than two complete sets of chromosomes per cell nucleus, which has been considered a ubiquitous phenomenon in plant evolution and diversification (Soltis et al. 2009). The estimation of polyploidy incidence is widely variable in the literature, ranging from 30 to 35 % (Stebbins 1971) to 70 % (Masterson 1994) for angiosperms. Otto and Whitton (2000) developed a simple model to estimate the incidence of polyploidy based on transitions between odd and even basic chromosome numbers. Using such approach, they suggested that polyploidization occurs in approximately 2–4 % of speciation events in angiosperms and 7 % in ferns. In light of these results, the authors affirmed that polyploidy is likely to be one of the most predominant mechanisms of sympatric speciation in plants.

The remarkable advances in genomic studies have revealed ancient cases of polyploidy. Using phylogenetic analysis of expressed sequence tags (EST), Jiao et al. (2011) identified two events of whole genome duplication (WGD), which occurred around 319 and 192 million years

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ago, shortly before the diversification of extant seed plants and flowering plants, respectively. Therefore, it is accepted that all seed plants have experienced at least one round of WGD in their evolutionary history, characterizing a paleopolyploid ancestry (Renny-Byfield and Wendel 2014).

The elucidation of the causes and consequences of polyploidy has been the focus of several reviews in the last hundred years (Stebbins 1947, 1950, 1971; Harlan and de Wet 1975; Levin 1983; Soltis and Soltis 1995, 1999, 2009; Ramsey and Schemske 1998; Otto and Whitton 2000; Wolfe 2001; Osborn et al. 2003; Yang et al. 2011; Ramsey and Ramsey 2014). These studies have provided a wide range of information about different aspects of polyploidy, including classification, frequency, mechanisms of origin and ancient polyploidy events, as well as its ecological, genetic and evolutionary consequences.

The revelation that a large number of plant species have a polyploid genome, including several important crops, has attracted the attention of plant breeders for the application of artificial polyploidy as a tool for crop improvement. In this context, the work at hand presents a review focused on the numerous applications of polyploidy in plant breeding and the methods for polyploidy induction and detection, as well as some examples of successfully induced polyploid crops of commercial relevance.

Polyploidy classes and modes of origin

A polyploid individual arising within one or between populations of a single species is denominated autopolyploid, while the term allopolyploid refers to individuals of hybrid origin (Stebbins 1950) (Fig. 1). The identification of each class is frequently accomplished by analyzing the pairing and inheritance patterns. The presence of more than two homologous chromosomes in autopolyploids may contribute to the formation of multivalents during meiosis. Due to non-preferential pairing, the offspring of a cross between two autopolyploids will exhibit a different ratio from that of the classic Mendelian cross (1:2:1), characterizing a polysomic inheritance (Ramsey and Schemske 1998; Tayalé and Parisod 2013).

Allopolyploids are often divided into two sub-classes: true and segmental allopolyploids. The formation of true allopolyploids involves hybridization between distantly related species. In this case, the divergent chromosome complements do not pair with each other, resulting in the formation of bivalents during meiosis and in a disomic inheritance pattern. On the other hand, segmental allopolyploids originate from hybridization between closely related species with partially differentiated genomes (Stebbins 1950). Therefore, segmental allopolyploids may undergo univalent, bivalent and/or multivalent pairing during meiosis, being considered intermediate types between true allopolyploids and autopolyploids (Sybenga 1992).

Different mechanisms have been proposed to explain how polyploids arise in nature. Two major pathways are known to lead to polyploidy in plants: somatic doubling and formation of unreduced reproductive cells. Somatic doubling is associated with mitotic events such as endomitosis or endoreduplication, which may occur either in a zygote cell or in apical meristematic tissues, giving rise to mixoploids or even completely polyploid organisms. Despite being constantly used to attain artificial polyploids, somatic doubling is supposed to have a minor role in the origin of natural polyploid organisms (Ramsey and Schemske 1998).

The production and fusion of unreduced reproductive cells have been pointed out as the most predominant pathway leading to polyploidy in plants. The capacity of producing unreduced gametes is a heritable feature evidenced in many plant species. Besides genetic control, environmental factors such as temperature, herbivory, wounding, water deficit and nutrients shortage influence the production of unreduced gametes (Ramsey and Schemske 1998). Once formed, the unreduced gamete can fuse either with another unreduced gamete (bilateral polyploidization) or with a reduced one (unilateral polyploidization).

Cytologically, two processes may lead to the formation of unreduced gametes, namely the first division restitution (FDR) and the second division restitution (SDR), depending on the meiotic stage in which the restitution occurs. FDR involves errors during meiosis I, which may occur due to the absence of chromosome pairing in zygotene/pachytene and/or non-segregation of homologous chromosomes in anaphase I. In SDR, chromosome pairing and division are normal during meiosis I, but sister chromatids do not segregate in anaphase II. Such abnormalities promote restitution of the somatic chromosome number in the reproductive cells and result in the formation of dyads or triads (Bretagnolle and Thompson 1995; Ramanna and Jacobsen 2003). Each mechanism of meiotic restitution has a different genetic consequence with regard to the maintenance of heterozygosity. The unreduced gametes originated by FDR will possess two non-sister chromatids and may contain approximately the same heterozygosity levels of their parents. In contrast, when an unreduced gamete is formed through SDR it will have two sister chromatids, resulting in a lower level of heterozygosity when compared to its parents. Such difference in the heterozygosity level has a crucial role in determining the success or failure in the establishment of a recently formed polyploid, either in the context of plant breeding or in wild populations (Bretagnolle and Thompson 1995).

Applications of polyploidy in plant breeding

Episodes of polyploidy have clearly played a major role in the evolution and speciation of plants. Polyploidization events often seem to be associated with increases in vigor and adaptation of the newly formed polyploid to novel conditions. According to Van de Peer et al. (2009), the competitive advantage of polyploids over their diploid progenitors is mostly related to transgressive segregation, i.e., formation of extreme phenotypes, and increased vigor. Using phylogenetic approaches, Fawcett et al. (2009) evidenced that many different plant lineages have independently experienced whole genome duplication events around the time of the Cretaceous–Tertiary (KT) extinction. These authors also suggested that some changes promoted by polyploidy allowed the polyploid individuals to survive the environmental changes of the KT boundary and outcompete many of their diploid progenitors. These changes included increase in phenotypic variability, heterosis, mutational robustness, subfunctionalization, and alterations in the reproduction modes. Such superior features exhibited by polyploid individuals have led to an increased interest in developing synthetic polyploids for application in crop breeding programs.

