

Advances and perspectives in the generation of polyploid plant species

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Abstract Whole-genome duplication (polyploidy) occurs frequently and repeatedly within species of plants. According to the source of the genomes giving origin to a polyploid plant species, these are classified into allopolyploid (when two or more genomes are combined through either intraspecific or interspecific hybridization) and autopolyploid (when a single genome becomes duplicated). According to the time period in which polyploidy occurred plant species are classified as paleopolyploid (ancient polyploids), mesopolyploid (less ancient polyploids), and neopolyploid (recent polyploids). Many plant species appearing as diploid are actually paleopolyploids (ancient polyploids) derived from at least one event of whole-genome duplication followed by a process known as diploidization, which consists in massive gene loss and genomic reorganization (diploidized paleopolyploids). Many polyploid species of plants have been shown to present morphological and physiological

characteristics making them further attractive for industry than their lower ploidy level counterparts. Polyploidy is a fundamental but relatively underexplored biological process. With the aim of understanding the factors involved in the formation of polyploid plant species, many studies have been carried out on synthetic polyploidy obtained by mitotic inhibitors and hybridization. However, the rapid progress of genetic engineering techniques makes genetic modification (GM) to become a feasible strategy for obtaining polyploid plants. In this review we discuss advances made about factors known to influence plant polyploidy and we suggest that in a future, this knowledge could be used for generating polyploids *in vitro* by GM and for crop improvement.

Keywords Plants · Polyploidy · Cell cycle · Mitosis and meiosis

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Introduction

Polyploidy is a very common phenomenon in species of angiosperms and vascular plants (Moghe and Shiu 2014; Wendel 2000). Polyploid species can be classified into allopolyploid and autopolyploid based on the origins and levels of ploidy (Chen 2010; Chen et al. 2006). An autopolyploid results from doubling a diploid genome, while allopolyploids are formed by the combination of two or more sets of distinct

genomes. In addition to polyploidy, plant species have been shown to be either intraspecific or interspecific hybrids (Mavarez et al. 2006; Rieseberg et al. 2003) and many plants showing an apparent diploid inheritance are actually paleopolyploids (ancient polyploids), which derived from at least one event of whole-genome duplication (WGD) followed by massive gene loss and genomic reorganization through a process known as diploidization (Wolfe 2001). *Arabidopsis* (Blanc et al. 2003; Vision et al. 2000), rice (Yu et al. 2005), and maize (Gaut 2001) are good examples of diploidized paleopolyploids. The ancestors of many polyploid plant species remain to be unknown, but in some polyploid plant species including taxa of *Brassica* (Liu et al. 2014) and *Gossypium* (Rauf et al. 2006) among others, physiological and morphological adaptations have been described that can confer them an increased resistance to adverse biotic and abiotic factors in comparison to their diploid ancestors (Table 1), and that could lead to evolution and speciation of such polyploid taxa (Madlung 2013; Wendel 2000).

Polyploidy induction has been successfully applied to crop, ornamental, and medicinal plants in order to obtain lines exhibiting new agronomical characteristics. This procedure has provided plants that are seedless, with larger fruits and flowers, and with enhanced pest resistance and physical stress tolerance (An et al. 2014; Tu et al. 2014; Yang et al. 2014). The presence in polyploid crop species of larger fruits, leaves, and kernels can improve their marketing in comparison to their diploid counterparts, and because polyploid species exhibit features adaptive to the presence of various biotic and abiotic stresses—such as drought, salinity, extreme temperatures, and resistance to various pathogenic diseases—these plants have the potential to adapt to future climate changes (Brochmann et al. 2004; Hahn et al. 2012). Thus, cultivation of polyploid species could reduce economic losses.

The induction of polyploidy in horticultural and agronomic plant species is based on the application of dinitroaniline antimicrotubule drugs such as colchicine, oryzaline, and triflurarin (Table 2). Among the negative effects reported in polyploid species are infertility, erratic bearing, brittle wood, watery fruit, and reduction in plant height and number of fruits per plant (Urwin 2014; Van Laere et al. 2011). In this sense, it is still necessary to work to eliminate the

negative effects of genomic doubling and genomic hybridization. Also, many reviews have documented the disadvantages of polyploidy and the problems found for reducing the problems present in polyploid plants (Comai 2005; Moghe and Shiu 2014; Neiman et al. 2013). In this paper, we document the molecular advances made and the new perspectives in the study of the formation of polyploid plants of horticultural and agronomic plant species. This knowledge can be applied in the future both for decreasing the negative effects of synthetic polyploids and for crop improvement.

Factors affecting ploidy level of plants

Major routes of polyploid plant formation are via unreduced gametes and somatic doubling (Ramsey and Schemske 1998; Coyne and Orr 2004). The somatic doubling is caused by cells not entering division, but reverting to interface, and thus to a repeated event of DNA synthesis. This is the most common process of polyploidization in plants and is due to failure in the cell cycle control signaling between the G2 and the M phases. This process may occur in zygotic, embryonic or sporophytic tissue. Spontaneous genome duplication in these tissues can also produce viable polyploidy (d'Amato 1984; Lee et al. 2013).

Regarding unreduced gametes can be produced by pre-meiotic genome doubling and by post-meiotic genome duplication, also termed post-meiotic restitution (PMR) or post meiotic doubling (PMD) (De Storme and Geelen 2013). The former mechanism has not been extensively studied in plants. However, the presence of male meiocytes containing double the amount of chromosomes in *Turnera* hybrids (Fernández and Neffa 2004), and the formation of giant tetrads in *Brassica* hybrids and orchids (Mason et al. 2011; Teoh 1984), have been assumed to indicate pre-meiotic chromosome duplication in these species.

The generation of polyploidy by PMR consists in the formation of $2n$ gametes and their subsequent fusion. Meiotically formed haploid spores undergo an extra round of genome duplication. The fusion of these non-reduced gametes can lead to polyploidy. This process is due to failure during the M phase of meiosis, causing that the homologous chromosomes paired in tetrads remain united during the anaphase, which

