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REVIEW PAPER

# The role of transposable elements in the evolution of aluminium resistance in plants

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## Abstract

**Aluminium (Al) toxicity can severely reduce root growth and consequently affect plant development and yield. A mechanism by which many species resist the toxic effects of Al relies on the efflux of organic anions (OAs) from the root apices via OA transporters. Several of the genes encoding these OA transporters contain transposable elements (TEs) in the coding sequences or in flanking regions. Some of the TE-induced mutations impact Al resistance by modifying the level and/or location of gene expression so that OA efflux from the roots is increased. The importance of genomic modifications for improving the adaptation of plants to acid soils has been raised previously, but the growing number of examples linking TEs with these changes requires highlighting. Here, we review the role of TEs in creating genetic modifications that enhance the adaptation of plants to acid soils by increasing the release of OAs from the root apices. We argue that TEs have been an important source of beneficial mutations that have co-opted OA transporter proteins with other functions to perform this role. These changes have occurred relatively recently in the evolution of many species and likely facilitated their expansion into regions with acidic soils.**

**Keywords:** Acid soils, *cis* elements, citrate transporter, malate transporter, mutation, transposon.

## Introduction

Transposable elements (TEs) or transposons are found in the genomes of most species and often represent a large proportion of the genome in plants (Bennetzen, 2000; Tenaillon *et al.*, 2010; Negi *et al.*, 2016). They comprise a large group of mobile genetic elements showing a diverse range of sequences and open reading frames. TEs are characterized by their ability to change their positions in the genome or *transpose*. Transposition requires conserved sequences to be present and a specific set of proteins that are provided either by the TE itself (autonomous elements) or by similar elements encoded elsewhere (*trans* activation of non-autonomous elements). TEs generate different types of mutations as they either multiply across the genome or excise from one place in the genome and insert into another. In addition to transposition, TEs can induce other genetic rearrangements such as translocations, inversions and duplications as they recombine throughout the genome (Hua-Van *et al.*, 2011; Lisch, 2013). TEs are an important source of spontaneous mutations (Paquin and Williamson, 1986; Green, 1988; Bennetzen, 2000) and their expression and activity can also increase in response to different biotic and abiotic stresses (Capy *et al.*, 2000; Makarevitch *et al.*, 2015). On occasions these mutations can be beneficial to the organism, and specific TEs have now been associated with the adaptation of plants to a range of environmental stresses (Vitte *et al.*, 2014; Negi *et al.*, 2016).

Aluminum (Al) toxicity is a major abiotic constraint limiting root growth in acid soils. Al is common in most soils and

Abbreviations: ALMT, aluminum-activated malate transporter; LTR, long terminal repeat; MATE, multidrug and toxic compound extrusion; MITE, miniature inverted-repeat transposable element; MRL, multi-retrotransposon-like; OA, organic anion; TE, transposable element; TSS, transcription start site.

generally harmless to plants when pH is above 5.0. However, when the soil becomes more acidic, the concentration of soluble Al cations increases and the molar fraction of the highly toxic trivalent cation species ($Al^{3+}$) becomes predominant. Many plant species are detrimentally affected by prolonged exposure to these Al cations with the inhibition of root growth being a key symptom (Singh *et al.*, 2017). Stunted root systems limit the capacity for water and nutrient uptake (Kochian *et al.*, 2015; Lynch and Wojciechowski, 2015). Plants have evolved different mechanisms to adapt to acid soils and most of the important crop species show a significant genotypic variation in Al resistance. Resistance mechanisms can be broadly divided into those that *exclude* Al from plant tissues, especially the root apices that are critical to root growth, and those mechanisms that enable plants to better *tolerate* the Al that is absorbed by the cells. Comprehensive reviews of these resistance mechanisms are available elsewhere (Taylor, 1991; Matsumoto, 2000; Hiradate *et al.*, 2007; Kochian *et al.*, 2015).

When plants are treated with toxic concentrations of Al, the activity of certain TEs is enhanced (Milla *et al.*, 2002; Mao *et al.*, 2004; Yang *et al.*, 2007; Zhen *et al.*, 2007; Mattiello *et al.*, 2010; Chen *et al.*, 2011; Guo *et al.*, 2017). TEs have been detected in the transcribed regions of some genes associated with Al resistance or in their flanking regions. While the role of genomic changes in enhancing acid-soil tolerance has been discussed previously (Magalhaes, 2010; Ryan and Delhaize, 2010; Delhaize *et al.*, 2012), the growing number of examples implicating TEs with these changes deserves a more thorough review. This article examines the evidence linking TE activity with increased tolerance to acid soils by increasing organic anion efflux from roots.

## The increased expression of certain organic anion transporters is linked with an important mechanism of Al resistance in plants

A widespread mechanism of Al resistance in plants that excludes Al from the sensitive root apices involves the release (or efflux) of organic anions (OAs) from the root apices (Fig. 1). The OAs commonly released by crop plants are citrate and malate (Ryan *et al.*, 2011). The current model proposes that these anions bind the toxic Al cations in the apoplast, which reduces Al uptake into the cells and minimizes other damaging interactions in the cell wall. By protecting the sensitive growing zone, the OA efflux helps to maintain root growth in acid soil. OA efflux from the root apices is facilitated by specific transport proteins in the plasma membrane. The expression of genes encoding these transporters and the activity of the transporter proteins are often increased by exposure to Al. In species such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.), OA efflux is the major mechanism of Al resistance and the relative expression of the genes involved is closely correlated with OA efflux and Al resistance (Delhaize *et al.*, 2012). In other species, OA efflux is one of several mechanisms contributing to resistance and the relationship between OA efflux and resistance is weaker.

