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Environmental stress and transposons in plants

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Transposons were once thought to be junk repetitive DNA in the genome. However, their importance gradually became apparent as it became clear that they regulate gene expression, which is essential for organisms to survive, and that they are important factors in the driving force of evolution. Since there are multiple transposons in the genomes of all organisms, transposons have likely been activated and increased in copy number throughout their long history. This review focuses on environmental stress as a factor in transposon activation, paying particular attention to transposons in plants that are activated by environmental stresses. It is now known that plants respond to environmental stress in various ways, and correspondingly, many transposons respond to stress. The relationship between environmental stress and transposons is reviewed, including the mechanisms of their activation and the effects of transposon activation on host plants.

Key words: transposon, environmental stress, plant, epigenetics

INTRODUCTION

The genomes of all living organisms, including humans, contain transposons, which are mobile genes. Transposons, also called transposable elements, can replicate or move specific DNA sequences from one genome locus to another. How they acquired these unique features is not yet clear, but similarities with the structure of virus-like DNA sequences have led some researchers to believe that they originated from viruses (Hayward, 2017). One notable difference from viruses is that transposons are not infectious. In other words, while viruses move between cells, transposons do not transfer between cells but only move around the genome in a single cell. Transposons are present in multiple copies in the genomes of all organisms, suggesting that they have undergone repeated amplification and selection over a long period. Many extant transposons have mutations within their genes and can no longer transpose. These transposons are like extinct volcanoes. On the other hand, some transposons that still retain the ability to transpose have been reported in many species. These transposons are like dormant volcanoes that are activated by some trigger.

What is the trigger for their activation? This review focuses on environmental stress as one of the factors that can activate transposons. Plants are thought to be better adapted to cope with environmental stresses than animals because their growing environment cannot be substantially altered by moving around like animals. I will discuss environmental stresses in more detail later, but begin with a general description of transposons found in plants.

TRANSPOSONS IN PLANTS

Transposons can be divided into two major groups based on the characteristics of their moving style (Wicker et al., 2007). The first group is retrotransposons, which use their encoded reverse transcriptase to synthesize DNA from RNA, thereby increasing the copy number of transposons. This moving style is generally referred to as a copy-and-paste type of transposition. Retrotransposons are especially abundant in plants and are often a major genome component. For example, in maize, retrotransposons comprise 80% of the genome (Jiao et al., 2017), and in wheat, 90% of the genome (Charles et al., 2008). According to their DNA sequence structure, retrotransposons can be classified into several types: those with long terminal repeats (LTRs) at both ends of the DNA sequence are called LTR-type retrotransposons, and the remaining non-LTR retrotransposons are further divided into two types named LINEs and SINEs (long and short interspersed nuclear elements, respectively). The two kinds of non-LTR retrotransposons are also found in

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large copy numbers in plants. Some of these non-LTR retrotransposons are autonomous, capable of producing the enzymes necessary for transposition on their own, while others are non-autonomous copies.

The other group is called DNA-type transposons, which take the so-called cut-and-paste moving style by cutting themselves out of their original position and moving to a new location on the genome (Sahebi et al., 2018). For DNA-type transposons to move, they need transposase, which is encoded by the transposon itself. The transposon has an inverted repeated sequence at each end, and the transposase recognizes this sequence and cuts the transposon out of the genomic sequence. The transposon is then reinserted into the new genomic sequence. Several DNA-type transposons in plants are also active, and some are used as essential breeding tools. Details will be explained later.

TRANSPOSONS ACTIVATED BY ENVIRONMENTAL STRESS IN PLANTS

Plants inhabit a large area of the Earth. Most plants produce the nutrients necessary for their growth through photosynthesis, and flowering plants pass to the next generation as seeds. Plants in the seed phase can move over a wide area, but they cannot move like animals once they have landed and rooted. While the basic life cycle is common among plant species, their growing environments vary, from icy regions to the tropics and deserts. Although plants are highly adaptable to such environments, transient changes in their growing environment are stressful for them. Here is an introduction to the types of environmental stresses in plants and to the transposons activated by these stresses.

