On the Role of Transposable Elements in the Regulation of Gene Expression and Subgenomic Interactions in Crop Genomes

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ABSTRACT

Transposable elements (TEs) represent a major and variable portion of plant genomes, and recent progress in genetics and genomics has highlighted the importance of different TE species as a useful genetic tool in crop breeding. TEs can cause changes in the pattern of gene expression, and regulate gene function by various means such as cis- or trans-regulation of nearby genes through insertion at promoter, intron, exon and downstream regions, and transproduction of short interfering RNAs (siRNAs) via two RNA-directed DNA methylation (RdDM) pathways. siRNAs generated through different RdDM pathways differ in length and have variable effects on TEs. For instance, noncoding siRNAs of 20–60 nt produced by RNA polymerase IV (dicer-independent) and 21/22 nt by Pol II (dicer-dependent) have only minor effects on TEs compared with 24 nt siRNAs produced by Pol IV (dicer-dependent pathways). Following whole-genome duplication (WGD) events after polyploidization in allopolyploids, TEs from either parent are able to induce siRNAs to regulate the complex polyploid genome. Those designated as ‘controllers’ usually reside in the dominant parent and affect the TEs of the recessive parent. Subgenomic cross-talk thus appears to contribute to epigenetic regulation as well as reshuffling or restructuring of subgenomes and creation of novel patterns of gene expression and variation in local or global copy number. In this review, we focus on recent progress in unraveling the role of TEs in gene expression regulation via TE-derived siRNAs in the context of polyploid plant evolution and environmental stress, and explore how ancient WGD and recent polyploidy affected the evolution of TE-induced epigenetic mechanisms.

Abbreviations: AGO2/4/6: AGRONAUT 2/4/6; Al: aluminum; BF: biased fractionation; BnSp11-1: Brassica napus S-locus protein 11-1; bp: base pair; BrFT2: Brassica rapa flowering locus T2; Chr: Chromosome; CLSY1: Classy 1; CMT3: Chromomethylase 3; CYP78A9: Cytochromes 78 (a member of Cytochromes P450) located on chromosome A09 of Brassica napus; DCL1/2/3/4: DICER-LIKE 1/2/3/4; DDM1: ATP-dependent DNA helicase 1; DP: duplicated; DRM1/2: domain-rearranged methyltransferase 1/2; ds-siRNA: Distinct class of siRNA; dsRNA: double stranded RNA; En/Spm: enhancer/suppressor; epi-siRNA: epigenetically-activated siRNA; FD: flowering locus D; FLCL: flowering locus C; FT: flowering locus T; FWA: flowering wageningen; gDNA: genomic DNA; gMSALT3: glycine max salt tolerance-associated gene on chromosome 3; GP: Golden and Pallas; gc-siRNA: gene-specific siRNA; HvAACT1: Hordeum vulgare Al-activated chalcone synthase transporter 1; JreCHSsubA: Juglans regia Chalcone synthase subgenome A; JreCHSsubB: Juglans regia Chalcone synthase subgenome B; JreSRG1: Juglans regia senescence-related gene 1; kb: kilo base; LF: least fractionation; LINE: long interspersed nuclear element; LTR-RT: long terminal repeat retro-transposon; MET1: Methyltransferase 1; MF: most fractionation; MF1: most fractionation 1; MF2: most fractionation 2; miRNA: MicroRNA; MITE: miniature inverted-repeat transposable elements; MLKS2: maize LINE KASH AlSINE-like; MRL: multi-retrotransposon-like; MYB: myeloblastosis, proto-oncogene protein; MYS: millions years; NAT: natural antisense transcripts; nat-siRNA: natural antisense siRNA; ncRNA: non-coding RNA; NLR: nucleotide-binding leucine-rich repeat; nt: nucleotide; ONAC045: NAM, ATAF, and CUC 045, a transcription factor family; ORF: open reading frame; OsCDPK7: Oryza sativa calcium-

KEYWORDS

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1. Introduction

Based on their sequence organization, preferences for genome insertion and sequence similarities, the various classes of transposons appear to share an evolutionary history with various parasitic viruses (Krupovic and Koonin, 2015). Their ability to infect and proliferate within eukaryotic genomes appears to be responsible not only for the large variation in genome size within related taxa but in many organisms, especially plants, has also contributed to ongoing evolutionary success (Wells and Feschotte, 2020). In plants, TEs facilitate an arsenal of mechanisms by which genomes may rapidly acquire new adaptations in response to environmental challenges. Although intrinsically mutagenic, mechanisms such as RNA interference, DNA methylation and histone modifications have either evolved or been co-opted to suppress the damaging effect of unrestrained transposition and genome expansion. In combination these two genomic innovations (transposition and genome expansion) have over the past × million years provided an extraordinary range of mechanisms for the subtle and responsive regulation of gene transcription and associated feedback systems. Given the ability of TEs to generate widespread, rapid and selectively responsive changes to plant genomes, understanding these processes in crop plants is likely to represent a key step in crop improvement in the face of challenges like climate change.

TEs were first discovered by Nobel laureate Barbara McClintock (McClintock, 1965) following her observations of genetic instability in maize. However, the term transposon was not coined until nine years later by (Hedges and Jacob, 1974). A TE is a DNA sequence that can incorporate features to allow its mobilization within a genome; they are thus also referred to as mobile elements or “jumping genes”. Based on the mechanism of TE transposition, TEs are grouped into two classes, namely class I retrotransposons (RTs) and class II DNA transposons (Slotkin and Martienssen, 2007; Wicker et al., 2007) (Figure 1). RTs move or are synthesized through a two-step “copy-and-paste” mechanism via an RNA intermediate (Dombroski et al., 1994; Chen et al., 2013). By contrast, DNA transposons transpose through the “cut-and-paste” transposition mechanism (Feschotte and Pritham, 2007; Muñoz-López and García-Pérez, 2010) (Wicker et al., 2007), which requires the involvement of several transposase enzymes but does not involve an RNA intermediate. Thus, retrotransposons increase their copy number more rapidly than DNA transposons, although both contribute to inflation of genome size (Jianxin and Bennetzen, 2004).

For a long time, TEs were regarded as “junk DNA” (Graur, 2013; Palazzo and Gregory, 2014), a term coined by Susumu Ohno in the 1970s while studying DNA sequence duplication (Ohno, 1972). Four years later, Richard Dawkins provided an in-depth definition of the selfish nature of gene in his book “The Selfish Gene” (Dawkins, 1976) in which he also postulated a gene-centric interpretation of “natural selection and evolution” (Davis, 2017). Since the 1980s, TE were referred to as “parasitic or selfish DNA”, given that they use the host machinery for their own propagation (as reviewed in (McLaughlin and Malik, 2017). More recently, the contribution of TEs to mutation, generation of genetic diversity and regulation of gene expression has become widely recognized (Hollister et al., 2011). Indeed, even though a large proportion of TE DNA may be not directly involved in gene expression - the so-called inactive TEs - they may still exert effects as a physiochemical consequence of
genome organization on three-dimensional chromatin conformation and dynamics (Golicz et al., 2020; Karaaslan et al., 2020). Upon activation, as a result of environmental or other cues (see section 2.3.2. below), TEs may be translocated within the genome, in the course of which inter-individual structural variations may be generated following excision and insertion (Xing et al., 2009). This ability has been harnessed using several different types of TEs, to develop research tools, such as the Ac/Ds (Fladung and Polak, 2012; Yu et al., 2012; Xuan et al., 2016; Mielich et al., 2018b), Tn and Mu (Lisch and Jiang, 2009) and Tos17 (Hirochika, 2001) systems. Such resources have been used for construction of mutant libraries to study gene function, in reconstruction of phylogenies (Kriegs et al., 2006), generation of novel germplasm, and in mammals for identification of onco-genes (Carlson and Largaespada, 2005), gene therapy (Ivics and Izsvak, 2006; Wilson et al., 2007; Hackett et al., 2010). Several excellent reviews address the direct role of TEs as insertional mutagens (Bennetzen, 2005; Lisch, 2013; Bennetzen and Wang, 2014; Chuong et al., 2017; Hirsch and Springer, 2017), so we will not discuss these in detail here.

Active TEs can carry tightly regulated noncoding elements that may be under selection. As such, they may contribute to adaptation and fitness of an organism in the context of different environments or life histories. These elements may include sequences for noncoding RNAs and transcription factor (TF) binding sites (Gong et al., 2015; Chuong et al., 2017). Recently, there has been increasing interest in (and consequently understanding of) the multiples roles that TE-induced small RNAs (sRNAs) play in plants, affecting processes such as reproductive development (Wang et al., 2018) including genome reprogramming

**Figure 1.** Classification, structure and transposition mechanisms of TE in plants. (a) TE classification into two main classes is based on the mechanism of their transposition and subclasses based on the chromosomal integration. Class I retrotransposons (RTs) transposed in copy and paste manner through RNA-intermediate whereas Class II DNA transposons by cut and paste. They are further subdivided into super-families and families. (b) Regarding TE structure, abbreviations used for the genes/protein coding domains include: long terminal repeats (LTR), long interspersed nuclear elements (LINE), short interspersed nuclear elements (SINE), capsid protein (GAG), aspartic protease (AP), integrase (INT), reverse transcriptase (RT), polymerase (Pol), polymerase B (Pol B), RNase H (RH), envelop (env), acidic amino acid triad (DDE or DDD), tyrosine recombinase (YR), Endonuclease (EN), Open reading frame (ORF) of unknown function, apurinic endonuclease (APE), transposase (Tpase), replication protein A (RPA), YR with YY motif (Y2) and helicase (HEL). Here, green triangle target site duplications (TSD), yellow triangle terminal inverted repeats (TIR), purple box extended coding region, pink box showed one or more additional open reading frame's containing region and blue box represent noncoding region with diagnostic features. (c) RTs transposition occurs in two steps: transcription of intermediate RNA (iRNA) from original retroelement DNA and complimentary DNA (cDNA) formation via a reverse transcriptase. This newly copied RT integrates into a target site in the genome. Transposition of DNA TE requires two terminal inverted repeats (TIRs) which contain two functional domains for cleavage and transposase binding for insertion to a new location in the genome.
in pollen (Zhang, Ramming, et al., 2019), meiosis (Martinez and Köhler, 2017) and the regulation of germ cell fate in Arabidopsis, maize and rice as reviewed by (Van Ex et al., 2011). Among the different classes of sRNA species, the small interfering RNAs (siRNAs) play a major role in epigenetic silencing of TE (Ito, 2013). However, although it was originally thought that such regulation was mediated solely by DNA methylation (Ito, 2013), growing evidence suggests that siRNAs produced from the TE by RdDM are a major driver of the epigenetic machinery, both via dicer-dependent and dicer-independent mechanisms (Wierzbicki et al., 2009; McCue et al., 2013; Liu, Shao, et al., 2014; Matzke and Mosher, 2014; McCue et al., 2015; Zhai et al., 2015; Cuerda-Gil and Slotkin, 2016; Panda et al., 2016; Ye et al., 2016; Johnson et al., 2017). The epigenetic silencing of TEs is described in more detail in section 2.2.

