2   INVITED REVIEW

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4   **Impact of transposable elements on polyploid plant genomes**

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12   **Running title**

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1 **ABSTRACT**

2 Background

3 The growing wealth of knowledge on whole plant genome sequences is highlighting the key

4 role of transposable elements (TEs) in plant evolution, as a driver of drastic changes in

5 genome size and as a source of an important number of new coding and regulatory sequences.

6 Together with polyploidization events, TEs should thus be considered the major players of

7 evolution of plants.

8 Scope

9 This review outlines the major mechanisms by which TEs impact plant genome evolution and

10 how polyploidy events can affect these impacts and vice versa. These include direct effects on

11 genes, by providing them with new coding or regulatory sequences, an effect on the

12 epigenetic status of the chromatin close to genes, and more subtle effects by imposing diverse

13 evolutionary constraints to different chromosomal regions. These effects are particularly

14 relevant after polyploidization events. Polyploidization often induce bursts of transposition

15 probably due to a relaxation in their epigenetic control, and, at short term, this can increase

16 the rate of gene mutations and changes in gene regulation due to the insertion of TEs next to

17 or into genes. At longer times, TE bursts may induce global changes in genome structure due

18 to inter-element recombination including losses of large genome regions and chromosomal

19 rearrangements that reduce the genome size and the chromosome number as part of a process

20 called diploidization.

21 Conclusions

22 TEs play an essential role in genome and gene evolution, in particular after polyploidization

23 events. Polyploidization can induce TE activity that may explain part of the new phenotypes

24 observed. TEs may also play a role in the diploidization that follows polyploidization events.

25 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 biass; neofunctionalization; chromosomal rearrangement.

1 **INTRODUCTION**

2 Transposable elements (TEs) are mobile genetic elements present in virtually all genomes.

3 Among all different types of TEs, Long Terminal Repeat (LTR) retrotransposons and

4 Miniature Inverted Transposable Elements (MITEs) are in general the most abundant TEs in

5 plant genomes (Casacuberta and Santiago, 2003). The bigger size of LTR retrotransposons,

6 makes them, by far, the most prevalent in all sequenced plant genomes comprising between

7 2,5% in *Utricularia gibba* (Ibarra-Laclette *et al*., 2013) and 90% of the genome in *Fritillaria*

8 species (Ambrožová *et al*., 2011).

9 Together with polyploidization, TE amplification is considered the main mechanism to plant

10 genome increase and, more generally, for plant genome evolution (Wendel *et al*., 2016;

11 Casacuberta *et al*., 2016). In fact, as discussed below, polyploidization and TE amplification

12 are not two completely independent mechanisms. On the contrary these two phenomena

13 greatly influence one another reinforcing their potential to drive plant genome evolution.

14 The role of TEs in the evolution of plant genes and genomes is not only a key for long term

15 plant evolution in the wild, but has also been of paramount importance for the recent crop

16 domestication and breeding (Olsen and Wendel, 2013). In this article we will review the links

17 between polyploidization and TEs dynamics, as well as the role that TEs have played in the

18 evolution of plant genomes both in the wild and during crop domestication and breeding.

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20 **LTR RETROTRANSPOSONS AND THE EXPANSION AND CONTRACTION OF**

21 **PLANT GENOMES**

22 Although all plant genomes contain an important fraction of TEs, with LTR retrotransposons

23 being the most abundant, the prevalence of particular families is highly variable among

24 species and even among varieties of the same species. In many cases a limited number of TE

25 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 approximately 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 as, for example the *Grande* LTR retrotransposon (Gómez-Orte *et al*., 2013) which shows 1450 copies in the maize inbred line B73 whereas 3500 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 less than 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 silencing weakening. 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 like 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 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), or *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 in the TE promoters suggests a transcriptional activation mechanism, but a decrease in silencing associated to 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 it 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, that 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). Transposable elements can amplify and redistribute transcription factor binding sites (TFBS) 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. TEs 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 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 them stress-inducibility. 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). 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 a siRNA that regulates a gene encoding a 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 (Hénaff *et al*., 2015; Ewing, 2015) allows analysing 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 evaluating more globally to what extent TEs are involved in crop domestication and breeding traits.