The most widespread consequence of polyploidy in plants is the increase in cell size, caused by the larger number of gene copies and referred to as the "gigas" effect (Fig. 1). Consequently, polyploid individuals may exhibit larger organs compared to their diploid counterparts, such as roots, leaves, tubercles, fruits, flowers and seeds (Stebbins 1950). Nonetheless, increase in cell size does not always lead to increased size of the whole plant or its organs, since the number of cell divisions in polyploids is often reduced (Stebbins 1971). Polyploid plants also have lower growth rates, and tend to flower later or over a longer period of time than related diploids, which is a desirable feature for ornamental breeding (Levin 2002). The reduction in fertility is another common consequence of autopolyploidy and may result from issues concerning the multivalent formation and meiotic irregularities (Stebbins 1971). Therefore, autopolyploidy induction in breeding programs is usually restricted to crops cultivated for their vegetative organs and those with vegetative propagation, due to the low rates of viable seed production (Paterson 2005). The breeding for seedless fruits is an exception, since in this case the low number of seeds is a desirable characteristic, such as in the triploid watermelon (Crow 1994). In addition, autopolyploidy may positively affect the tolerance to some stresses, such as nutrient deficiency, drought, water deficit, temperature, pests and pathogens (Levin 2002).

The concepts of genome "buffering" and heterozygosity have been widely applied in polyploid breeding programs

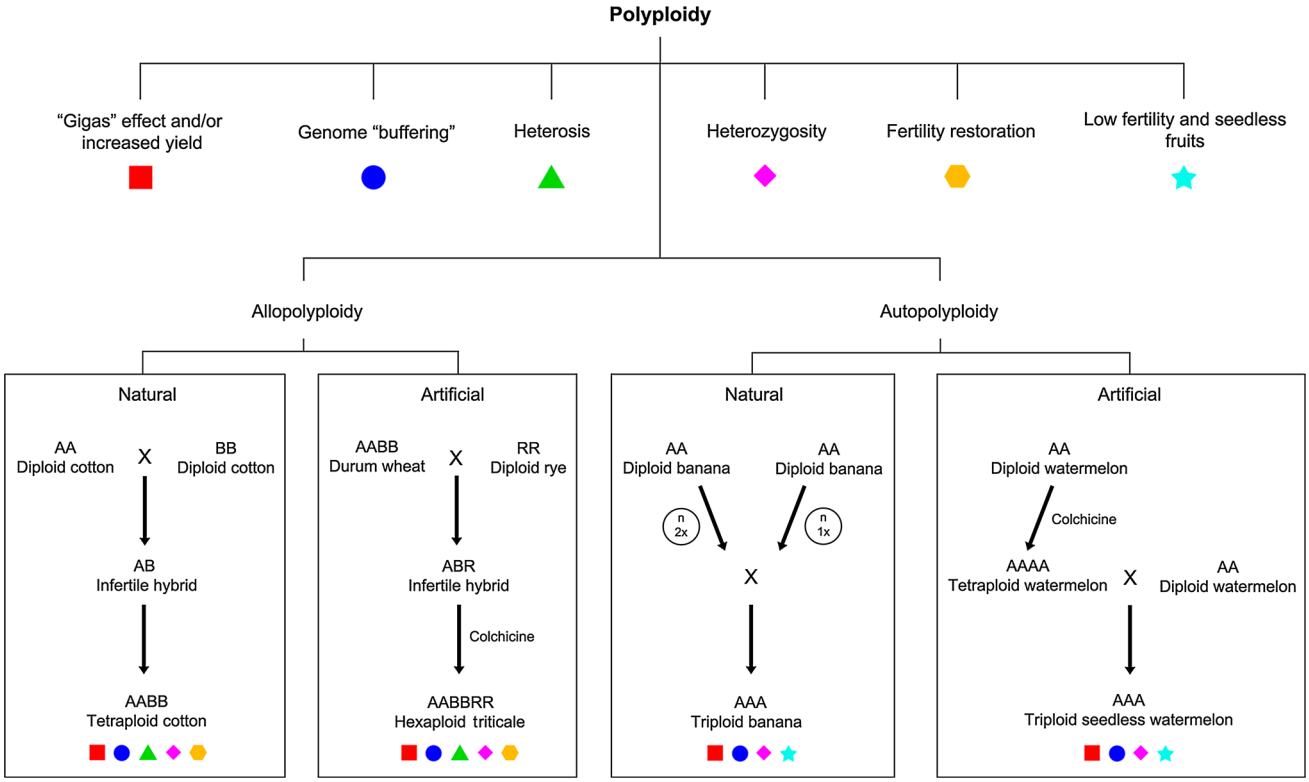

Fig. 1 Schematic representation of four cultivated species and some of the main polyploidy consequences for application in crop improvement. The *symbols* "n 1*x*" and "n 2*x*" refer to reduced and unreduced reproductive cells, respectively

(Fig. 1). Genome redundancy promotes a "buffering" effect in which the deleterious alleles are masked by the extra copies of wild-type alleles. Thus, the duplicated genes offer a protective effect against single-locus deleterious mutations and inbreeding depression (Soltis and Soltis 2000; Comai 2005). Another benefit of genome redundancy is the possibility of functional diversification of redundant gene copies, in which one member of a duplicated gene pair mutates and acquires a novel function, without compromising essential functions (Adams and Wendel 2005). The increment in heterozygosity is another feature that accompanies polyploidy. In allopolyploids, the combination of two or more divergent genomes results in high levels of heterozygosity, which is fixed due to disomic inheritance within each genome. Moreover, autopolyploids are also expected to have higher levels of heterozygosity compared to their related diploids due to polysomic inheritance and the possibility of outcrossing occurrence (Moody et al. 1993; Osborn et al. 2003). Higher levels of heterozygosity have been positively related to vigor increment in autotetraploid maize (Randolph 1942), potato (Mendoza and Haynes 1974) and alfalfa (Katepa-Mupondwa et al. 2002).

Interspecific hybridization is accepted as an important evolutionary force for adaptation and speciation in plant groups (Barton 2001). Allopolyploids frequently display superior vigor in comparison with the mean of its two progenitors. Such hybrid vigor, also referred to as heterosis (Fig. 1), generally points to increases in biomass, stature, growth rate, fertility levels and/or stress tolerance of the hybrid, and has been considered one of the most important aspects for crop improvement (Chen 2010). The hexaploid bread wheat (*Triticum aestivum* L.; AABBDD) is an example of natural allopolyploid species, originated through multiple hybridizations. The most accepted hypothesis suggests that an initial cross between *Triticum urartu* Tumanian ex Gandilyan (AA) and *Aegilops speltoides* Tausch. (BB) resulted in the tetraploid hybrid *Triticum turgidum* L. (AABB), or durum wheat. Posteriorly, one or more hybridization events between *Aegilops tauschii* Coss. (DD) and the allotetraploid *T. turgidum* originated the hexaploid bread wheat (Haider 2013). The allohexaploid *T. aestivum* is the most widely cultivated species of wheat, exhibiting desirable features for bread making, followed by *T. turgidum*, which is the most suitable for pasta production (Pauly et al. 2013).