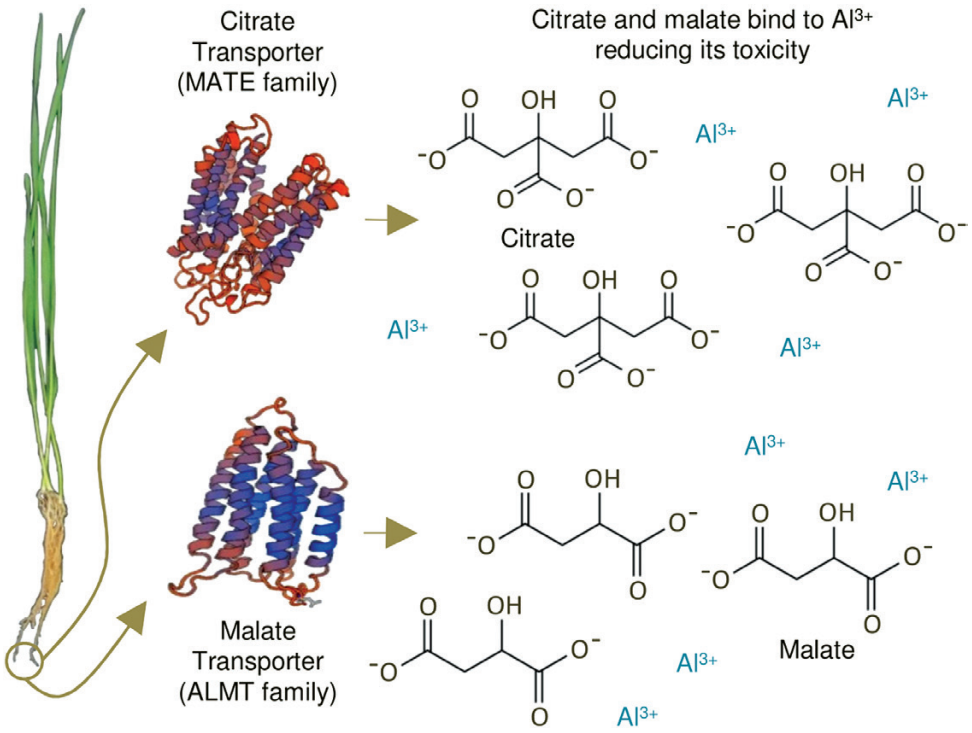


**Fig. 1.** Aluminium (Al) resistance based on the efflux of organic anions by the roots. In acid soils, toxic aluminium cations ($Al^{3+}$) impact root growth. The Al toxicity is reduced when organic anions (citrate and/or malate) released by the roots bind to $Al^{3+}$. Two families of transporters (ALMT and MATE) facilitate the transport of organic anions to the outside of root cells and higher expression of the genes encoding these transporters is associated with higher efflux of citrate and/or malate and greater Al resistance. Three-dimensional structures for ALMT and MATE transporters were built by SWISS-MODEL (Biasini *et al.*, 2014) based on sequences of *TaALMT1* (GenBank DQ072260) and *HvAACT1* (GenBank KX278713).

The first genes encoding malate and citrate transporters associated with Al resistance were identified in wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and sorghum (*Sorghum bicolor* L.) (Sasaki *et al.*, 2004; Furukawa *et al.*, 2007; Magalhaes *et al.*, 2007; Wang *et al.*, 2007). More than 30 additional genes encoding OA transporters have been linked with Al resistance in other species including most important crops (Table 1). These OA transporters are encoded by two gene families: the *Al-activated malate transporter* (*ALMT*) family encodes anion channels that release malate from cells, and the *multidrug and toxic compound extrusion* (*MATE*) family encodes co-transporters that release citrate from cells (Takanashi *et al.*, 2014; Palmer *et al.*, 2016; Sharma *et al.*, 2016). Some of the genes in Table 1 have a strong genetic and physiological association with Al resistance, but for others, the links remain correlative and further confirmation is required.

The founder member of the ALMT family is *TaALMT1* from wheat. This gene encodes an anion channel and controls the major Al resistance mechanism by facilitating the Al-activated efflux of malate from roots (Sasaki *et al.*, 2004). Other members of this gene family have now been characterized in detail, but only a few contribute to Al resistance in a similar fashion to *TaALMT1*. The remainder encode anion channel proteins with diverse functions including the regulation of stomatal aperture, anion homeostasis and fruit development (Palmer *et al.*, 2016; Sharma *et al.*, 2016). Some ALMTs are permeable to γ-aminobutyric acid (GABA) and might have other functions transducing stress signals via GABA concentrations (Ramesh *et al.*, 2018). ALMT proteins are usually

**Table 1.** *List of plant genes/candidate genes encoding organic anion (OA) transporters, which are involved in Al resistance, and the presence of transposons (TE) insertions near or within them*

| Gene[a] | OA | Species | TE insertion[b] | Reference |
|---|---|---|---|---|
| Genes where the upstream regions (at least 1.5 kb) have been sequenced[c] | | | | |
| *TaALMT1* | Malate | *Triticum aestivum* | No | Sasaki *et al.* (2006) |
| *SbMATE* | Citrate | *Sorghum bicolor* | Upstream region | Magalhaes *et al.* (2007) |
| *AtALMT1* | Malate | Arabidopsis | No | Kobayashi *et al.* (2007) |
| *ScALMT1* | Malate | *Secale cereale* | Inside intron | Collins *et al.* (2008) |
| *AtMATE* | Citrate | Arabidopsis | No | Liu *et al.* (2009) |
| *AetALMT1* | Malate | *Aegilops tauschii* | No | Ryan *et al.* (2010) |
| *HvAACT1* | Citrate | *Hordeum vulgare* | Upstream region | Fujii *et al.* (2012) |
| *ScAACT1* | Citrate | *Secale cereale* | Downstream region | Silva-Navas *et al.* (2012) |
| *HlALMT1* | Malate | *Holcus lanatus* | No | Chen *et al.* (2013) |
| *ZmMATE1* | Citrate | *Zea mays* | Flanking regions | Maron *et al.* (2013) |
| *TaMATE1B* | Citrate | *Triticum aestivum* | Upstream region | Tovkach *et al.* (2013) |
| *BdALMT1* | Malate | *Brachypodium distachyon* | Upstream region[d] | Contreras *et al.* (2014) |
| *GmMATE75* | Citrate | *Glycine max* | No | Liu *et al.* (2016*a*) |
| *VuMATE1* | Citrate | *Vigna umbellata* | No | Liu *et al.* (2016*b*) |
| *OsFRDL4* | Citrate | *Oryza sativa* | Upstream region | Yokosho *et al.* (2016) |
| *SlALMT9* | Malate | *Solanum lycopersicum* | Inside intron | Ye *et al.* (2017) |
| *CcMATE1* | Citrate | *Cajanus cajan* | No | Daspute *et al.* (2018) |
| *VuMATE2* | Citrate | *Vigna umbellata* | No | Liu *et al.* (2018) |
| *HvAACT1* | Citrate | *Hordeum vulgare* | Upstream region | Kashino-Fujii *et al.* (2018) |
| Genes whose flanking regions were not sequenced | | | | |
| *BnALMT1* | Malate | *Brassica napus* | Not in coding region | Ligaba *et al.* (2006) |
| *BnALMT2* | Malate | *Brassica napus* | Not in coding region | Ligaba *et al.* (2006) |
| *ZmMATE2* | Citrate | *Zea mays* | No | Maron *et al.* (2010) |
| *ScFRDL2* | Citrate | *Secale cereale* | Not in coding region | Yokosho *et al.* (2010) |
| *MsALMT1* | Malate | *Medicago sativa* | Not in coding region | Chen *et al.* (2011) |
| *CgALMTs*[e] | Malate | *Citrus grandis* | Not in coding region | Yang *et al.* (2012); Guo *et al.* (2017) |
| *CsALMTs*[e] | Malate | *Citrus sinensis* | Not in coding region | Yang *et al.* (2012); Guo *et al.* (2017) |
| *GmALMT1* | Malate | *Glycine max* | Not in coding region | Liang *et al.* (2013) |
| *EcMATE1* | Citrate | *Eucalyptus camaldulensis* | Not in coding region | Sawaki *et al.* (2013) |
| *EcMATE3* | Citrate | *Eucalyptus camaldulensis* | Not in coding region | Sawaki *et al.* (2013) |
| *BsALMT1* | Malate | *Brachypodium stacei* | No | Contreras *et al.* (2014) |
| *BdMATE1* | Citrate | *Brachypodium distachyon* | Not in coding region | Contreras *et al.* (2014) |
| *BdMATE2* | Citrate | *Brachypodium distachyon* | Not in coding region | Contreras *et al.* (2014) |
| *BoMATE* | Citrate | *Brassica oleracea* | Not in coding region | Wu *et al.* (2014) |
| *CsMATEs*[e] | Citrate | *Citrus sinensis* | Not in coding region | Guo *et al.* (2017) |
| *BoALMT1* | Malate | *Brassica oleracea* | Not in coding region | Zhang *et al.* (2018) |

[a]*HvAACT1* is shown twice due to the identification of independent TE insertions.
[b]Absence of TEs is based on the available sequences (promoter and/or gene or only coding region—cDNA).
[c]For *AetALMT1* and *CcMATE1*, less than 1.5 kb of the upstream region was sequenced.
[d]Probably.
[e]More than one sequence has been found for these transporters.