Polyploidy is a common phenomenon in the evolutionary history of plants and other eukaryotes such as certain groups of fish and amphibians. Polyploids can result either from whole genome duplication (WGD) events, resulting in autopolyploids, or hybridization between two existing diploids or diploid with tetraploid to form an allopolyploid (in the case of hexaploid wheat). In the latter case, a chromosome doubling step is generally required to provide pairing of homologous chromosomes, as in the evolution of stable, allopolyploid wheat and brassica species (Madlung and Wendel, 2013; Oliver et al., 2013; Soltis et al., 2015; Shimizu-Inatsugi et al., 2017). Post-polyploidisation genome reshuffling can enhance diversity in de novo allopolyploids, possibly due to both homologous exchanges through genetic recombination (Szadkowski et al., 2010) and nonhomologous exchanges through translocation/deletion (Challoub et al., 2014; Samans et al., 2017). Whilst polyploidy may initially lead to a doubling of gene numbers and opportunity for neo- and sub-functionalisation of some of the paralogs (Comai, 2005; Te Beest et al., 2011; del Pozo and Ramirez-Parra, 2015; Edger et al., 2017; Yao et al., 2019), it is generally followed by a pattern of gene loss (Gao, Wang, et al., 2016; Emery et al., 2018; Tong et al., 2018), especially where genomic regulation may be complicated by the proliferation of interacting regulatory elements (Chen and Ni, 2006; Song and Chen, 2015). In many diploid plants already rich in TE contents, polyploidy may further increase the complexity of TE roles and interactions. For example, TEs represent about 80% of the hexaploid wheat genome (Cantu et al., 2010), 67% of the tetraploid cotton genome (Wang et al., 2016), 61.83% of the B. napus oilseed rape (Chen et al., 2020) and 49% of the dodecaploid sugarcane (De Setta et al., 2014) genomes. As such, the ability to study TE function in larger genomes is severely hindered by their high abundance.

The dynamic nature of TEs represents a major source of genome and gene variation in both animals and plants (Kazazian, 2004; Barrón et al., 2014; Buckley and Adelson, 2014; de Carvalho et al., 2016; Li et al., 2018; Wicker et al., 2018; Zhang, Hu, et al., 2019), with functional changes in the patterns of gene transcription influenced either directly by, or in combination with, the presence of TEs at given genome positions, their transposition to other locations, or by the considerable diversity of TE-derived small RNAs (Lanciano and Mirouze, 2018). These topics are well covered by excellent reviews (Parisod et al., 2010; Hollister et al., 2011; Parisod and Senerchia, 2012; Lisch, 2013; Chuong et al., 2017; Vicent and Casacuberta, 2017) in relation to polyploid genome evolution and crop plants. However, to date, there has been little coverage of the complexity of subgenome interactions within polyploids, where TE contributions to variation in genomic regulation may result from changes in chromatin dynamics.

Here, we review recent progress in understanding how TEs affect genetic variation in various plant species and present examples of their contribution to crop adaptation and improvement. We first address the mutagenic role of TEs, their relationship to stress (be it genetic or environmental) and contribution to plasticity of gene expression. We then focus on the impact of TE-derived small RNAs on the expression of nearby genes (cis-effect) and subgenome paralogues (trans-effect). We conclude with an exploration of how such interactions may increase regulatory complexity in polyploid crops.

2. TEs as endogenous mutagens and transcriptional modifiers

The transposable and insertional nature of TEs render them a highly plastic endogenous mutagen that may become active following some form of environmental or genetic stress. This mutagenic ability has also been harnessed in development of mutation libraries, for study of functions of genes inactivated by TE insertions, such as “the Sleeping Beauty Transposons System” which was utilized for identification of cancerous genes (Narayanavari et al., 2017), and the “piggyBac Transposon System” for transgenesis of insects, germline mutagenesis in mice and transposon-
based gene therapy in humans (Ivics and Izsvak, 2006; Wilson et al., 2007; Hackett et al., 2010). As mentioned above the Ac/Ds (Fladung and Polak, 2012; Yu et al., 2012; Xuan et al., 2016; Mielich et al., 2018b), Tn and Mu (Lisch and Jiang, 2009) systems have similarly been used in plants.

The interaction between TEs and “stress” is, however, a complex theme, that has fascinated generations of researchers since the early works of Barbara McClintock (McClintock, 1983). Today, we know that TE transcription (in case of RTs) and excision (in case of DNA TEs) are induced when cells and organisms face some form of “unfamiliar conditions”. These conditions may be essentially of a genetic nature such as the genomic shock following plant hybridization and polyploidization (Feliner et al., 2020), or may be simply represented by various environmental conditions that plants may face during their life cycle (e.g., temperature, water stress deficit, nutrient deficit) (Oustric et al., 2019; Balfagón et al., 2020; Yadav et al., 2020). A related, but distinct, feature of the complex interplay between TEs and stress (intended here in its broadest term) is the potential of these mobile elements to confer stress responsiveness to the genes in the vicinity of their location. The effects that TEs have on the expression of nearby genes clearly depends on where they integrate in the genome (Sigman and Slotkin, 2016). As we will detail in sections further below, TEs can cause up- or down-regulation of a neighboring gene, but also interfere with the processing of the premRNA (e.g., by altering the splicing process) or be integrated within the coding sequence to be transcribed as additional exons (exonization). In particular, the capacity of TEs to act as cis-acting factors (i.e., as enhancers or repressors of transcription) has been initially proposed on the basis of the evidences of the preferential association of LTR-RTs (especially COPIA elements) in the vicinity of stress-responsive genes in a number of plant genomes (Naito et al., 2009; Bolger et al., 2014; Xü, Brockmoller, et al., 2017). If an LTR-RT is located inside a promoter, for example, its transcription factor (TF) binding sites (located in the long terminal repeats, LTRs) may bind specific TFs determining up- or down regulation of the proximal gene or cause a change in the promoter specificity (Dubin et al., 2018). More recently, in a large collection of tomato accessions, the polymorphisms generated by the insertion of TEs have been studied both in relation to the global transcriptional changes and also with respect to the variation observed in transcript lengths. Most importantly, genes related to pathogen resistance and response to environmental stresses were enriched for the presence of various TE insertion polymorphisms (Dominguez et al., 2020). This association may thus reflect the preference of COPIA elements for inserting, once transposed, into specific genomic locations (i.e., in proximity of stress-related genes); these preferential insertions may have thus been fixed in natural populations given their potential adaptive value. COPIA-like elements have been shown to preferentially co-locate with environmental-responsive genes in Arabidopsis (Quadrana et al., 2019), maize (Makarevitch et al., 2015), wild tomato [S. pennellii, (Boiger et al., 2014]) and wild tobacco [N. attenuata, (Xu, Brockmoller et al., 2017)].

Several recent studies have highlighted the role of native trans-positional mutations of TEs in crops [reviewed by (Grzebelus, 2018)]. TEs can insert within any open reading frame, intron, 5′- or 3′- cis-regulatory elements or remote trans-regulatory sequences. Some TEs show insertion bias, for instance mPing preferably inserts into the 5′ flanking region rather than in the exons of genes and even de novo insertions have been filtered by selection (Naito et al., 2009). Similarly, TE elements of Athila, a member of the Metaviridae family, preferably target heterochromatin, as do members of Pseudoviridae family, which are less likely to be inserted into euchromatic regions (Pereira, 2004). TEs are preferably located in upstream regions compared to downstream regions of genes (Warnefors et al., 2010). TE insertions have many potential consequences. First, they can result in local or cis-effect, knock-out or knock-down, changes in gene expression. Second, activation of flanking genes can occur either on the provision of novel de novo cis-regulatory elements that may act as enhancers/ repressors of TFs (Ito et al., 2011), or by the outward reading of promoters following the insertion of a TE into the gene (Martienssen et al., 1990; Barkan and Martienssen, 1991; Morgan et al., 1999; Girard and Freeling, 2000) as well as inducing changes in the chromatin structure of gene promoter regions (Hollister and Gaut, 2009; Lisch, 2009; Eichten, et al., 2012). Third, alterations in splicing patterns of RNA precursors result in alternate transcripts which may subsequently translate into alternate proteins. Finally, (in human) the generation of natural antisense transcripts (NATs; noncoding RNAs transcribed from the strand opposite to a coding sequence), which are recognized today as global gene regulators are often initiated following the insertion of TEs, particularly in case of humans (Zinad et al., 2017). However, in Arabidopsis, such NATs may interfere with the
expression of cognate sense transcripts/genes or other noncoding RNAs (Xu, Wang, et al., 2017; Zhao et al., 2018). The consequence of expression changes in an inserted gene may of course be detrimental, but in a minority of cases, may be beneficial for the plant, eventually allowing adaptation to specific environments (Thieme and Bucher, 2018; Baud et al., 2019; Lei et al., 2020), seed dormancy (Fedak et al., 2016) and genetic tuning of crop growth cycles (Li et al., 2016). Furthermore, NATs reduced to phased small interfering RNAs (pha-siRNAs) (Yu et al., 2016) that may play a role in epigenetic regulation of TE. The impact of TEs on nearby genes and biogenesis of small RNAs (sRNAs) are detailed in the following sections.

2.1. Proximal effects of TEs

There is considerable evidence that TE insertion may increase or decrease the transcription of nearby genes. Interestingly, some TE insertions in the up- and down-stream regions (so-called cis-regulatory regions) may enhance gene expression and contribute to beneficial phenotypic traits. TEs can also insert into exonic- and intronic-regions; in these cases, they directly alter the coding region and/or the original splicing pattern of the target gene, but may also modify, as we will see below, the gene expression profile (Table 1).

2.1.1. Introns

Although there is no universal intron requirement for gene expression in eukaryotes, the majority of TE insertions in the introns of genes affect gene transcription. Indeed, in many cases, the involvement of introns was reported to contribute to altered transgene expression (Zhang, Zhang, et al., 2019). For example, in soybean, insertion of Tgmt-CACTA TE on the intron-1 of Flavonoid 3’-hydroxylase gene produced t* allele responsible for the stable gray trichome color (Zabala and Vodkin, 2008). A 259-640-bp insertion of an LTR-RTs into the intron of B. rapa Flowering Locus T2 (BrFT2), resulted in mutation of the allele which caused delayed flowering irrespective of growing season (Zhang, Meng, et al., 2015). Similarly, in tomato, a Rider insertion causes the 24.7-kb duplication of the DEF11 gene at the SUN locus resulting in elongated fruit shape (Xiao et al., 2008). There are several excellent examples in maize wherein insertion of Mutator element in the introns of the three homeobox genes Knotted1, Rough Sheath1 and Liguleless3 causes ectopic expression resulting in improper leaf development (Greene et al., 1994; Schneberger et al., 1995; Muehlbauer et al., 1999). Moreover, in another study, a MuI1.5-kb insertion in the first intron of the Adh1-S3034 gene encoding alcohol dehydrogenase-1 (ADH1) reduced the transcript levels through inhibition of transcription (Bennetzen et al., 1984). Furthermore, TE insertions into the intronic regions can be responsible for the transition of reproductive to nonreproductive organs, for delayed flowering and also for fruit morphological variations. For instance, insertion of Enhancer/Suppressor (En/Spm) mutator-like elements of an ancestral species of Ipomoea in the second intron of the floral homeotic gene DUPLICATED (DP), was responsible for the substitution of reproductive organ to perianth organs i.e. petals and sepals in Japanese morning glory (Ipomoea nil) (Nitasaka, 2003).

