Annals of Botany **120**: 195–207, 2017
doi:10.1093/aob/mcx078, available online at https://academic.oup.com/aob

ANNALS OF BOTANY
Founded 1887

INVITED REVIEW: PART OF A SPECIAL ISSUE ON POLYPLOIDY IN ECOLOGY AND EVOLUTION

Impact of transposable elements on polyploid plant genomes

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Received: 10 March 2017 Returned for revision: 3 April 2017 Editorial decision: 8 May 2017 Accepted: 23 May 2017

• **Background** The growing wealth of knowledge on whole-plant genome sequences is highlighting the key role of transposable elements (TEs) in plant evolution, as a driver of drastic changes in genome size and as a source of an important number of new coding and regulatory sequences. Together with polyploidization events, TEs should thus be considered the major players in evolution of plants.
• **Scope** This review outlines the major mechanisms by which TEs impact plant genome evolution and how polyploidy events can affect these impacts, and vice versa. These include direct effects on genes, by providing them with new coding or regulatory sequences, an effect on the epigenetic status of the chromatin close to genes, and more subtle effects by imposing diverse evolutionary constraints to different chromosomal regions. These effects are particularly relevant after polyploidization events. Polyploidization often induces bursts of transposition probably due to a relaxation in their epigenetic control, and, in the short term, this can increase the rate of gene mutations and changes in gene regulation due to the insertion of TEs next to or into genes. Over longer times, TE bursts may induce global changes in genome structure due to inter-element recombination including losses of large genome regions and chromosomal rearrangements that reduce the genome size and the chromosome number as part of a process called diploidization.
• **Conclusions** TEs play an essential role in genome and gene evolution, in particular after polyploidization events. Polyploidization can induce TE activity that may explain part of the new phenotypes observed. TEs may also play a role in the diploidization that follows polyploidization events. However, the extent to which TEs contribute to diploidization and fractionation bias remains unclear. Investigating the multiple factors controlling TE dynamics and the nature of ancient and recent polyploid genomes may shed light on these processes.

Key words: Transposable element, plant genome, polyploidization, silencing, genome stress, exaptation, genome dominance, diploidization, fractionation bias, neofunctionalization, chromosomal rearrangement.

INTRODUCTION

Transposable elements (TEs) are mobile genetic elements present in virtually all genomes. Among all different types of TEs, long terminal repeat (LTR) retrotransposons and miniature inverted transposable elements (MITEs) are in general the most abundant TEs in plant genomes (Casacuberta and Santiago, 2003). The larger size of LTR retrotransposons makes them, by far, the most prevalent in all sequenced plant genomes, comprising between 2·5 % in *Utricularia gibba* (Ibarra-Laclette *et al*., 2013) and 90 % of the genome in *Fritillaria* species (Ambrožová *et al*., 2011).

Together with polyploidization, TE amplification is considered the main mechanism to increase the plant genome and, more generally, for plant genome evolution (Casacuberta *et al*., 2016; Wendel *et al*., 2016). In fact, as discussed below, polyploidization and TE amplification are not two completely independent mechanisms. On the contrary, these two phenomena greatly influence one another, reinforcing their potential to drive plant genome evolution.

The role of TEs in the evolution of plant genes and genomes is not only a key for long-term plant evolution in the wild, but has also been of paramount importance for recent crop domestication and breeding (Olsen and Wendel, 2013). In this article we will review the links between polyploidization and TE dynamics, as well as the role that TEs have played in the evolution of plant genomes both in the wild and during crop domestication and breeding.

LTR RETROTRANSPOSONS AND THE EXPANSION AND CONTRACTION OF PLANT GENOMES

Although all plant genomes contain an important fraction of TEs, with LTR retrotransposons being the most abundant, the prevalence of particular families is highly variable among species and even among varieties of the same species. In many cases, a limited number of TE families have increased their copy number in one lineage (El Baidouri and Panaud, 2013). For example, a single type of LTR retrotransposon explains most of the *Capsicum annuum* genome expansion (Park *et al*., 2012), and a single Ty3/gypsy-like retrotransposon, *Ogre*, makes up approx. 38 % of the genome of *Vicia pannonica* (Neumann *et al*., 2006). In some cases, a family's potential for amplification is shared by several related species (Estep *et al*., 2013), but it is also usual to observe a TE family with a high copy number in one species that presents a low copy number in a close relative (Hawkins *et al*., 2009). Moreover, important differences can even be observed among varieties of the same

species such as, for example, the *Grande* LTR retrotransposon (Gómez-Orte *et al*., 2013) which shows 1450 copies in the maize inbred line B73 whereas 3500 copies are found in 'Palomero Toluqueño'.

Although the presence of a single or a few highly repetitive TE families in a genome is usual, genomes with several TE families with similar copy numbers have also been observed. For example, although LTR retrotransposons account for almost 50 % of the genome of *Pinus taeda* (loblolly pine), the three most common repetitive elements represent <5 % the genome (Wegrzyn *et al*., 2014). All these data suggest that the capacity for TEs to invade genomes may depend on both the element and the genome, with some elements being able to escape the control in a particular genome, and some genomes being more permissive to the TE proliferation. Moreover, the amplification of TEs is not constant during evolution, and periods where TEs are relatively quiescent alternate with periods in which some TEs increase their numbers dramatically, resulting in genome expansions (Qin *et al*., 2014), suggesting that genome control over TEs is not constant over time. TE activity is tightly controlled by epigenetic mechanisms (Bennetzen and Wang, 2014; Ito and Kakutani, 2014). The permissiveness of some genomes to TEs may be related to a lower silencing efficiency. On the other hand, it is known that silencing can be influenced by the environment, and a transient release of silencing may be one of the reasons behind TE proliferation bursts (Willing *et al*., 2015).