Table 1 Features described in commercially important polyploid crops

Characteristics	Commercial name	Species, line or variety	Ploidy number	References
Genetic	Agave	<i>Agave fourcroydes</i> Lem.	$2n = 3x = 90$ $2n = 4x = 120$	Tamayo-Ortón et al. (2015)
Increase in the size of the genome			$2n = 5x = 150$	
Increase of genetic variability			$2n = 4x = 120$	
Presence of new genetic units			$2n = 6x = 180$	
	Banana	<i>Musa acuminata</i> Colla	$2n = 3x = 33$	Davey et al. (2013)
	Canola	<i>Brassica napus</i> L.	$2n = 4x = 76$	Lysak et al. (2005)
	Indian mustard	<i>Brassica juncea</i> L.	$2n = 4x = 72$	Liu et al. (2014)
	Ethiopian mustard	<i>Brassica carinata</i> A. Braun	$2n = 4x = 68$	
	Cotton	<i>Gossypium hirsutum</i> L.	$2n = 3x = 39$	Rambani et al. (2014)
		<i>Gossypium tomentosum</i>	$2n = 3x = 39$	
	Kiwifruit	<i>Actinidia arguta</i> (Siebold & Zucc.) Planch. ex Miq.	$2n = 4x = 116$	McNeillage and Considine (1989)
		<i>Actinidia deliciosa</i> (A.Chev.) C.F.Liang & A.R.Ferguson	$2n = 6x = 174$	
	Peanut	<i>Arachis hypogaea</i> L.	$2n = 4x = 40$	Kochert et al. (1996)
	Rice	<i>Oryza punctata</i> Kotschy ex Steud.	$2n = 4x = 48$	Wang et al. (2009)
		<i>Oryza malampuzhaensis</i> Krish. et Chand.	$2n = 4x = 48$	
		<i>Oryza minuta</i> J.Presl	$2n = 4x = 48$	
		<i>Oryza alta</i> Swallen	$2n = 4x = 48$	
		<i>Oryza grandiglumis</i>	$2n = 4x = 48$	
		<i>Oryza latifolia</i>	$2n = 4x = 48$	
	Sugar cane	<i>Saccharum officinarum</i> L.	$2n = 8x = 80$	Premachandran et al. (2011)
		<i>Saccharum spontaneum</i>	$2n = 12x = 120$	
	Tobacco	<i>Nicotiana tabacum</i> L.	$2n = 4x = 48$	Kovarik et al. (2008)
	Wheat	<i>Triticum urartu</i> Tumanian ex Gandilyan	$2n = 2x = 14$	Wang et al. (2014)
		<i>Triticum turgidum</i> L.	$2n = 4x = 48$	
		<i>Triticum aestivum</i> L.	$2n = 6x = 42$	
Physiological	Balady mandarin	<i>Citrus reticulata</i> Blanco	$2n = 4x = 36$	Elyazid and El-Sherief (2014)
	Grape myrtle	<i>Lagerstroemia indica</i> L.	$2n = 4x = 96$	Ye et al. (2010)
	Egyptian clover	<i>Trifolium alexandrinum</i> L.	$2n = 4x$	El-Naby et al. (2012)
	Old maid	<i>Catharanthus roseus</i> L.	$2n = 4x$	Xing et al. (2011)
	Oil palm	<i>Elaeis guineensis</i> Jacq.	$2n = 4x = 64$	Samala and Te-chato (2012)

Table 1 continued

Characteristics	Commercial name	Species, line or variety	Ploidy number	References
Increase in cell size and decrease in the number of nuclei per unit area	Potato	<i>Solanum commersonii</i> Dunal	$2n = 4x = 48$	Cardi (1998)
Slow ontogeny		<i>Solanum tuberosum</i> L.	$2n = 4x = 48$; $2n = 6x = 72$	
Morphological	Rangpur lime	<i>Citrus limonia</i> Osbeck	$2n = 4x$	Allario et al. (2011)
Increased size of leaves, flowers, and stems	Tobacco	<i>Nicotiana glauca</i> Link & Otto	$2n = 4x$	El-Morsy et al. (2009)
	Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	$2n = 4x = 44$	Ahmad et al. (2013)
	Banana	<i>Musa acuminata</i> Colla	$2n = 4x = 44$	Hamill et al. (1992)
	Citrus	Swingle' citrusmelo [<i>C. paradise</i> × <i>Poncirus trifoliata</i> (L.) Raf]	$2n = 4x = 36$	Guerra et al. (2014)
Larger seeds		Citrange 'Troyer,' (<i>C. sinensis</i> (L.) Osb. x <i>P. trifoliata</i>)	$2n = 4x = 36$	
Longer roots		Citranges 'Fepagro C 13' and 'Fepagro C 37,' (<i>C. sinensis</i> cv. <i>Pêra</i> x <i>P. trifoliata</i>)	$2n = 4x = 36$	
Darker colored leaves	Cotton	<i>Gossypium arboreum</i> L.	$2n = 4x = 52$	Rauf et al. (2006)
	Hops	<i>Humulus lupulus</i> L.	$2n = 4x = 40$	Trojak-Goluch and Skomra (2013)
	Kiwifruit	<i>Actinidia chinensis</i> Planch.	$2n = 4x = 116$	Wu et al. (2012)
	Lychnis	<i>Lychnis senna</i> Siebold et Zucc.	$2n = 4x = 48$	Chen et al. (2006)
	Mopane	<i>Colophospermum mopane</i> Kirk ex Benth.) J. Léonard	$2n = 4x$	Rubulza et al. (2007)
	<i>Petunia</i>	<i>Petunia</i> × <i>hybrida hort. ex E.Vilm.</i>	$2n = 3x = 21$; $2n = 4x = 28$	Ning et al. (2009)
	Tobacco	<i>Nicotiana glauca</i> Link & Otto	$2n = 4x = 36$	El-Morsy et al. (2009)
	Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai	$2n = 3x = 33$	Pradeepkumar (2011)
	Black locust	<i>Robinia pseudoacacia</i> L.	$2n = 4x = 44$	Wang et al. (2013)
	Honeysuckle	<i>Lonicera japonica</i> Thunb.	$2n = 4x = 36$;	Li et al. (2009a)
Ecological				
Tolerance to extreme drought or cold at high altitudes and latitudes.	Fourwing saltbush	<i>Atriplex canescens</i> (Pursh) Nutt.	$2n = 6x = 54$	Hao et al. (2013)
Resistance to pests	Orange	<i>Citrus sinensis</i> Osbeck	$2n = 4x = 36$	Shafeizargar et al. (2013)
	Rangpur lime	<i>Citrus limonia</i> Osbeck	$2n = 4x$	Allario et al. (2013)
	Rice	<i>Oryza Sativa</i> L.	$2n = 4x = 48$	Tu et al. (2014)
	Tobacco	<i>Nicotiana benthamiana</i> Domin	$2n = 4x = 48$; $2n = 4x = 96$	Deng et al. (2012)

Table 2 Compounds used in the synthesis of polyploid species

Compounds	Commercial name	Species	Ploidy level of wild type to level of ploidy gain in synthetic species	References
Colchicine	Balady mandarin	<i>Citrus reticulata</i>	$2n = 2 \times$ to $2n = 4x$	Elyazid and El-Shereif (2014)
	Kiwifruit	<i>Actinidia chinensis</i>	$2n = 2x$ to $2n = 4x$	Wu et al. (2012)
	Petunia	<i>Petunia \times hybrida</i>	$2n = 2x$ to $2n = 3x$ and $2n = 2x$ to $2n = 4x$	Urwin (2014)
	Lavandin	<i>Lavandula \times intermedia</i>	$2n = 2x$ to $2n = 4x$	Ning et al. (2009)
	Watermelon	<i>Citrullus lanatus</i>	$2n = 2x$ to $2n = 4x$	Hasnain et al. (2003)
Oryzaline	Banana	<i>Musa acuminata</i>	$2n = 2x$ to $2n = 4x$	Salles Pio et al. (2014)
	Bugle Lily	<i>Watsonia lepida</i>	$2n = 2x$ to $2n = 4x$	Ascough et al. (2008)
	Butterfly	<i>Buddleja madagascarensis \times B. crispa</i>	$2n = 2x$ to $2n = 4x$	Dunn and Lindstrom (2007)
	Lilac	<i>Syringa vulgaris \times S. pinnatifolia</i>	$2n = 2x$ to $2n = 4x$	Rose et al. (2000)
Trifluralin	Rose	<i>Rosa rugose</i>	$2n = 2x$ to $2n = 4x$	Kermani et al. (2003)
	Garlic	<i>Allium sativum</i>	$2n = 2x$ to $2n = 4x$	Cheng et al. (2012)
	Jimsonweed	<i>Datura stramonium</i>	$2n = 2x$ to $2n = 4x$	Amiri et al. (2010)
	Peace lily	<i>Spathiphyllum wallisii</i>	$2n = 2x$ to $2n = 4x$	Eeckhaut et al. (2004)
	Ranunculus	<i>Ranunculus asiaticus</i>	$2n = 2x$ to $2n = 4x$	Dhooghe et al. (2009)
	Rose	<i>Rosa chinensis minima</i>	$2n = 2x$ to $2n = 4x$	Zlesak et al. (2005)