The terms "biotic stress" and "abiotic stress" are often used when considering stress on plants. Biotic stress, as the term implies, is stress that is exerted on plants by other organisms, including weeds, pathogens and insect pests. Abiotic stress, on the other hand, includes drought, salt, high temperatures, low temperatures, ultraviolet radiation, high light intensity and an excess or deficiency of certain nutrients. When plants are exposed to these stresses, changes occur in various factors in the genome (Shinozaki et al., 2003). Sometimes the scale of these changes is such that chromatin structure is altered, while at other times they result in changes in the expression of specific genes (Kim, 2021). These latter transient changes are epigenetically regulated, and transposons are known to be activated during this regulatory response. I will first explain which transposons are activated by environmental stresses in plants before describing the mechanism of transposon activation.

Regarding the activation of a transposon, there are two stages of activation. The first stage is activation at the transcriptional level, and the second is activation at the transpositional level. Some transposons that are transcriptionally activated by environmental stresses encode full-length enzymes that are required for transposition. In such cases, transposition of the transposon is observed. It is important to note that not all transposons that show activation at the transcriptional level will transpose. Therefore, when discussing the activation of a transposon, it is necessary to separate these two stages of activation. The majority of environmental stress-responsive transposons in plants are retrotransposons. Specific retrotransposons reported to date that are transcriptionally activated by environmental stresses are summarized in Table 1. Many other retrotransposons are also activated by environmental stress. For example, the transcriptional activity of diverse retrotransposons has been observed in rice under drought and salt stress (Jiao and Deng, 2007). Various retrotransposons are also activated in arabica coffee trees under drought stress (Lopes et al., 2013). Recently, genome-wide analysis has become possible in various plant species, and it has been reported that LTR-type retrotransposons in sunflowers are activated by phytohormone-induced abiotic stress (Mascagni et al., 2020). Retrotransposons are also reportedly activated in poplar by drought, cold or high-temperature stress (Vangelisti et al., 2019). Stress-induced activation of retrotransposons was also reported in conifers. Several retrotransposons are activated by heat stress, abscisic acid and salicylic acid treatment in Scots pine (*Pinus sylvestris* L.) (Voronova et al., 2014). Heat stress experiments showed that some *Ty3/gypsy* retrotransposons were more highly expressed than other retrotransposons in cedar (Ujino-Ihara, 2020). Another example of stress-responsive retrotransposons was reported in Aleppo pine (*Pinus halepensis* Miller) (Fox et al., 2018). Activation of both *Ty1/copia* and *Ty3/gypsy* retrotransposons was found in the recovery process after 46 days of irrigation suspension. Retrotransposons are activated by high-temperature stress not only in land plants but also in the Mediterranean seagrass *Posidonia oceanica* (Vangelisti et al., 2020). Plant stresses include tissue culture, callus formation and stresses during the creation of hybrids through crossbreeding, and other reviews should be consulted for more information on these stress responses (e.g., Negi et al., 2016).

MECHANISMS OF TRANSPOSON ACTIVATION BY ENVIRONMENTAL STRESS IN PLANTS

Two effective mechanisms exist for the activation of transposon transcription by environmental stress. The first is that environmental stresses induce transcriptional activation through the interaction of specific transcription factors with the promoter sequence of the transposon. Various specific DNA elements associated with particular molecules that initiate different stress