Other examples of natural allopolyploids with industrial relevance are the tetraploid cotton species *Gossypium hirsutum* L. (upland cotton; AADD) and *Gossypium barbadense* L. (Egyptian cotton; AADD). Their origin dates back to 1.5 million years and involved the hybridization between an A-genome species, like *Gossypium herbaceum* L. or *Gossypium arboreum* L., and a D-genome cotton species, probably *Gossypium raimondii* Ulbrich (Fig. 1). According to Jiang et al. (1998), the D subgenome of both allotetraploid cotton species, *G. hirsutum* and *G. barbadense*, possesses some of the quantitative trait loci (QTLs) influencing fiber yield and quality. However, only the diploid species with the A-genome produces suitable fibers for spinning, while the fibers of D-genome species are not spinnable. Moreover, none of the diploid cotton species provides fibers with the same high quality and the same yield as the two AADD allotetraploid species. Such observations suggest that the combination of the A and D genomes resulted in the formation of a polyploid hybrid that produces a fiber with quality superior to that of both diploid parents (Renny-Byfield and Wendel 2014).

In addition to the mentioned advantages of polyploidy for crop improvement, polyploids may also be induced for other purposes, such as to restore the fertility of sterile hybrids (Fig. 1) and to serve as a bridge for genetic transfer when direct crossing between two species is not feasible (Dewey 1980). Hybrids (AB) between distant taxa are commonly sterile due to the lack of homologous chromosomes for pairing during meiosis (Hegarty et al. 2008). Therefore, induced genome duplication is applied in breeding programs to overcome the sterility of newly synthesized hybrids, as the presence of an additional copy of both divergent genomes (AABB) enables the proper pairing during meiosis. Olsen et al. (2006) successfully restored the fertility of the intergeneric sterile hybrid × *Chitalpa tashkentensis* Elias & Wisura [*Catalpa bignonioides* Walt. × *Chilopsis linearis* (Cav.) Sweet] by inducing polyploidization with the anti-tubulin agent oryzalin. The allotetraploids of × *C. tashkentensis* obtained by these authors were fertile and stable, allowing their application for introgression of desirable traits in × *Chitalpa* breeding programs.

Bridge crossing is a strategy employed for transferring genes between two species with different ploidy levels through transitional fertile allopolyploids. For instance, Buckner et al. (1961) developed a bridge hybrid to transfer desirable traits from Italian ryegrass (*Lolium multiflorum* Lam.; $2n = 2x = 14$) to tall fescue (*Festuca arundinacea* Schreb.; $2n = 6x = 42$). The direct cross between Italian ryegrass and tall fescue is not possible. However, both species can successfully cross with meadow fescue (*Festuca pratensis* Huds.; $2n = 2x = 14$). Thus, the researchers were able to transfer the desirable traits by initially crossing Italian ryegrass with meadow fescue, which results in a sterile hybrid that has its genome doubled to form a fertile tetraploid bridge hybrid ($2n = 4x = 28$). Posteriorly, this bridge hybrid was repeatedly crossed with tall fescue for the selection of hexaploid tall fescue ($2n = 6x = 42$) individuals displaying the desirable features of Italian ryegrass. The same technique has been applied for gene

introgression in other relevant crops, such as tobacco (Burk 1967), cowpea (Fatokun 2002), wheat (Chhuneja et al. 2007) and cotton (Ram 2014).

Methods for polyploidy induction and detection

Polyploids may be induced through sexual polyploidization or somatic doubling. Before the discovery of colchicine in the 1930s, sexual polyploidization was commonly used for obtaining polyploids (Ramanna and Jacobsen 2003). This method has been effectively used in breeding programs of potato, alfalfa, red clover, yams, rose, lily and several other species of economic interest (Peloquin et al. 1999; Ramanna and Jacobsen 2003). Sexual polyploidization is based on the fusion of unreduced reproductive cells, and may be unilateral, when involving the fusion of one reduced and one unreduced gamete, or bilateral, when both gametes are unreduced. The major advantage of inducing sexual instead of somatic polyploids is that they combine genetic effects of both the increased ploidy levels (i.e., genome buffering, increased levels of gene expression, neofunctionalization) and the meiotic recombination (i.e., genetic variability through independent segregation and crossing over), allowing the maintenance of high levels of heterozygosity (Ramsey and Schemske 1998; Peloquin et al. 1999).

For some crops, such as triploid banana and plantain, sexual polyploidization may be the most efficient way to produce polyploids (Ramanna and Jacobsen 2003). However, the major hindrance to the application of sexual polyploidization is the low frequency of unreduced gametes production. In general, unreduced reproductive cells are generated at a low rate, varying from 0.56 % in non-hybrid species to 27.52 % in hybrids. Nonetheless, the ability to produce these gametes is a heritable condition that can be increased in some plant populations by selection (Ramsey and Schemske 1998). In addition, several attempts to induce the production of unreduced gametes have been made in the last decades, which included treatments with temperature, nitrous oxide (N_2O), anti-tubulin agents and ethyl methane sulphonate (EMS), as well as gene silencing by RNA interference (RNAi) and virus-induced gene silencing (VIGS) (Dewitte et al. 2012). Such advances in the induction and manipulation of unreduced gametes have facilitated the application of sexual polyploidization in breeding programs that require high levels of heterozygosity, and in the cases where somatic polyploidization is not feasible (Ramanna and Jacobsen 2003; Dewitte et al. 2012).

Somatic, or mitotic, polyploidization involves the induction of chromosome doubling in somatic tissues, and has been achieved in several crop species. Before the discovery of colchicine by Blakeslee and Avery (1937), attempts to induce somatic polyploidy were made via other methods, such as exposure to high or low temperature (Blakeslee and Avery 1937). Randolph (1932) obtained tetraploid maize using a high-temperature treatment during the initial development of the embryos. Posteriorly, Dorsey (1936) used the same method and succeeded in producing polyploids of rye and wheat. However, the breakthrough in polyploidy induction was only achieved after the aforementioned work of Blakeslee and Avery (1937), which announced the great power of the alkaloid colchicine for inducing plant polyploidy.

Colchicine is an alkaloid extracted from meadow saffron (*Colchicum autumnale* L.) and the most widely used antimitotic agent for polyploidy induction (Planchais et al. 2000). The mechanism of action of colchicine involves its binding to α- and β-tubulin dimers, inhibition of microtubule polymerization during the cell cycle and prevention of chromosome/chromatid migration during anaphase. Consequently, cytokinesis will also be compromised, resulting in the formation of cells with doubled chromosome number. Colchicine has low affinity for plant tubulins and must be used at millimolar levels for effective polyploidy induction in plants (Dhooghe et al. 2011). Besides, through the use of colchicine, artificial plant polyploidy may also be achieved with other classes of antimitotic agents, such as the herbicides dinitroanilines (trifluralin and oryzalin) and phosphoric amides (amiprophos-methyl and butamiphos). These substances have higher affinity for plant tubulins. Therefore, micromolar concentrations of such agents might produce the same results as colchicine treatment (Planchais et al. 2000).