results in cells having a complete chromosome complement. During the second meiotic division cells will generate diploid, unreduced gametes, which when joined to a normal gamete will produce a sterile triploid zygote, and when combined with another unreduced gamete, a tetraploid zygote (Soltis and Soltis 1999). Diploidization of egg cells has also been observed in potato, sugarcane and evergreen blackberry (Dowrick 1996; Bastiaanssen et al. 1998; Ramanna and Jacobsen 2003).

In gametic non-reduction and somatic doubling, genes specific for the cell cycle and meiosis—e.g. cyclin-dependent kinases (CDKs), cyclins (CYCs), tardy asynchronous meiosis (TAM), and omission of second division 1 (OSD1)—have been shown to be affected and regulated by external factors such as low temperature, darkness and growth regulators. The relation of all these factors is illustrated in Fig. 1 and described in the following sections.

Deregulation of CDK/CDC complexes and polyploidization

CDKs are a large family of serine/threonine protein kinases with an important role in ensuring that cells progress in an orderly fashion along the different

stages of cell division (Coudreuse and Nurse 2010; Doonan and Kitsios 2009). The progression of the cell cycle involves kinase activities from CDK/CYC complexes that coordinate the transition from one phase of the cell cycle to the next.

Studies made in *Arabidopsis* have reported seven different classes of CDKs named CDKA through CDKF, and an additional class of CDK-like proteins was termed as CLKs (Menges et al. 2005; Tank and Thaker 2011). Of these CDK's, the major drivers of the cell cycle in plants are the A and B type cyclin-dependent kinases (CDKA and CDKB, respectively). Failures in gene regulation disturbing the function of CDKs, or resulting in the inactivation of CDKA and CDKB, have been shown to affect progression of the cell cycle.

The inactivation in yeast of p34^{CDC2/CDC28}—functional homologues of CDKAs—causes uncoupling of the S and M phases (Bezooijen et al. 1973; Pak et al. 1982). This decoupling of the cell cycle could generate a high susceptibility to ploidy level changes (Cross et al. 1995). Moreover a dominant negative form of the *Arabidopsis* CDKA;1 gene in tobacco plants resulted in an overall reduction of cell division rate, thus yielding smaller plants. The G1/G2 ratio of these plants remains unaltered, demonstrating that CDKA;1

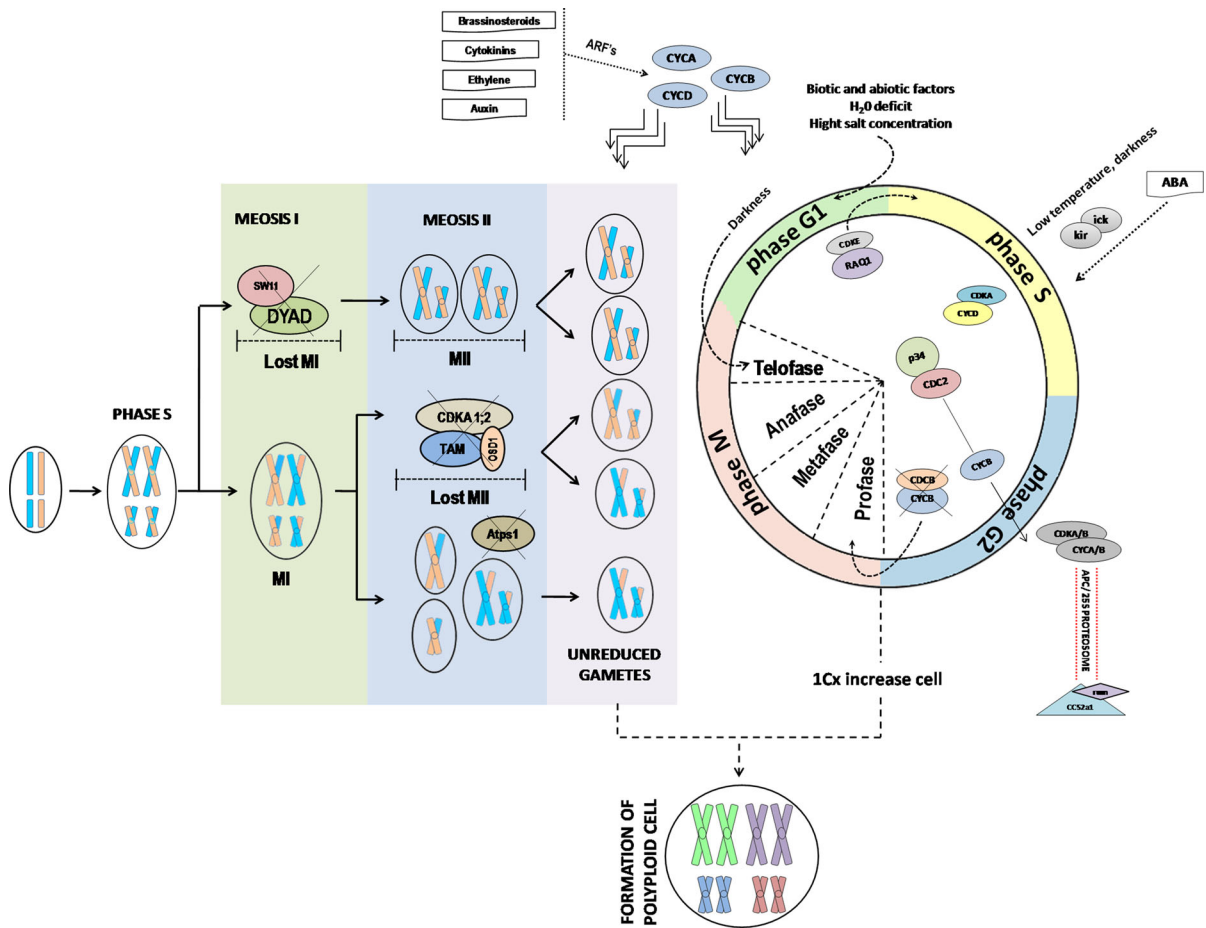


Fig. 1 The diagram illustrates the factors that can cause genomic duplication and formation of unreduced gametes. a Genome doubling can be caused by presence of several abiotic and biotic factors. For example, in the presence of H_2O_2 and low temperatures, the complex CDKE;1/RAO1 can sense the response by induction of transcription factors involved in the function of RNAPol II and trigger the transcription of genes related to the cell cycle. In response to the biotic stress caused by infection of plant with pathogenic fungi, the CDKE;1/RAO1 complex can induce brassinosteroids that, in turn, can induce the synthesis of auxins and increase the production of ethylene, which together with cytokinins and gibberellins induces the expression of CYCA, CYCB, and CYCD. In addition, ABA and low temperatures can activate the ICK/KRP complex and induce the activation of signaling cascades allowing for the G1–S transition; in which formation of the CDKB/CYCD complex plays an important role. Stress events in general can prolong the DNA replication phase. Subsequently, the cell prepares for entering mitosis, in which the CDKB/CYCB complex is important. A failure in the CDKB/CYCB complex may lead to arrest of the M phase. Also, naturally, the formation of the p34/cdc2 complex induces the expression of CYCDB, important for the transition from G2 to M. However, the failure of the p34/