The differential activity of particular TEs may be due to the capacity of some TEs to counteract genome silencing or to stochastic activation of particular TEs due to general weakening of silencing. Indeed, it has been shown that plant retrotransposons can escape host silencing (Hernández-Pinzón *et al*., 2012), in some cases by expressing anti-silencing factors (Fu *et al*., 2013). On the other hand, TE transcription, and in some cases their transposition and amplification, can be reactivated under particular situations such as in particular mutant backgrounds with reduced DNA methylation, some environmental conditions or after genome rearrangements (Vicient, 2010; Ito and Kakutani, 2014). For example, the expression of some TEs is activated in the pollen vegetative nurse cell surrounding the sperm cells, which triggers the production of small interfering RNAs (siRNAs) to ensure the maintenance of the epigenetic silencing of TEs in the following generation (Martínez *et al*., 2016). In addition, some TEs are activated under different stress conditions. Indeed, biotic and abiotic stresses activated the transcription of the tobacco *Tnt1* retrotransposon (Grandbastien *et al*., 2005), cold and salt stresses activated the amplification of the rice MITE *mPing* (Naito *et al*., 2009), heat stress activated the transcription of the *Arabidopsis thaliana* retrotransposon *ONSEN* (Cavrak *et al*., 2014) and its mobilization (Ito *et al*, 2016), and *in vitro* culture activated the mobilization of different *Oryza sativa* (rice) and maize TEs (Hirochika, 1997; Kaeppler *et al*., 2000). In some of these cases, the presence of stress-associated transcription factor-binding sites (TFBSs) in the TE promoters suggests a transcriptional activation mechanism, but a decrease in silencing associated with stress could also account for the widespread association of stress and TE reactivation (Tittel-Elmer *et al*., 2010). The stress activation of TEs may produce an increase in TE-related mutations, some of which may result in adaptive mutations to the stress situation, as has been proposed for the arabidopsis *ONSEN* retrotransposon (Ito *et al*, 2016). Some changes in the genome, such as interspecific crosses and polyploidization events, have also been shown to lead to global epigenetic changes and activation of TE transcription (Table 1), and have, in some cases, been considered 'genome stresses' (Yaakov and Kashkush, 2012). This relationship will be further explored in a dedicated section (see below).

Although TE amplification leads to larger genomes, their turnover and loss can also occur (Bennetzen and Wang, 2014). Unequal homologous recombination and illegitimate recombination may reduce genome TE content, and differences in their efficiency may contribute to the differences in the TE content between genomes (Bennetzen and Wang, 2014). Homologous recombination between the LTRs of a single retrotransposon results in internal domain removal, leaving behind a single recombinant LTR, or solo-LTR; these are highly abundant in some plant genomes (Vicient *et al*., 1999). If the recombination occurs between LTRs of two TEs, it may produce not only the loss of TE sequences but also the loss of additional genomic sequences (Vicient *et al*., 2005) or it may produce chromosomal rearrangements, including duplications, inversions and translocations (Ma *et al*., 2004).

The rate of inter-element recombination is variable among species, LTR retrotransposons and chromosomal regions (Bennetzen and Wang, 2014). For example, heterochromatin has lower recombination rates and, as a consequence, these regions contain lower ratios of solo-LTRs to intact elements (Tian *et al*., 2009). The processes of LTR retrotransposon removal by recombination seems to be highly efficient because in most plant genomes the majority of intact LTR retrotransposon elements found were recently inserted (Bennetzen and Wang, 2014).

In summary, the TE content of a particular genome is the result of an equilibrium between proliferation and elimination processes, and may result in plant genomes with a very different TE content (from 2·5 to 90 %). Whereas potential advantages and disadvantages of a high TE content have been proposed, the actual phenotypic consequences of this large variability in TE content and genome size are not obvious. It has recently been proposed that the balance between the TE content in different genome regions may be, in fact, more relevant than the total number of TEs in a genome (Freeling *et al*., 2015).

IMPACT OF TRANSPOSONS IN GENE CODING AND REGULATION IN PLANTS

A significant number of plant genes are derived from TEs in a process known as exaptation, and TEs have also contributed to the evolution of introns, exons and promoters (Zhao *et al*., 2016). The mechanisms by which TEs can modify genes are diverse (Contreras *et al*., 2015). The most obvious is the insertional inactivation of the coding or the regulatory regions of the gene. However, the insertion of a TE inside a gene may also generate more subtle mutations such as changes in the protein sequence encoded, changes in the pattern of expression or new splicing variants (Huang *et al*., 2015). TEs can carry ready-made promoters and/or enhancers, enabling the dissemination of discrete regulatory elements (Rebollo *et al*., 2012). TEs can

TABLE 1. *Examples of studies reporting reorganization of, or expression changes related to, the transposable elements after polyploidy in plants*