2.1.2. Exons

Similar to introns, TE insertion in exons may also reduce transcript levels. For example, in maize plants, MuI elements were found in the two mutants mlks2-1 and mlks2-2 of Maize LINC KASH AtSINE-like2 (MLKS2). The MLKS2 is a pleiotropic gene controlling multiple functions such as (i) affecting root hair nuclear morphology, (ii) complex stomatal development, (iii) multiple aspects of meiosis, and (iv) pollen viability (Gumber et al., 2019b). Similarly, in soybean expression of the salt-tolerance conferring gene GmSALT3 (salt tolerance-associated gene on chromosome 3) was higher in the roots of the salt-tolerant cultivar “Tiefeng 8” compared to the salt-sensitive cultivar “85-140” and associated with limiting the accumulation of sodium ions in the shoot. Further, molecular analysis showed that behind the reduced expression of the GmSALT3 gene in salt-sensitive cultivar there was a 3.78-kb insertion of Copia RT in exon 3, resulting in expression of a truncated transcript (Guan et al., 2014). Moreover, SINE insertion in the open reading frame (ORF) of FLOWERING WAGENINGEN (FWA) gene controls gene expression by DNA methylation of CG through methyltransferase 1 (MET1) and the chromatin remodeling gene, ATP-dependent DNA helicase 1 (DDM1). Proper expression of FWA depends upon TE insertion that delayed the flowering time in A. thaliana (Kinoshita et al., 2007). This “delayed flowering time” (for more detail see section 2.3.1) suggests that not all types of TE insertion into exons has a negative consequence but can also help plants to adapt to their changing environment.
Table 1. Impact of TE insertion as cis-acting element on nearby gene.

| Insertion position | TE species | Insertion size | Gene name | Location | Plant species | Impact | Reference |
|--------------------|------------|----------------|-----------|----------|--------------|--------|-----------|
| Intron             | Mu1        | 1.4-kb         | Adh1      | Intron-1 | Z. mays      | It reduced the levels of messenger RNA expression by depressing RNA processing or transcription | (Bennetzen et al., 1984) |
| Muator             | 310-bp     | Knoteed1       | Intron-3  | Z. maize | Ectopic expression, improper development of the leaf mutation | (Greene et al., 1994) |
| Mutaor             | 2-kb       | Rough Sheath1  | Intron-1  | Z. maize | Ectopic expression, improper development of the leaf mutation | (Schneeberger et al., 1995) |
| Tpn, EnvSpn-like   | 1.2-kb     | DUPUCATED1     | Intron-2  | I. nil   | It causes the substitution of reproductive organs to peniania organs (petals and sepals) resulted in double flower phenotype | (Nitsazaka, 2003) |
| Rider              | 24.7-kb    | DEF1L          | N/A       | S. lycopersicum | Responsible for stable gray trichome color | (Xiao et al., 2008) |
| Tgmt CACTA         | 20.5-kb    | N/A            | Intron-1  | G. max   | It causes the elongation of fruit shape | (Zabala and Vodkin, 2008) |
| LTR                | 259-640-bp | BTF2           | Intron-2  | B. rapa  | It causes the delaying in flowering time | (Zhang, Meng, et al., 2015) |
| MITE-element       | 20-bp      | ST1            | Intron-2  | O. sativa | It causes quantitative resistance to maize rough dwarf disease | (Zhang, Tao, et al., 2016) |
| Helitron           | 2.6-kb     | RabGDs         | Intron-10 | Z. mays  | It causes the substitution of reproductive organs to peniania organs (petals and sepals) resulted in double flower phenotype | (Liu, Deng, et al., 2020) |
| Exon               | Mu1        | 1.4-kb         | MLKS2     | Z. mays  | Ectopic expression, improper development of the leaf mutation | (Muellbauer et al., 1990) |
| Up/-down-stream    | Acid       | 800-bp         | SBEI      | P. sativum | Aberrant transcript of SBEI production has resulted in the production wrinkled seed | (Bhattacharya et al., 1990) |
| Trat1              | N/A        | Nitrate reductase | 7 Upstream from ATG | N. tabacum | It increases the expression level of diverse genes related to cold stress | (Grandbastien et al., 1997) |
| Grett              | 10.4-kb    | VmybA1a        | 7 Upstream from ATG | V. vinifera | Loss of pigmentation in grape skin color | (Kobayashi et al., 2004) |
| Tourist            | 143-bp     | AP2-like       | 5` UTR; Exon-1; Intron-1 | Z. mays | It causes the allelic variation in the downstream genes at Vgt1 locus (responsive to flowering time) triggered adaptation. | (Salvi et al., 2007) |
| Tourist-like       | 456-bp - 1.9-kb | SMMATE        | 1.4-kb Upstream from ATG | S. bicolor | It increases the gene expression of MATE in root apex and responsible for Al-tolerance | (Magalhaes et al., 2007) |
| Triton1            | 310-bp     | Trichosanthin  | 482-bp Upstream from ATG | T. rilowii | It provides the co-regulatory element and alter the promoter of TCS gene resulted in the regulation of gene expression related to light | (Yu et al., 2007) |
| Renovator          | 5.5-kb     | Pit            | 244-bp Upstream from ATG | O. sativa | It increases resistance to rice blast disease | (Hayashi and Yoshida, 2009) |
| mPing              | N/A        | Diverse genes related to diverse stresses | 7 Upstream from ATG | O. sativa | It activates the gene expression related various hormones (ABA, SA etc.) and other stresses such as Cold, Dehydration and disease resistance | (Naito et al., 2009) |
| Stowaway-like element; Ds-like element MITE | 141; 221; 915-bp | GST           | 5.59; 757; 1045-bp Upstream from ATG | O. sativa | They influence the promoter resulted in the reduced expression of GST weakens the herbicide detoxification mechanism | (Hu et al., 2011) |
| -Hopscoth          | 4.9-kb     | tb1            | 58.5-bp Upstream from ATG | Z. mays | Increased apical dominance | (Studer et al., 2011) |
| -ONSEN             | N/A        | Heat Shock TF  | 7 Upstream from ATG | A. thaliana | Its heat shock element binds with HSF and can regulate the transcriptional circuits in response to heat stress | (Ito et al., 2007) |
| CACTA-like         | 1-kb       | HvAAT1         | 4.8-kb Upstream from TSS | N. vulgare | It enhances the Aluminum tolerance | (Matsunaga et al., 2012) |
| Copia-like         | 254-bp     | Ruby, MYB TF   | 501-bp Upstream from ATG | C. sinensis | Enhanced expression results in purple coloration “Sicilian Blood Oranges” | (Butelli et al., 2012) |
| Sukkolo-like       | 11.1-kb    | TaMATE1-I8     | 1.5- and 2.5-bk Upstream from ATG | T. aestivum | It confronts the citrate efflux from root and then enhance the Al resistance | (Tavkach et al., 2013) |
| mPing              | 430-bp     | OsDREB1A       | 1.5- and 2.5-bk Upstream from ATG | O. sativa | Enhance cold, salt and drought stress tolerance | (Kawabata et al., 2011) |

(Continued)
Table 1. Continued.

| Insertion position | TE species | Insertion size | Gene name | Location | Plant species | Impact | Reference |
|--------------------|------------|----------------|-----------|----------|---------------|--------|-----------|
| mPing 430-bp       | ZFP252     | 446-bp upstream from ATG | O. sativa | Enhance salt and drought stress tolerance | (Yasuda et al., 2013) |
| mPing 430-bp       | ONAC045    | 263-bp upstream from ATG | O. sativa | Enhance cold, salt and drought stress tolerance | (Yasuda et al., 2013) |
| mPing 430-bp       | OsCDPK7    | 17-bp upstream from ATG | O. sativa | It increases the gene expression under cold stress | (Yasuda et al., 2013) |
| mPing 430-bp       | ZFP252     | 446-bp upstream from ATG | O. sativa | It increases the gene expression under salt stress | (Yasuda et al., 2013) |
| mPing N/A          | ONAC045, TF| 263-bp upstream from ATG | O. sativa | It increases the gene expression under salt stress | (Yasuda et al., 2013) |
| CACTA-like 5.1-kb  | ZmCCT      | 2.5-kb upstream from ATG | Z. mays | Reduce the photoperiod sensitivity and accelerated the maize adaptability to long-day environment | (Yang et al., 2013) |
| Sukkula-like 11.1-kb | TaMATE1-4B | 25-bp upstream from ATG | T. aestivum | TE insertion enhance the expression of TaMATE1B resulted in the increase tolerance to Aluminum stress | (Garcia-Oliveira et al., 2014) |
| Tourist-like 6-kb  | SmMATE     | 1.4-kb upstream from the ATG | S. bicolor | Allelic variation due to TE insertion enhance the Al tolerance and increase grain yield | (Caniato et al., 2014) |
| Tourist-like 276-bp | TaHSP16.9-3A | 142-bp downstream from TGA | T. aestivum | It increases the gene expression that enhance the heat tolerance | (Li et al., 2014) |
| Hoeman N/A         | Diverse cold and UV response genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to cold and UV stress | (Makarevitch et al., 2015) |
| Naiba N/A          | Diverse cold responsive genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to cold stress | (Makarevitch et al., 2015) |
| Gyna N/A           | Diverse cold responsive genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to cold stress | (Makarevitch et al., 2015) |
| Etug N/A           | Diverse heat and salt responsive genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to Heat- and high salt stress | (Makarevitch et al., 2015) |
| Pedi N/A           | Diverse heat responsive genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to Heat stress | (Makarevitch et al., 2015) |
| Alaw N/A           | Diverse salt responsive genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to High salt stress | (Makarevitch et al., 2015) |
| Ipiki N/A          | Diverse salt and UV responsive genes | ? Upstream from ATG | Z. mays | It increases the expression level of diverse genes related to High salt and UV stress | (Makarevitch et al., 2015) |
| MITE 82-bp         | ZmNAC111   | 572-bp upstream from ATG | Z. mays | It represes the gene expression and enhance the drought tolerance | (Mao et al., 2015) |
| Copia-like 3.9-kb   | MYB TF     | 2.7-kb upstream from ATG | G. hirsutum | Increased the gene expression controlling fiber development | (Wang et al., 2016) |
| LINE-element 13-mb  | ERF gene   | 1.04-kb upstream from ATG | G. hirsutum | Increased the gene expression controlling trichome development | (Wang et al., 2016) |
| Helitron 3.6-kb     | BnSP11-1   | 106-bp upstream from ATG | B. napus | Alter the mating system that might facilitate the speciation | (Gao, Zhou, et al., 2016) |
| Multiple species of RT and DNA TE 30-kb | Zm1 | 1.9-kb upstream from ATG | Z. tattie (a fungal plant pathogen of T. aestivum) | Multiple TE insertions contribute in the alteration of melanin accumulation and facilitate adaptation. | (Krishnan et al., 2018) |
| Multi-retrotransposon-like 15.3-kb | HvAACT1 | 7.2kb upstream from ATG | H. vulgare | It promotes the adaptation of barley to acidic soil | (Kashino-Fujii et al., 2018) |
| CACTA-like 3.9-kb  | BnaA9.CYP7A9 | 3.9-kb upstream from ATG | B. napus | Enhance the silique length and seed weight by affect auxin metabolism | (Shi et al., 2019) |
| Copia 4.8-kb       | BnSHP.A9   | 252-bp upstream from ATG | B. napus | It represes the gene expression of BnHSP.A9 and enhance pod shattering resistance | (Liu, Zhou, et al., 2020) |
**2.1.3. Promoters, up- and downstream regions**