IMPACT OF TRANSPOSONS IN 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 the *Rosales* and *Brassicales* divergence (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 of *Gypsy*-like retrotransposons, whereas most *Copia*-like retrotransposons and most DNA TEs seem to preferentially insert in euchromatin (Contreras *et al*., 2015). Second, selection tends to eliminate deleterious insertions, concentrating TE insertions in gene-poor regions such as the heterochromatic repetitive regions. Third, 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).

1   The epigenetic silencing of the TEs accumulating in the heterochromatin reinforces the

2   heterochromatic state of these regions (Bierhoff *et al*., 2014) which is essential for the normal

3   functioning of these important chromosomal regions (Dernburg *et al*., 1996). In addition, the

4   concentration of TEs in pericentromeric regions may help centromeres to resist microtubule

5   tension during mitosis and meiosis (Freeling *et al*., 2015) and retrotransposon insertion into

6   the centromeres contributes to the centromere rapid evolution (Han *et al*., 2016), which is

7   important for the evolution of the species. On the other hand, recent results show that TEs in

8   pericentromeric regions frequently contribute replication origins somehow compensating the

9   scarcity of genes which are the preferred source of origins of replication (Vergara *et al*.,

10   unpubl. res.).

11   The high concentration of TEs near centromeres may also have other important consequences.

12   The size of the heterochromatic pericentromeric regions and the concentration of TEs in them

13   vary among plants. Whereas Arabidopsis has relatively small pericentromeric TE-rich

14   regions, the closely related *Arabis alpina* has a bigger genome, with a higher content of

15   retrotransposon elements which seem to have expanded its pericentromeric regions (Willing

16   *et al*., 2015). Therefore, ancestral genes that have remained in gene-rich regions in

17   Arabidopsis may have been incorporated into gene-poor pericentromeric regions in *A. alpina*,

18   and this may lead to different consequences. The recombination is usually strongly reduced in

19   pericentromeric heterochromatic regions and, in consequence, the evolution of these pairs of

20   orthologous genes may be different in the two species. The bigger pericentromeric region of

21   *A. alpina* correlates with a more important reduction of meiotic recombination in

22   pericentromeric regions as compared with Arabidopsis (Willing *et al*., 2015), which may

23   exacerbate this consequence. Long pericentromeric regions with a high concentration of TEs

24   may therefore constitute particular chromosomal compartments with specific evolutionary

25   constraints which may be well suited for the evolution of particular types of genes.

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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 evolving 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 in these regions many of its species specific genes (in preparation).

THE TIGHT LINKS BETWEEN POLYPLOIDY AND TRANSPOSABLE ELEMENTS 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 mechanisms (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 than 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. But on the other hand, gene duplication allows genomes to cope with a higher TE activity, as 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 it 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.*, 2013).

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 to this process (Springer *et al*., 2016). These changes are limited to the first generations after polyploidy which will be followed by the re-establishing of TE silencing. However, the consequences of 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-establish 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 parentals *Arabidopsis thaliana* and *Arabidopsis arenosa* (Madlung *et al*., 2005), the *Wis*2-1a retrotransposon showed high transcriptional activity in newly synthesized wheat amphiploids compared to 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

1   *et al*., 2010) and the *Au* SINE in wheat polyploids (Ben-David *et al*., 2013). Moreover, it has

2   been shown that some TEs proliferate after polyploidization. For example, the *Tekay* families

3   proliferate after *Orobanche gracilis* polyploidization (Piednoël *et al*., 2013) and the

4   *Stowaway*-like MITEs transpose following allopolyploidization events in wheat and *Brassica*

5   species (Sarilar *et al*., 2011; Yaakov and Kashkush, 2012). Moreover, a massive TE

6   derepression was observed after hybridization of three diploid *Helianthus* species (Kawakami

7   *et al*., 2010). However, polyploidization is not always accompanied by an increase of TEs.