350–500 amino acids long with five to seven transmembrane domains (Delhaize *et al.*, 2007; Dreyer *et al.*, 2012; Sharma *et al.*, 2016). At least some of the ALMT transporters function as tetramers (Zhang *et al.*, 2013).

MATE transporters were first identified in prokaryotic cells, where they facilitate the efflux of a variety of secondary compounds including xenobiotics (Putman *et al.*, 2000; Moriyama *et al.*, 2008). MATE proteins are 400–700 amino acids long with 12 membrane-spanning domains. They are divided into three phylogenetic families and 14 small subfamilies with the plant members in subfamily 2B (Moriyama *et al.*, 2008). The MATEs characterized in plants transport a diverse range of compounds involved in different functions including mineral nutrition, transport of secondary metabolites, and hormone signalling (Takanashi *et al.*, 2014). The first *MATE* genes linked with Al resistance were the *SbMATE* in sorghum (Magalhaes *et al.*, 2007) and the *aluminum-activated citrate transporter* (*HvAACT1*) in barley (Furukawa *et al.*, 2007; Wang *et al.*, 2007).

ALMT and MATE proteins share no sequence homology, indicating that these transporters have evolved in a convergent manner to perform similar functions (Delhaize *et al.*, 2007; Ryan and Delhaize, 2010). In other words, the same phenotype (Al resistance) is achieved by similar mechanisms (OA efflux from roots) via transporters from different families. In some species only one of these transporters contributes to Al resistance (e.g. barley) whereas in other species members of both families contribute to Al resistance in the same plant (see Table 1).

Why should members from distinct transporter families evolve a role in Al resistance? The two key features common to the ALMT and MATE transporters are, firstly, that they facilitate OA efflux from cells and, secondly, that their substrates (malate and citrate) form stable complexes with $Al^{3+}$. Both are essential requirements if the OAs are to protect the roots by reducing the concentration of free Al ions in the apoplast. Many other substrates, including certain secondary metabolites and peptides, can bind Al strongly as well (Kidd *et al.*, 2001, Poschenrieder *et al.*, 2008), but these more complex compounds require extra energy and resources for their synthesis and transport. Malate and citrate anions, by contrast, are small, energetically cheap to synthesize and prevalent in living cells. Because they are so common, many genes are likely to encode transporters that move these substrates across cellular membranes (Ryan and Delhaize, 2010). Spontaneous mutations that increase the expression of specific *MATE* or *ALMT* genes in the apical tissues of roots have the potential to increase OA release from those cells and enhance Al resistance.

## Plant transposons: balancing between parasitism and beneficial genetic change

Many different types of TEs have been described in living cells. Two broad classes represent the first division in TE taxonomy, and further subdivisions into subclasses, orders, superfamilies, families, and subfamilies depend on the sequence similarity (DNA and protein) and phylogenetic data of the elements (Wicker *et al.*, 2007; Lisch, 2013; Gozukirmizi *et al.*, 2016). Plant genomes contain representatives from both classes, but the majority belong to Class I, which require an RNA intermediate for transposition. During transposition, Class I TEs remain in the same position and a copy produced by reverse transcription inserts elsewhere in the genome. This explains why some Class I TEs, such as the long terminal repeat (LTR) retrotransposons, are very prevalent in plants (Vitte *et al.*, 2014). TEs that do not require RNA intermediates are grouped in Class II, and these elements excise from one site in the genome and then insert at another site. Class II includes the *Mutator* superfamily, the *CACTA* superfamily and the miniature inverted-repeat transposable elements (MITEs) among others. Some TEs may have singular characteristics from both classes. *Helitrons*, for instance, are DNA transposons that transpose via a 'rolling circle' mechanism. Because they replicate by a copy-and-paste mechanism, *Helitrons* are similar to Class I elements. However, the 'rolling circle' mechanism does not require an RNA intermediate (Wicker *et al.*, 2007; Lisch, 2013; Gozukirmizi *et al.*, 2016).

The association between TE transposition and the generation of mutant phenotypes in plants was reported nearly 70 years ago (McClintock, 1950). The hypothesis that segments of DNA could change their position in the genome challenged the status quo that then held genes were in a stable arrangement along the chromosome (Ravindran, 2012). TEs were initially seen as unimportant or 'junk DNA' and their importance was not fully realized for decades. It took almost 40 years to characterize the TEs in maize (*Zea mays* L.) and understand the molecular basis of the *Dissociation* (*Ds*) and *Activator* (*Ac*) loci that explained the chromosomal changes that caused sectored kernel pigmentation (Fedoroff *et al.*, 1983; Lazarow *et al.*, 2013). The current view is that mutations generated by TE activity are important drivers of genetic change and adaptation (Bennetzen, 2000; Bennetzen and Wang, 2014). Indeed, more than 50 TE-induced phenotypic changes have been directly linked with domestication or diversification of cultivated plants (Vitte *et al.*, 2014).

The mutations generated by TEs can be divided into three main groups: transposition (mutations that occur from an insertion or excision), recombination (where similar TEs dispersed throughout the genome cause inter- or intra-chromosomal rearrangements and sequence duplications) and exaptation (where sequences of the TEs are co-opted to perform functions that generate new phenotypes). The insertions or excisions of TEs that occur inside coding regions or introns can disrupt transcription or cause frameshifts that affect splicing or protein function. For example, TE excision generates a chromosomal break that can lead to point mutations or frameshifts if a small number of bases (called footprints) are added or deleted as the DNA reconnects. Indeed, the imperfect repair of DNA after TE excision is associated with a large number of mutations with evolutionary significance in rice, maize, wheat, and barley (Wicker *et al.*, 2016). TE-dependent recombinations of sequences can be so severe that in some cases they disrupt the gene collinearity between related plant species (Morgante *et al.*, 2005). TE insertions do not necessarily occur randomly in the genome. For instance, Class II

TEs in maize and sorghum are more frequently found in low-copy regions and the sequences flanking genes rather than in the coding regions themselves (Zhang *et al.*, 2000; Lisch, 2002; Wei *et al.*, 2016), while LTR retrotransposons are primarily found inserted within each other (SanMiguel *et al.*, 1996). Furthermore, Class II and low-copy-number Class I TEs are enriched in the upstream promoter sequences of all categories of plant genes, including stress-induced genes in maize and rice (Baucom *et al.*, 2009; Naito *et al.*, 2009; Bennetzen and Wang, 2014; Makarevitch *et al.*, 2015). TEs that insert in the promoter regions of genes have the potential for altering gene expression in a number of ways. They can either up- or down-regulate expression of the genes or change their tissue-specific expression (Selinger and Chandler, 2001; Lisch, 2013; Dhadi *et al.*, 2015). The ability of some TEs to increase gene expression is related to them containing transcription start sites or binding sites for transcription factors that would not normally influence the neighbouring genes (Thornburg *et al.*, 2006; Fujii *et al.*, 2012). Remarkably, TEs can even impact the expression of genes located more than 50 kb away from their insertion sites (Studer *et al.*, 2011), although this is quite rare in plants (Bennetzen and Wang, 2018).