Species	Auto/Allo	TE	TE type	Effect	Reference
Synthetic (short-term reorganization)					
Aegilops charonensis × *Triticum monococcum*	Allo	Diverse	Diverse	Methylation changes.	Shaked *et al.* (2001)
Aegilops sharonensis × *Triticum monococcum*	Allo	*Wis*2-1A	LTR retrotransposon	Transcriptional activation with impact on adjacent genes.	Kashkush *et al.* (2002, 2003)
Arabidopsis thaliana × *Arabidopsis arenosa*	Allo	*Sunfish*	En-Spm-like transposon	Transcriptional activation and epigenetic changes.	Madlung *et al.* (2005)
Arabidopsis thaliana × *Arabidopsis arenosa*	Allo	Diverse	Diverse	Methylation changes and variation in siRNAs in the first generation.	Ha *et al.* (2009)
Arabidopsis thaliana × *Arabidopsis arenosa*	Allo	Diverse	Diverse	Differential repression of TEs by RNAi in the two sub-genomes.	Chen *et al.* (2008)
Arabidopsis thaliana × *Arabidopsis lyrata*	Allo	*CAC, Ac-III*	DNA transposons	No evidence of increased mobility or loss of elements from parental origin and methylation changes.	Beaulieu *et al.* (2009)
Arabidopsis thaliana × *Cardaminopsis arenosa*	Allo	MITE	MITE	Changes in DNA methylation.	Madlung *et al.* (2002)
Brassica carinata × *Brassica rapa*	Allo	Diverse	Diverse	Methylation changes.	Xu *et al.* (2012)
Brassica rapa and *Brassica oleracea*	Allo	Diverse	Diverse	Mobilization in the first generation and reduced in subsequent generations.	An *et al.* (2014)
Brassica rapa × *Brassica oleracea*	Allo	Diverse	Diverse	Methylation changes.	Xu *et al.* (2009)
Brassica rapa × *Brassica oleracea*	Allo	Diverse	Diverse	Changes in TE-derived miRNAs.	Fu *et al.* (2016)
Nicotiana sylvestris × *Nicotiana tometosiformis*	Allo	*Tnt1*	LTR retrotransposon	Increase in mobility and loss of elements from parental origin.	Petit *et al.* (2010)
Oryza sativa	Auto	Diverse	Diverse	Hypermethylation that in some cases affects the expression of neighbouring genes. Changes in siRNA abundance.	Zhang *et al.* (2015)
Oryza sativa	Auto	Diverse	Diverse	Changes in miRNAs related to retrotransposons and DNA transposons.	Guo *et al.* (2017)
Spartina alterniflora × *Spartina maritima*	Allo	*Ins2, Cassandra, Wis*-like	hAT DNA transposon, TRIM, LTR retrotransposon	Loss of elements especially of maternal origin and epigenetic changes.	Parisod *et al.* (2009)
Triticum turgidum × *Aegilops tauschii*	Allo	*Au*	SINE	Mobilization, loss and epigenetic changes (hypermethylation after a few generations).	Ben-David *et al.* (2013)
Triticum turgidum × *Aegilops tauschii*	Allo	*Minos*	MITE	Mobilization (but no burst of copy number) and epigenetic changes (hypermethylation after a few generations).	Yaakov and Kashkush (2012)
Triticum turgidum × *Aegilops tauschii*	Allo	*Veju*	TRIM	Hypomethylated in the first S1 generation and hypermethylated in the S4 generation.	Kraitshtein *et al.* (2010)
Triticum turgidum × *Aegilops tauschii*	Allo	Diverse	Diverse	No mobilization.	Mestiri *et al.* (2010)
Triticum turgidum × *Aegilops tauschii*	Allo	*Balduin, Apollo,Thalos*	DNA transposons	Changes in methylation where hypermethylation was predominant. Lack of massive mobilization.	Yaakov and Kashkush (2011)
Triticum turgidum × *Aegilops tauschii*	Allo	*Veju, Wis*2-1A	TRIM, LTR-retrotransposon	siRNAs were reduced and CpG methylation decreased.	Kenan-Eichler *et al.* (2011)
Natural (long-term reorganization)					
Aegilops crassa, *Aegilops cylindrical*, *Aegilops geniculata* and *Aegilops triuncialis*	Allo	Diverse	LTR retrotransposon	Some TE families increase their mobilization and some suffer massive loss, depending on the polyploids.	Senerchia *et al.* (2014)
Arabidopsis suecica and *A. arenosa*	Auto/Allo	Ac-like	DNA transposon	Differential amplification and fixation of particular elements.	Hazzouri *et al.* (2008)
Arachis spp.	Allo	*AhMITE*1	MITE		Gowda *et al.* (2011)

(Continued)

Table 1. *Continued*

Species	Auto/Allo	TE	TE type	Effect	Reference
				Recent activation of the element, possibly because of the hybridization followed by allopolyploidization.	
Biscutella laevigata	Auto	Diverse	LTR retrotransposons	Analyses of the dynamics of LTR retrotransposons following autopolyploidy.	Bardil *et al.* (2015)
Brachiaria decumbens	Auto/Allo	Diverse	LTR retrotransposons	Transcriptional activation.	Santos *et al.* (2015)
Brassica napus	Allo	Diverse	CACTA, LTR retrotransposon	Insertion of a TE in a sub-genome contributed to significant high levels of cytosine methylation and structural divergences between genome orthologues.	Wang *et al.* (2012)
Brassica rapa	Allo	Diverse	Diverse	Biased distribution of TEs among sub-genomes.	Cheng *et al.* (2016)
Brassica rapa × *Brassica oleracea*		*BraSto*	MITE	Moderate amplification.	Sarilar *et al.* (2011)
Brassica rapa × *Brassica oleracea* Sarilar et al. (2013)	Allo	*Athila*-like, *BraSto, Bot*1	LTR	retrotransposonMITECACTA	No massive structural changes.
Brassica spp.	Allo	Diverse	Diverse	Different amplification of TEs depending on the genome.	Liu *et al.* (2014)
Brassica spp.	Allo	Diverse	Diverse	Small RNA-mediated silencing of transposons near genes causes position-effect downregulation.	Woodhouse *et al.* (2014)
Brassica spp.	Allo	*Bot*1	CACTA	Differential amplification in the two sub-genomes.	Alix *et al.* (2008)
Capsella bursa-pastoris	Allo	Diverse	Diverse	Increase in copy number but only in the gene-rich regions and not in the centromeres.	Ågren *et al.* (2016)
Coffea arabica	Allo	Diverse	LTR retrotransposon	Differential insertions in the two sub-genomes.	Yu *et al.* (2011
Coffea canephora × *Coffea eugenioides*	Allo	Diverse	Diverse	Increase in copy number.	Lopes *et al.* (2013)
Crocus spp.	Allo	Diverse	Diverse	TE markers used to identify allopolyploid parental species.	Alsayied *et al.* (2015)
Glycine max	–	Diverse	Diverse	Differential insertions in the two sub-genomes.	Innes *et al.* (2008)
Glycine max and *Phaseolus vulgaris*	–	Diverse	Diverse	TE-associated epigenetic gene regulation.	Kim *et al.* (2015)
Gossypium arboretum × *Gossypium raimondii*	Allo	Diverse	Diverse	Loss of sequences mostly of maternal origin.	Grover *et al.* (2007)
Gossypium hirsutum	Allo	*Gorge*3, *copia*, diverse	LTR retrotransposon, LINEs	Deletions in the TE genome fractions and limited transpositions.	Hu *et al.* (2010)
Gossypium hirsutum	Allo	Diverse	Diverse	TE differential activity according to the genome fraction.	Li *et al.* (2015)
Gossypium hirsutum	Allo	CRG	LTR retrotransposon	Differential amplification in the centromere of sub-genomes.	Luo *et al.* (2012)
Gossypium spp.	Allo	Diverse	LTR retrotransposons	Changes in distribution and copy number in centromeres.	Han *et al.* (2016)
Gossypium spp.	Allo	Diverse	Diverse	TE influence on genome fractionation.	Renny-Byfield *et al.* (2015)
Gossypium spp.	Allo	Diverse	Diverse	Spread of TEs in the early stages of polyploidy formation between the genomes from the diploid progenitors of a polyploid.	Zhao *et al.* (1998)
Gossypium spp.	Allo	Diverse	LTR retrotransposon	Differential amplification.	Guo *et al.* (2014)
Helianthus anomalus, *Helianthus deserticola* and *Helianthus paradoxus*	Allo	Diverse	LTR retrotransposons	Increase in copy number.	Kawakami *et al.* (2010)
Helianthus anomalus, *Helianthus deserticola* and *Helianthus paradoxus*	Allo	Diverse	LTR retrotransposons	Increase in copy number.	Ungerer *et al.* (2006, 2009); Staton *et al.* (2009)
Nicotiana repanda and *Nicotiana nudicaulis*	Allo	Diverse	Diverse	Reduction in TE copy numbers depending on species and TE families during diploidization.	Renny-Byfield *et al.* (2013)
Nicotiana spp	Allo	Diverse	SINEs, MITEs and LTR retrotransposons	Increase in copy number and loss of sequences mostly of paternal origin.	Parisod *et al.* (2012)
Nicotiana sylvestris × *Nicotiana tomentosiformis*	Allo	*Tnt*1, *Tnt*2, *Tto*1	LTR retrotransposon	Loss of sequences mostly of paternal origin and new insertions.	Petit *et al.* (2010)
Nicotiana tabacum	Allo	Diverse	Diverse	Loss of sequences mostly of paternal origin.	