cdc2 complex or the degradation of the complexes involving CDKs and CDYs by means of the APC/25 proteasome—which can in turn be activated by the presence of mitotic inhibitors (rum and CSS52)—can cause the arrest of the cell cycle and to an increase in the 1CX values of the cell. If such cells are exposed to long periods of darkness, they may be subject of several genomic duplication events resulting in a polyploid cell. b Two important events have been described in the formation of unreduced gametes, the first of these events is caused by the failure of the SWI1/DYAD complex resulting in the separation of sister chromatids and to the arrest of the M1 phase of meiosis, which results in the formation of triploids and unreduced gametes. Triploid gametes may result from the non-equivalent distribution of chromosomes in cells or due to arrest of the S phase. The second event involves the poor or null activity of the CYCA1;2/TAM and OSD1 complex that in plants can cause the arrest at Meiosis II, originating the formation of unreduced gametes. Additionally, affectation of Atps1 can cause parallel orientation of mitotic spindles during Metaphase II, arresting Meiosis II and resulting in the formation of unreduced gametes. Crossing of unreduced gametes may lead to the formation of a polyploid

is essential at both G1/S and G2/M transitions of the cell cycle (Hemerly et al. 1995).

Otherwise, CDKA activity has also been shown to be important in the meiotic process. Dissmeyer et al. (2007) demonstrated that CDKA;1 activity in *Arabidopsis* is necessary for cytokinesis control through its effect on microtubule associated proteins (Dudits et al. 2007; Sasabe et al. 2011). More recently, Borowska-Wykret et al. (2013) showed that expression of a negative dominant allele CDKA;1.N146 results in defects in epidermis continuity (i.e., loss of individual cells and occurrence of gaps between anticlinal walls of neighboring pavement cells), indicating that CDKA;1 has an important role in regulation of plant development via its influence on the cytoskeleton and on plant cell walls.

In addition, expression of CDKB has been shown to be important for the G2–M transition (Francis 2011; Lipavská et al. 2011). The remarkable feature of the CDKB genes is that they are expressed only in mitotic cells, from the S-phase until the M-phase. The CDKB1 genes are expressed from the S phase and peak in G2, whereas the CDKB2 genes are expressed somewhat later from G2–M (Menges et al. 2005). Non degradation of cyclin B1 in tobacco and knockdown of CDKB2;1 in rice were demonstrated to lead to doubling cell DNA contents as a result of cells undergoing endoreduplication (Endo et al. 2014; Weingartner et al. 2004).

In general, other CDKs (CDKC to CDKF) have been implicated in the regulation of the mRNA involved in biogenesis and as sensor regulatory signals between specific transcription factors in response to cellular stress, hormones, and plant development. For example, it has also been suggested that CDKC and CDKG play a role in regulation of mRNA processing in the nucleus (Doonan and Kitsios 2009; Fulop et al. 2005). CDKDs and CDKF;1 have been shown to participate in cotranscriptional processing and stability of a set of small RNAs and transcripts involved in their biogenesis through changes in the phosphorylation of RNAPII CTD by CDKF;1 and CDKDs (Hajheidari et al. 2012; Umeda et al. 2005), and the only CDK that to date has been shown to be involved as a sensor signal regulatory of external stresses is CDKE. The role of CDKE;1/RAO1 as a CDK integrating cellular response to environmental signals with division or elongation has been demonstrated. However, it has been demonstrated that CDKE;1/

RAO1 does not directly interact with any other cyclin components, but has a role as a sensitive relay between specific stress induced transcription factors actively bound to the promoter and RNA polymerase II, thereby directly affecting transcription under stresses such as presence of H₂O₂ and cold (Boruc et al. 2010; Ng et al. 2013).

Finally, regarding CDK's, it is important to mention that CDKG has proved most closely related to Ph1 kinase (Yousafzai et al. 2010; Zheng et al. 2014), which enhances the fidelity of chromosome pairing in hexaploid wheat (Greer et al. 2012). In *Arabidopsis*, mutation in the *cdkg1* gene leads to a temperature-sensitive failure of meiosis in late Zygotene/Pachytene, which is associated with defective formation of the synaptonemal complex, reduced bivalent formation and crossing over, and formation of aneuploid gametes. The CDKG/CYCLINL complex is essential for the final steps of chromosome synapsis during male gamete formation.

Other important factors in the regulation of the cell cycle are cyclins. A-type cyclins (CYCA), B-type cyclins (CYCB), and D-type cyclins (CYCD) are major cyclin classes involved in cell cycle regulation. CYCAs are mainly present between the S and the M phases, and CYCBs are present in G2–M transition and during mitosis (De Veylder et al. 2007; Francis 2011). Studies in *Arabidopsis* indicated that CYCA and CYCB3;1 contribute to distinct meiosis-related processes, CYCA being important for chromosome segregation and CYCB3;1 preventing ectopic cell wall formation (Bulankova et al. 2013). Also, null mutations of CYCA2;3 semidominantly promoted endocycles and increased the ploidy levels achieved in mature organs, but they did not significantly affect the proportion of cells that underwent endoreduplication. Apparently CYCA2;3 negatively regulates endocycles and acts as a key regulator of ploidy levels by endoreduplication (Imai et al. 2006).

D-type cyclins have been shown to respond to external signals, such as hormonal and plant developmental signals. In *Arabidopsis*, CYCD2 and the related CYCD4;1 respond to sucrose availability and levels (Nieuwland et al. 2009; Riou-Khamlichi et al. 2000), and CYCD3 genes mediate responses to the key phytohormone cytokinin in the cell cycle (Dewitte et al. 2007; Riou-Khamlichi et al. 1999). Also, Sozzani et al. (2010) showed that CYCD genes are directly regulated by transcription factors known to have key

developmental roles. The response of CYCD to sensors of external conditions in plants is mediated by direct phosphorylation of the plant homologue of the retinoblastoma protein (RB) (Cruz-Ramírez et al. 2012; Dick and Rubin 2013).

As mentioned above, it appears as if the function of both CDK's and CYC's is important for the progression of the cell cycle and a failure in their regulation could result in cell cycle arrest. In that regard, the mechanisms for regulation of cyclin-dependent kinases (CDKs) involves the formation of CYC/CDK complexes and of their inhibitors. The CYCD/CDK complexes control the G1/S transition by inhibiting RBR, resulting in the transcription of genes involved in DNA replication. CYCB/CDK complexes control G2/M transition. The role of CYCA/CDK complexes is less clear, but they appear to play various roles in maintaining the S phase and in the G2/M transition (Churchman et al. 2006). In addition, several genes inhibiting and interacting with CDK have to date been identified, which have been designated as *CDK1* and *CDK2* (inhibiting), *ICK1* and *ICK2* (interacting) (Lui et al. 2000; Wang et al. 1997), and Kip-related proteins (KIPs) (Verkest et al. 2005).