Since many of the mutations caused by TEs are detrimental to the host, organisms have evolved mechanisms to reduce their activity. Epigenetic mechanisms, such as DNA methylation and demethylation, can moderate TE activity and suppress their parasitic-like behaviour (Kim and Zilberman, 2014; Bewick *et al.*, 2016; Bennetzen and Park, 2018). Sometimes these epigenetic processes function imperfectly and affect the expression of neighbouring, non-target genes (Hollister and Gaut, 2009; Lisch and Bennetzen, 2011; Le *et al.*, 2014). Therefore, a balance is required between the activation and inactivation of TEs which minimizes their detrimental effects without losing the benefits that sometimes flow from the genetic variation they create.

## Transposons alter the expression of organic anion transporters involved in Al resistance

Figure 2 classifies the TEs that have been detected inside or near specific OA transporters associated with Al resistance. While the coding regions are known for most of these genes, the sequence from the upstream flanking regions (usually ≥1.5 kb) is only available for 18 of them (Table 1) and fewer have sequence from the downstream regions. In nine of these genes, TEs have been detected upstream, downstream, or in the transcribed regions. In the case of the barley gene *HvAACT1*, two independent insertions have been reported (Fig. 3). Most of these TEs enhance Al resistance by increasing OA efflux from the roots, but others appear to have no effect or even decrease Al resistance.

### *TE insertions near OA transporters that increase Al resistance*

TE insertions have been detected near Al-resistance genes encoding OA transporters in barley, wheat, rice, sorghum, *Brachypodium distachyon*, and rye (*Secale cereale* L.) (Magalhaes *et al.*, 2007; Fujii *et al.*, 2012; Silva-Navas *et al.*, 2012; Tovkach *et al.*, 2013; Yokosho *et al.*, 2016; Kashino-Fujii *et al.*, 2018). All of these transporters except one are MATE-type transporters that facilitate citrate efflux. The exception is an ALMT-type transporter in *Brachypodium distachyon*. These TEs vary in classification (Fig. 2) and are positioned at a range of distances from the coding regions (Fig. 3) as detailed below.

Al resistance in barley is controlled by a single major gene, *HvAACT1* on chromosome 4H (Minella and Sorrells, 1997; Furukawa *et al.*, 2007; Wang *et al.*, 2007). *HvAACT1* encodes a MATE transporter that facilitates the Al-activated efflux of citrate from the root apices. Al-resistant cultivars of barley show a constitutively higher level of *HvAACT1* expression in the apices than sensitive cultivars. In some resistant cultivars this is caused by a 1023-bp *CACTA*-like transposon (Class II) located in the 5′ untranslated region (UTR) approximately 4.8 kb upstream of the *HvAACT1* start codon (Fujii *et al.*, 2012). Among a range of barley genotypes tested, those with this TE grew better in $Al^{3+}$-toxic conditions than others without the TE (Fujii *et al.*, 2012; Ferreira *et al.*, 2018). More recently, another independent insertion affecting Al resistance was detected 6.6 kb upstream of *HvAACT1* (Kashino-Fujii *et al.*, 2018). This is a 15.3-kb-long multi-retrotransposon-like (MRL) sequence which includes LTRs. It is referred to as 'an insertion' but it may be a mix of more than one element. Cultivated barley accessions containing this other insertion also showed greater *HvAACT1* expression in the root apices and improved resistance to Al stress as long as the *HvAACT1* promoter region is demethylated (Kashino-Fujii *et al.*, 2018).

In wheat, the *TaMATE1B* gene on chromosome 4B controls the constitutive release of citrate from root apices. Relatively few genotypes show this phenotype (Ryan *et al.*, 2009) but those that do possess an 11.1-kb TE inserted 25 bp upstream of the *TaMATE1B* start codon. This insert contains a 3.9-kb *Sukkula*-like TE (Class I) (Tovkach *et al.*, 2013) that is linked with greater *TaMATE1B* expression. The association between this TE and Al resistance among different genotypes is not strong because most of the variation in Al resistance is determined by malate efflux via TaALMT1 (Garcia-Oliveira *et al.*, 2014; Aguilera *et al.*, 2016). Nevertheless, many of the most Al-resistant cultivars from Brazil (e.g. cv Carazinho, cv IAC5-Maringá and cv Toropi) combine the superior alleles of *TaALMT1* and *TaMATE1B* (Pereira *et al.*, 2015; Aguilera *et al.*, 2016; Pereira, 2018).

In rice, Al resistance is a complex trait involving multiple mechanisms of Al exclusion and Al tolerance (Yamaji *et al.*, 2009). Most of the 30 or more genes that regulate these mechanisms are induced by Al via a C2H2 zinc finger-type transcription factor called Aluminium Resistance Transcription Factor1 (ART1) (Yamaji *et al.*, 2009; Tsutsui *et al.*, 2011). Transcription factors from this family in other species, including Arabidopsis (e.g. AtSTOP1), have also been implicated in the regulation of Al-resistance genes (Sawaki *et al.*, 2009, 2014; Chen *et al.*, 2013; Liu *et al.*, 2016*a*,*b*, 2018; Daspute *et al.*, 2018). One of the genes induced by ART1 in most *japonica* rice lines is *Ferric Reductase Defective3-like 4* (*OsFRDL4*), which encodes a *MATE*-type transporter. Part of the phenotypic variation for Al resistance