(Continued)

TABLE 1. *Continued*

Species	Auto/Allo	TE	TE type	Effect	Reference
					Renny-Byfield *et al.* (2011)
Orobanchaceae gracilis	Auto	Diverse	LTR retrotransposons	Increase in copy number and loss of some TE families.	Piednoël *et al.* (2013)
Orobanche austrohispanica, *Orobanche densiflora* and *Orobanche gracilis*	Allo	Diverse	LTR retrotransposons	Increase in copy number.	Piednoël *et al.* (2015)
Oryza minuta	Allo	hAT	DNA transposon	Gene silencing due to DNA methylation differences within promoter regions that were associated with a TE insertion.	Sui *et al.* (2014)
Oryza punctata × *Oryza officinalis*	Allo	Diverse	Diverse	Loss of sequences mostly of paternal origin and mobility.	Lu *et al.* (2009)
Oryza sativa	Auto	Diverse	Diverse	Changes in siRNAs and methylation associated with TEs.	Li *et al.* (2014)
Spartina angelica	Allo	*Skipper*	LTR retrotransposons	Transcriptional activation.	Chelaifa *et al.* (2010)
Spartina anglica	Allo	Diverse	Diverse	Few new integration sites were found in the allopolyploid genome compared with the parental genomes.	Baumel *et al.* (2002)
Thinopyrum intermedium	Allo	Diverse	LTR-retrotransposon	Burst of Ty3/gypsy centromeric retrotransposon during allopolyploidization.	Divashuk *et al.* (2016)
Triticum aestivum	Allo	*Veju, BARE*1	TRIM, LTR retrotransposons	Methylation changes.	Zhao *et al.* (2011)
Triticum aestivum	Allo	Diverse	Diverse	Increased siRNA density for TEs in one genome.	Li *et al.* (2014)
Triticum aestivum	Allo	Diverse	Diverse	TEs are involved in part of the genomic rearrangements after polyploidization events.	Chantret *et al.* (2005); Isidore *et al.* (2005)
Triticum aestivum	Allo	*CRW*, *Quinta*	LTR retrotransposon	TEs are involved in the centromere rearrangements after polyploidization.	Li *et al.* (2013)
Triticum aestivum	Allo	Sabrina	LTR retrotransposon	Differential amplification in the sub-genomes.	Sehgal *et al.* (2012)
Triticum aestivum	Allo	Fatima	LTR retrotransposon	Differential amplification in the sub-genomes.	Salina *et al.* (2011)
Triticum aestivum	Allo	Diverse	Diverse	TEs are involved in part of the gene specificities among genomes.	Golovnina *et al.* (2010)
Triticum aestivum	Allo	Diverse	Diverse	Differential amplification in the sub-genomes.	Salse *et al.* (2008)
Triticum spp., *Aegilops* spp. and allopolyploids	Allo	Stowaway-like	MITEs	Genome-specific proliferation and non-additive quantities in the polyploids.	Yaakov *et al.* (2013*a*)
Triticum spp., *Aegilops* spp. and allopolyploids	Allo	Diverse	Diverse	Some TE families proliferate in specific genomes reactivated following polyploidization. The changes that occur following polyploidization events are unique to each TE family.	Yaakov *et al.* (2013*b*)
Triticum turgidum × *Aegilops tauschii*	Allo	Diverse	Diverse	Predominantly mobility but also loss.	Chantret *et al.* (2005); Charles *et al.* (2008)
Zea mays	Allo	*Ji, Opie*	LTR retrotransposons	Increase in copy number.	Estep *et al.* (2013)
Zea mays	Allo	*CRM*1	LTR retrotransposon	Expansion associated with polyploidization event.	Sharma *et al.* (2008)
Zea spp and *Sorghum* spp	Allo	Diverse	Diverse	Spread of TEs in *Zea* after an ancient genome duplication.	Gaut *et al.* (2000)

amplify and redistribute TFBSs, creating new regulatory networks or rewiring new genes into the existing ones (Hénaff *et al*., 2014). The mobility of TEs containing transcriptional regulatory elements may endow genomes with a transcriptional plasticity that could be very useful for rapid adaptation to changing conditions.