Initially, colchicine was applied to plants established in the soil by immersion of a seed or twig in solution, spraying of the leaves, or repeated application of single drops of solution to a bud (Blakeslee and Avery 1937). Posteriorly, Murashige and Nakano (1966) first reported an in vitro procedure that resulted in the spontaneous polyploidization of tobacco calli. In this study, the increase in the number of subcultures resulted in the development of polyploid and aneuploid calli. Considering these results, the authors suggested that tissue culture was a potential tool for artificial polyploidization. The in vitro environment allows greater control and standardization of the polyploidization process, improving the efficiency of the method and the relative rates of polyploid plants formation. The success of an in vitro polyploidization procedure depends on many factors, such as the preexistence of a well-established protocol for the in vitro regeneration of the target species, type and concentration of the antimitotic agent, time of exposure, the method of antimitotic solution application, and the type of explant. This way, the development of a protocol for in vitro polyploidization requires

the conduction of several tests to obtain the most suitable combination of antimitotic agent concentration and exposure time for each species (Dhooghe et al. 2011).

After induction of chromosome doubling, it is important to confirm the success of the experiment in yielding polyploid plants. The methods for identification of polyploid individuals are classified as direct and indirect. Indirect methods involve the examination of physiological and/or morphological traits, especially those related with stomata. In comparison with their diploid relatives, polyploid plants usually display larger stomata in lower density, and the number of chloroplasts per guard cell is higher. Such stomata features have been efficiently used to distinguish the polyploid regenerants of several plant species, such as red clover (Evans 1955), ryegrasses (Speckmann et al. 1965), orchids (Silva et al. 2000), pear (Kadota and Niimi 2002), grapes (Yang et al. 2006), African marigold (Sajjad et al. 2013) and Balady mandarin (Elyazid and El-Shereif 2014).

The indirect procedures for polyploidy detection are usually rapid and simple. Nonetheless, they are often inaccurate and the confirmation through direct methods, such as chromosome counting and nuclear genome size measurement by flow cytometry, is usually necessary. Chromosome counting has been considered the most accurate method to detect polyploid variants. However, cytogenetic techniques are often laborious, requiring highly specific protocols for each species (Doležel et al. 2007). Alternatively, flow cytometry is a rapid, reliable and simple method to measure the ploidy level and confirm the success of polyploidy induction, allowing the analysis of a large number of target plants in a short period of time (Roy et al. 2001). In flow cytometry analysis, the ploidy level is inferred indirectly by its correlation with the relative or absolute DNA content—the DNA ploidy level. Therefore, assuming that an increment in the DNA content corresponds to increments in chromosome number, the DNA content of an exemplar with a known ploidy level can be used as a reference standard to determinate the DNA ploidy level of an unknown sample (Doležel et al. 2007) (Fig. 2).

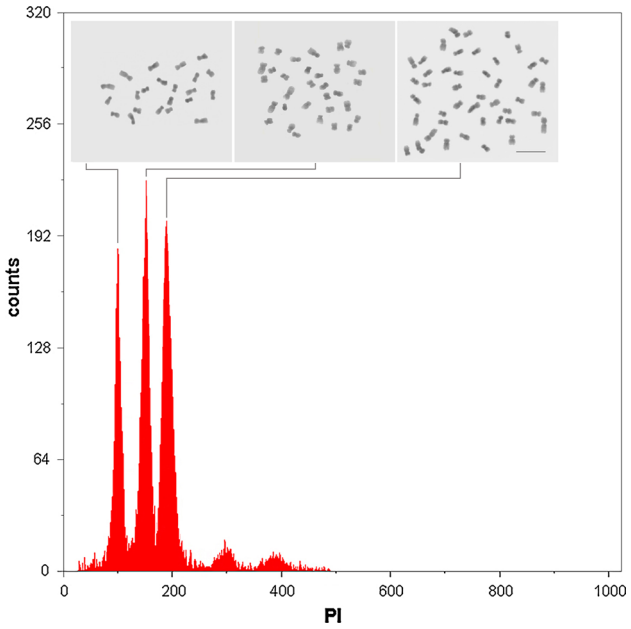

Fig. 2 Polyploidy detection in *Coffea* through chromosome counting and flow cytometry. Karyotypes of *C. canephora*, "Híbrido de Timor" (*C. arabica* × *C. canephora*) and *C. arabica* are represented from *left* to *right*, evidencing the chromosome numbers of $2x = 22$, $3x = 33$ and $4x = 44$, respectively. The *histogram* represents the G_0/G_1 peaks (above—the correspondent chromosome number) from nuclear suspensions of the same exemplars. Based on the DNA ploidy level of the diploid species *C. canephora* (channel 100, 2C = 1.43 pg) it is possible to estimate the DNA ploidy level of the triploid "Híbrido de Timor" (channel 146, 2C = 2.10 pg) and of the tetraploid species *C. arabica* (channel 186, 2C = 2.66 pg). *Bar* 5 μm

Impacts of polyploidy induction on crop improvement

According to Simmonds (1980), approximately 40 % of the cultivated species are polyploids. Examples of natural polyploid cultivars are listed in Table 1, which includes some of the most widely cultivated species worldwide. High expectations were created following the perception of the advantages provided by polyploidy in natural populations and especially after the discovery of colchicine properties for easily inducing polyploidy in different plant species. Attempts to induce polyploidy were made in several crop species between the 1930s and 1970s, such as sugar beet, rye, grape, watermelon, red clover, alsike clover and various ornamentals. Nonetheless, only a small number of artificial polyploids (Table 1) met the initial expectations and have in fact become relevant to the market (Dewey 1980).

Although polyploids have been obtained in a large number of crop plants, they do not always exhibit higher quality and/or yield than their diploid relatives, or the improvement occurs in organs that are not of interest for trade. As highlighted by Dewey (1980), each crop species responds differently to polyploidization, depending on their original ploidy level, genome structure, reproduction mode, perenniality and the plant organ for which the crop is cultivated. The reduction in fertility is also a hindrance to the use of induced polyploids, especially when the organs of interest are reproductive, i.e., fruits or seeds (Dewey 1980). For ornamental breeding, reduced fertility is not a problem, since larger and more beautiful flowers may offset the lower number of flowers and seed production (Schifino-Wittman and Dall'Agnol 2003).