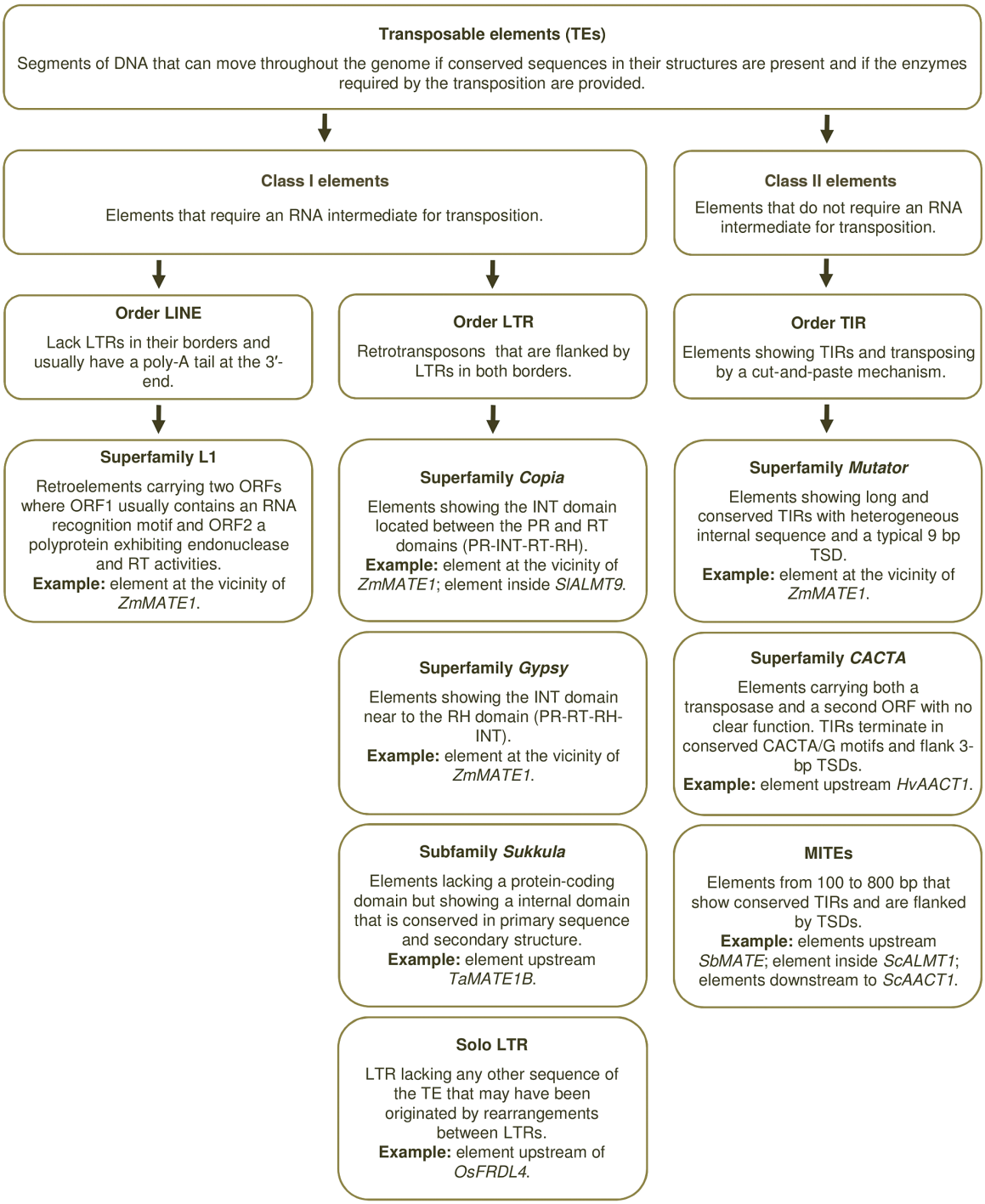


**Fig. 2.** Taxonomy of the elements found to be associated with organic anion transporter genes that contribute to Al resistance in plants. The multi-retrotransposon-like (MRL) sequence upstream of *HvAACT1* (Kashino-Fujii *et al.*, 2018) was not considered because it contains a mix of LTR elements from different superfamilies. INT, integrase; LTR, long terminal repeat; ORF, open reading frame; PR, protease; RH, RNase H; RT, reverse transcriptase; TIR, terminal inverted repeat; TSD, target site duplication.

in rice is explained by greater *OsFRDL4* expression and citrate efflux, which are directly linked with a 1213-bp solo LTR inserted 615 bp upstream of the *OsFRDL4* transcription start site (TSS) (Yokosho *et al.*, 2011, 2016).

In sorghum, Al resistance is controlled by a major QTL on chromosome 3 ($Alt_{SB}$), which contains a *MATE* gene called *SbMATE* (Magalhaes *et al.*, 2007). In the absence of Al toxicity, *SbMATE* is expressed equally in the root apices of Al-resistant and sensitive genotypes of sorghum but no citrate efflux occurs. When the plants are treated with Al, *SbMATE* expression increases over several days and the increase in expression is closely correlated with citrate efflux and enhanced Al resistance (Magalhaes *et al.*, 2007). The polymorphisms in *SbMATE* between resistant and sensitive genotypes occur in a ~6-kb region encompassing part of the transcribed region and an insert ~1.4 kb upstream of the predicted TATA box (Caniato *et al.*, 2014). This insert harbours a Class II TE called a *Tourist*-like MITE and the number of copies of the MITE and flanking

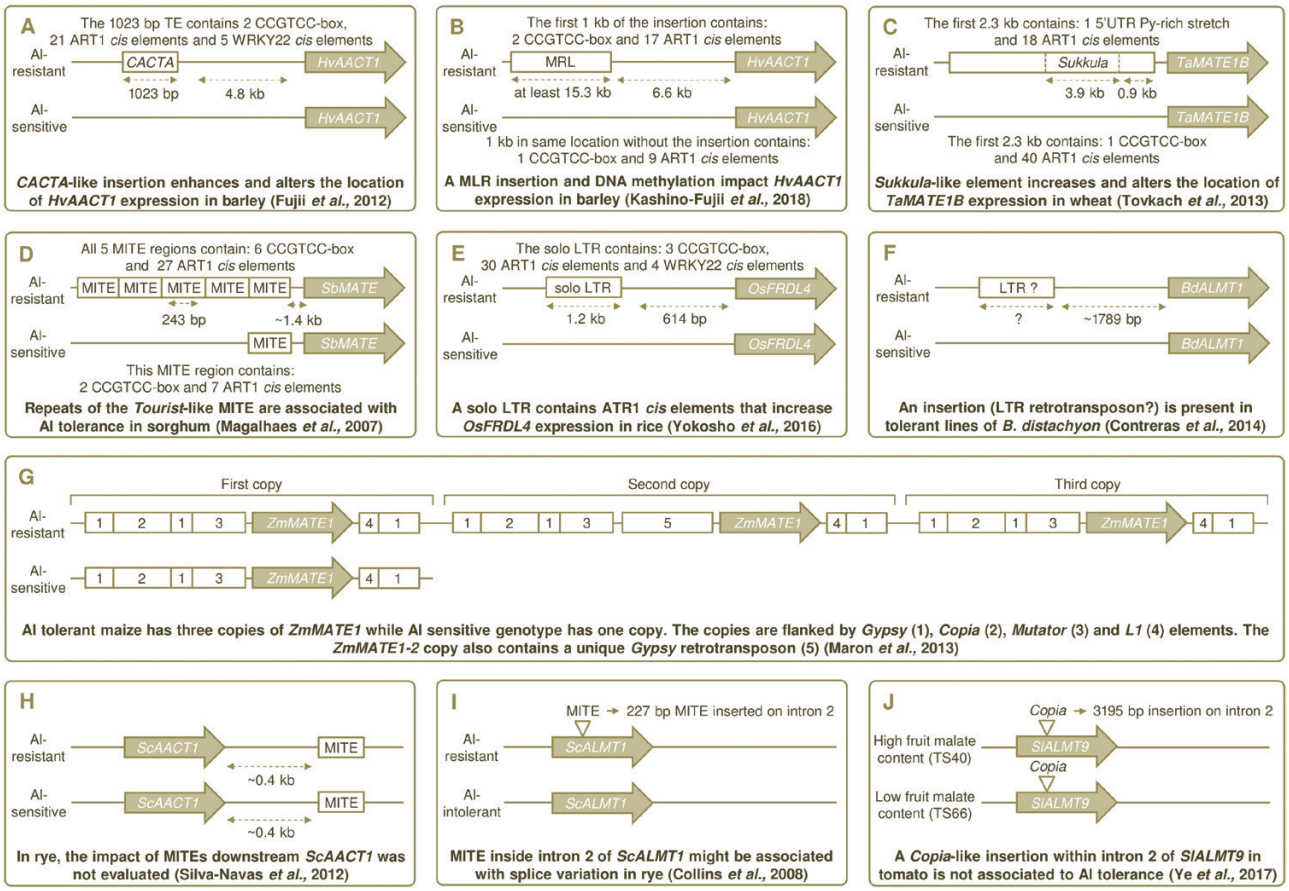


**Fig. 3.** Schematic representation of transposable elements that are associated with organic anion transporters genes/candidate genes. Putative *cis* elements discussed in the text are shown in (A–E). In (B), MRL indicates a multi-retrotransposon-like sequence. In (E), the numbers of *cis* elements for ART1 and WRKY22 in the solo LTR near *OsFRDL4* are different from the ones reported previously (Yokosho *et al.*, 2016; Li *et al.*, 2018). Here, we consider a larger range of affinity levels for ART1 and the sequence (T/C)TGAC(T/C) and its reverse complement for WRKY22.