8   For example, no significant increase in the copy number of *Au* SINE was found in newly

9   formed allopolyploid *Triticum aestivum* (wheat) lines (Ben-David *et al*., 2013), in the

10   allopolyploid *Spartina anglica* (Parisod *et al*., 2009) or in re-synthesized *Brassica napus*

11   allotetraploids (Sarilar *et al*., 2013). There may also be differences in activation among

12   different TE families within a single genome, as it has been seen after *Aegilops* allotetraploidy

13   where some gypsy-like retrotransposons proliferate whereas other remained quiescent

14   (Senerchia *et al*., 2014). But the effect on a particular TE family may also depend on the

15   parental species, as it has been shown for the *Sabine* retrotransposon that proliferates in

16   particular wheat polyploids and is massively eliminated in others (Senerchia *et al*., 2014). It

17   seems therefore that the response to polyploidization varies among genomes and TE families.

18   Most TEs present in genomes are defective copies no longer able to transpose, and therefore

19   old TE families will probably not respond to an activation stimulus such as the one potentially

20   linked to polyploidization. In addition, different TE families can be regulated differently

21   within a single genome depending, among others, on the type of TEs, their copy number,

22   chromosome localization and promoter sequences. For example, TEs mainly controlled by

23   promoter methylation may be more prone to reactivation by a polyploidization-related de-

24   methylation, than those requiring a more specific transcriptional activation. And, on the other

25   hand, different genomes differ in their TE control efficiency due, among others, to differences

1 in siRNA populations and methylation status. Finally, a certain degree of stochasticity in TE

2 activation may also contribute to the differences observed on the consequences of

3 polyploidization on TE populations.

4 An increasing amount of data indeed indicates that polyploidization may induce epigenetic

5 changes, such as modifying DNA methylation at TEs (Parisod and Senerchia, 2012; Zhang *et*

6 *al*., 2015). For example, a widespread, DNA methylation variation in TEs was observed in

7 autotetraploid rice accompanied by changes of 24-nt siRNA abundance (Zhang *et al*., 2015).

8 The demethylation of TEs was observed in newly formed allopolyploids (Yaakov and

9 Kashkush, 2011; Parisod *et al*., 2009) and, after few generations, survivors gradually returned

10 to their original TE methylation state (Zhang *et al*., 2015). This seems to be a general trend.

11 For example, many *Veju* TRIM sequences were hypomethylated in the first generation of the

12 newly formed wheat allohexaploid returning to a methylation state similar to the original in

13 the subsequent generations (Kraitshtein *et al*., 2010). The observed methylation alterations,

14 either hyper- or hypomethylation, depend on the TE family and are reproducible (Yaakov and

15 Kashkush, 2012). For example, in rice and wheat while retrotransposons showed mainly

16 hypomethylation in the first generation of newly formed allopolyploids, class II DNA

17 elements were hypermethylated (Zhang *et al*., 2015; Yaakov and Kashkush, 2011).

18 As a summary, polyploidization may lead to the transient activation of some TEs. The extent

19 of this phenomenon depends on the type of event (auto or allo-poplyploidization) and on the

20 nature of the genome, and will affect particular families of TEs that may be more prone to

21 activation. In addition, the relaxed selection in polyploids, due to the increase of gene copies,

22 may also allow for a higher TE insertion retention, which will also contribute to an increase of

23 TE copy number.

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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 to polyploidization will therefore induce changes in gene expression. Genes located near reactivated TEs after polyploidization could be then 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 subgenome control of the 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 allopoplyploids, show genome dominance, some, which probably are autopolyploids, do not (Woodhouse *et al*., 2014). Different mechanisms have been proposed for such intergenomic 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 (for example,

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 subgenome in the stabilized allotetraploid (Garsmeur *et al*., 2014). In *B.rapa*, transposon-derived 24-nt RNAs target the upstream region of genes preferentially located in the recessive subgenome (Woodhouse *et al*., 2014). This has lead 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 as more divergent the parental species are. Thus, whereas in an autopolyploid no differences are expected, in an allopolyploid from species of different genus 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 suppose 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 comparing

subgenomes. 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 a 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

subfunctionalization 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 lead to its loss of function in *B. napus* (*B. rapa* x *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 has driven the deletion of the *hardness* locus, which controls grain hardness, in

different subgenomes 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

1 new coding or regulatory sequences, a more indirect effect on the epigenetic status of the