Because of the variety and importance of CDKs and CYCs in the regulation of the cell cycle, the repression or expression of the activity of some complexes involving cyclins—e.g. CDKA/CYDC, CDK (ICK/KRP, SIM and CCS5)—can lead to the arrest of the cell cycle (Acosta et al. 2011; Yang et al. 2011), to a decrease in ploidy level, and to the consequent decrease in cell size (Cebolla et al. 1999). In *Arabidopsis*, tomato, and tobacco the ICK/KRP proteins showed inhibition of CDK activity in vitro (Bisbis et al. 2006; Jasinski et al. 2002) and the deregulation in these complexes could cause cell cycle arrest.

Other complex involved in change in ploidy level is p34cdc2/CYB. In eukaryotes, the loss of activity of p34cdc2 was suggested to cause insufficient expression of CYCB, and over-expression of the inhibitor p25 would lead to the generation of polyploidy (Correa-Bordes and Nurse 1995; Moreno and Nurse 1994). Because an alteration in p34cdc2 activity can affect chromosome condensation, separation of sister chromatids, and cytokinesis (Satterwhite et al. 1992; Sawin and Mitchison 1995), there would be changes in cellular control during or after mitosis that could result in genome changes. In eukaryotes, there are

indications that the loss of p34cdc2 is responsible for polyploidy (Grafi and Larkins 1995).

As describe above for all CDKs and CYCs, deregulation of CDKA, CDKB, CYCA, CYCB, CYCD, and of complexes such as CDK (ICK/KRP, SIM, and CCS5), p34cdc2/CYB, among others, are majorly related with cell cycle arrest and are able to cause genomic doubling. The regulatory importance during the cell cycle of CDKs, CYCs, and their complexes has been demonstrated in commercially important plants. Table 3 shows NCBI GenBank (<http://www.ncbi.nlm.nih.gov/>) accession or ID numbers of genes of CDKA, CDKB, CYCA, CYCB and CYCD that are supported by a publication.

To date, these genes have been analyzed in most economically important diploid crop plants. However, in order to gain information on these genes and on their future use, either for improvement of species or for formation of polyploid species, it is important to analyze these genes in polyploid species in order to know if they present the same characteristics of organization, regulation and function as those reported for the diploid species.

Genes involved in the formation of unreduced gametes in plants

The formation of unreduced gametes caused by failures during meiosis can be due to the omission of the first (MI) or second meiotic (MII) divisions (De Storme and Geelen 2013; Ramanna and Jacobsen 2003). Since the 1980s, several plant genes involved in abnormalities of meiosis have also been reported, for example, wheat *msg* (Joppa et al. 1987) and barley *tri* (Finch and Bennett 1979) were found to condition the formation of reduced eggs without effects on pollen production. Also, the genes restitution pollen (*rp*) and jumbo pollen (*jp*) in *Medicago* condition 2n pollen formation by disorientation of meiotic spindles during metaphase II, and failure of cytokinesis during the second meiotic division was observed (McCoy and Smith 1983). It has been suggested that the production of unreduced gametes through meiotic restitution could have been an important mechanism for the widespread occurrence of polyploidy in nature (Wagenaar 1968).

Unreduced gametes formed by meiotic restitution can be the result of mechanisms known as first division restitution (FDR), second division restitution (SDR),

Table 3 Plant genes reported to be involved in genomic doubling (endorreduplication) and formation of unreduced gametes

Genes	Commercially name	Species	Ploidy level (x)	Gene name (GenBank accession number or ID number denoted by '*')	References
Cyclin-dependent kinase (CDKs)	CDKA	Alfalfa	2	Medsa; CDKA;1;1 (M58365), Medsa CDKA;2; 1 (X70707)	Hirt et al. (1991)
	Arabidopsis	<i>Arabidopsis thaliana</i>	2	CDKA;1 (NM_114734)	Erfe et al. (2000)
	Maize	<i>Zea mays</i>	2	CDKA;1 (GRMZM2G008327)*	Colasanti et al. (1991)
	Norway spruce	<i>Picea abies</i>	2	Picab;CDKA;1; (X77680)	Kvarnheden et al. (1998)
	Pea	<i>Pisum sativum</i>	2	CDKA;3 (GRMZM2G174596)* Pissa;CDKA;1; (X53035)	Dante et al. (2014) Feiler and Jacobs (1990)
	Petunia	<i>Petunia hybrida</i>	3	Pissa;CDKA;2;1 (AB008187)	Shimizu and Mori (1998)
	Rice	<i>Oryza sativa</i>	2	Pehy;CDKA;1; (Y13646) Orysa;CDKA;2;1 (X60374) Orysa;CDKA;1; (X60375)	Tréhin et al. (1998) Hashimoto et al. (1992)
	Snapdragon	<i>Antirrhinum majus</i>	2	Antma;CDKA;1; (X97637) Antma;CDKA;2;1 (X97638)	Fobert et al. (1996)
	Soybean	<i>Glycine max</i>	2	Glyma;CDKA;1;1 (M93139) Glyma;CDKA;1;2 (M93140)	Miao et al. (1993)
	Tobacco	<i>Nicotiana tabacum</i>	2	Nicta;CDKA;1;3 (D50738) Nicta;CDKA;1;4 (AF289467)	Setiady et al. (1996) Sorrell et al. (2001)
	Alfalfa	<i>Medicago sativa</i>	2	Medsa;CDKB;1; (X97315) Medsa;CDKB;2;1 (X97315)	Magyar et al. (1997)
	Aspen	<i>Populus tomentosa</i>	2	Medsa;CDKB;2;2 (DQ136188)	Zhiponova et al. (2006)
	Maize	<i>Zea mays</i>	2	ProCDKB (EU822323)	Li et al. (2009b)
	Rice	<i>Oryza sativa</i>	2	CDKB;1;1 (GRMZM2G495626)* Orysa;CDKB;1;2 (D64036)	Dante et al. (2014) Kidou et al. (1994)
	Snapdragon	<i>Antirrhinum majus</i>	2	Antma;CDKB;1; (X97639) Antma;CDKB;2;1 (X97640)	Fobert et al. (1996)
	Sunchoke	<i>Helianthus tuberosus</i>	6	Heltu;CDKB;2;1 (AY063463)	Freeman et al. (2003)
	Tobacco	<i>Nicotiana tabacum</i>	4	Nicta;CDKB;1;1 (AF289465) Nicta;CDKB;1;2 (AF289466)	Sorrell et al. (2001)
	Tomato	<i>Lycopersicon esculentum</i>	2	Lyces;CDKB;1;1 (AJ297916) Lyces;CDKB;2;1 (AJ297917)	Joubès et al. (2000).