sequences is positively correlated with Al resistance. However these MITEs only account for part of the variation in expression because important SNPs were detected in intron 2. Other *trans*-acting elements may affect *SbMATE* expression as well because the integration of the $Alt_{SB}$ locus into different genetic backgrounds generates variable phenotypes (Melo *et al.*, 2013).

TEs could be implicated in Al resistance in two final examples (*Brachypodium* spp. and rye) but further experiments are required to directly demonstrate their impact. Contreras *et al.* (2014) found that the significant variation in Al resistance among a range of diploid (*B. distachyon*; $2n$=10) and allotetraploid (*B. hybridum*; $2n$=30) *Brachypodium* accessions was correlated with malate efflux from the roots. The Al-resistant genotypes showed greater expression of the *BdALMT1* gene than sensitive accessions and all resistant genotypes possessed a large insert ~1789 bp upstream of the first ATG. The insert has not been fully sequenced and a complete description is not available, but there is a LTR at that position in the *Brachypodium* genome (Contreras *et al.*, 2014). Nevertheless, these findings do establish a link between the insertion adjacent to *BdALMT1*, greater *BdALMT1* expression, and increased malate efflux. In rye, both ALMT- and MATE-type transporters contribute to Al resistance by controlling malate and citrate efflux, respectively (Fontecha *et al.*, 2007; Collins *et al.*, 2008; Yokosho *et al.*, 2010; Silva-Navas *et al.*, 2012). One of the candidate *MATE* genes involved, *ScAACT1*, resides on chromosome 7RS (Silva-Navas *et al.*, 2012) and its expression was greater in a resistant line than a sensitive line. MITE insertions (*Stowaway* family) were detected downstream of the coding region in the resistant and sensitive lines but the sequences and their insertion sites were different. Additional work is required to determine whether these differences can account for the contrasting levels of *ScAACT1* expression and Al resistance.

## *How do TEs increase the expression of Al-resistance genes?*

The preceding discussion provided examples of where TE insertions appear to improve the Al resistance of plants by enhancing the expression of genes in the root apices. Several mechanisms can explain this behaviour and Fig. 4 provides a stylized explanation for one mechanism. The expression of genes can be increased if the sequence of the TE contains transcriptional enhancer activity that alters the spatial or temporal expression pattern of adjacent genes. This mechanism has been attributed to the enhanced expression of several stress-responsive genes in maize (Makarevitch *et al.*, 2015) and it also may explain the impact of TEs on the expression of OA

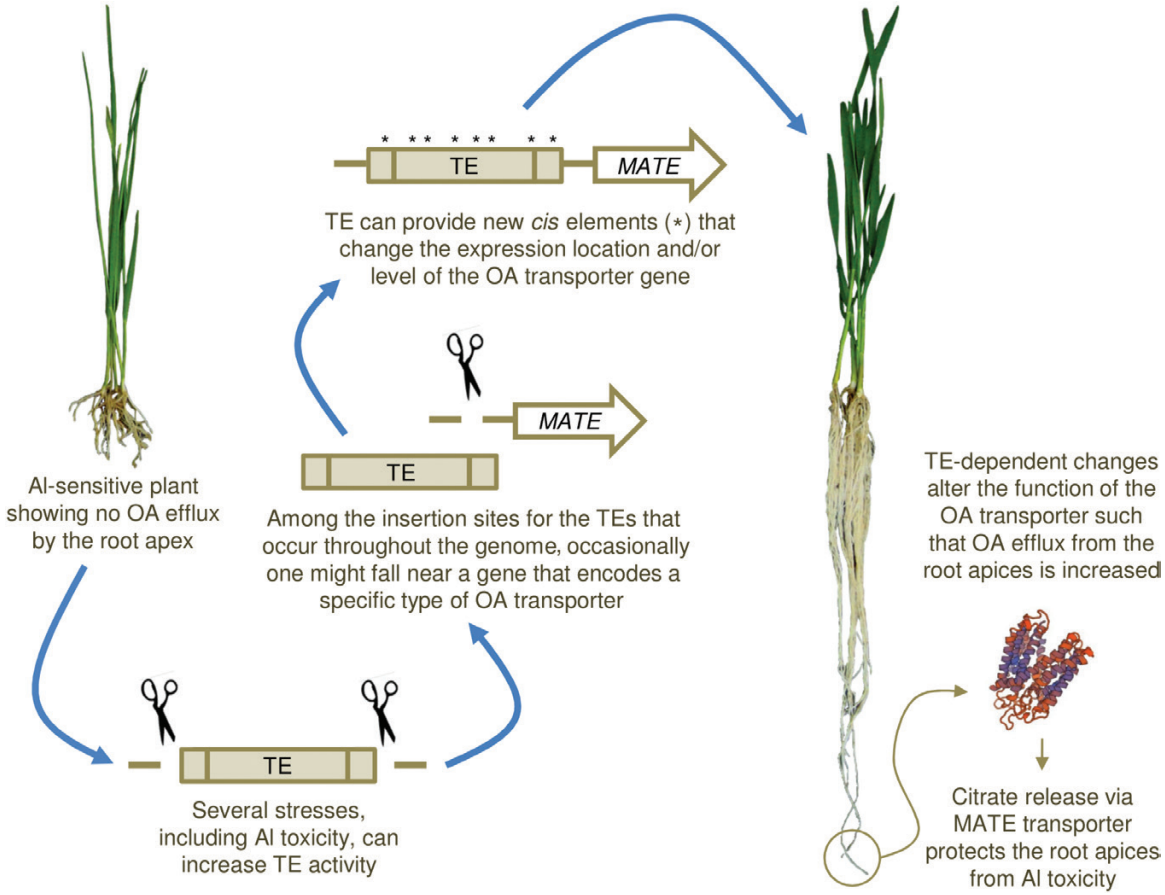


**Fig. 4.** An illustration of how transposable elements (TEs) can change the expression of organic anion (OA) transporter genes in plants. As an example, the TE represented here is a Class II element and the OA transporter gene belongs to the MATE family

transporter genes. For example, in Al-sensitive cultivars of barley, expression of *HvAACT1* is greater in the vascular bundle of roots than in the cortical cells and root apices. This localization supports the proposed function of HvAACT1, which is to export citrate from the xylem parenchyma into xylem to accompany iron movement to the shoots (Fujii *et al.*, 2012). Indeed, other MATE transporters have been ascribed similar functions in Arabidopsis, rice and perhaps wheat (Durrett *et al.*, 2007;Yokosho *et al.*, 2009;Tovkach *et al.*, 2013). However, in Al-resistant barley genotypes that possess the 1023-bp *CACTA*-like TE insertion, *HvAACT1* expression is expanded to include cells at the root apices. The TE sequence has promoter activity and contains additional TSSs both of which increase gene transcription. This was confirmed in transgenic studies that used promoters derived from Al-resistant and -sensitive barley to drive expression of *HvAACT1* or green fluorescent protein in transgenic barley plants (Fujii *et al.*, 2012). Promoter studies of this kind have also been used to confirm the effect of TEs on *TaMATE1B* expression in wheat and *OsFRDL4* expression in rice (Tovkach *et al.*, 2013; Yokosho *et al.*, 2016). A second example in barley is the MRL insertion located farther upstream of *HvAACT1* because it also contains multiple TSSs that increase *HvAACT1* expression (Kashino-Fujii *et al.*, 2018).