2 chromatin close to genes, but also more subtle effects by imposing different evolutionary

3 constraints to different chromosomal regions. Because of this, TEs are considered together

4 with polyploidy as the major drivers of plant gene evolution. But these are not two

5 independent sources of variability, as polyploidy can induce TE activity and TEs explain

6 some of the new variability associated to polyploidy. In addition, genomes tend to diploidize

7 after polyploidization. The extent to which TEs contribute to diploidization and fractionation

8 bias remains an open question but it is clear that polyploid speciation is a promising model to

9 investigate the multiple factors controlling TE dynamics, and that understanding TE activity

10 will bring light on the dynamics of polyploid genomes.

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1   **FIGURE LEGENDS**
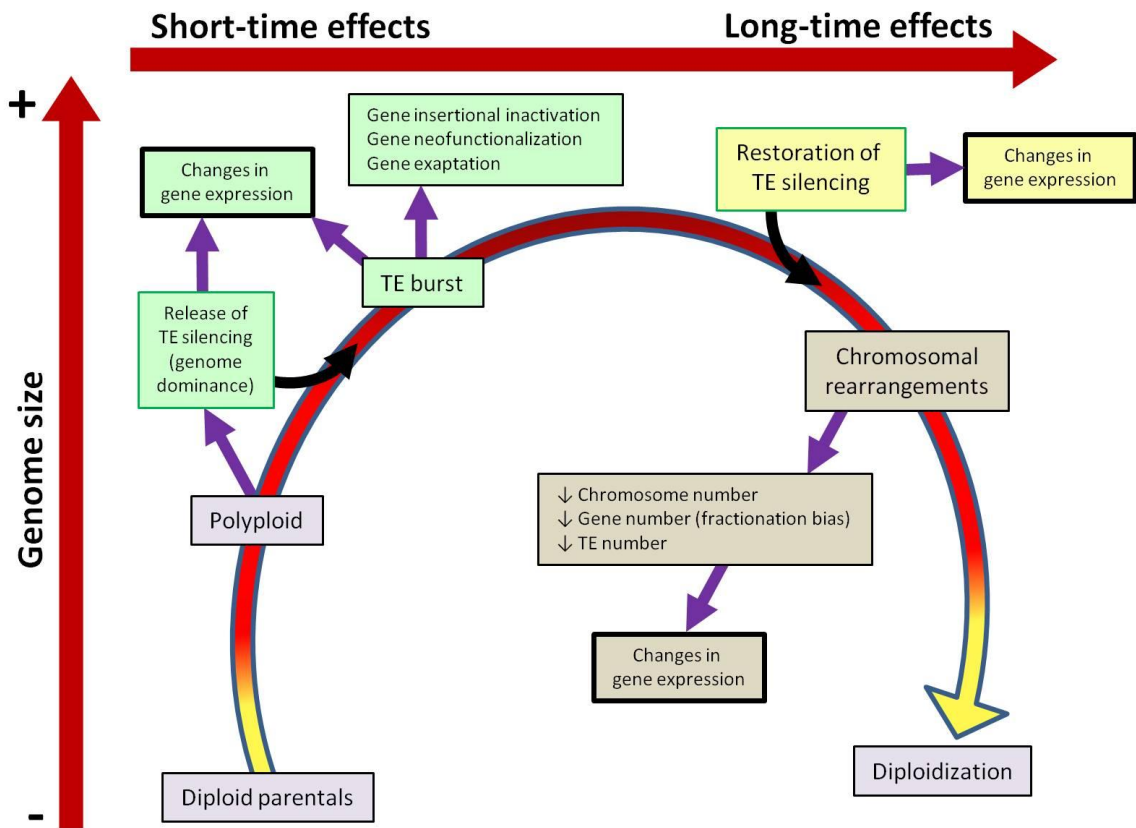
2