In addition to insertion into introns and exons, also the TE insertions into the upstream (including the promoter and enhancer/repressor regions) and downstream regions may play a significant role in plant responses to developmental and environmental cues. Recent adoption of high-throughput profiling of accessible chromatin regions (ACRs) in plants illuminated the potential of TEs for generation of novel regulatory elements (Noshay et al., 2020) on a whole genome level, with nearly 20% of ACRs located within an annotated TE. Genome-wide studies also demonstrated that TE insertions can alter the epigenetic state of the neighboring sequence and expression of adjacent genes. However, the relationship between TE insertions, heterochromatin spreading and gene expression appears to vary across species. A study in maize (Eichten et al., 2012a) showed altered methylation levels and presence of heterochromatic marks up to 1,200 base pairs from the TE insertion site, but the property was family specific with Copia and Gypsy RTs but not LINEs contributing to heterochromatin spreading. Genes located near heterochromatin spreading TEs were also reported to have lower expression levels. A comparative analysis between sorghum and Arabidopsis (Wyler et al., 2020), revealed that although TEs are more abundant in sorghum their impact on methylation spreading and expression of neighboring genes appears to be smaller than in Arabidopsis. In rice, the extent of methylation spreading was also shown to be age, type and genomic position dependant, with older LTR-RTs and those found in pericentromeric regions displaying higher levels of methylation spreading (Choi and Purugganan, 2018). In addition, gene expression was affected only if the TE insertion took place within the gene body.

In those rare cases where TE insertions in cis provided beneficial effects, we can distinguish at least two different phenotypic outcomes. The first is the modification of organ size and color, for example fruit shape, color, size and length, or fiber development. For instance, the emergence of white grape varieties can be reconstructed to have been due to the insertion of a TE (Gret) in the upstream region of Myb TF gene controlling anthocyanin synthesis. Molecular analysis revealed that insertion of this RT-LTR in the promoter region was responsible for the loss of pigmentation (Kobayashi et al., 2004). The second case includes those TE events imparting adaptation to new environmental conditions, like, for example, day length-dependent flowering time. In maize plants, an insertion of a MITE-element in the 2-kb noncoding cis-regulatory region located 70-kb upstream of the AP2-like TF gene on chromosome 8 [corresponding to a major flowering time QTL, Vegetative to generative transition 1 (Vgt1)] caused the allelic variation in Vgt1 which resulted in expression changes of the downstream gene. Hence, the novel regulatory variant in a distant upstream region was a driver of genetic adaptation for maize breeding (Salvi et al., 2007). Similarly, after insertion of Triton1, a species of MITE-element, the presence of an additional cis-regulatory element altered the chromatin structure of the promoter (TP9) of the Trichosanthin (TCS) gene resulted in altered regulation of gene expression (Xu et al., 2007). Also in maize, composite insertion (CI) generated by Ac transposable elements induced ectopic expression of the gene pericarp color 2 (p2) (Su et al., 2020). Expression of p2 was activated due to TE mediated mobilization of the enhancer element of the neighboring p1 gene.

In *B. napus*, TE insertions may alter the mating system (transitioning from out-crossing to self-fertilizing) by inducing changes in the transcript levels of the BnSP11-1 gene. This change is important as it may aid in the process of speciation and evolution. Genetic analysis showed that a 3.6 kb insertion of a nonautonomous Helitron TE was found in the promoter of BnSP11-1. After TE insertion, the endogenous enhancer and the cis-regulatory elements were disrupted, causing the loss of expression of BnSP11-1. Thus Helitron transposons are involved in the alteration of mating system and facilitation of speciation (Gao, Zhou, et al., 2016). Also, TE may enhance the pod shattering resistance of *B. napus*. Pod shattering resistance is controlled by SHATTERPROOF1 (SHP1). Results showed that a copia LTR-RT insertion (4.8 kb) was found in the promoter of BnSHPA9.1 and was involved in repressing the expression of the BnSHP.A9.1 gene. This association analysis suggested that the above TE insertion can be used as a breeding marker for pod resistance (Liu, Zhou, et al., 2020). In another example, a CACTA-like transposable element inserted in the upstream region of CYP78A9, a gene encoding a P450 monooxygenase, acts as a positive regulator of silique length in rapeseed. It is expressed in the silique valves, and its levels were higher in a long than a short silique variety due to increased accumulation of auxin. Transgenic experiments confirmed the involvement of the above TE type in the higher expression of this gene (Shi et al., 2019).

Since TEs are of course also abundant in polyploid genomes, the study of these mobile elements is also interesting considering the impact of polyploidizations...
on TE dynamics. For example, despite being a diploid species, maize genome shows signatures of ancient allopolyploidy, has experienced large-scale genome rearrangements, loss of repetitive DNA elements and chromosomal duplications [as reviewed in (Gaut et al., 2000)]. Moreover, many genes experienced homoeologous loss although regulatory and developmental related genes are retained in excess following WGD (Soltis et al., 2015).

The regulatory role of TE as an insertional mutation in response to environmental stresses such as cold, heat, salt and UV is discussed by (Makarevitch et al., 2015). They demonstrated that in maize, several specific classes of TE families were specifically enriched in the upstream regions of differentially expressed genes responsive to each stress. Further, analyses of stress responsive transcripts and proximal region of TEs showed that the TEs may cause changes in the local enhancer elements. TEs cause polymorphic variation in stress responsive genes by altering their regulatory mechanism. Distance of TE insertion from TSS at upstream region also influence as it controls the transcriptional mechanism of adjacent genes. For instance, in Brassica species such as B. rapa and B. oleracea, several LTR-RTs are found in less than 2-kb and 100-bp of distance from the nearby genes, respectively and influence the process of transcription. LTR driven transcription may produce sense or antisense transcripts of nearby genes, with the effects of activating or silencing the corresponding genes. For example, in B. rapa 15 and in B. oleracea 55 LTR-RTs produced the antisense transcripts which may interfere with the adjacent gene expression when the others produce sense transcripts and thus enhance adjacent gene expression (Zhao et al., 2013).

### 2.2. Interactions between TE-induced sRNAs and epigenetic regulation

#### 2.2.1. Types and biogenesis of sRNAs

The sRNAs ranging from 20-24 (nt) carry out important regulatory tasks in plants, influencing cellular and developmental functions such as gene expression regulation, reproductive transitions, paramutation and genomic imprinting (Borges and Martienssen, 2015). Based on the involvement of RNA-dependent RNA polymerases (RDRs) (Polydore and Axtell, 2018) proposed a revised sRNA classification. According to this classification, sRNAs are divided into two groups i.e., RDR-independent and RDR-dependent. The first group includes micro RNAs (miRNAs), inverted repeat small interfering RNAs (ir-siRNAs), and natural antisense siRNAs (nat-siRNAs) that are further divided into cis-nat-siRNAs and trans-nat-siRNAs. In the second group, RDR-dependent ones are pha-siRNAs and heterochromatic siRNAs (hc-siRNAs) that further divided into trans-acting siRNAs (ta-siRNAs) and epigenetically activated siRNAs (ea-siRNAs) (Figure 2). Biogenesis of miRNAs begins from specific locations (endogenous genes) in the genomic DNA (gDNA) which are first transcribed into long primary transcripts (pri-miRNAs) by RNA polymerase II (Pol II) (Axtell and Meyers, 2018). These pri-miRNAs are single stranded, polyadenylated RNA (ssRNA) molecules of less than 300-nc which are converted into hairpin-like structures (Axtell, 2013). From here, DICER-LIKE 1 (DCL1) cleaves pri-miRNAs into shorter stem-loop structures known as precursor miRNAs (premiRNAs). Finally, DCL1 processes again the premiRNAs into mature miRNAs, with a length of 20-22 nt, containing both the active and the complementary strand (Borges and Martienssen, 2015). The siRNAs, the major 2nd class of small RNAs are instead produced from TEs, immature mRNA transcripts, tandem repeats, hairpin RNAs, natural sense- and antisense pairs, duplicates including pseudogene-induced anti-sense transcripts and cognate gene derived sense mRNAs, and exogenous sources such as RNA viruses and transgenes (Phillips et al., 2007).

Here, long double stranded RNA (dsRNA) molecules served as the precursor of siRNAs (Axtell and Meyers, 2018), which arise from pairing of sense- and anti-sense transcripts. Long dsRNA molecules can be synthesized by RNA-dependent RNA polymerase 2/6 (RDR2/6). Then, dsRNAs are cleaved by different dicer elements including DCL 3/4 into pha-siRNAs and secondary siRNAs or hc-siRNAs. There are two subclasses of hc-siRNAs, including ta-siRNAs and ea-siRNAs. Among, the most abundant siRNAs of 24 nt in length are hc-siRNAs, whose biogenesis requires transcription by RNA polymerase IV (Pol IV). Here, 26-50-nc dsRNAs molecules are synthesized by RDR2 and then processed to mature het-siRNAs of 21-nc by DCL3. However, in case of pha-siRNAs, in the first step Pol II transcribed double stranded mRNA or long noncoding RNA region into single strand molecule that hydrolyzed by RNA induced silencing complexes (RISCs) of 21/22-nc miRNA or 21-nc siRNA (Axtell and Meyers, 2018). After that, SUPPRESSOR OF GENE SILENCING 3 (SGS3) protein protects the transcript from further degradation by binding at 3’ end and that later on duplexed by RDR6. Here, DCL4 cleaved into 21-nc siRNA that loaded into RISC complex by ARGONAUTE 1 (AGO1) protein.
Interestingly, one pha-siRNA formed from one precursor in a phased manner or head-to-tail pattern (that’s why it called “pha-siRNA”). There are two types of pha-siRNA loci reported to date. For examples, 1) 21/22-nc miRNA directed dominant pha-siRNA producing loci are present in almost all land plants and 2) 24-nc dominant pha-siRNA loci are only encoded in monocots and are uncommon in male sex determinant tissues (Polydore et al., 2018). Conversely, biogenesis of other secondary RDR-independent siRNAs such as cis-nat-siRNAs and trans-nat-siRNAs are transcribed by Pol II into partially mis-matched dsRNA molecule that cleaved into nat-siRNAs of 21-nc by DCL1 and 24-nc by DCL4 and finally loaded into RISCs complex by their respective AGO protein. The cis-nat-siRNAs are produced from overlapping genomic region (two genes) and transnat-siRNAs derived from two or more different genes that are complementary and nonoverlapping genomic region (Röther and Meister, 2011). There are two examples of ir-siRNAs reported in plants with 21/22 nt length are generated from precursors of 2100 and 6800-nc (Lindow et al., 2007). Here, Pol II transcribe into ssRNA molecule having stem-loop hairpin structure that hydrolyzed into 20-24nc of ir-siRNAs by all kinds of DCLs (Chitwood and Timmermans, 2010). After that similar to nat-siRNAs, they loaded into RISCs by their respective AGOs. Thematic of biogenesis of sRNAs is presented in Figure 2.