Several genetic and epigenetic changes occur after both natural and induced polyploidization. Genetic alterations

Table 1 Examples of polyploid crops and their classification regarding the commercial interest, origin (synthetic/natural), formation process (auto-/allopolyploidization)

Common name	Specific name	Commercial interest	Origin	Formation process	Ploidy level and chromosome number	References
Alfalfa	*Medicago sativa* subsp. *sativa* L.	Forage	Natural	Autopolyploidy	$4x = 42$	Small and Jomphe (1989)
Banana	*Musa acuminata* Colla	Edible fruits	Natural	Autopolyploidy	$3x = 33$	Dantas et al. (1999)
Potato	*Solanum tuberosum* L.	Tubercle	Natural	Autopolyploidy	$4x = 48$	Carputo et al. (2003)
Sweet potato	*Ipomea batatas* (L.) Lam.	Tubercle	Natural	Autopolyploidy	$6x = 90$	Roullier et al. (2013)
Leek	*Allium ampeloprasum* L.	Cooking vegetable	Natural	Autopolyploidy	$4x = 32$	Levan (1940)
Yam	*Dioscorea alata* L.	Tubercle	Natural	Autopolyploidy	$3x = 60$; $4x = 80$	Arnau et al. (2009)
Kiwifruit	*Actinidia chinensis* Planch.	Edible fruits	Natural	Autopolyploidy	$4x = 116$	Hopping (1994)
Kiwifruit	*Actinidia chinensis* var. *deliciosa* (A. Chev.) A. Chev.	Edible fruits	Natural	Autopolyploidy[a]	$6x = 174$	Hopping (1994)
'Tahiti Lime'	*Citrus latifolia* (Yu. Tanaka) Tanaka	Edible fruits	Natural	Allopolyploidy	$3x = 27$	Morton (1987)
Rapeseed	*Brassica napus* L.	Oil and Culinary	Natural	Allopolyploidy	$4x = 38$	Nagaharu (1935)
Indian mustard	*Brassica juncea* (L.) Czern.	Oil and Culinary	Natural	Allopolyploidy	$4x = 36$	Nagaharu (1935)
Ethiopian mustard	*Brassica carinata* L.	Oil and Culinary	Natural	Allopolyploidy	$4x = 34$	Nagaharu (1935)
Plums	*Prunus domestica* L.	Edible fruits	Natural	Allopolyploidy	$6x = 48$	Bennett and Leitch (1995)
Tobacco	*Nicotiana tabacum* L.	Industrial	Natural	Allopolyploidy	$4x = 48$	Leitch et al. (2008)
Bread wheat	*Triticum aestivum* L.	Grain	Natural	Allopolyploidy	$6x = 42$	Haider (2013)
Durum wheat	*Triticum turgidum* L.	Grain	Natural	Allopolyploidy	$4x = 28$	Haider (2013)
Cotton	*Gossypium hirsutum* L. and *Gossypium barbadense* L.	Industrial	Natural	Allopolyploidy	$4x = 52$	Jiang et al. (1998)
Coffee	*Coffea arabica* L.	Beverage	Natural	Allopolyploidy	$4x = 44$	Clarindo and Carvalho (2008)
Sugarcane	*Saccharum officinarum* L.	Industrial	Natural	Allopolyploidy	$8x = 80$	Premachandran et al. (2013)
Peanut	*Arachis hypogaea* L.	Nuts	Natural	Allopolyploidy	$4x = 40$	Raina and Mukai (1999)
Oat	*Avena sativa* L.	Grain	Natural	Allopolyploidy	$6x = 42$	Ansari and Thomas (1983)
Cranberry hibiscus	*Hibiscus acetosella* Welw. Ex Hiern	Ornamental	Natural	Allopolyploidy	$4x = 72$	Contreras and Ruter (2009)
Strawberry	*Fragaria* × *ananassa* (Weston) Duchesne ex Rozier	Edible fruits	Natural	Allopolyploidy	$8x = 56$	Whitaker (2011)
Tetraploid Rye	*Secale cereale* L.	Grain/Forage	Synthetic	Autopolyploidy	$4x = 28$	Müntzing (1951)
Tetraploid Westerwolds ryegrass	*Lolium perenne* L. 'Grasslands Tama'	Forage	Synthetic	Autopolyploidy	$4x = 28$	Armstrong (1981)
Tetraploid Italian ryegrass	*Lolium multiflorum* L. 'Grasslands Moata'	Forage	Synthetic	Autopolyploidy	$4x = 28$	Armstrong (1981)
Tetraploid Red clover	*Trifolium pratense* L.	Forage	Synthetic	Autopolyploidy	$4x = 28$	Levan (1948)

Table 1 continued

Common name	Specific name	Commercial interest	Origin	Formation process	Ploidy level and chromosome number	References
Triploid Sugar beet	*Beta vulgaris* L.	Industrial	Synthetic	Autopolyploidy	$3x = 27$	Kinoshita and Takahashi (1969)
Triploid Watermelon	*Citrullus vulgaris* Schard.	Edible fruits	Synthetic	Autopolyploidy	$3x = 33$	Crow (1994)
Tetraploid *Rhondodendron*	*Rhododendron minus* 'Epoch'	Ornamental	Synthetic	Autopolyploidy	$4x = 52$	Kehr (1971)
Triploid cassava 'Sree Harsha'	*Manihot sculenta* 'Sree Harsha'	Tubercle	Synthetic	Autopolyploidy	$3x = 54$	Sreekumari et al. (1999)
Snapdragons	*Antirrhinum majus* L. 'Tetra Giant'	Ornamental	Synthetic	Autopolyploidy	$4x = 32$	Tolety and Sane (2011)
Lilies	*Lilium* spp. L.	Ornamental	Synthetic	Autopolyploidy	$3x = 36$; $4x = 48$	Zhou et al. (2011)
Kobus magnolia	*Magnolia kobus* 'Norman Gould'	Ornamental	Synthetic	Autopolyploidy	$4x = 76$	Parris et al. (2010)
Chamomile	*Matricaria chamomilla* L.	Medicinal	Synthetic	Autopolyploidy	$4x = 36$	Das (2015)
Triploid marigold	*Tagetes erecta* × *patula*	Ornamental	Synthetic	Allopolyploidy	$3x = 18$	Jalil et al. (1974)
Triticale	× *Triticosecale* Wittmack	Grain	Synthetic	Allopolyploidy	$6x = 42$; $8x = 56$	Mergoum and Gómez-Macpherson (2004)
Tulip	*Tulipa* spp. L.	Ornamental	Synthetic/natural	Autopolyploidy/ allopolyploidy	$3x = 36$; $4x = 48$	Marasek-Ciolakowska et al. (2012)
Rose	*Rosa* L.	Ornamental	Synthetic/natural	Autopolyploidy/ allopolyploidy	$3x = 21$; $4x = 28$; $5x = 35$; $6x = 42$	Yokoya et al. (2000)
Chrysanthemum	*Chrysanthemum* L.	Ornamental	Synthetic/natural	Autopolyploidy/ allopolyploidy	$4x = 36$; $6x = 54$; $8x = 72$; $10x = 90$	Liu et al. (2012)
Apple	*Malus* spp. Mill.	Edible fruits	Synthetic/natural	Autopolyploidy/ allopolyploidy	$3x = 51$; $4x = 68$	Janick et al. (1996)
Banana	*Musa* spp.	Edible fruits	Synthetic/natural	Autopolyploidy/ allopolyploidy	$3x = 33$; $4x = 44$	Silva et al. (2001)
Grape	*Vitis* spp. L.	Edible fruits	Synthetic/natural	Autopolyploidy/ allopolyploidy	$3x = 57$; $4x = 76$	Motosugi et al. (2002)