TEs can also affect the expression of neighbouring genes if their sequences contain *cis*-regulatory elements that recognize certain transcription factors. For instance, the solo LTR inserted near *OsFRDL4* in an Al-resistant rice (cv Nipponbare) contains nine *cis*-acting elements that recognize the ART1 transcription factor. This compares with only two *cis*-acting elements in a sensitive cultivar (cv Kasalath) that lack the insert (Yokosho *et al.*, 2016). It is proposed that the greater number of *cis* elements causes more interaction between ART1 and the promoter, which increases *OsFRDL4* expression and citrate efflux (Yamaji *et al.*, 2009;Yokosho *et al.*, 2016). The core motif of the *cis*-acting elements of ART1 is GGN(T/g/a/C)V(C/A/g)S(C/G), where the bases shown in lowercase show weaker ART1-biding affinity when compared with the bases shown in uppercase (Tsutsui *et al.*, 2011). In the same way, *cis* elements that recognize another transcription factor, OsWRKY22, are present in the solo LTR upstream from *OsFRDL4* (Li *et al.*, 2018). OsWRKY22 belongs to the WRKY family of transcription factors which bind with W-box sequences (T/C)TGAC(T/C). The 25-fold induction of OsWRKY22 expression under Al treatment and the large number of *cis* elements in the TE near *OsFRDL4* is consistent with these elements increasing *OsFRDL4* expression under Al stress (Li *et al.*, 2018). Since the core sequences for the transcription factors ART1 and OsWRKY22 are relatively short, other *cis*-acting elements might be required to control the specificity between these transcription factors (Delhaize *et al.*, 2012).

As part of this review, we analysed the TE insertions upstream of *SbMATE*, *HvAACT1*, *TaMATE1B*, and *OsFRDL4* to determine whether putative *cis* elements for ART1/STOP1- and WRKY22-like transcription factors are present. We also used the PlantCARE database (Lescot *et al.*, 2002) to detect other *cis* elements that could affect gene expression (Fig. 3; Supplementary Fig. S1; Supplementary Tables S1–S5 at *JXB* online). This analysis used the following sequences: the two TE insertions upstream of *HvAACT1* in barley (the 1023-bp *CACTA*-like transposon in cv Murasakimochi and the first 1 kb of the MRL insertion in cv FM404), the first 2.3 kb of the *Sukkula*-like transposon upstream of *TaMATE1B* in wheat (cv Carazinho), the 455 pb region containing the MITE insertion upstream of *SbMATE* in sorghum (line TX430), and the 1213-bp solo LTR upstream of *OsFRDL4* in rice (cv Nipponbare) (Magalhaes *et al.*, 2007; Fujii *et al.*, 2012; Tovkach *et al.*, 2013; Yokosho *et al.*, 2016; Kashino-Fujii *et al.*, 2018). Possible biding sites for ART1/STOP1 and WRKY22 were searched manually while *cis* elements registered in the Plant CARE database were detected by submitting the sequences to the program (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/). This *in silico* analysis identified common *cis*-acting elements in promoter and enhancer regions as well as the TSS in all the TEs. It also detected five *cis*-acting elements of WRKY22 in the 1023-bp TE insertion upstream of *HvAACT1* and four *cis*-acting elements in the solo LTR upstream of *OsFRDL4*, but no *cis* elements were present in the TEs near *SbMATE*, *TaMATE1B* or in the first 1 kb of the MRL insertion upstream of *HvAACT1*. We found possible binding sites for ART1 in the solo LTR upstream of *OsFRDL4*, as identified by Yokosho *et al.* (2016), and similar ART1/STOP1 binding sites in the TEs near *HvAACT1* (first 1 kb of the MRL insertion and the 1023 bp TE) and in the MITE near *SbMATE*. An ART1/STOP1-like protein reportedly contributes to the Al resistance of sorghum (Huang *et al.*, 2018) but a direct interaction between that protein and these *cis* elements in the MITE has not been demonstrated. Similarly, the role of these putative *cis* elements upstream of *HvAACT1* is unclear but it is important to note that *HvAACT1* expression is not induced by exposure to Al (Furukawa *et al.*, 2007). We also found that the number of *cis* elements for ART1/STOP1-like transcription factors was reduced by the insertion of the *Sukkula*-type TE upstream of *TaMATE1B* in wheat compared with the first 2.3 kb upstream of *TaMATE1B* without the TE insertion (Tovkach *et al.*, 2013), but another motif with possible transcriptional activity (the 5′UTR pyrimidine-rich sequence TTTCTTCTCT; Daraselia *et al.*, 1996) was detected 369 bp upstream from the coding region but only in the *Sukkula*-type TE insertion. Whether this motif is important for increasing *TaMATE1B* transcription is uncertain but it is consistent with Tovkach *et al.* (2013), who showed that a promoter derived from 1.5 kb of the 5′ end of that insertion generated stronger expression than a promoter without this region. Finally, multiple copies of another motif (CCGTCC-box) previously associated with expression in meristematic cells (Chaubet *et al.*, 1996) was detected in the TEs near *SbMATE*, *OsFRDL4*, and *HvAACT1* (both the 1023-bp insertion and the first 1 kb of the MRL insertion). While this finding is consistent with the expression of these genes in the root apices (which contain meristematic tissue) additional promoter studies are required to determine whether any of these putative *cis* elements are indeed affecting gene expression.

### *Enhanced Al resistance through sequence duplication: a role for TEs?*

Repeated blocks of sequence can be generated by TEs and some of these have resulted in gene duplications that have beneficial phenotypes. For instance, a *Copia*-like retrotransposon named *Rider* contributed to the domestication of tomato (*Solanum lycopersicum* L.) by altering fruit shape. The *Rider* TE caused this change by inducing a 24.7 kb duplication that increased expression of the *IQD12* gene encoding an *IQ67* domain-containing protein (Xiao *et al.*, 2008). The duplication arose when the TE failed to stop reverse-transcribing its own 3′ LTR and continued to produce a ~25-kb fragment that included the gene (Xiao *et al.*, 2008; Flagel and Wendel, 2009). Another example is the *R-r* complex that controls anthocyanin production. The *R-r* locus in maize contains a series of homologous repeats and the *CACTA*-like TEs present at the breakpoints thus implicated these TEs in the chromosomal rearrangements (Walker *et al.*, 1995). Finally, *Helitrons* are another group of TEs that can duplicate sequences. These elements encode proteins with the rolling-circle replication initiator domain and a DNA helicase domain, which are required for transposition. *Helitrons* have been an important source of genetic diversity in maize (Morgante *et al.*, 2005) and all other investigated angiosperms. These types of mutations have also been implicated in the adaptation of plants to acid soils as illustrated by the following examples.