Not only the biogenesis process of sRNAs is different compared to miRNAs as discussed above. They differ in many ways, for example, siRNAs play central role in transcriptional gene silencing and miRNAs regulate post-transcription gene silencing (Axtell and Meyers, 2018). Interestingly, in the case of miRNAs, one locus can produce one miRNA while many siRNAs duplexes can be produced from a single locus, respectively (Phillips et al., 2007). Another important difference between miRNAs and siRNAs is that the former are conserved both in plants and animals, whereas the latter vary even in different accessions/genotypes of an organism (Bartel and Bartel, 2003). Furthermore, in some cases, sRNAs are conserved even at a locus, chromosome, or cultivar level depending upon their size. For example, in barley, (Hackenberg et al., 2016) investigated the generation (different sizes) and types of sRNAs in the barley cultivars Golden Promise and Pallas. They reported that 20-nt miRNAs were statistically over-expressed in ‘Pallas’ on chromosomes 3H and 6H compared to ‘Golden Promise’ whereas 21-nt miRNAs were over-expressed in ‘Pallas’ only on 4H. In contrast, 22-nt

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**Figure 2.** A proposed model of small RNA classification and their biogenesis based on the involvement of RNA-dependent RNA polymerase (RDR). Small RNAs are grouped into two groups i.e., RDR-independent includes microRNA (miRNAs), inverted repeat small interfering RNAs (ir-siRNAs), and natural antisense siRNAs (nat-siRNAs) that further divided into cis-nat-siRNAs and trans-nat-siRNAs. RDR-dependent ones are phased siRNAs (pha-siRNAs) and heterochromatic siRNAs (hc-siRNAs) that are further divided into trans-acting siRNAs (ta-siRNAs) and epigenetically activated siRNAs (ea-siRNAs). For more details related to biogenesis see text.
miRNAs and other sRNAs derived from repetitive elements were under-expressed in ‘Pallas’ on 5H compared to ‘Golden Promise’. Interestingly, siRNAs of 24 nt derived from repetitive elements were equally distributed in both cultivars on all chromosomes. Results also showed that most of the siRNAs were generated from the 3' terminal region of 1H and the 5' terminal region of 5H. Moreover, sRNAs which were highly expressed in ‘Golden Promise’ were responsive to stress and iron-binding. In general, whilst in both cultivars 23/24-nt sRNAs were found to be involved in (repressive) chromatin modification and genome stability, the 20/21-nt sRNAs may be more cultivarspecific. Among all types of sRNAs, siRNAs primarily contribute to DNA methylation pathways to silence TEs, as we detail in the following section.

### 2.2.2. Role of sRNAs in epigenetic regulation of TE

To avoid mutagenic activity following TE expression and their transposition, plants have established several mechanisms to inhibit TE activity (Kim and Zilberman, 2014). Epigenetic regulation of TE transcription may be mediated through one or more epigenetic marks that result from mechanisms such as DNA/RNA methylation, histone modification and consequent alterations in nucleosome positions, as well as processes associated with small nuclear RNA (snRNA) and other noncoding RNAs (ncRNA) (Bernatavichute et al., 2008; Chodavarapu et al., 2010). Among these, the prominent regulatory mechanism in eukaryotes is DNA methylation, including the most heavily-studied 5mC mark (methylation on the fifth position of the pyrimidine ring of cytosine) (Suzuki and Bird, 2008; Law and Jacobsen, 2010). Recently the importance of the 6 mA mark (methylation on the sixth position of the purine ring of adenine) has been largely appreciated (Liang et al., 2017; Zhou et al., 2018). A recent study in rice reported that 5-methylcytosine overlaps with 6-methyladenine at CG sites in gene bodies and is complementary to 6 mA at CHH sites in TEs (Zhou et al., 2018). Among the methylation targets such as CG, CHG, and CHH (where H is the nucleotide A, T, or C), CG is the most abundant in plants, and is frequently associated to TE silencing and maintenance (Deniz et al., 2019). Plants have specific enzymes for methylation in each of these sequence contexts. For example, cytosines in CpG (C and G, dinucleotide) are methylated by MET1 [methyltransferase 1, subfamily of DNA methyltransferase enzymes (DNMT enzymes)]; CHG by chromomethylase 3 (CMT3); and CHH is established by domain rearranged methyltransferase 1 and 2 (DRM1 and DRM2) (Jeltsch, 2010).

Many studies have reported TE silencing mechanisms that operate without the aid of RdDM [an epigenetic regulatory process in which noncoding RNAs established the methylation state at a specific DNA sequence, (Erdmann and Picard, 2020)] such as the CMT3/CMT2 and MET1 pathways that are recruited via H3K9me2 (Lister et al., 2008; Stroud et al., 2013; Zemach et al., 2013; Stroud et al., 2014). However, RdDM pathways are required for the maintenance of TE methylation. Hence, we can conclude that DNA methylation relies on RdDM activity, since methylation levels cannot be established using non-RdDM pathways (Stroud et al., 2013; Zemach et al., 2013).

In recent years, with progress in whole-genome sequencing, there is growing evidence that TEs could induce a large number of sRNAs; many of them are siRNAs that function as central players in DNA methylation via the RdDM pathway (Li et al., 2015). These TE-derived siRNAs may guide cleavage of the TE transcript itself in a typical PTGS process (Matzke and Mosher, 2014), but also play a key role in preventing the genome from the nucleic acid invaders such as viruses (Carthew and Sontheimer, 2009). The siRNAs have been reported to knock down or knock-out the gene expression endogenously by various mechanisms in different eukaryotic organisms (Deng et al., 2017). Several classes of siRNAs were found to be involved in the silencing of the genes at level of PTGS. The PTGS-linked siRNAs such as ta-siRNAs and nat-siRNAs can mediate gene expression in plants at different developmental stages and under different environmental conditions. For example, 21–24 nt siRNAs produced via RdDM pathways from the 82-bp MITE element inserted into the promoter of the ZmNAC111 gene increased gene expression resulting in improved water use efficiency and enhanced the expression of drought tolerance related genes under water stress in maize (Mao et al., 2015). Moreover, the above study suggested that the MITE insertion into the ZmNAC111 gene occurred after domestica tion and then spread among germplasm of temperate region. Thus, it provides the genetic basis of natural variation in the mechanism of drought tolerance in maize. In plants such as Arabidopsis, rice and maize, a majority of siRNAs affecting gene expression are linked with TE inserted in genes or in their regulatory region (Slotkin et al. 2009) (Mao et al., 2015; Deng et al., 2017). For more details concerning the role of siRNAs and other noncoding RNAs produced from TE see Table 2.
### 2.2.3. Cross-talk between TEs and the methylome

On the basis of siRNAs biogenesis via RdDM mechanisms, there are two models (both consisting of dicer-dependent and dicer-independent routes) that may establish the methylation state of TEs. In the first model, Pol II recognizes the binding sites of a TE at an active locus and transcribes the ssRNA via two routes. In the first, dicer-independent route, ssRNA is directly loaded into ARGONAUTE 4 (AGO4) protein following trimming activity, producing a distinct class of siRNAs (d-siRNAs, 20-60 nt). These d-siRNAs are similar at the 5′ end but differ at the 3′ by one nt whose production may depend on distributive 3′–5′ exonuclease activities. The d-siRNAs and AGO4 complex next recruits the DRM 2 protein resulting in the DNA methylation of TE (Ye et al., 2016). In the second, dicer-dependent route, Pol II generated an ssRNA which is subsequently duplexed by RDR6. The original strand is spliced by DCL2/4 into 21/22 nt siRNAs and then loaded into AGO 2/6 proteins. After that, this complex recruit DRM 2 (in a manner similar to the first route) to methylate the above similar TE (Nuthikattu et al., 2013; McCue et al., 2014; Fultz et al., 2015; Cuerda-Gil and Slotkin, 2016; Panda et al., 2016) (Figure 3a). The methylation level established by Pol II-induced pathways is not so strong and may leave some marks for the initiation of Pol IV activity. To maintain epigenetic control, Pol IV recognizes the Pol II-directed sites or marks by the assistance of two Pol IV-interacting proteins namely Classy 1 (CLSY1) (Law et al., 2011) and Sawadee Homeodomain Homolog 1/DNA-binding transcription factor (SHH1/DTF1) (Law et al., 2013; Zhang et al., 2013). The Pol IV dicer-independent route is similar to that of Pol II, as it is the initiator of RdDM in both models, and also produces similar 20-60 nt d-siRNAs to silence the TE. However, in the second route, following a “one precursor for one siRNA model”, each Pol IV enzyme produces one siRNA (Zhai et al., 2015), with RDR2 duplexing each transcribed strand of 30-40 nt. These Pol IV-induced double-stranded RNAs (p4dsRNAs) are spliced into 24 nt siRNAs by DCL3 and then loaded as a guide strand into the AGO4 protein domain. Each complex recruits DRM1/2 with the help of Pol V interacting protein such as SU(VAR)3-9 HOMOLOG (SUVH) 4/5/6 to silence the TE by altering its H3K9me2 histone structure (Wierzbiicki et al., 2009; Johnson et al., 2014; Liu, Shao, et al., 2014; Matzke and Mosher, 2014; Fultz et al., 2015; Zhai et al., 2015) (Figure 3b).