Transposbale elements may also influence the expression of neighbouring genes by epigenetic effects (Contreras *et al*., 2015). TEs are the main target of silencing mechanisms which keep their activity under a threshold to avoid compromising genome viability. As a consequence, TEs are usually heavily methylated and are associated with heterochromatic epigenetic marks (Ito and Kakutani, 2014). The insertion of a TE close to a gene can attract silencing epigenetic marks and modify its expression, as, for example, in the case of the repression of the flowering regulator *FWA* in arabidopsis (Kinoshita *et al*., 2007) or the regulation of the sex determination gene in *Cucumis melo* (melon) (Martin *et al*., 2009). The analysis of maize populations has shown that differences in DNA methylation are associated with changes in the expression of about 300 genes, and that many of the differentially methylated regions are associated with TEs (Eichten *et al*., 2013). In arabidopsis, a general negative correlation exists between methylation of TEs and expression of the neighbouring genes (Hollister and Gaut, 2009), and it has been proposed that the genome distribution of TEs may contribute to the balanced transcription of gene networks (Freeling *et al*., 2015). TEs also seem to be at the origin of an important number of microRNA (miRNAs) (Piriyapongsa and Jordan, 2008). For example, many regulatory miRNA genes are derived from TEs in rice (Li *et al*., 2011) and in the green alga *Volvox carteri* (Dueck *et al*., 2016).

The close relationship between stress, TE activation and TE potential to modify gene expression can make these elements important players in plant adaptation to stress conditions. As already explained, TEs usually contain stress-inducible promoters (Cavrak *et al*., 2014), and their insertion close to genes may confer stress inducibility on them. For example, the rice MITE *mPing* inserts preferentially upstream of genes, making them stress inducible (Naito *et al*., 2009), and the stress-induced retrotransposon *ONSEN* can generate abscisic acid-insensitive mutations in arabidopsis (Ito *et al*., 2016). A total of 33 % of the genes expressed under stress in maize contain a TE in their promoter region, many of which also respond to stress (Makarevitch *et al*., 2015). In addition, it has been shown that TEs can regulate stress response genes through TE-derived siRNAs. Indeed, it has been shown that the epigenetic activation of the arabidopsis *Athila* retrotransposon induces the production of an siRNA that regulates a gene encoding an RNA-binding protein involved in stress granule formation (McCue *et al*., 2012).

The recent development of bioinformatic tools to detect TE polymorphisms using short reads from re-sequencing data (Ewing, 2015; Hénaff *et al*., 2015) allows analysis of the prevalence of particular TE insertions in crop varieties or populations. This should help to assess the impact of TEs in crop domestication and breeding. As an example, a recent analysis of melon varieties showed that TEs are responsible for an important part of the variability selected during melon breeding (Sanseverino *et al*., 2015). The fast growing number of plants and plant varieties for which the genome is available will allow more global evaluation of to what extent TEs are involved in crop domestication and breeding traits.

IMPACT OF TRANSPOSONS ON PLANT GENOME STRUCTURE

In addition to the local impact of transposons on genes, TEs can have a profound impact on genome structure and affect gene expression at a global scale. As already discussed, recombination between two TEs can potentially produce deletions of the interleaving genome sequence, or create chromosomal rearrangements. Examples of such processes have been observed in maize where the *Ac* element produced deletions, inversions and translocations (Weil and Wessler, 1993), or in arabidopsis where different types of TEs generated segmental duplications that occurred after divergence of the *Rosales* and *Brassicales* (Hughes *et al*., 2003). TE-mediated karyotype differences may be an important mechanism contributing to reproductive isolation, species diversification in plants and crop domestication.

Although there are examples of TEs that insert preferentially in gene-rich chromosomal arms (Du *et al*., 2010), the regions around the centromeres and telomeres usually contain a higher TE density. This is the result of different combined mechanisms. First, some TEs target heterochromatin for insertion (Contreras *et al*., 2015). This is frequently the case for *Gypsy*-like retrotransposons, whereas most *Copia*-like retrotransposons and most DNA TEs seem to insert preferentially in euchromatin (Contreras *et al*., 2015). Secondly, selection tends to eliminate deleterious insertions, concentrating TE insertions in gene-poor regions such as the heterochromatic repetitive regions. Thirdly, the rate of elimination of TEs by intra- or inter-element recombination is lower in the heterochromatic repetitive regions because they show a lower recombination rate (Zamudio *et al*., 2015).

The epigenetic silencing of the TEs accumulating in the heterochromatin reinforces the heterochromatic state of these regions (Bierhoff *et al*., 2014) which is essential for the normal functioning of these important chromosomal regions (Dernburg *et al*., 1996). In addition, the concentration of TEs in pericentromeric regions may help centromeres to resist microtubule tension during mitosis and meiosis (Freeling *et al*., 2015), and retrotransposon insertion into the centromeres contributes to the rapid evolution of the centromere (Han *et al*., 2016), which is important for the evolution of the species. On the other hand, recent results show that TEs in pericentromeric regions frequently contribute replication origins, somehow compensating for the scarcity of genes which are the preferred source of origins of replication (Vergara *et al*., unpubl. res.).

The high concentration of TEs near centromeres may also have other important consequences. The size of the heterochromatic pericentromeric regions and the concentration of TEs in them vary among plants. Whereas arabidopsis has relatively small pericentromeric TE-rich regions, the closely related *Arabis alpina* has a larger genome, with a higher content of retrotransposon elements which seem to have expanded its pericentromeric regions (Willing *et al*., 2015). Therefore, ancestral genes that have remained in gene-rich regions in arabidopsis may have been incorporated into gene-poor pericentromeric regions in *A. alpina*, and this may lead to different consequences.

The recombination is usually strongly reduced in pericentromeric heterochromatic regions and, in consequence, the evolution of these pairs of orthologous genes may be different in the two species. The larger pericentromeric region of *A. alpina* correlates with a more important reduction of meiotic recombination in pericentromeric regions as compared with arabidopsis (Willing *et al*., 2015), which may exacerbate this consequence. Long pericentromeric regions with a high concentration of TEs may therefore constitute particular chromosomal compartments with specific evolutionary constraints which may be well suited for the evolution of particular types of genes. Interestingly, it has been recently shown that the very long heterochromatic pericentromeric regions of *Solanum lycopersicum* (tomato) are enriched in tomato-specific genes, whereas older genes found in all plants are depleted from these regions (Jouffroy *et al*., 2016), suggesting that these low-recombining regions may allow the evolution of new gene functions while maintaining the rest of the genome relatively constant. Results from our laboratory suggest that tomato is not an isolated case and other genomes such as melon, which has also expanded its TE-rich pericentromeric regions (Sanseverino *et al*., 2015), may also concentrate many of its species-specific genes in these regions (C.M.V. and J.M.C., unpubl. res.).