3   **Figure 1. The close connections of polyploidization and TE dynamics.** Polyploidization is

4   accompanied by a release of TE silencing, which may be different for parental or maternal

5   inherited TEs. This release, in addition of activating TE mobilization, may induce changes in

6   the regulation of genes located near TEs. The burst of TEs will produce new TE insertions

7   that can modify coding capacity of genes or their regulation. The release of TE silencing is

8   reverted after few generations and TE sequences become again the target of epigenetic

9   silencing mechanisms. The silencing of TEs, including the new insertions resulting from the

10   TE burst, will influence the expression of genes located nearby. This may result in changes of

11   gene expression with respect to the early phases of polyploidy but also with respect to the

12   diploid parentals. TEs will also be important for the diploidization of the polyploid genome,

13   as the different TE copies may provide sequence homology for recombination leading to

14   deletions and chromosome rearrangements.

1 Table 1.- Examples of studies reporting reorganization of- or expression changes related to
2 the transposable elements after polyploidy in plants.
3

Species	Auto/Allo	TE	TE-type	Effect	Reference
Synthetic (short-term reorganization)					
Aegilops charonensis x *Triticum monococcum*	Allo	Diverse	Diverse	Methylation changes	Shaked *et al.*, 2001
Aegilops sharonensis x *Triticum monococcum*	Allo	*Wis*2-1A	LTR-retrotransposon	Transcriptional activation with impact on adjacent genes	Kashkush *et al.*, 2002, 2003
Arabidopsis thaliana x *Arabidopsis arenosa*	Allo	*Sunfish*	En-Spm-like transposon	Transcriptional activation & epigenetic changes	Maldung *et al.* 2005
Arabidopsis thaliana x *Arabidopsis arenosa*	Allo	Diverse	Diverse	Methylation changes and variation in siRNAs in the first generations	Ha *et al.*, 2009
Arabidopsis thaliana x *Arabidopsis arenosa*	Allo	Diverse	Diverse	Differential repression of TEs by RNAi in the two subgenomes	Chen *et al.*, 2008
Arabidopsis thaliana x *Arabidopsis lyrata*	Allo	*CAC, Ac-III*	DNA transposons	No evidence of increased mobility or loss of elements from parental origin & methylation changes	Beaulieu *et al.*, 2009
Arabidopsis thaliana x *Cardaminopsis arenosa*	Allo	MITE	MITE	Changes in DNA methylation	Madlung *et al.*, 2002
Brassica carinata x *Brassica rapa*	Allo	Diverse	Diverse	Methylation changes	Xu *et al.*, 2012
Brassica rapa & *Brassica oleracea*	Allo	Diverse	Diverse	Mobilization in the first generations and reduced in subsequent generations.	An *et al.*, 2014
Brassica rapa x *Brassica oleracea*	Allo	Diverse	Diverse	Methylation changes	Xu *et al.*, 2009
Brassica rapa x *Brassica oleracea*	Allo	Diverse	Diverse	Changes in TE-derives miRNAs	Fu *et al.*, 2016
Nicotiana sylvestris x *Nicotiana tometosiformis*	Allo	*Tnt1*	LTR-retrotransposon	Increase in mobility & loss of elements from parental origin	Petit *et al.*, 2010
Oryza sativa	Auto	Diverse	Diverse	Hypermethylation that in some cases affects the expression of neighboring 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 x *Spartina maritima*	Allo	*Ins2, Cassandra, Wis*-like	hAT DNA transposon, TRIM, LTR retrotransposon	Loss of elements specially from maternal origin & epigenetic changes	Parisod *et al.*, 2009
Triticum turgidum x *Aegilops tauschii*	Allo	*Au*	SINE	Mobilization, loss & epigenetic changes (hypermethylation after few generations)	Ben-David *et al.*, 2013
Triticum turgidum x *Aegilops tauschii*	Allo	*Minos*	MITE	Mobilization (but no burst of copy number) & epigenetic changes (hypermethylation after few generations)	Yaakov and Kashkush, 2012
Triticum turgidum x *Aegilops tauschii*	Allo	*Veju*	TRIM	Hypomethylated in the first S1 generation and hypermethylated in the S4 generation	Kraitshtein *et al.*, 2010