In the RdDM pathway an important feature of chromatin material is the nucleosome positioning. A
recent study (Rothi et al., 2020) showed that the RdDM impact on the nucleosomes occurs via Switch/Sucrose Non-Fermenting (SWI/SNF) chromatin remodeling complex (required for the DNA methylation on intact nucleosomes). In Arabidopsis, subunits of this SWI/SNF complex may interact with other silencing elements such as HISTONE DEACETYLASE 6 (HDA6) and MICRORCHIDIA 6 (MORC6) to silence the TE (Liu et al., 2016; Yang et al., 2020), which shows the importance of SWI/SNF complex as
it is involved in various prospects of gene silencing. The scope of TE silencing can be expanded, as in recent findings from D. Zilberman’s group (Choi et al., 2020) showing that DNA methylation jointly with the histone protein H1 repress the TE and other aberrant transcripts by interfering with their transcription mechanism. Furthermore, they also reported that loss of H1 functioning not only altered nucleosomes poisoning globally resulting in the weakly de-represses of TE, but also strongly activates the hypomethylated TE through mutation of DNA MET1. This raises another question of what happens if Pol IV (the main factor of RdDM pathway) also loses its function and how this could impact phenotypic expression. For example, loss of Pol IV function does not cause a noticeable pollen defect in Arabidopsis but does result in arrest of pollen development in Capsella rubella. In Capsella, in fact, the distance of TE from gene is large (Wang et al., 2019). In another example, mutation in the Pol IV-dependent RdDM pathway induced lethal but specific reproductive faults in B. rapa in the form of aborted seed (Grover et al., 2018). In rice, OsDCL3α plays a major role (among 535,054 24-nt siRNA clusters, ~82% were OsDCL3α-dependent) in the processing of 24-nt siRNAs produced from the MITEs. Impairment in the functionality of OsDCL3α causes changes in the expression of genes involved in the homeostasis of gibberellin and brassinosteroid leads to negative impact on the phenotypes such as dwarfism, widening of flag leaf angle, and reduction in the number of secondary branches (Wei et al., 2014). The scope can be widened as MITE elements are present in several other crops including sorghum and maize (Feschotte et al., 2002; Han et al., 2013), thus the association of 24-nt siRNAs with TE processed by DCL3 broadly act as functional regulators of gene expression (Wei et al., 2014). However, in Arabidopsis, some reports stated that Pol IV could produce the siRNAs independently without the aid of DCL3 (Yang et al., 2016; Ye et al., 2016). These findings suggest a dicer-independent route for siRNAs production. Moreover, DCL3-independently produced siRNA possesses some unique features such as length being approximately of 20-60-nt and often differ by one nt at the 3’end compared with normally produced 24-nc siRNAs. The 21/22-nt siRNAs (generated from model one, Pol II), can associate with other nontarget mRNAs of TEs and thereby interfere with gene expression of nearest genes. In rice, siRNAs in the RdDM pathway methylate the global TE presence especially DNA transposon in the CHG and CHH cytosine sequence contexts and suppress the expression of nearby genes harboring double alleles following WGD. Also, siRNAs minimizing the transposition rate of TE, stabilize chromosomal integrity, down-regulate the expression level of neighboring genes and reduce the negative impact of genome-dosage resulting in the rapid adaptation of neo-polyploids to WGD (Zhang, Liu, et al., 2015). In mammals, PIWI-RNAs control a vast number of transcripts and lncRNAs related to the testis (Watanabe et al., 2015), it has been suggested that TE-induced sRNAs perform a variety of regulatory roles both in plants and animals (Watanabe et al., 2015).

2.3. TE-induced mechanisms contribute to crop adaptation and plasticity

2.3.1. Impact/modification on flowering time

During plant domestication, our ancestors placed an intense selective pressure on improving plant species leading to striking modifications of plant phenotypes. Evolution of new phenotypes such as the ability to adapt to low temperatures and alteration of flowering time (a trait that has universally received selective pressure in crop plants) helped plants move from tropical and/or semi-temperate to temperate climates eventually leading to the establishment of new ecotypes and cultivars (Olsen and Wendel, 2013; Song and Cao, 2017).

Vernalization, the exposure of a plant species/seed to a low temperature to produce flowering/trigger germination, is an excellent example of species adaptation to a new environment following migration (Figure 4). For example, the shift of spring to winter-type rapeseed on its migration from Southern to Northern Europe was accompanied by the insertion of the Tourist-like MITE element in the upstream- and intronic region of the BnFLC.A10 gene. Results showed that the allelic variation of this TE was the major cause of differentiation between spring and winter ecotypes. Furthermore, the winter ecotype evolved from the spring ecotype through selection pressure at the BnFLC.A10 locus during domestication (Hou et al., 2012). In another study on B. napus, researchers (Yin et al., 2020) found 4422-nt of hAT and 5625-nt of LINE insertion within BnFLC.A10 and a 810 bp insertion of MITE in BnFLC.A2. Consequences of these TE insertions modified gene expression patterns and resulted in differential responses to vernalization. Furthermore, the authors found the 621 bp insertion of a MITE element in the promoter region of BnFLC.A10 acts as a transcriptional enhancer and as such appeared to shape
rapeseed vernalization and adaptation. They also showed that when this above insertion (in the promoter of $BnFLC.A10$) was absent, then the functional allele of $BnFLC.A2$ primarily contributed the vernalization demand. To summarize, they concluded that a MITE insertion in the region upstream of $BnFLC.A10$ together with a functional allele of $BnFLC.A2$ are necessary for expression of the winter ecotype.

A recent study of the $B. napus$ pangenome (eight genomes including spring-, semi-winter- and winter-ecotypes) shed further insight into the role of TE species in the evolution of different ecotypes (Song et al., 2020). This study examined the structure of FLC gene homologues ($BnaA02.FLC$, $BnaA10.FLC$ and $BnaC02.FLC$) in the subgenomes of $B. napus$ (including those of its diploid progenitors $B. rapa$ and $B. oleracea$), which contains multiple copies and several homologues associated with flowering time. The results showed that four TE species inserted in the promoter and coding region of FLC homologue, $BnaA10.FLC$ were explicitly associated with the three different ecotypes. In spring-type cultivars No2127 and Westar, a 5,565-bp LINE transposon was identified in the first exon. In contrast, the four semi-winter types ZS11, Zheyou7, Gangan and Shengli carried a 4421-nt hAT-element in the promoter region, while the three winter-types Quinta, Tapidor and Darmour-bzh carried a 621-nt MITE insertion in the upstream region. Furthermore, there was also specificity of TE species within the semi-winter type, as a 1,656-nt LTR was only present in the promoter region of Shengli and Zheyou7. Interestingly, in Arabidopsis, TE insertions were recorded exclusively within the (single-copy) FLC locus and not in other flowering time related loci such as SUPPRESSOR of CONSTANS 1 (SCO1), FLOWERING LOCUS T (FT) and FLOWERING LOCUS D (FD). Reduction in the regulation of vernalization enables plants to adapt well under drought/hot summer areas and facilitates a rapid lifecycle, while conversely an increase in vernalization facilitates adaptation toward more northerly latitudes (Quadrana, 2020).

3. Polyploid robustness and TE-induced siRNAs

Polyploidy refers to the condition in which a diploid organism acquires one or more additional sets of
chromosomes or unreduced gametes. It occurs frequently in flowering plants, with nearly 70% of angiosperms having undergone at least one round of WGD in their progenitors, suggesting a selective advantage in the evolutionary terms (Soltis et al., 2009; Jiao et al., 2011).

Consequences of polyploidy appeared in the form of both short-term and long-term benefits. Short-term benefits include (i) masking of deleterious mutations, (ii) instant alterations in physical properties due to increased nucleus/cell size, and (iii) buffering against the transposition burst and its subsequent generation of large-effect mutations, whereas long-term benefits include (i) enhanced invasiveness and colonization potential, (ii) increased tolerance for self-pollination, (ii) deterioration in the purifying selection against the harmful mutations—enhanced the frequencies of beneficial alleles responsive to dynamic environment, and (iv) the opportunity to expand genetic variation via local introgression (as reviewed in (Baduel et al., 2018). Conversely, after WGD, entire sets of chromosomes also create some short and long term challenges such as meiotic disruption (i.e., alteration in chromosomes numbers or lack of intersubgenomic homology can lead to meiotic disorders), gene dosage effects, lack of suitable mates for de novo allopolyploids (especially when they are few in numbers), increased genetic load, deceleration of selection on beneficial mutations and growth rate (due to larger genome size), and diploidization (a cradle for diversification) (Comai, 2005; Madlung and Wendel, 2013; Baduel et al., 2018). Polyploidy enhances the meiotic recombination rate (homeologous and nonhomeologous exchanges) which is associated with an increase in both TE abundance and reshuffling of the genome (Bartolomé et al., 2002; Pecinka et al., 2011). Furthermore, WGD can lead to genome/chromosome reorganization, such as changes involved in major restructuring and epigenetic repatterning, mainly in TE-rich fractions of the genome. As such, allopolyploidy is the best model to investigate novel genetic variation occurring after genome combination (Vicent and Casacuberta, 2017). Type-specific proliferation and insertion of TE in subgenomes reshapes epigenetic mechanism (as we shall discuss in detail in following sections). Among the various subclasses of RTs, the most abundant are LTRs, which are mainly distributed in heterochromatic regions, while the less abundant DNA TEs are more common in gene-rich regions. In allopolyploids, the abundance of TE species is not the same for each subgenome (Ågren et al., 2016). As we explain below, the subgenomic TE-biased selection results in considerable variation in the controlling epigenetic mechanisms leading to gene evolution and diversification.

3.1. Impact of WGD on TE in polyploids

A sudden and massive increase of TEs following polyploidization could be demonstrated in several paleopolyploid plant species or more recent polyploids, including Z. mays (Jiao et al., 2017), B. napus (Sun et al., 2017), T. aestivum (Consortium, 2014) and C. bursa-pastoris (Ågren et al., 2016). Conversely, in some polyploids, such as in cotton, TE expansion occurred in the parents before the polyploidization event and their relative abundance remained unchanged globally after allotetraploid formation (Zhang, Hu, et al., 2015). The consequences of WGD in polyploids can be different in the various subgenomes. For example, in allotetraploid cotton, more structural changes have been recorded in the A subgenome compared to the D subgenome. Moreover, a higher number of TEs, a larger number of lost and damaged genes and a higher overall rate of evolution have been noted in the A subgenome. By contrast, centromeric RTs from the D subgenome occupied the same position on the chromosomes of the A subgenome following the allopolyploidy event. Very recently in Juglans regia (Zhang, Zhang, et al., 2020) genome duplication caused little to extensive gene expression divergence. In first case, the two copies of JreCHSubA and JreCHSubB encoding chalcone synthase, showed closely correlated gene expression, which may indicate that both copies were responsible for the biosynthesis of the flavonoids and that there was very little functional divergence. In the second case, JreSRGI, a gene involved in plant senescence, the copy on the A subgenome was normally expressed in immature fruit and somatic embryo, while the copy in subgenome B was not transcribed in these tissues. The changes in the promoter regions between these two copies which only display a sequence identity of 45% likely explain these expression differences.

The emergence of polyploidy resulted in the phenomenon of global subgenomic bias and dominance. Following polyploidy or hybridization-induced merging of divergent genomes, a form of “genomic shock” occurs, leading to a wide range of rapid genetic and epigenetic changes as a result of conflict between subgenomes. In this genomic tussle, one subgenome generally becomes dominant over the others leading to subgenomic bias regarding gene content, regulation and expression (Bird et al., 2018). This phenomenon
has been reported in *B. napus* and *Z. mays* (ref here). However, in *G. hirsutum* and *T. aestivum*, no genome dominance phenomenon has been reported (Pfeifer *et al.*, 2014; Harper *et al.*, 2016; Fang *et al.*, 2017). However, there is a strong correlation between genome that has been target for genomic selection and its domestication for positively selected genetic characters related to developmental and environmental traits that showed bias toward subgenomes (Zhang, Hu, *et al.*, 2015). Indeed, in cotton, the A subgenome showed positive selection toward genes related to fiber yield and quality, whereas the D subgenome carried signatures of selection related to stress tolerance genes (Fang *et al.*, 2017). In *B. napus*, it was suggested that the A subgenome-specific selection promoted stress tolerance, while ecotype improvement was mainly caused by asymmetrical selection within the C subgenome (Lu *et al.*, 2019).