Table 1. Stress-activated transposons in plants

Plant species	TE	Group	Stress	Evidence for mobility	References
Arabidopsis thaliana	*Athila*	Gypsy	Heat	No	Buchmann et al., 2009
	AtCopeg1	Copia	Nutrition starvation, salt, cytokinin, abscisic acid	No	Duan et al., 2008
	At2G06045	Copia	Salt, osmotic stress, cold, heat, abscisic acid	No	Zeller et al., 2009
	ONSEN/*Atcopia78*	Copia	Heat, high-intensity light	Yes	Tittel-Elmer et al., 2010, Matsunaga et al., 2012
	AtGP1, *EVD*	Copia	Elicitation with bacterial flagellin	Yes	Yu et al., 2013
Citrus limon	*CLCoy1*	Copia	Wounding, salt	No	De Felice et al., 2009
Citrus sinensis	*CIRE1*	Copia	Wounding, auxin	No	Rico-Cabanas and Martínez-Izquierdo, 2007
	Tcs1, *Tcs2*	Copia	Cold	No	Butelli et al., 2012
Cucumis melo	*Reme1*	Copia	UV light	No	Ramallo et al., 2008
Hibiscus syriacus	*HRET1*	Gypsy	Wounding	No	Jeung et al., 2005
Hordeum vulgare	*BAGY1*	Gypsy	Senescence	No	Ay et al., 2008
	BARE-1	Copia	Abscisic acid	No	Suoniemi et al., 1996
	OARE1	Copia	Salicylic acid	No	Kimura et al., 2001
Nicotiana tabacum	*Queenti*	Copia	Cryptogein (fungal elicitin), hydrogen peroxide	No	Anca et al., 2014

response signals, such as phytohormones and elicitors, have been conserved in the 5′ LTR of plant retrotransposons (Casacuberta and González, 2013). These regulatory sequences are similar to well-known motifs that are required for activation of stress-responsive genes. One example is *ONSEN*, a retrotransposon found in *Arabidopsis thaliana* and activated by high-temperature stress; transcription of *ONSEN* is activated upon exposure to 37 °C (Ito et al., 2011). The 5′ LTR of *ONSEN* contains a *cis* sequence called the heat shock element (HSE), and binding of a heat shock factor to the HSE allows *ONSEN* to respond to high-temperature stress (Cavrak et al., 2014).

The other mechanism is that transposon sequences, which are suppressed by epigenetic modifications including DNA methylation under non-stress conditions, are turned on by changes in epigenetic modifications that arise from environmental stress. Plants show changes in epigenetic modifications due to environmental stresses. As a result, various gene expression patterns change, including transposons (Kumar et al., 2013). It is expected that the heterochromatin state will loosen, and transcription factors will become more accessible. Here, I describe DNA methylation levels that are altered by stress, and transposons and their stress responses in host plants. In tomatoes, it has been reported that an LTR-type retrotransposon called *Rider* is transcriptionally activated by drought stress and abscisic acid and that DNA methylation regulates this activation (Benoit et al., 2019). *Tam3*, a DNA-type transposon of *Antirrhinum majus*, is markedly activated at low temperatures (15 °C) and almost completely inactivated at high temperatures (25 °C). This characteristic of the transposon in response to low-temperature stress is unique to *Tam3* but is found to be tightly related to DNA methylation. Fifty copies of *Tam3* are present in the *Antirrhinum majus* genome and one transposed copy was identified. Methylation of the 3′ terminal region of the *Tam3* sequence was found to be low at low temperatures and high at high temperatures, and the changes were reversible with temperature shift and restricted to this region. In addition, the *Tam3* transposase did not bind to methylated DNA. Thus, reversible methylation of the *Tam3* terminal region was found to be closely related to the temperature-sensitive transposition of *Tam3* (Kitamura et al., 2001).

EFFECTS OF ACTIVATED TRANSPOSONS IN HOST PLANTS

There are many known examples of transposons in genomes regulating gene expression in the host. Some transposon-like sequences are reported to regulate the expression of neighboring genes through epigenetic modifications, even though they have already lost the ability to transpose (Gazzani et al., 2003; Lippman et al., 2004; Martin et al., 2009; Sasaki et al., 2012). In this section, the relationship between stress-responsive transposons and the host genome will be highlighted.