Triticum turgidum x *Aegilops tauschii*	Allo	Diverse	Diverse	No mobilization	Mestiri *et al.*, 2010
Triticum turgidum x *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 x *Aegilops tauschii*	Allo	*Veju, Wis*2-1A	TRIM, LTR-retrotransposon	siRNA were reduced and CpG methylation decreased	Kenan-Eichler et al., 2011
Natural (long-term reorganization)					
Aegilops crassa, Aegilops cylindrical, Aegilops geniculata & *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	Recent activation of the element, possibly because of the hybridization followed by allopolyploidization	Gowda *et al.*, 2011
Biscutella laevigata	Auto	Diverse	LTR-retrotransposons	Analyses of the dynamics of LTR-RTs 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 TEs in a subgenome 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 subgenomes	Cheng *et al.*, 2016
Brassica rapa x *Brassica oleracea*		*BraSto*	MITE	Moderately amplification	Sarilar *et al.*, 2011
Brassica rapa x *Brassica oleracea*	Allo	*Athila*-like, *BraSto*, *Bot*1	LTR-Retrotransposon MITE CACTA	No massive structural changes	Sarilar *et al.*, 2013
Brassica spp.	Allo	Diverse	Diverse	Different amplification of TEs depending on the genome	Liu *et al.*, 2014
Brassica spp.	Allo	Diverse	Diverse	smRNA-mediated silencing of transposons near genes causes position-effect down-regulation.	Woodhouse *et al.*, 2014
Brassica spp.	Allo	*Bot*1	CACTA	Differential amplification in the two subgenomes	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 subgenomes	Yu *et al.*, 2011
Coffea canephora x *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 subgenomes	Innes *et al*, 2008
Glycine max & *Phaseolus vulgaris*	-	Diverse	Diverse	TE associated epigenetic gene regulation	Kim *et al.*, 2015
Gossypium arboretum x *Gossypium raimondii*	Allo	Diverse	Diverse	Loss of sequences mostly from maternal origin	Grover *et al.*, 2007
Gossypium hirsutum	Allo	*Gorge*3, *copia*, Diverse	LTR retrotransposons, 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 subgenomes	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 in 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 & *Helianthus paradoxus*	Allo	Diverse	LTR retrotransposons	Increase in copy number	Kawakami *et al.*, 2010
Helianthus anomalus, Helianthus deserticola & *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 & loss of sequences mostly from paternal origin	Parisod *et al.*, 2012
Nicotiana sylvestris x *Nicotiana tomentosiformis*	Allo	*Tnt*1, *Tnt*2, *Tto*1	LTR-Retrotransposon	Loss of sequences mostly from paternal origin & new insertions	Petit *et al.*, 2010
Nicotiana tabacum	Allo	Diverse	Diverse	Loss of sequences mostly from paternal origin	Renny-Byfield *et al.*, 2011
Orobanchaceae gracilis	Auto	Diverse	LTR-retrotransposons	Increase in copy number & loss of some TE families	Piednoël *et al.*, 2013
Orobanche austrohispanica,	Allo	Diverse	LTR retrotransposons	Increase in copy number	Piednoël *et al.*, 2015

Species	Type	TE name	TE type	Description	Reference
Orobanche densiflora, and Orobanche gracilis					
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 x *Oryza officinalis*	Allo	Diverse	Diverse	Loss of sequences mostly from paternal origin & 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 to the parental ones	Baumel *et al.*, 2002
Thinopyrum intermedium	Allo	Diverse	LTR-retrotransposon	Burst of Ty3/gypsy centromeric retrotransposon in 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 subgenomes	Sehgal *et al.*, 2012
Triticum aestivum	Allo	Fatima	LTR retrotransposon	Differential amplification in the subgenomes	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 subgenomes	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.*, 2013a
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.*, 2013b
Triticum turgidum x *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

1