As genome dominance is a heritable phenomenon (Woodhouse *et al.*, 2014), the dominant subgenome established upon the first polyploidy event (R1) remains dominant in the subsequent events (R2, R3 etc.). The changes occurring in gene expression balance is therefore largely dependent on the differences in TE abundance in the parents following the WGD event as hypothesized by (Woodhouse *et al.*, 2014). Moreover, it was demonstrated that the TE-induced siRNAs residing in the dominant subgenome impact on the level of gene expression of the recessive subgenome in *B. rapa* (Woodhouse *et al.*, 2014). However, it appears that increasing TE number does not result in a higher TE activity, possibly due to the relaxation of selective pressure and hybrid breakdown in the TE silencing mechanism (Springer *et al.*, 2016). In other words, TE transcription is not necessarily correlated to its mutagenic potential given that it also results in impairment of siRNA control systems (Ito *et al.*, 2011). For example in the allotetraploid *C. bursa-pastoris*, the enhanced TE contents in genic regions is likely the result of relaxed TE buffering (Ågren *et al.*, 2016). However, the situation is clearly complex as in *B. napus*, following the allopolyploidization of *B. oleracea* and *B. rapa*, the increase of TE content was reflected in enhanced TE activity (An *et al.*, 2014). Therefore, considerable further research is necessary before we reach a comprehensive understanding of the mechanisms underlying these changes.

In some cases, polyploidy may decrease the genomic population of TE elements (Renny-Byfield *et al.*, 2011). For example, in allotetraploid *Nicotiana* loss of TE elements was evidenced throughout the genome. Particularly prominent was the loss of all families of Ty3-gypsy RTs in *N. tabacum* compared with its parents. Moreover, a comparative analysis of allotetraploid *N. tabacum* with its diploid parents showed that sequence loss was more prominent from the paternal subgenome of *N. tomentosiformis* than from the maternal *N. sylvestris* subgenome. Given that, before tetraploidization, the female parent had experienced a recent TE burst and subsequent homogenization that may cause the biased genomic deletion from the male parent. The relaxation of epigenetic silencing mechanisms in the early generations following polyploidization induces TE transposition and recombination processes between/among TEs, resulting in novel phenotypes. However in later generations, TEs play a major role in regulating genome expansion by silencing local TEs through RdDM pathways (epigenetic regulation) and by promoting the association with chromatin modifications (Springer *et al.*, 2016). Generally, following polyploidization, TEs play an important role in reorganization to rebalance the genome after a WGD event (Vicient and Casacuberta, 2017). However, considerable research is needed on a case-by-case basis in order to gain deeper understanding of the role and relative importance of specific TEs within this process.

### 3.2. Impact of TE insertions on polyploid subgenomes

Following TE insertion, mutation occurred in gene and its expression regulation by TE-derived siRNA through various RdDM pathways, could not distinguish polyploids from their parental diploids. However, in *B. rapa* and Arabidopsis, TE-induced 24-nt siRNAs preferentially reside upstream of genes in the dominant subgenome with relatively little impact on the recessive subgenome (Woodhouse *et al.*, 2014). Furthermore, following polyploidization, the merging of the two subgenomes includes the bringing together of two sets of TEs. TE-derived siRNAs from one subgenome may methylate or silence or activate those from the other subgenome(s) (Cao *et al.*, 2003; Wierzbicki *et al.*, 2009; Matzke and Mosher, 2014; Fultz *et al.*, 2015) (Figure 4). Such interplay constitutes the so-called “trans-effect”. Polyploids containing two or more sets of related genomes appear to add additional TE roles and impose complicated multigenome interactions on the TEs. Such a role of TEs is particularly noticeable in relatively recent polyploids which have become major crops such as wheat, oilseed rape, cotton and peanut which contain high TE contents (ranging from 50 to 80%) (Cantu *et al.*, 2017).
2010; Wang et al., 2016; Sun et al., 2017). Given the prevalence of polyploidy in plant evolution, such complex levels of interaction are also apparent in many diploids such as maize, soybean, and cabbages (B. oleracea, B. rapa) which are all paleopolyploids with clearly detectable and quite complete subgenomes (Shoemaker et al., 2006; Lee et al., 2012; Schnable et al., 2012; Liu, Liu, et al., 2014).

### 3.3. Specific TE activities in polyploids

As described above, mobile TEVs contribute as a primary source of genetic and genomic variation. They can cause chromosomal shuffling or rearrangements through chromosomal recombination, and hence may regulate closely linked genes. (Bennetzen and Wang 2014). Apart from the fact that TEVs have the hallmarks of selfish DNA, the host organism/cells may co-opt TEVs in order to modify existing genes or create novel ones. A considerable number of studies have shown TE activation following hybridization and polyploidy as reviewed in (Feliner et al., 2020) but much less is known concerning how the different types of TEVs respond to process of hybridization and what are the consequences of their insertion sequence on gene function. That said, a study by An et al. (2014) addressed these questions and reported the effect of allopolyplody between B. oleracea and B. rapa in multiple self-pollinated generations. By designing 92 different TE primers amplifying 548 loci in order to detect polymorphism among RTs, they showed successively decreasing levels of genetic variation created by novel mutations from LTR-RTs > TIRs > LINEs > SINEs and that these variations were higher from F1-F2 than from the later generations F3-F5 (An et al., 2014). Moreover, specific TE classes may infect and proliferate within one genome or subgenome. For example, a comparative analysis of allotetraploid Aegilops spp. such as Ae. crassa, Ae. cylindrica, Ae. geniculata, Ae. triuncialis with their diploid progenitors such as Ae. tauschii, Ae. caudata, Ae. comosa, and Ae. umbellulata revealed that Gypsy-like RTs are more likely to be active in new tetraploids than diploids whereas other classes remain silent. This effect may also be associated with particular parental species, for example, Sabine RTs is more abundant and diverse in Ae. cylindrica but massively eliminated in Ae. geniculata, whereas they appear to be inactive in other polyploid species. Interestingly, the molecular mechanism behind the deletion of the above RTs in Ae. geniculata remains ambiguous, however, specific elimination of Sabine insertions cannot simply occur due to an illegitimate recombination (Devos et al., 2002; El Baidouri and Panaud, 2013) but also due to homeologous recombinations. Thus, the effects of WGD/polyploidization may differ both among subgenomes and within specific TE families. Hence, variations in the abundance of repetitive elements upon polyploidization can result in changes to genome structure, gene expression and developmental traits. As reviewed in (Chen, 2007) repetitive elements may be responsible for variation in characters including inbreeding depression, hybrid vigor, diploidization and apomixis. The transition from the formation of a neopolyploid to a stabilized species involves modifications in the chromatin material, cis- and trans-acting effects. RdDM, and other regulatory pathways controlling expression pattern of homeoeologous genes resulted in noticeable phenotypic alteration that may trigger the genetic diversity and adaptive radiation (Chen, 2007). Moreover, regulatory mechanisms within one genome can be different for a TE species and it also depends on TE numbers, location on the chromosome as well as the promoter sequences. For instance, TEVs commonly regulated at the promoter region by DNA methylation. As we know, TE control efficiency may vary among species because of differences in siRNA numbers and governing/methylation procedure (Vicient and Casacuberta 2017).

### 3.4. Interaction of TE-derived siRNAs in silencing polyploid subgenomes

It is reasonable to infer that subgenomic sets of TE-derived siRNAs may methylate, silence or activate the other similarly localized TEVs residing in the other subgenome(s) (Cao et al., 2003; Wierzbicki et al., 2009; Matzke and Mosher, 2014; Fultz et al., 2015). Following allopolyplidization, novel and important genome-wide interactions occur between the two different suites of siRNAs and TEVs. These heterochromatic siRNAs function to suppress TEVs in both cis- and trans-, so that TEVs are no longer able to mobilize freely like they do in their two parents (Wendel et al., 2016). In synthetic autotetraploid rice, there is variation in siRNA expression associated with TEVs located within the 4-kb flanking region of genes (Zhang, Liu, et al., 2015). Interestingly, within the same mentioned-above region, class I TEVs showed no changes in siRNA abundance for a few methylation marks, whereas there were significant changes in class II TEVs (i.e., MULE_MUDR, Harbinger, Stowaway and DNA-Other) as compared with diploid rice. These four types of DNA transposons were more likely to
surround genes and were hypermethylated in CHG and CHH sequence contexts. Furthermore, the expression level of siRNAs was reported to be higher in tetraploid than in diploid rice and was also consistent with siRNA suppression of genes following WGD.

An exciting study by (Zhang, Tao, et al., 2016) demonstrated that TE-derived siRNAs causes allelic variation with opposing functions that can contribute to adaptation to disease resistance in rice. In detail, they showed effects on the transcription factor WRKY45, which globally regulates the resistance mechanism to bacterial disease caused by *Xanthomonas oryzae*. At the WRKY45 locus, the two alleles WRKY45-1 (Os05g257770, a transcription factor on the chromosome 5) and WRKY45-2 are differing by the insertion of two similar MITE-like elements of 500-nt in the intron of first allele. Results showed that attack of pathogenic *X. oryzae* induces the expression of WRKY45-1, the TE is hijacked, and the expressed small RNA (osa-miRNA185) then processed to a siRNA, TE-siR185, which is mainly 24-nt in length. This TE-siR185 could target a homologous ectopic TE of another locus for methylation via RdDM consequently interferring with the expression of the host gene ST1 (Os08g10150, a leucine-rich repeat receptor kinase-type protein on the chromosome 8) harboring target TE. The methylated TE suppresses the expression of its host gene ST1, hereby becoming inactivated due to the pathogen attack. By contrast, the allelic line carrying WRKY45-2, which did not have the TE insertion, exhibited normal resistance to the pathogen (Zhang, Tao, et al., 2016). We speculate that this working mode of TE-siRNAs might be common for all subgenomic interactions, given that a majority of TE families are shared in allopolyploids (Figure 5).

Our understanding of the roles that TEs play in the interactions between polyploid subgenomes is still fragmentary. Most studies to date have shown expression divergence amongst polyploid homoeologous genes (Zhang, Gou, et al., 2020). In order to develop a deeper understanding, it is important to investigate TEs and subgenome interactions over different time-scales. The modern domesticated *Brassica* allopolyploids provide a useful framework for such studies, because it is possible to regenerate synthetic allopolyploid hybrids among the diploid species of “U’s Brassica Triangle” (Nagaharu, 1935). For example, in comparing the progenitor diploids *B. rapa* (AA genome) and *B. oleracea* (CC genome), with the recent allopolyploid *B. napus* (AACC) (Chalhoub et al., 2014), it was found that, of 29,736 homoeologous gene pairs, at least one homoeolog was expressed in at least one tissue. Thus in 4,665 (15.7%) and 5,137 (17.3%) gene pairs, homoeolog C_n or A_n contributed more, respectively, demonstrating biased expression in both tissues. In root, leaf, flower and silique tissues from the other reference genome of the *B. napus* cultivar ‘ZS11’, 32 to 40% of the homoeologous genes diverged regarding expression ratios (>2 or <1/2, FDR < 0.001 and p-value <= 0.05) (Wang and Elgin, 2011; Chalhoub et al., 2014; Liu, Liu, et al., 2014). Also, in a parallel comparison of homoeologous gene pairs among synthetic allopolyploids, 26–31% of A_n and C_n duplicated genes displayed homoeolog bias expression levels toward A or C genome, and nearly half of them were shared among different hybrids (Zhang, Pan, et al., 2016). Among different subgenomes derived from the Brassicaceae-lineage-specific whole-genome triplication (WGT), occurring ~ 15 MYs ago, significant ‘genome dominance’ is observed in all extant Brassica species including *B. rapa*, *B. oleracea*, and *B. napus* (Wang et al., 2011; Cheng et al., 2012; Liu, Liu, et al., 2014). The analysis of RNA-seq data generated from callus, root, leaf, stem, flower, and silique of *B. oleracea*, *B. rapa* and *B. napus* revealed that the genes in the less fractioned subgenome (LF, which experience less deletion of duplicated genes following WGD) were dominantly expressed over their paralogs/orthologs in more fractioned subgenomes (MF1 and MF2). Similarly, there is evidence for biased gene expression in less fractionated genome regions in many other paleopolyploids, including *B. rapa* and *Zea mais* (Schnable et al., 2011; Cheng et al., 2012; Tang et al., 2012).