A rice transposon, *mPing*, was the first MITE (miniature inverted-repeat transposable element) with transpositional activity to be recognized in plants and animals and is actively transposed in the rice variety 'Ginbouzu' (Jiang et al., 2003; Nakazaki et al., 2003). While all common Japanese rice cultivars, including 'Nipponbare', have around 50 copies of *mPing*, more than 1,000 copies exist in 'Ginbouzu' due to its active transposition. It has been shown that *mPing* has high transposition activity even under normal growing conditions in the rice variety 'Ginbouzu' and that it is easily transposed to the gene region. In addition, genes with *mPing* insertions in their promoter region tend to confer low-temperature or salt stress responsiveness (Naito et al., 2009). It is currently believed that part of the sequence within *mPing* functions as a stress-responsive transcriptional regulator and controls downstream gene expression as a selective promoter.

A MITE inserted into the promoter of the NAC gene *ZmNAC111* is associated with spontaneous variation in maize drought tolerance (Mao et al., 2015). The 82-bp MITE, when expressed in Arabidopsis, suppresses *ZmNAC111* expression via RNA-directed DNA methylation and histone (H3K9) demethylation. Interestingly, the MITE insertion into the *ZmNAC111* promoter appears to have occurred after maize domestication. Identifying the MITE insertion provides insight into the genetic basis of natural variation in maize drought tolerance.

Transposons can affect gene regulation on a genome-wide scale by carrying potential transcriptional regulatory signals. Examination of the poplar methylome at single-nucleotide resolution using high-throughput bisulfite sequencing revealed that methylation levels of transposons in the promoter regions of genes increase under drought stress conditions (Liang et al., 2014). Transcription factor genes whose methylation and expression increase with drought treatment may play an important role in the drought stress response of poplar through changes in DNA methylation.

Stress-responsive transposons can sometimes have negative effects on host plants. In Arabidopsis, activated *Athila* retrotransposons produce small interfering RNAs (siRNAs) in *trans* that regulate stress response genes. When the *Athila* transposon is activated, homologous siRNAs increase (Slotkin et al., 2009). One of these siRNAs can repress the stress response gene *UBP1b* in *trans*; *UBP1b* is activated under stress conditions, and repression of *UBP1b* by *Athila* may negatively affect the host.

SUMMARY AND PERSPECTIVES

Transposons are present in the genomes of all organisms, not just plants. Furthermore, the complement of transposons is not a single sequence but multiple copies forming a family, suggesting that transposons have been activated and have transposed throughout the long history of living organisms. Environmental stresses may be involved in transposon activation, and activated transposons affect the regulation of gene expression in the host genome (Fig. 1). It is important to remember that dramatic environmental changes are also expected