Table 3 continued

Genes	Commercially name	Species	Ploidy level (x)	Gene name (GenBank accession number or ID number denoted by ‘*’)	References	
Cyclins (CYCs)						
CYCA	Arabidopsis	<i>Arabidopsis thaliana</i>	2	CYCA1;2/TAM (844075)	Magnard et al. (2001)	
				CYCA2;1 (Z31589)	Ferreira et al. (1994)	
				CYCA2;2 (Z31402)		
				CYCA2;3 (NM_101426)	Theologis et al. (2000)	
	Madagascar periwinkle	<i>Catharanthus roseus</i>	2	CYCA2;4 (NM_106686)		
				CYS (D86385.1)	Ito et al. (1997)	
	Maize	<i>Zea mays</i>	2	eyeZm2w (NP_001105387)	Hsieh and Wolniak (1998)	
				CYCA1;1 (GRMZM2G017081*)	Renaudin et al. (1994)	
	Spotted monkey flower	<i>Minulus guttatus</i>	4	CYCA1;2 (GRMZM2G007113*)	Hsieh and Wolniak (1998)	
				mCYCA (EU363012.1)	Sweigart et al. (2008)	
Tobacco	<i>Nicotiana tabacum</i>	2	N1eycA59 (X92965.1)	N1eycA30 (X92967.1)	Reichheld et al. (1996)	
			N1eycA19 (X92966.1)			
Tomato	<i>Lycopersicon esculentum</i>	2	N1eycA105 (X92964.1)			
			Lyces;CycA1;1 (Y17225)	Lyces;CycA2;1 (Y17226)	Joubès et al. (1999)	
			Lyces;CycA1;1 (AJ243451)	Lyces;CycA2;1 (AJ243452)	Joubès et al. (2000)	
			Lyces; CycA3;1 (AJ243453)			
			SlCycA1 (CAB46641)		Guo et al. (2010)	
Tobacco	<i>Nicotiana tabacum</i>	2	SlCycA2 (CAB46642)			
			SlCycA3 (CAB46643)			
			N1eycA59 (X92965.1)	N1eycA30 (X92967.1)	Reichheld et al. (1996)	
			N1eycA19 (X92966.1)			
			N1eycA105 (X92964.1)			
			CYCB2;2 (GU009976.1)			
			ProCYCB (FJ262735)			
			CYM (D86386.1)			
			CYCB1;3 (GRMZM2G005619*)			
			P1ssar;eyeB1 (AB008189)			
CYCB	Arabidopsis	<i>Arabidopsis thaliana</i>	2	eyeB (X62820)	Hata et al. (1991)	
				Lyces;CycB1;1 (AJ243454.1)	Joubès et al. (2000)	
				Aspen	<i>Populus tomentosa</i>	
				Madagascar periwinkle	<i>Catharanthus roseus</i>	
				Maize	<i>Zea mays</i>	
Pea	<i>Pisum sativum</i>	2		Sterken et al. (2009)		
				Li et al. (2009b)		
Soybean	<i>Glycine max</i>	2		Ito et al. (1997)		
				Sun et al. (1999)		
Tomato	<i>Lycopersicon esculentum</i>	2		Shimizu and Mori (1998)		
				Hata et al. (1991)		

Table 3 continued

Genes	Commercially name	Species	Ploidy level (x)	Gene name (GenBank accession number or ID number denoted by ‘*’)	References
	Tobacco	<i>Nicotiana tabacum</i>	2	Lyces;CycB2;1 (AJ243455) cycB1 (Z37978.2)	Qin et al. (1995)
CYCD	Maize	<i>Zea mays</i>	2	CYCD2;1 (GRMZM2G075117*) CYCD5;1 (GRMZM2G006721*) CYCD5;2 (GRMZM2G007130*)	Gutiérrez et al. (2005) Quiroz-Figueroa and Vázquez-Ramos (2006)
	Pea	<i>Pisum sativum</i>	2	Pissa;cycD3;1 (ABO08188)	Shimizu and Mori (1998)
	Tomato	<i>Lycopersicon esculentum</i>	2	Lyces;CycD3;1	Joubès et al. (2000)
OSD1	Arabidopsis	<i>Arabidopsis thaliana</i>	2	OSD1/GIG1/UV14 (824955*)	d’Erfurth et al. (2009)
AtPSI	Arabidopsis	<i>Arabidopsis thaliana</i>	2	PSI (840337*)	d’Erfurth et al. (2008)

Genes involved in formation of unreduced gametes

or indeterminate meiotic restitution (IDR). In FDR-type mechanisms 2n spores are genetically equivalent to the gametes formed by an omission of MI, in the SDR type the genotypic constitution of the 2n gametes is equivalent to those formed by a complete loss of MII, and in the IDR type 2n gametes varied between those in FDR and SDR (Ramanna and Jacobsen 2003).

Until the present, there are few studies in plants linking the function of genes involved in omission of MI and MII. In the following paragraphs we will describe some proteins that have proved to be relevant in the meiotic process, the failure in their regulation or their inactivation resulting in the omission of meiosis I or II.

Siddiqi et al. (2000) have shown that the mutant allele *dyad* in *Arabidopsis* affects male and female meiosis due to the loss of activity of SWI1/DYAD, which may result in the separation of sister chromatids in MI and the termination of female meiosis (Agashe et al. 2002; Mercier et al. 2001). Gametophytes presenting the mutant *dyad* have a low number of gametes, of which 60 % are triploid.

Also the proteins CYCA1 and CYCA2 are known as TAM (tardy asynchronous meiosis) and are required for MI and progression of MII. Mutations in these proteins lead to the production of unreduced gametes (Wang et al. 2004; d’Erfurth et al. 2010). Homozygotic loss of alleles of CYCA1;2/TAM causes that 30 % of female meiocytes complete the first meiotic division, but fail to proceed to the second meiotic division, thus chromatids do not separate and, consequently, the resulting cells (unreduced gametes) may give rise to a polyploid. Cromer et al. (2012) have reported that CYCA1;2/TAM forms an active complex with the cyclin-dependent kinase CDKA;1, and that the expression of a synthetic non-degradable CYCA1;2/TAM invokes the entry into a third meiotic division. Hence, TAM/CYCA1;2 is an essential regulator of meiotic cell cycle progression that promotes entry into MII and mediates exit from meiosis, most presumably through the regulation of CDKA;1.

Another factor that causes disturbances in synapsis and bivalent formation in male and female meiosis is SDS (SOLO DANCERS). SDS contains a C-terminal domain resembling known B2-type cyclins, which suggest that SDS is a meiosis-specific B2-like cyclin that regulates prophase I and meiotic cell cycle progression (Chang et al. 2009).

An protein that deserves mention is named *omission of second division 1* (OSD1)—also termed GIGAS CELL1 (GIG1) or UVI4-Like (UVI4-L) and its paralog, UVI4 (for UV-B-insensitive 4)—and in *Arabidopsis* it is required for entering meiosis II and is also important for avoiding the second meiotic division (d'Erfurth et al. 2009). Meiocytes in which CYCA1; 2/TAM, and OSD1 were lost could complete the first meiotic division, but failed to enter the second mitotic division, producing paired chromosome instead of tetrads. The loss of OSD1 in plants causes 100 and 85 % of unreduced gametes in males and females, respectively, which may produce polyploid offspring. The exact role of OSD1 in meiotic progression is still unknown. Iwata et al. (2011) have demonstrated that UVI4 physically binds to FZY-RELATED (FZR), a well-known APC/C activator, thereby inhibiting the activation of the APC/C ubiquitin ligase complex. Similarly, OSD1 interacts with CDC20/FZY, another activator of the APC/C complex, and mutant forms of OSD1 ectopically induce somatic endomitosis, which indicates that OSD1 not only controls meiotic progression but also regulates the exit from it, and it is believed that this gene plays an important function by directly or indirectly changing the activity of CDK. In *Arabidopsis*, it has been shown that the loss of function of *osd1* and *uvi4* cause endoreduplication and lethality of female gametes. This lethality could be partially suppressed by a mutation in the APC activator CCS52a1. Mutation of the *cpr5* (gene involved in disease resistance to bacterial pathogens) suppressed many defects of *osd1* and *uvi4* mutants, while the *uvi4* mutation enhanced the *cpr5* defect in trichome branching and disease resistance. This indicates that CPR5 interacts with OSD1 and UVI, playing a role in cell cycle regulation (Bao and Hua 2014).