[a] There is still debate on whether *A. chinensis* var. *deliciosa* is an autopolyploid of *A. chinensis* or an allopolyploid between *A. chinensis* and other *Actinidia* taxa (Mertten et al. (2012)

include structural chromosome rearrangements, aneuploidy, direct changes in the DNA sequence (point mutations), loss of duplicated genes and gene conversion. Epigenetic changes also occur, promoting variations in gene expression levels without altering the DNA sequence itself. This phenomenon is triggered by modifications in the chromatin compaction levels (e.g., DNA methylation and histone acetylation), RNA interference and dosage compensation (Osborn et al. 2003; Soltis et al. 2004).

In most cases, the exact contribution of each progenitor to the genome of natural polyploids is unknown. Therefore, the use of synthetic polyploids, such as those of *Brassica* L. (Song et al. 1995), wheat (Kashkush et al. 2002) and *Arabidopsis* Heynh. (Lee and Chen 2001), has provided evidence for the occurrence of genetic and epigenetic changes, as well as their effects on gene expression and emergence of new phenotypes. Immediate and long-term disturbances in the genome, transcriptome, epigenome and other "-omes" are intrinsic to polyploidy (Renny-Byfield and Wendel 2014). Thus, they may explain why induced polyploids do not always reach the initial expectations and overcome their diploid progenitors, or even why tetraploids, for instance, are not twice as productive, vigorous or resistant than their diploid progenitors. Nonetheless, such disturbances have the potential to produce novel genotypic and phenotypic variations, which may be useful for artificial selection in plant breeding programs.

Raphanobrassica is a widely known example of a failed attempt to gather commercially relevant traits of two distinct species in a polyploid. In 1928, Georgi Karpechenco performed an experiment whose objective was to produce a fertile hybrid that would unite the roots of radish (*Raphanus sativus* L.; $2x = 18$) and the leaves of cabbage (*Brassica oleracea* L.; $2x = 18$), the most economically important characteristics of each species. The F1 hybrids ($2x = 18$) resulting from this cross were viable, although infertile. Through the spontaneous formation and fusion of unreduced reproductive cells, some of these hybrid plants occasionally produced viable seeds, which originated fertile allotetraploid plants with $4x = 36$ chromosomes, denominated *Raphanobrassica*. Unfortunately, although fertile, the allopolyploid *Raphanobrassica* displayed the leaves of radish and the roots of cabbage (McNaughton 1973).

Triticale (×*Triticosecale* Wittmack) is the first human-made cereal grain and the most remarkable example of a successful synthetic allopolyploid crop (Mergoum and Gómez-Macpherson 2004). Triticale originated from the intergeneric cross between species of wheat and rye, followed by colchicine-promoted induction of chromosome doubling. Two forms of triticale have been synthesized, the octoploid and the hexaploid. The octoploid triticale ($8x = 56$) combines the genomes of the hexaploid bread wheat (*T. aestivum*; $6x = 42$) and the cultivated diploid rye (*Secale cereale* L.; $2x = 14$). The hexaploid form of triticale ($6x = 42$), the most cultivated worldwide, results from the cross between the tetraploid durum wheat (*T. turgidum*; $4x = 28$) and diploid rye (Ammar et al. 2004) (Fig. 1). The major objective of breeders when developing triticale was to combine the market quality of wheat grains with the robustness of rye. Triticale plants have an appearance similar to wheat, except for the larger spikes and kernels and greater growth vigor (Poehlman 1987). Triticale has exhibited high yield potential even under less favorable environmental conditions. However, despite constituting a good source of protein and energy, it is mainly used as animal feed and very little as human food, being considered as inferior quality for wheat-like bread making due to both grain-related and non-grain-related factors (Baier et al. 1994; Peña 2004). In a few cases of wheat shortage, triticale has been used by small landholders, alone or blended with wheat, for the production of homemade breads. Currently, the main objectives of further triticale breeding programs are to improve its grain quality and to make it a more attractive grain for the human food industry (Peña 2004).

Among the achieved induced autopolyploids, examples of some that actually became relevant for cultivation and trade are the following:

1. Triploid sugar beet (*Beta vulgaris* L.; $3x = 27$): Sugar beet is a crop of major importance for sugar production in temperate areas, and exists in diploid ($2x = 18$), triploid ($3x = 27$) and tetraploid ($4x = 36$) forms (Smulders et al. 2010). Since the 1970s, most of the sugar beet varieties are the synthetic triploid forms, which are cultivated mainly in Europe and in the United States (OECD 2008). Triploid sugar beets are produced by crossing male diploid sterile plants with tetraploid pollinators or by reciprocal crossing, i.e., between male tetraploid sterile plants and diploid pollinators (Kinoshita and Takahashi 1969). Triploid sugar beets have larger roots than diploid ones, but maintain the same sugar content of the diploids and thus yield more sugar per unit area. Moreover, triploid sugar beets are highly sterile and do not produce seeds, which is not a disadvantage, since only their roots are relevant for commercial purposes (Dabholkar 2006).
2. Triploid seedless watermelon (*Citrullus vulgaris* Schrad.; $3x = 33$): The reduced fertility related to abnormal meiotic pairing has been a beneficial result of autotriploidy in watermelon breeding. Triploid seedless watermelons were first produced by Kihara in 1939, who started the experiment by treating a normal diploid ($2x = 22$) plant with colchicine to obtain a tetraploid from ($4x = 44$), and then used the

pollen of the diploid to pollinate the stigma of the induced tetraploid, producing the triploid progeny (Fig. 1). However, since the triploids were infertile, they did not produce sufficient viable pollen for pollination and fruit development. Consequently, diploid plants were planted in the same area of the triploids to supply the required pollen for seedless fruit production (Crow 1994). Seedless watermelons are popular in Israel, Japan and the Northern Territory in Australia, and comprise around 10 % of the United States' market (Hancock 1997; Tran-Nguyen et al. 2013; U.S. Department of Agriculture 2013). The costs for producing triploid watermelons are high for various reasons, namely, requiring the hand pollination of tetraploid plants to obtain triploid seeds; more difficult germination and establishment of the triploid seeds; and a pollinizer variety having to be grown together with the triploid one. The cost for seeds of the triploid seedless variety is almost four times higher than of the seeded diploid, which results in a higher end-market price (Boyhan et al. 2000).