### 3.5. Polyploidy reshapes the TE-induced siRNAs epigenetic mechanism

Polyploidy contributes to reshuffle and reshape the genome, providing the opportunity for enhanced adaptability through the rewiring of gene regulatory networks (Adams and Wendel, 2005). After WGD, dramatic mutations occur that can impact cell and subsequently whole organism size, genomic stability, gene expression and evolutionary rate (Soltis and Soltis, 2009; Jiao et al., 2018). Moreover, polyploidization in both auto- and allopolyploids may frequently cause genomic instabilities, chromosome imbalances, regulatory incompatibilities and/or reproductive failures, especially in cases where genome dosage responses are ineffective (Chen, 2007).

With the advance of next-generation sequencing techniques, more and more studies are providing deep insights on the alterations polyploidization might have
in genome restructuring and epigenetic repatterning, with profound effects on the TE fractions (Parisod and Senerchia, 2012; Zhang, Liu, et al., 2015). The variation in the underlying mechanism of DNA methylation and its impact on neighboring genes on genome doubling can be observed in newly formed autotetraploid rice (Zhang, Liu, et al., 2015). This study showed that hypermethylation of DNA TE appeared predominantly in CHG and CHH sequence contexts and was accompanied by changes in siRNA abundance following WGD. This suggested a role of the RDdM pathway to methylate DNA TE, resulting in suppressed expression of nearby genes with double alleles (“bi-allelic” gene expression, when both copies of a gene are actively transcribed and if one copy transcribed is termed as “monoallelic”). Changes in the epigenetic mechanism following polyploidy is not always the same in all polyploids. For instance, in nascent allopolyploids of Spartina anglica (fam. Poaceae) the cytosine methylation occurring in CpG contexts was abundant near TE insertion sites (Parisod et al., 2009). Moreover, more obvious genome-wide changes and TE methylation were apparent in the maternal subgenome. This interesting finding indicated that merging of divergent genomes resulted in TEs fueling epigenetic changes (Parisod et al., 2009; Yaakov and Kashkush, 2010). In the case of bread wheat (allohexaploid T. aestivum), the methylation changes that transcriptionally demethylated TE occurred predominantly in early generations (1-4) and abundantly in CpG contexts in the vicinity of TE insertions (Yaakov and Kashkush, 2010); up to 54% CpG sites were flanking to the three DNA TE species Balduin, Apollo, and Thalos. This finding suggested that allopolyploidization induced a high level of methylation alterations in regions flanking by DNA transposons compared to other genomic regions. To gain further insight on the role of polyploidy in reshaping epigenetic mechanism, we have the excellent example of hexaploid Brassica (B. juncea, AABB × B. oleracea, CC) generated via grafting (Cao et al., 2016). Results indicated that the polyploidization induced siRNAs which changed the demethylation pattern, and changes were prominent in both the TE and exonic regions. Moreover, these changed siRNAs altered the expression pattern of genes associated to flowering time and gibberellin. However, this trend can survive only for a few generations before returning to its original methylation state via the process of TE buffering (Zhang, Liu, et al., 2015). As discussed above, the epigenetic mechanisms controlling TEs following polyploidization alter the chromatin behavior, decrease the expression level of nearby genes, and increase their copy number. Changes that occur in this manner have been demonstrated to be heritable (Vicent and Casacuberta, 2017).

The variation in the expression levels of duplicated genes in allopolyploid subgenomes may be due to differences in their male and female parents, a phenomenon defined as maternal dominance (Alaniz-Fabián et al., 2020). This is more common in ancient polyploids, such as wheat, than in newly formed ones (Feldman et al., 2012), indicating that the establishment of genome dominance needs several generations (Woodhouse et al., 2014). TE buffering (TE silencing) mechanism is usually affecting only one of the subgenomes, and because of this, the female parent may contribute to the siRNAs that repress TE (of male
parent) resulting in a higher repression occurred in the paternal subgenome, probably in early generations after polyploidization (Zhang, Liu, et al., 2015). Besides, as the abundance of 24-nt siRNAs are different in two subgenomes. For example, in a stabilized allopolyploid, if one parent has more TEs and a greater fraction of TE are specifically located in the proximity of genes then that subgenome usually becomes recessive and the epigenetic machinery to regulate TE is inherited from the dominant subgenome. Genome dominance also relies on biased fractionation (BF) following WGD, the frequency of fractionation (gene loss) in duplicated genes or gene regions negatively correlated with gene expression, and overexpression of genes occur more in LF regions than in MF ones (Renny-Byfield et al., 2014). Further, BF provides the variable TE location effect, for instance, the down-regulation of gene expression induced by endogenous TEs can be different between co-existing subgenomes (in a nucleus) that may drive the biased gene expression between/among overlapping (duplicated) regions (Woodhouse et al., 2014; Renny-Byfield et al., 2015; Liang et al., 2017). Moreover, in B. rapa TE-induced 24-nt siRNAs preferentially target the TEs present in the recessive subgenome (Woodhouse et al., 2014). Further, in the recessive subgenome TE-induced siRNAs could mutate/alter the less transcribed gene more easily without impacting the phenotype. However, if such phenotypic changes are more visible, then it may highlight the genetic diversity existed in that parentage.

The consequences of WGD can, however, at least in some occasions, be reversible. This is evident in several plant species where diploidization process was initiated. The process might have started due to the fractionation of duplicated genes in the recessive subgenome (due to the so-called “subgenome dominance”, a phenomenon in which one subgenome preferentially retained more duplicated gene blocks of ancestral duplicated genes and showed biased gene expression) resulting in LF and MF (Salse, 2016). Such biased fractionation after WGD, for instance, has been observed by (Woodhouse et al., 2014). Moreover, scientists reported that epigenetic mechanisms based on 24-nc targeted TEs (in their 1kb flanking region) were less prominent in genes present in LF region compared to the MF region (Woodhouse et al., 2014; Cheng et al., 2016). So, we can say that epigenetic influence will be in general higher on the expression of nearby genes of the recessive subgenome. Because autopolyploids are less diverse than allopolyploids (Cheng et al., 2016), and do not experience genome dominance and biased fractionation, so we can assume that the TE-induced 24-nt siRNAs activity can bring more phenotypic changes in duplicated genes produced by the event of allopolyploidy compared to that of autopolyploidy.

4. Closing remarks and future perspective

Appreciation of the functional significance of TEs has developed greatly since their early definitions as junk DNA, selfish (Dawkins, 2016) or genomic parasites (McLaughlin and Malik, 2017). Upon transposition, TEs have the capability to induce mutation in the host gene altering its function. This mutagenic capacity of TEs has been used to develop useful genetic tools such as the collection of Ac/Ds mutants in popular (Fladung and Polak, 2012), rice (Xuan et al., 2016) and Candida albicans (Mieli et al., 2018a). TE insertion on host plant genomes and their interactions contributed in several ways to gene expression regulation through both cis- (landing in the flanking region and impacting the nearby genes) and trans-acting mechanisms (producing siRNAs and then epigenetically silencing the TEs at the TE active locus via RdDM pathways). Direct insertion of a TE in a gene coding region can lead to structural variation through insertions/deletions (indels) and/or subsequent duplications, resulting in altered gene function.

WGD following polyploidization increased TE contents massively and then allowed recombination to occur between and among TEs; as a consequence of wide scale mutation in genes, gene loss and restructuring of genome occurred. As such, polyploidization results in a balancing of the plant genome. As a result of hybridization, the merging of two different subgenomes additionally results in the merging of two sets of TEs. TEs from both subgenomes subsequently induce the siRNAs to regulate subgenomic complexities. Usually, siRNAs from the dominant parent impact on TEs located at nearby genes as well as targeting the ectopic homologous TE residing at a distant locus of the recessive parent. This subgenome cross-talk not only refines the gene expression in polyploid plants but can also create novel genes. However, siRNA-based epigenetic control by RdDM does not distinguish between diploids and polyploids.

Glossary

Apomixis: Asexual formation of the seed of flowering plants without meiosis and fertilization.

Bias fractionation: Mechanism following WGD where one chromosome is targeted for more events of gene loss with respect to its homologous.
**Cis-effect/Trans-effect on gene expression:** Cis-effects caused by those regulatory elements that are located on the same DNA molecule where is the target gene. On the other hand, the trans-effect mutations affect gene expression in a diffusible manner, such as transcription factors.

**Diploidization:** The process of transforming a polyploid genome back into a diploid state.

**DNA methylation:** It is an epigenetic mechanism in which a methyl group (CH₃) is attached to DNA molecule resulted in the gene modification and changing gene expression.

**Hybrid vigor (or heterosis):** The increase of yield/biomass in the hybrid with respect to its parental genotypes.

**Least fractionation (LF):** If 70% of genes in each subgenome showed collinearity with Arabidopsis following polyploidy is called least fractionated blocks and the phenomenon is least fractionation.

**Medium fractionation (MF1):** If 46% of genes in each subgenome showed collinearity with Arabidopsis following polyploidy is called medium fractionated blocks and the phenomenon is medium fractionation.

**Most fractionation (MF2):** If 36% of genes in each subgenome showed collinearity with Arabidopsis following polyploidy is called most fractionated blocks and the phenomenon is most fractionation.

**Post-transcriptional gene silencing:** It is an RNA degradation mechanism in which dsRNAs spread throughout the genome in an organism from their initiating loci and processed into siRNAs by the help of RDRs, RNA helicases and other proteins that silence TE or other DNA molecules.

The control of gene expression in a cell to inhibit the expression of a certain gene at the translation stage (occurred in cytosol) is post-transcriptional gene silencing.

**Subgenomic bias/dominance:** The differences in the patterns of gene loss, gene expression and DNA methylation between the subgenomes of a polyploidization event.

**TE buffering:** TE burst often creates deleterious mutations and that in accumulation enhanced the fitness cost of a species. At whole genome level TE induced the buffering mechanism that deteriorate the negative impact of deleterious mutation hence reduced the fitness cost.

**TE silencing:** It is the form of transcription gene silencing (TGS). In TGS mechanism, DNA methylation (mainly by the involvement of siRNAs) and histone modification repress the TE transcription/particular part of a DNA.

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