THE TIGHT LINKS BETWEEN POLYPLOIDY AND TRANSPOSABLE ELEMENT DYNAMICS

Whole-genome duplication (WGD) events, leading to polyploids, are a common theme in plant evolution. With the only exception of *Gymnosperms*, polyploidy is widespread in plants, either natural or domesticated, and it has been recognized as an important speciation mechanism (Adams and Wendel, 2005; Soltis *et al*, 2015; Shimizu-Inatsugi *et al*., 2017). Polyploidyzation has a profound impact on genomes. Reproductive isolation, heterosis, gene redundancy, change in mating systems, changes in cellular architecture, problems in meiosis and mitosis, gene regulatory changes and epistatic instability are some of the possible consequences of polyploidy (Soltis *et al*., 2015). Duplicated genes can be lost, retained or maintained, often acquiring new functions (Adams and Wendel, 2005). As a result, polyploids often show different phenotypes compared with their diploid progenitors that may contribute to their adaption to the environment or to their utility for agriculture (Gaeta *et al*., 2007).

Polyploidization is frequently accompanied by an increase on TE content (Fig. 1) (McClintock, 1984). This can be the result of an induced burst of transposition. However, on the other hand, gene duplication allows genomes to cope with a higher TE activity, as a TE's mutagenic capacity is buffered by the duplication of essential genes. This increase in TE insertions may lead not only to the inactivation of duplicated genes but also to changes in gene functions. In some cases, as has been described in the allotetraploid *Capsella bursa-pastoris*, the increase of TE abundance in gene-rich regions seems to be the result of a relaxed selection rather than of an increase in TE activity (Ågren *et al*, 2016). However, in other cases, an increase of TE activity has also been reported (An *et al*., 2014).

When two different genomes are combined in an allopolyploid, an induction of TE activity can be the result of the loss of epigenetic silencing associated with this process (Springer *et al*., 2016). These changes are limited to the first generations after polyploidy which will be followed by the re-establishment of TE silencing. However, the consequences of a TE transposition burst can be extended for many more generations. Even in the absence of new transposition events, recombination between TEs, expected to be more frequent due to their higher abundance, could counteract genome expansion but also induce gene losses, gene mutations and genome restructuring. In summary, under this scenario, TEs play a key role in re-establishing a new equilibrium after genome duplication.

Transcriptional analyses in different allopolyploid plants and their parental diploids suggest that allopolyploidization induces TE transcription (Table 1). For example, an increase in the RNA levels of three *En-Spm*-like elements and a Ty-1 copia-like retrotransposon was detected in synthetic arabidopsis polyploids compared with the parents *Arabidopsis thaliana* and *Arabidopsis arenosa* (Madlung *et al*., 2005), the *Wis*2-1a retrotransposon showed high transcriptional activity in newly synthesized wheat amphiploids compared with its diploid parents (Kashkush *et al*., 2003) and the expression of Tip100 in allopolyploid coffee, *Coffea arabica*, is higher than in its parents *C. eugenioides* and *C. canephora* (Lopes *et al*., 2013).

Moreover, the copy number of TEs is frequently higher in polyploids than in their related diploid species. This is the case of the *Tnt1* retrotransposon in the allotetraploid tobacco (Petit *et al*., 2010) and the *Au* SINE in wheat polyploids (Ben-David *et al*., 2013). Moreover, it has been shown that some TEs proliferate after polyploidization. For example, the *Tekay* families proliferate after *Orobanche gracilis* polyploidization (Piednoël *et al*., 2013) and the *Stowaway*-like MITEs transpose following allopolyploidization events in wheat and *Brassica* species (Sarilar *et al*., 2011; Yaakov and Kashkush, 2012). Moreover, a massive TE derepression was observed after hybridization of three diploid *Helianthus* species (Kawakami *et al*., 2010). However, polyploidization is not always be accompanied by an increase of TEs. For example, no significant increase in the copy number of *Au* SINE was found in newly formed allopolyploid *Triticum aestivum* (wheat) lines (Ben-David *et al*., 2013), in the allopolyploid *Spartina anglica* (Parisod *et al*., 2009) or in re-synthesized *Brassica napus* allotetraploids (Sarilar *et al*., 2013). There may also be differences in activation among different TE families within a single genome, as has been seen after *Aegilops* allotetraploidy where some gypsy-like retrotransposons proliferate whereas other remained quiescent (Senerchia *et al*., 2014). However, the effect on a particular TE family may also depend on the parental species, as has been shown for the *Sabine* retrotransposon that proliferates in particular wheat polyploids and is massively eliminated in others (Senerchia *et al*., 2014). It seems, therefore, that the response to polyploidization varies among genomes and TE families. Most TEs present in genomes are defective copies no longer able to transpose, and therefore old TE families will probably not respond to an activation stimulus such as the one potentially linked to polyploidization. In addition, different TE families can be regulated differently within a single genome, depending, among others, on the type of TEs, their copy number, chromosome localization and promoter sequences. For example, TEs mainly controlled by promoter methylation may be more prone to reactivation by a polyploidization-related de-methylation