Little is known about the regulation of OSD1, but recently it has been found that CYCA1;2/TAM-activated CDKA;1 phosphorylates OSD1 in vitro, indicating that CYCA1;2/TAM, OSD1, and APC/C form a functional network that regulates meiotic cell cycle progression (Cromer et al. 2012). It has also been demonstrated that OSD1 modulates the activity of APC/C in a gradient-dependent manner, the process being controlled through phosphorylation of OSD1 by CYCA1;2/TAM (De Storme and Geelen 2013). CYCA1;2/TAM may be degraded by APC-C, whereas

OSD1 regulates this degradation in a gradient-dependent manner allowing entry in MI and MII.

Finally, another gene known to have a direct relationship with the production of unreduced gametes is AtPS1 (*Arabidopsis thaliana* PARALLEL SPINDLES 1), coding for a plant-specific protein with two highly conserved domains: an N-terminal forkhead-associated (FHA) domain and a C-terminal PINC domain. Due to the presence of their catalytic domains, it has been speculated that AtPS1 plays a regulatory role in the quadripolar orientation of MII spindles (d'Erfurth et al. 2008). The phenotype of mutants bearing the *Arabidopsis* gene AtPS1 results from the parallel orientation of the meiotic spindles during metaphase II, instead of the normal tetrahedral configuration. This results in the formation of a single plane of division and originates dyads containing diploid spores instead of a tetrad of haploid spores (Andreuzza and Siddiqi 2008). However, as no targets have been identified to date, more research is needed to elucidate the mechanisms involved in establishment of MII polarity.

Nowadays, there is little research aimed at studying the genes involved in the omission of MI and MII, most studies to date having been conducted in the *Arabidopsis* model, however, it would be interesting to study these genes in plants with commercial importance. Between 2005 and 2013, 28 genomes of diploid crops—such as rice, chickpea, bamboo and barley (Bevan and Uauy 2013)—were sequenced, but in the same time period only one genome of hexaploid bread wheat was sequenced. Although the genomes of many polyploid species remain to be known, several molecular analysis methods have been used to learn differences in genetic expression between polyploid species and their diploid progenitors. Such methods include comparative genome analysis, high-throughput DNA sequencing, high-resolution melting analysis (HRM), high-throughput RNA sequencing, and molecular marker-based genetic mapping (Aversano et al. 2012; Rambani et al. 2014).

Advances made in sequencing of crop genomes provide a powerful tool for in silico analysis of genes involved in the cell cycle and meiosis (and of the regulation of their genetic expression) aimed at finding possible differences in structure and function in polyploid relative to diploid species. The information obtained supplemented with further research might

suggest whether these genes are involved in endoreduplication and meiosis, and could thus be used for the genetic manipulation and improvement of polyploid crop species.

Growth regulators and their influence in the cell cycle

Extrinsic factors such as plant growth regulators affect cell elongation and division (Muller and Leyser 2011). Auxin is a plant hormone that is important in the induction of cell-cycle entry and in the expression of genes regulating cell-fate determination (Blilou et al. 2005; Smolarkiewickz and Dhonukshe 2013). The control by auxin of the transcriptional mechanism is based on binding of transcriptional activators known as auxin-response factors (ARFs) (Tiwari et al. 2003). In the absence or at low levels of auxin, ARFs proteins dimerize with the auxin/indole-3-acetic acid (Aux/IAA) proteins, the dimer functioning as transcriptional repressors inhibiting the expression of CDKB 2;1, CYCA2;4, and CYCD 3;2, thus arresting the cellular cycle. However, high concentrations of auxin induce the cellular cycle (Ishida et al. 2010; Sanz et al. 2011).

Experiments in cell cultures have shown that growth regulator treatments induce extra rounds of DNA replication. The presence of auxins and cytokinins induce the increase of nuclear DNA in pea (Libbenga and Torrey 1973), tomato (De Jong et al. 2009) and rice (Meguro and Sato 2014). At the molecular level, cytokinins induce the rapid activation of the regulatory cycle through tyrosine dephosphorylation of CDKA, which is required to enter mitosis and meiosis (Srivastava and Handa 2005; Zhang et al. 1996).

Regarding gibberellins (GAs), it has been demonstrated that they control DNA synthesis during the development of the hypocotyl in *Arabidopsis* (Gendreau et al. 1999). Perraza et al. (1998) suggested that gibberellic acid stimulates the development of the plant as a direct effect of endoreduplication. Gibberellins can stimulate development of trichomes, as was demonstrated in *Arabidopsis* mutants deficient in gibberellic acid through induction of GL1 (Glabrous1).

Ethylene plays a key role throughout fruit development and ripening of climacteric fruits and has been broadly studied (Llop-Tous et al. 2000; Srivastava and Handa 2005). Ethylene has also been demonstrated to induce extra rounds of DNA synthesis in cucumber (Dan et al. 2003) and *Populus* (Love et al. 2009).

Other hormones that have proven to have an indirect relationship with cell division are the brassinosteroids (Bishop and Koncz 2002). In silico studies have shown that the gene *BR11* of *Arabidopsis* encodes a leucine rich repeat receptor kinase (LRRRK) (Li and Chory 1997) that is crucial for many plant signaling processes, such as plant architecture (De Smet et al. 2012), flower abscission (Jin et al. 2000), and responses to stress (Marshall et al. 2012). The BRs are involved in root gravitropism in an IAA-dependent manner. BRs also affect the biosynthesis of other hormones (cytokinin) (Jang et al. 2000) and enhance ethylene production (Sakurai and Fujioka 1993). While BR did not directly affect the process of endoreduplication, its direct relationship with other hormones involved in this process (cytokinins, auxin and ethylene) positioned it as an indirect regulator that may contribute to polyploidy.

Environmental factors affecting genome size

Polyploids generally appear to be particularly common in extreme environments, including those present in the subarctic regions, glaciated areas, and the arid zones (Brochmann et al. 2004; Madlung 2013), which suggest that genome doubling per se is tightly associated with environmental change. Plants have probably developed mechanisms allowing them to adjust their cell cycle in response to environmental cues. In wheat and in maize, water stress reduces plant size and prolongs the duration of the cell cycle in meristems as a result of a decreased activity of CDK (Granier et al. 2000; Schuppler et al. 1998). Li et al. (2012) observed in polyploid species of *Arabidopsis* a direct relation between the expression of the ICK1, ICK2, and ICK5 genes and the dimensions of stomata, which affects water acquisition by plants. It may be inferred that environmental factors such as drought trigger a series of mechanisms allowing polyploid species to withstand extreme conditions. Possibly genes exist that are directly and consistently regulated by genome doubling (Madlung 2013).