3. Tetraploid red clovers (*Trifolium pratense* L.; $4x = 28$): Several commercial tetraploid varieties of red clover have been produced since the discovery of colchicine in 1937, primarily by Swedish researchers. The first successful polyploidy induction in red clover was accomplished by Levan during the World War II through colchicine treatment, whereas reproducible techniques only became available in the 50s (Boller et al. 2012). Although the most common method for obtaining tetraploids in red clover is colchicine doubling, N_2O and sexual polyploidization through unreduced gametes have also been reported. In some cases, the induced tetraploid forms exceed their diploid counterparts in many aspects, displaying increased disease resistance, persistence, winter hardiness and forage dry matter yield. The tetraploid cultivar 'Sally', for instance, exceeded in 72 % the seed yield of a diploid cultivar. The tetraploid varieties of red clover are cultivated mostly in Europe, and their low rate of seed production and high seed prices have been limiting factors to their widespread use (Taylor and Quesenberry 1996). Another example of artificial tetraploid variety of red clover is 'Grasslands Pawera' ($4x = 28$), from New Zealand, which was developed by selection and breeding after colchicine treatment of the diploid variety 'Grasslands Turoa' ($2x = 14$) (Hay et al. 1978).
4. Tetraploid rye (*S. cereale*; $4x = 28$): Artificial tetraploids of rye have been induced since the 1930s; thereafter, many tests have been performed about their agricultural value and grain quality (Hagberg and Ellerström 1959). The first artificial autotetraploid rye was produced by Dorsey in 1936 using high-temperature shock treatment of the diploid Stålråg ($2x = 14$) at the time of the first zygotic division (Müntzing 1951). The further work and selection in the populations obtained by Dorsey resulted in the development and marketing of a new variety of rye named 'Dubbelstål' ($4x = 28$) (Müntzing 1951; Hagberg and Ellerström 1959). Similarly, the tetraploid rye variety referred as 'Tetra Petkus' ($4x = 28$), which is widely popular in Germany, was developed by Dr. W. Laube in 1950 through colchicine treatment of the diploid 'Petkus' ($2x = 14$) (Hancock and Overton 1960). In 1951, this tetraploid variety was introduced in the United States for trade (Mulvey 1958). According to Hancock and Overton (1960), 'Tetra Petkus' was the first artificial polyploid variety of small grain crop to attain commercial relevance. Tetraploid varieties of rye are cultivated in limited amounts in Eastern Europe for grain production, and on large scale in the United States and other countries as a forage crop. In rye, the tetraploid forms have stiff-straw and baking qualities superior to the diploid varieties, although their yield is usually smaller (Schlegel 2006).
5. Tetraploid ryegrass (*Lolium* spp. L.; $4x = 28$): Polyploidy through colchicine has been induced in ryegrass since 1939 (Myers 1939). Tetraploid varieties of ryegrass have been widely cultivated for forage in Europe. Chromosome doubling in ryegrass has provided several superior qualities in the tetraploid cultivars compared to their diploid relatives, such as increase in water and soluble carbohydrate content, tolerance to drought, disease resistance, improvement of palatability and, consequently, increase in animal productivity (Nair 2004). Nonetheless, the choice between planting diploid or tetraploid cultivars depends on the environmental characteristics of the plantation region, since both ploidy levels may have different behaviors in each specific location (White and Lemus 2014). Two of the main tetraploid cultivars of ryegrass were developed by Dr. P. C. Barelay in 1962 at the Grasslands Division. In these experiments, seedlings of the diploids Westerwolds ryegrass (*L. multiflorum*) and 'Grasslands Paroa' (*Lolium perenne* L.) were treated with colchicine for chromosome doubling. The resulting tetraploid forms were released as cultivars by the names of 'Grasslands Tama' Westerwolds ryegrass (released in 1968) and 'Grasslands Moata' Italian ryegrass (released in 1981), respectively. Both cultivars are described as highly productive and palatable, and in many districts of New Zealand, Tama and Paroa have supplied high-valuable forage in spring and winter (Armstrong 1981; Wright 1983). Another popular and highly palatable tetraploid

cultivar released in the 1980s is the hybrid 'Grasslands Greenstone', derived from colchicine treatment of the diploid 'Grasslands Ariki' (a hybrid cultivar with 25 % introgression from *L. multiflorum*) (Anonymous 1990). Since then, several other tetraploid cultivars of ryegrass were released, such as 'Nevis', 'Quartet' and 'Ceres Horizon' in the 1990s, and 'Bealey', 'Banquet' and 'Grasslands Sterling' in the 2000s (Stewart 2006).

6. Ornamental crops: Polyploidy induction has been widely applied in ornamental crop breeding, since it often results in the extension of flower longevity, increase in flower size and deep flower colors. The genus *Rhododendron*, which includes the azaleas, has a large number of induced polyploid cultivars with commercial relevance (Jones et al. 2007). For instance, *Rhododendron minus* 'Epoch' ($4x = 52$) was the first artificial polyploid form of broad-leaved rhododendrons, obtained by colchicine treatment of the seeds of *Rhododendron carolinianum* Rehd. ($2x = 26$). The tetraploid *R. minus* 'Epoch' exhibits pale-pink, almost white flowers that are bigger in size and heavier in texture than the diploid *R. carolinianum* (Kehr 1971). Besides *Rhododendron*, autopolyploid cultivars of other ornamental plants have been released, such as the tetraploid *Antirrhinum majus* L. 'Tetra Giant' ($4x = 32$) (Tolety and Sane 2011), the triploid 'Navona' ($3x = 36$) and the tetraploids 'Val di Sole' and 'Brunello' ($4x = 48$) of *Lilium* L. spp. (Zhou et al. 2011), and the tetraploid *Magnolia kobus* 'Norman Gould' ($4x = 76$) (Parris et al. 2010).
7. Medicinal plants: Because of the increased number of gene copies present in polyploids, artificially induced polyploidy may lead to increases in enzymatic content and activity and several other effects that contribute to an enhanced production and qualitative changes in secondary metabolites (Dhawan and Lavania 1996). Chamomile (*Matricaria chamomilla* L.; $2x = 18$) is an important drug crop, being valuable mostly for its anti-inflammatory activities. Colchicine breeding in chamomile started in Europe around the 1950s. In 1962, the first tetraploid ($4x = 36$) variety, named Bodegol, was developed and released as a cultivar in Germany. In the follow decades, tetraploid varieties were released by other countries, such as Slovakia ('Goral' and 'Lutea' in 1995), Poland ('Zloty Lan' in 1972 and 'Dukar' in 2006), Romania ('Flora' and 'Margaritar') and Bulgaria ('Lazur' in 1980). The tetraploid forms of chamomile outperform their diploid relatives in both biochemical and morphological traits, like in the quantity of essential oils, bisaboloids, chamazulene, apigenin and flavonoids, as well as in the higher height, capitulum size and weight and dry seed weight (Das 2015). The cultivated tetraploid chamomile varieties 'Lutea' and 'Goral', for instance, have been shown to produce higher levels (above 20 %) of chamazulene, one of the valuable medicinal components of chamomile essential oil, than diploid cultivars (Gosztola et al. 2006). In the present days, almost one quarter of the chamomile varieties cultivated worldwide are tetraploids induced by colchicine, highlighting the success of polyploidy breeding establishment in this medicinal crop (Das 2015). Besides chamomile, Dhawan and Lavania (1996) revised the influence of artificial polyploidization on the concentration of useful secondary metabolites in other medicinal species, such as lavender (*Lavandula angustifolia* Mill.), caraway (*Carum carvi* L.), tea plant (*Camellia sinensis* (L.) Kuntze), and many others.