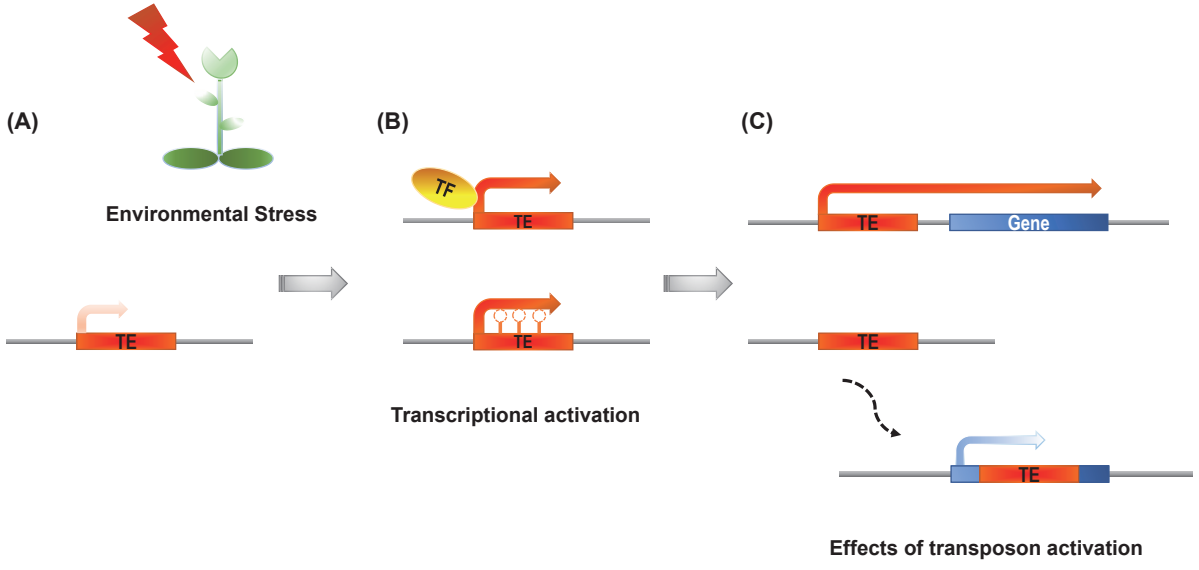

Fig. 1. The relationship between environmental stress and transposons. (A) Under normal conditions, transcription of most transposons (transposable elements; TEs) is turned off or very low. (B) When plants are subjected to environmental stress, stress-responsive transcription factors (TFs) bind to the promoter regions of TEs and increase the transcription of TEs. Environmental stress also increases the transcription of TEs by altering epigenetic modifications of TEs. (C) Activation of TEs causes changes in the expression of nearby genes. Some TEs also transpose, altering the expression of genes into which they are inserted.

to activate many extant transposons, and transposons are likely to be the driving force of genome evolution (Fedoroff, 2012; Lisch, 2013). Their roles are to serve as a source of mutation in plant genomes, to regulate gene expression in host plants and to be a transient information delivery system via siRNA. It is now becoming clear that transposon sequences, previously thought of as junk DNA, can play a great variety of biological roles.

Most of the transposon-mediated stress responses presented in this review are responses at the transcriptional level. There are few reports on the relationship between transpositional activity and environmental stress responses (Hashida et al., 2003; Ito et al., 2011). One reason for this is that there is no established method to efficiently detect retrotransposon transpositions in real time. If transposition occurs in a cell that is the source of a particular tissue in a plant, and that cell divides and multiplies, new transposon copies can be detected in every somatic cell that is derived from that single cell, but it is challenging to find new transpositions when analyzing DNA extracted from tissues comprising cells both with and without newly transposed transposons. Therefore, only when genomic DNA with a new insertion is passed on to germline cells will the insertion sequence be detectable in all cells of the next generation of individuals.

There are known to be preferential insertion sites for transposons. Some transposons are more likely to insert into heterochromatin regions, while transposition of others is biased toward euchromatin regions. What determines these biases is unknown, but the histone variant H2A.Z reportedly plays an important role in the preferential incorporation of *Ty1*/*copia* retrotransposons into environmentally responsive genes and exclusion from essential genes (Quadrana et al., 2019). The involvement of epigenetic modification marks in determining the insertion sites of such transposons is of interest, and it will be crucial to investigate how these marks change under environmental stress. In Arabidopsis, experiments with mutants of DNA methylation have reported the activation of several transposons (Hirochika et al., 2000; Miura et al., 2001; Mirouze et al., 2009; Tsukahara et al., 2009). Therefore, understanding how environmental stresses alter epigenetic modifications in plants will provide a critical perspective in understanding the mechanisms of transposon regulation by plants in nature.

As noted above, transposons are present in all plants. If we can artificially manipulate transposons in agriculturally important plants, we will be able to select valuable traits more efficiently in a shorter period than in the past, when such traits were selected by crossbreeding. Another advantage of breeding with endogenous transposons is that the improved crop will not be a GMO, and transient stress would control the transposition of transposons artificially. In the future, we expect to apply our research findings using model plants to the breeding of important crops, thereby unlocking the natural potential of plants.

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