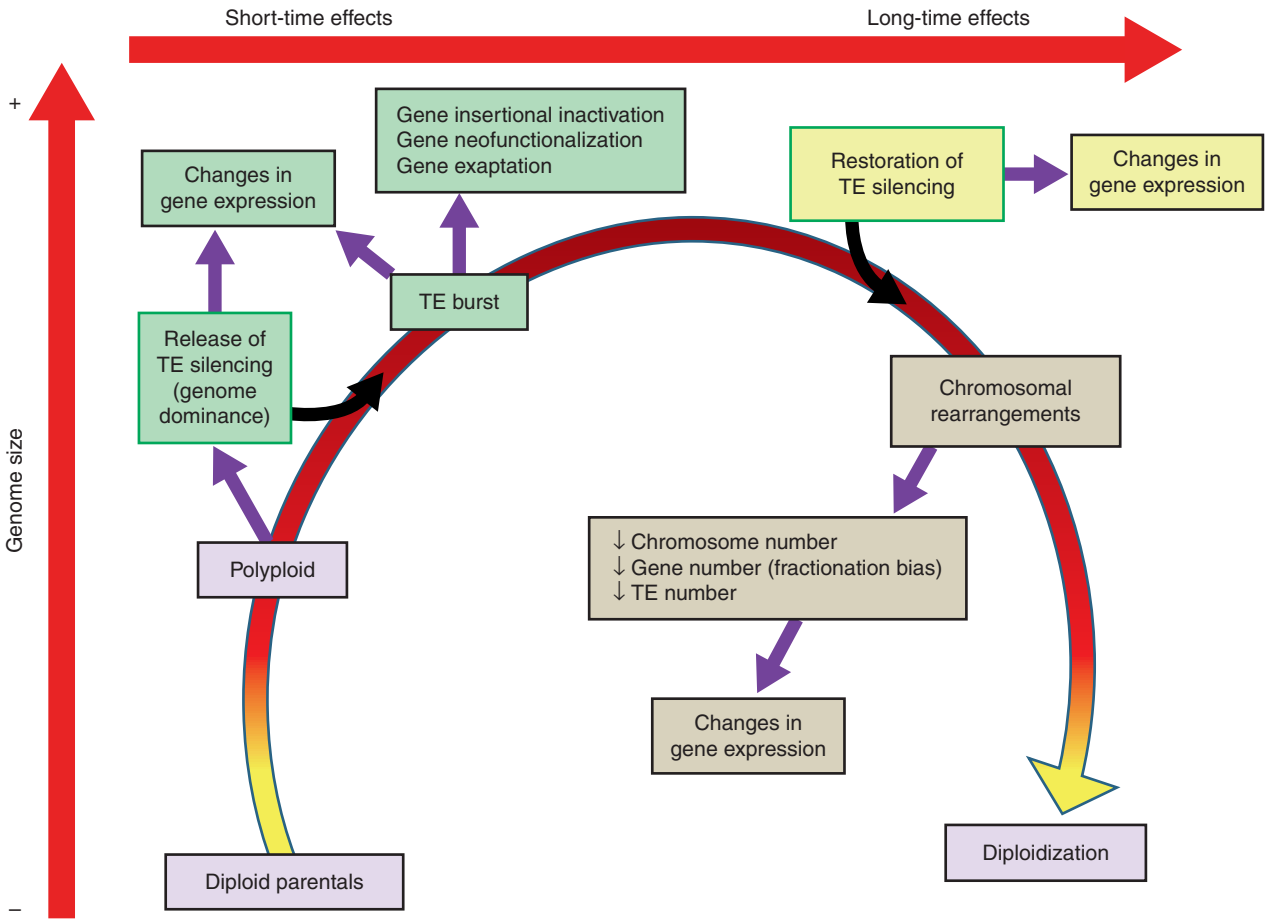

FIG. 1. The close connections of polyploidization and TE dynamics. Polyploidization is accompanied by a release of TE silencing, which may be different for parentally or maternally inherited TEs. This release, in addition to activating TE mobilization, may induce changes in the regulation of genes located near TEs. The burst of TEs will produce new TE insertions that can modify the coding capacity of genes or their regulation. The release of TE silencing is reversed after few generations, and TE sequences again become the target of epigenetic silencing mechanisms. The silencing of TEs, including the new insertions resulting from the TE burst, will influence the expression of genes located nearby. This may result in changes of gene expression with respect to the early phases of polyploidy but also with respect to the diploid parents. TEs will also be important for the diploidization of the polyploid genome, as the different TE copies may provide sequence homology for recombination, leading to deletions and chromosome rearrangements.

than those requiring a more specific transcriptional activation. Also, on the other hand, different genomes differ in their TE control efficiency due, among others, to differences in siRNA populations and methylation status. Finally, a certain degree of stochasticity in TE activation may also contribute to the differences observed on the consequences of polyploidization on TE populations.

An increasing amount of data indeed indicates that polyploidization may induce epigenetic changes, such as modifying DNA methylation at TEs (Parisod and Senerchia, 2012; Zhang *et al*., 2015). For example, a widespread, DNA methylation variation in TEs was observed in autotetraploid rice accompanied by changes of 24 nucleotide siRNA abundance (Zhang *et al*., 2015). The demethylation of TEs was observed in newly formed allopolyploids (Parisod *et al*., 2009; Yaakov and Kashkush, 2011) and, after a few generations, survivors gradually returned to their original TE methylation state (Zhang *et al*., 2015). This seems to be a general trend. For example, many *Veju* TRIM sequences were hypomethylated in the first generation of the newly formed wheat allohexaploid, returning to a methylation state similar to the original in the subsequent generations (Kraitshtein *et al*., 2010). The observed methylation alterations, either hyper- or hypomethylation, depend on the TE family and are reproducible (Yaakov and Kashkush, 2012). For example, in rice and wheat, while retrotransposons showed mainly hypomethylation in the first generation of newly formed allopolyploids, class II DNA elements were hypermethylated (Yaakov and Kashkush, 2011; Zhang *et al*., 2015).

As a summary, polyploidization may lead to the transient activation of some TEs. The extent of this phenomenon depends on the type of event (auto- or allopoplyploidization) and on the nature of the genome, and will affect particular families of TEs that may be more prone to activation. In addition, the relaxed selection in polyploids, due to the increase of gene copies, may also allow for a higher retention of TE insertions, which will also contribute to an increase in TE copy number.