Some crop species have been improved by a complex chain of interspecific hybridizations and/or crosses between different ploidy levels. Breeding strategies involving crosses between different ploidy levels is very common in apples, for instance. The triploid forms of apples have more advantageous features than the diploids, including more regular fruit bearing, larger fruits with higher commercial appeal and scab resistance. Tetraploid varieties have no commercial value because of their low-quality fruits and low resistance to cold, being mostly used to develop the triploid cultivars (Sedov 2014; Sedov et al. 2014). About ten percent of the commercial apple cultivars are spontaneous triploids, such as 'Baldwin' and 'Gravenstein' (Janick et al. 1996). More recently, eight triploid cultivars artificially developed by crossing different diploid and tetraploid forms were released in Russia (Sedov et al. 2014).

In grapes (*Vitis* spp. L.), tetraploid and triploid plants have been produced to obtain large-berried and seedless varieties, respectively (Dermen 1954; Park et al. 2002). Autotetraploid grapes induced by colchicine have often shown poor fruitfulness, low vigor, brittle shoots and decreased cold hardiness. Still, these artificial tetraploids have been used as bridges to overcome barriers in crossings between *Vitis rotundifolia* Michx., *Vitis vinifera* L. and *Vitis labrusca* L. The main cultivar grown in Japan, 'Kyoho' ($4x = 76$), is an allotetraploid between varieties of *V. vinifera* and *V. labrusca* (Morinaga 2001). The cultivars 'Osuzu' ($3x = 57$) and 'King Dela' ($3x = 57$) are important seedless triploid varieties produced by crossings between different diploid and tetraploid ones, including 'Kyoho' (Park et al. 2002).

Tulips are the third most sold flower crop worldwide, and comprise more than 1100 cultivars distributed in the commercial market. The majority of those cultivars are varieties of the species *Tulipa gesneriana* L., followed by

the Darwin hybrid tulips, which have been obtained by crossings between different cultivars of *T. gesneriana* and *Tulipa fosteriana* Hoog ex W. Irving. Darwin hybrid tulips are characterized by their increased plant vigor and larger flowers, and include diploid cultivars ($2x = 24$; e.g., 'Yellow Dover' and 'Purissima'), a majority of triploid cultivars ($3x = 36$; e.g., 'Apeldoorn', 'Ad Rem' and 'Pink Impression') and some tetraploid ones ($4x = 48$; e.g., 'Tender Beauty' and 'Ollioules') (Marasek-Ciolakowska et al. 2012). Mitotic polyploidy induction has also been applied in tulips, either to induce new polyploid varieties or to restore the fertility of interspecific hybrids (Eikelboom et al. 2001). In most cases, polyploid tulips are induced by exposure to N_2O, since the meristems are hidden in noses inside the bulbs, hampering the induction by colchicine. In addition, colchicine has been shown to be harmful for bulbous plants (Van Tuyl et al. 1992). Some examples of commercial varieties induced by N_2O treatment include 'Rambo', 'Hunter', 'Zorro' and 'Kung Fu' (Eikelboom et al. 2001). Oryzalin has also been successfully used for in vitro polyploidization in tulips, as an alternative to colchicine (Chauvin et al. 2006).

For many other crops, colchicine-induced plants have shown some improvements in characteristics of commercial relevance, such as significant fruit size increase in autotetraploids of kiwifruit (*Actinidia chinensis* Planch.) (Wu et al. 2012), increase in berry size of autotetraploid grapes (Notsuka et al. 2000) and higher fruit quality in autotetraploid watermelons (Jaskani et al. 2005). Although several of such recently induced polyploid forms have not yet reached the required market qualities, they comprise valuable germplasm sources for application in prospective breeding experiments.

Conclusions and future perspectives

Polyploidy has been widely studied in the last century and is arguably one of the most important mechanisms of adaptation and speciation in plants. Moreover, the fact that many of the most relevant crop species are polyploid has proven that polyploidy is also of great relevance for humans. The several consequences of polyploidy observed in natural populations have attracted great attention of plant breeders for the application of artificial polyploidy as a tool for crop improvement. The "gigas" effect is one of those direct consequences and, when occurring in organs of commercial interest, is a valuable feature for crop improvement. The phenomena of genome "buffering", heterozygosity and heterosis (hybrid vigor) deserve attention in plant breeding programs, as they may lead to the higher vigor displayed by polyploid organisms when compared to their diploid relatives.

Several protocols have been developed for polyploidy induction in a wide range of crop species. Since the discovery of colchicine, in vitro polyploidization using this antimitotic agent has been one of the most important applications for artificial polyploidy induction. Sexual polyploidization through the fusion of unreduced reproductive cells is also applied, especially when high levels of heterozygosity are required.

The initial expectations regarding polyploidy induction for plant improvement were extremely optimistic, especially after the discovery of colchicine. In the present days, only few successfully induced autopolyploids have commercial relevance. Nevertheless, polyploidy has become a highly valuable tool in plant breeding programs, and its application is not restricted to yielding improvement by the "gigas" effect promoted by autopolyploidy induction. Polyploids are also important as bridges for genetic transfer between species in which the direct cross is not possible, as well as to reestablish the fertility of sterile hybrids. Therefore, the application of polyploidy as a tool by plant breeders has allowed the development of increasingly productive and adapted cultivars.

The last decades have seen a remarkable advance in the field of polyploidy, and different mechanisms regarding its causes and consequences have been discovered. However, many questions are still unanswered, evidencing the need to conduct additional research and elucidate the effects of both auto- and allopolyploidy in plant genomes. A thorough knowledge about the connection between genomic changes and expression of novel phenotypes following polyploidy is very promising for crop improvement, and may allow plant breeders to manipulate polyploid genomes more accurately and achieve outstanding results.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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