Darkness and temperature have also been shown to generate variations in cell division, cell expansion, and DNA endoreduplication (Bertin 2005). Studies in vitro made under conditions of darkness have shown that the elongation of the epicotyl in pea and *Arabidopsis* involved an endocycle leading to an increase in DNA of 8C and 16C, while in light conditions those levels

were of 4C and 8C (Gendreau et al. 1997; Van Oostveldt and Van Parijs 1975). The same pattern was found in tomato and corn (Biradar et al. 1993; Smulders et al. 1994). Berckmans et al. (2011) described that light promotes cell division in hypocotyls and activates the transcription of *DELI*, which encodes an atypical E2F that inhibits endoreplication by repressing the expression of CCA52A1 (*Fzr/Cdh1*). In the dark, *DELI* expression is extinguished and hypocotyl cells undergo endoreplication (Berckmans et al. 2011). In the root meristem (unexposed to light) auxin signaling regulates the mitosis-to-endoreplication switch (Ishida et al. 2010).

Regarding temperature, studies in tomato have shown that an increase in temperature promoted a larger cell size, but slightly decreased the number of cells (Bertin 2005). This trend of increment in cell size and decrease in number of cells has also been observed in polyploid species, a phenomenon known as *gigas* (Lutz 1907; Tupper and Bartlett 1916). The ploidy-regulation of the progression of the cell cycle could explain the control of endoreduplication on cell size, due to an earlier cessation of mitotic activity (Galitski et al. 1999). Thus, endoreduplication precedes cell expansion, as has been documented in maize and tomato (Bertin 2005; Schweizer et al. 1995). Temperature could also play a role in the rate of progression of nuclei from a lower to a higher C-value, and contribute to increase the mean ploidy level. In *Rosa* sp. the effect of temperatures above 36 °C has the potential to increase gamete ploidy level. The high frequencies of diplogametes obtained in *Rosa* sp. at certain extreme temperatures support the hypothesis that polyploidization events could have occurred in adverse conditions; also suggesting the facilitation of polyploidization in the context of global change (Pécix, et al. 2011).

Finally, Adachi et al. (2011) showed in parsley (*Petroselinum crispum*) and tobacco that endoreduplication (and arrest of the cell cycle) could be adopted as a survival strategy under genotoxic stress conditions as a consequence of biotic stress caused by fungal elicitors (Logemann et al. 1995).

Perspectives: is genetic transformation and synthesis of polyploid species possible?

The genetic modification (GM) of plants to acquire characteristics of commercial interest has been

strongly supported in ornamental plants and important food species (Srinivasan et al. 2012; Xu et al. 2012). Although GM has helped to solve problems related to herbicide tolerance, disease resistance, nutrition, and phytoremediation (Dudareva et al. 2013; Dudareva et al. 2013; Verma et al. 2011) there is still controversy because some genetically modified crops have shown unintended harm to other organisms, reduced effectiveness of pesticides, and gene transfer to non-target species (Verma et al. 2011; Barrows et al. 2014).

The use of GM for the synthesis of polyploid species has not yet been implemented because there is little information regarding the selection of genes to use and because the ongoing controversy of the drawbacks of transformed plants. However the new biotechnological tools offer a number of alternatives, such as the transformation via chloroplast and vectors that allow the removal of cassettes of antibiotics once foreign DNA is inserted into the host (Day and Goldschmidt-Clermont 2011). Additionally, gene editing techniques like the use of zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALEN), and the clustered regulatory interspaced short palindromic repeats (CRISPR) associated nuclease (Cas) have allowed site-directed modifications in the genes of interest (Curtin et al. 2012; Feng et al. 2013; Upadhyay et al. 2013). These techniques have been used to induce mutations in crops of commercial interest such as tobacco, maize and wheat (Shukla et al. 2009; Upadhyay et al. 2013). At present, GM of plants is rapidly becoming a viable strategy for crop breeding (Gepts 2002; Hou et al. 2014).

For transformed plants to display a number of features it is usually required to insert two or more genes (Hou et al. 2014). As more genes are inserted, deleted, or regulated in a genome, the higher is the risk of unknown effects on human health. Obtaining polyploid species by GM should be feasible, since it is possible that manipulating a gene involved in genomic doubling will possibly lead to the acquisition of more features of interest.

In the previous sections we discuss important genes involved in the endoreduplication and formation of unreduced gametes, and we suggest that these genes could be used in the future for genetic transformation of diploid crops for obtaining their polyploid counterparts. Two of the disadvantages present in the GM of cell cycle genes are the redundancy of these genes in the genome and the generation of loss of function. In

this regard, transgene-induced RNA interference has proved to be a powerful strategy for overcoming gene redundancy in polyploids and for generating the loss of function in genes of interest (Lawrence and Pikaard 2003; Travella et al. 2006). Moreover, the applicability of the CRISPR/Cas9 system to target mutagenesis of paralogous genes in rice revealed that single, double, and triple mutants of CDKs genes could be created by a single sgRNA (Endo et al. 2014).

Interspecific hybridization is an important strategy for plant breeding, but its success depends largely on the compatibility of the genomes to be combined. In plant breeding, interspecific hybridization has often been limited by cross barriers, which are frequently due to ploidy level differences. Isolation of genes involved in 2n gamete production opens the way for new strategies in plant breeding programmes. RNA interference (RNAi), virus induced gene silencing (VIGS), or mutagenesis of the encoding gene using techniques such as site-directed mutagenesis could be used to knock down the level of specific proteins that play a role in formation of unreduced gametes (Brownfield and Kohler 2011). The translation of this knowledge from the model plant *Arabidopsis* to plant breeding work is yet to be initiated. However, the vision of crop generation via designed gametes is becoming realistic. Thus, GM of genes involved in the cell cycle and playing a role in the formation of unreduced gametes could be used for obtaining unreduced gametes in infertile plants with an impair number of sets of chromosomes, such as in triploids and pentaploids. Additionally, GM of cell cycle genes could also be used for obtaining polyploid plants from species found as diploids in nature like grapes, corn, banana, and carrot, among others.

Concluding remarks

Evidence of genetic and epigenetic changes in polyploids and their potential evolutionary benefit has been repeatedly discussed. Polyploids exhibiting valuable new phenotypic traits can occupy new niches and become ecologically and agriculturally important. Despite the importance of polyploid plant species, the mechanisms underlying their origin and adaptation are yet poorly understood, which has aroused interest to investigate the factors involved in the formation of polyploid species. As mentioned in this review,

failures during the cell cycle, both in mitosis and in meiosis, could derive in polyploidy. Understanding the factors involved in endoreduplication and formation of unreduced gametes, the best routes for formation of polyploid species, can in the future be used for the generation of polyploids and for crop improvement. The prospects of further studies are connected with the identification of genes regulating the cell cycle for generating transgenic plants with a reduced or elevated expression of these genes. The manipulation by GM of genes involved in the cell cycle and in the production of unreduced gametes is positioned as a tool feasible to be applied in commercial plants with the aim of enhancing features of commercial interest.

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