TRANSPOSABLE ELEMENT-MEDIATED GENE REGULATION IN POLYPLOIDS

As already explained, the epigenetic silencing of TEs can reduce the expression of adjacent genes and therefore changes in TE silencing can generate heritable variations in gene expression. The important changes in TE silencing associated with polyploidization will therefore induce changes in gene expression. Genes located near reactivated TEs after polyploidization could then be under the influence of active TEs instead of silenced ones, which can modify their chromatin status and transcriptional activity. Moreover, the reactivated TEs can generate new copies of themselves (accompanied in some cases by deletions from their original locations). If these altered TE locations are close to genes, this may produce changes in their transcriptional activities. Even if the decreases in TE silencing control are transitory, they may participate in reorganizing the functional genome after polyploidization, as shown in newly synthesized wheat polyploids (Kashkush *et al*., 2003).

Interestingly, the expression of duplicated genes in the progeny of allopolyploids usually shows differences depending on their paternal or maternal origin, a phenomenon called genome dominance. This is reflected, for example, in a differential sub-genome control of morphological traits (Feldman *et al*., 2012). Genome dominance is a characteristic more usual in ancient polyploids rather than in new synthetic ones, indicating that it takes some generations to be established (Woodhouse *et al*., 2014). In addition, although most ancient polyploids, which probably are allopolyploids, show genome dominance, some, which probably are autopolyploids, do not (Woodhouse *et al*., 2014). Different mechanisms have been proposed for such inter-genomic suppression of gene activity, including chromatin modifications and the differential suppression of genes near TEs (Feldman *et al*., 2012).

The process of suppression of the genes near TEs by induced methylation in a polyploid genome is generally higher in one of the two parental genomes. This may be due to the fact that only the female parent contributes to cytoplasmic TE-repressing factors (e.g. siRNAs) and, as a consequence, TEs in the maternal genome are expected to have a higher repression, at least in the very early phases of polyploidy (Zhang *et al*., 2015). Another possibility is that the two parental genomes have different TE repression efficiencies; for example, if one of the parental genomes has a greater TE content and/or if the TEs are closer to the genes, it will become the recessive sub-genome in the stabilized allotetraploid (Garsmeur *et al*., 2014). In *B.rapa*, transposon-derived 24 nucleotide RNAs target the upstream region of genes preferentially located in the recessive sub-genome (Woodhouse *et al*., 2014). This has led to the hypothesis that the parental genome with the lowest TE content may become the dominant genome in the polyploid (Woodhouse *et al*., 2014). Whatever the initial reason is, this difference initiates a cascade of processes based on the fact that a gene that is less transcribed is a gene that can be mutated or altered more easily without phenotypic consequences. These effects will be more important the more divergent the parental species are. Thus, whereas in an autopolyploid no differences are expected, in an allopolyploid from species of different genera this difference will be very important (Cheng *et al*., 2016).

ROLE OF TRANSPOSABLE ELEMENTS IN DIPLOIDIZATION

Although all plant genomes present signatures of one or more polyploidy events during their evolution, they do not exhibit chromosome numbers or genome sizes proportional to such duplication processes, indicating that polyploidy is, at least in part, reversible by a process called diploidization (Soltis *et al*., 2015). The mechanisms governing diploidization are largely unknown, although TEs are likely to be pivotal players through transposition but also by inducing recombination and various types of chromosomal rearrangements involving reductions in chromosome number and large-scale loss of repetitive sequences and duplicated genes. It is known that TEs may have played a major role during diploidization in *Nicotiana* (Lim *et al*., 2007) and maize (Bruggmann *et al*., 2006). Although intra-element recombination only produces relatively small deletions, a high number of these events may represent a major process in genome restructuring during diploidization (Vicient *et al*., 1999).

During diploidization, usually one of the parental genomes experiences greater sequence loss than the other, as was found in *Nicotiana* (Renny-Byfield *et al*., 2011), arabidopsis (Freeling and Thomas, 2006) and maize (Woodhouse *et al*., 2010). This phenomenon is called fractionation bias and can be explained, at least in part, by the bias in TE insertions when comparing sub-genomes. As already explained, it has been proposed that a different TE content between the two parental genomes may lead to the dominance, and the preferential gene retention, of the genome with the lowest TE load (Woodhouse *et al*., 2014).

The TE-associated epigenetic changes and DNA recombination events during diploidization may produce a high number of new alleles that could allow for adaptive evolution and, following a chaotic tetraploid period, some of the duplicated genes may suffer sub-functionalization or neofunctionalization. For example, the insertion of a non-autonomous Helitron element into the promoter of the self-incompatibility male-determining gene *BnSP11-1* had led to its loss of function in *B. napus* (*B. rapa* × *B. oleracea*) and an alteration in its mating system from self-incompatible to self-compatible, which had a great impact on the reproduction of the species (Gao *et al*., 2016). Moreover, different recombination events involving TEs have driven the deletion of the *hardness* locus, which controls grain hardness, in different sub-genomes of various polyploid wheat species (Chantret *et al*., 2005).

CONCLUDING REMARKS

The growing wealth of knowledge on whole-genome sequences for plant species and varieties is highlighting the major role played by TEs in the evolution of wild and domesticated plants. The impact of TEs in plant genomes includes direct effects on genes, by providing them with new coding or regulatory sequences, a more indirect effect on the epigenetic status of the chromatin close to genes, but also more subtle effects by imposing different evolutionary constraints on different chromosomal regions. Because of this, TEs are considered together with polyploidy as the major drivers of plant gene evolution. However, these are not two independent sources of variability,

as polyploidy can induce TE activity and TEs explain some of the new variability associated with polyploidy. In addition, genomes tend to diploidize after polyploidization. The extent to which TEs contribute to diploidization and fractionation bias remains an open question, but it is clear that polyploid speciation is a promising model to investigate the multiple factors controlling TE dynamics, and that understanding TE activity will shed light on the dynamics of polyploid genomes.

ACKNOWLEDGEMENTS

We apologize to those authors whose primary works could not be cited owing to space limitations. Work done at the laboratoy of J.M.C. and C.M.V. was supported by by the Spanish Ministerio de Economía y Competitividad [grants AGL2013-43244-R to J.M.C., AGL2016-78992-R to J.M.C. and C.M.V., and SEV-2015-0533 to J.M.C. and C.M.V.].

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