Sequence duplications have been implicated in the mechanisms of Al resistance in maize and wheat. Al resistance in maize is a polygenic trait, but a major QTL on chromosome 6 contains two *MATE* genes, *ZmMATE1* and *ZmMATE2* (Maron *et al.*, 2010). *ZmMATE1* encodes a citrate transporter whose expression was induced by Al in resistant lines more than in sensitive lines. This difference was not associated with polymorphisms in the gene or in *cis*-regulatory regions (Maron *et al.*, 2013). Instead, variation in gene expression was linked with the number of copies of *ZmMATE1* such that Al-sensitive lines (e.g. L53) have a single copy and Al-resistant lines (e.g. Al237) have three copies (Maron *et al.*, 2013). Each *ZmMATE1* copy is flanked by different TEs that are highly conserved between the copies (Maron *et al.*, 2013) except for *ZmMATE1-2*, which has a *Gypsy*-type retrotransposon (Class I) in its upstream region. It is possible the TEs flanking *ZmMATE1* were involved in the duplication events in the resistant line which then enhanced *ZmMATE1* expression.

*TaALMT1* is the major gene controlling Al resistance in wheat and the higher constitutive expression of *TaALMT1* in resistant lines is caused by tandemly repeated blocks of sequence (31–803 bp long) upstream of the coding region (Sasaki *et al.*, 2006; Raman *et al.*, 2008). These repeats occur in different arrangements but the number of repeats is generally correlated with the level of gene expression and malate efflux. Furthermore, promoter studies in transgenic plants have

demonstrated that these tandem repeats do increase transcriptional activity (Ryan *et al.*, 2010). While the origins of these repeats in wheat are unknown, it has been previously proposed that the rolling-circle DNA replication machinery used by *Helitrons* could generate tandem repeats of this kind (Delhaize *et al.*, 2007). The repeats could result from the inaccurate repair of damaged double-stranded DNA (Vaughn and Bennetzen, 2014) and from inaccurate DNA replication due to simply repeated sequences.

## Not all transposons associated with OA transporters increase Al resistance

The cases highlighted previously illustrate the beneficial role of TEs to Al resistance, but not all TE insertions will have this affect. In tomato, for example, the *SlALMT9* gene encodes a tonoplast-localized ALMT transporter that contributes to malate content in the fruit and resistance to Al stress (Ye *et al.*, 2017). A LTR transposon (superfamily *Copia*) was detected in the second intron of *SlALMT9*, but Al resistance is not controlled by this insertion. Instead, those phenotypes were linked to a 3-bp deletion in the promoter that disrupted the binding site of a WRKY transcription repressor (Ye *et al.*, 2017). This is an example of a TE inserted in the non-coding region of an OA transporter that has no apparent effect on the Al-resistance phenotype.

In rye, Collins *et al.* (2008) showed that the copy number and expression level of the *ScALMT1* gene on chromosome 7RS differed in Al-resistant and -sensitive genotypes. The Al-resistant haplotype (M39A-1–6) had five copies of *ScALMT1* of which two were induced by Al treatment, whereas the Al-sensitive haplotype (*M77A-1*) had two copies of *ScALMT1* of which only one was induced by Al (Collins *et al.*, 2008). The sequence obtained of the *ScALMT1* transcripts revealed that the Al-sensitive haplotype had a much greater proportion of splice variants, which may be caused by a 400-bp insertion in intron 2 harboring a 227-bp MITE (Collins *et al.*, 2008). Therefore, not only does the Al-sensitive rye have fewer copies of *ScALMT1*, but a TE may cause a further reduction in functional transcripts. The MITE insertion in *ScALMT1* is a possible example of a TE negatively affecting Al resistance. These examples suggest that the positive effect of TEs on Al resistance mainly come from their insertions into regions upstream of OA transporter genes rather than the transcribed regions.

## TE-dependent improvements to Al resistance are evolutionarily recent events

The TE-dependent mutations associated with Al resistance are relatively recent events in the evolution of those species and may have facilitated their wider expansion into regions with acid soils. The mutations near *HvAACT1* in barley, *OsFRDL4* in rice, *TaALMT1* and *TaMATE1B* in wheat, and *SbMATE1* in sorghum, as well as the multiple copies of *ZmMATE1* in maize, all occur rarely in those populations and most have not been detected in their progenitor species. So why should these genetic changes be recent events when Al has been prevalent in the earth's crust for a large part of the planet's history? One explanation is that the TE-dependent mutations may have occurred in a different 'aluminium environment' from the one during which higher lifeforms began evolving. Exley (2009) proposed that the concentration of 'biologically reactive' Al has increased through evolutionary time as the levels of silicic acid decreased. Silicic acid decreases the biological availability of Al by forming hydroxyaluminosilicates. As silicic acid levels fell, plants were gradually exposed to greater levels of Al stress (Exley, 2009). In this new 'aluminium environment' any TE-dependent mutations that increased the resistance of plants to biologically reactive Al would be selected for. This is discussed further below.

Al resistance in barley is likely to have had a single origin during its expansion from the Near East and Fertile Crescent to the Far East where acid soils are more common (Fujii *et al.*, 2012). The 1023-bp TE insertion upstream of *HvAACT1* has only been detected in resistant genotypes from China, Japan, and Korea, but not in any of the wild barley or progenitor species (Fujii *et al.*, 2012; Ferreira *et al.*, 2018). Novel alleles do occur near the same insertion site in a Chinese six-rowed barley, which suggests that the locus is prone to genetic rearrangements (Ma *et al.*, 2016). Tibetan wild barley (*Hordeum spontaneum*) diverged early from the Near East genotypes and could represent an additional centre of diversity and domestication (Wang *et al.*, 2015). When barley cultivation expanded towards Europe, the second TE insertion, named MRL, appears to have contributed to acid soil tolerance (Kashino-Fujii *et al.*, 2018). The MRL insertion is also rare since it was detected in only two out of 289 wild barley accessions screened and in 26 out of 274 cultivated barley genotypes. Interestingly, wild barley accessions with the MRL insertion do not have the same elevated levels of *HvAACT1* expression that the modern cultivars show. The reason for this was that the promoter of *HvAACT1* was heavy methylated in the wild barley accessions. As stated previously, DNA methylation plays an important role in reducing TE activity (Bewick *et al.*, 2016). Consequently, for the MRL sequence to enhance *HvAACT1* expression and improve Al resistance in cultivated barley material, the promoter had to be demethylated at some stage. Kashino-Fujii *et al.* (2018) argued that demethylation likely occurred during the early domestication of barley when natural hybridizations transferred the MRL sequence from the wild barley to domesticated barley accessions.

In rice, the solo LTR found in the promoter of *OsFRDL4* is more prevalent in *japonica* than in *indica* varieties but absent in six wild species examined (*Oryza rufipogon*, *O. barthii*, *O. glumaepatula*, *O. meridionalis*, *O. australiensis*, and *O. punctata*). This led Yokosho *et al.* (2016) to conclude that the insertion event happened at the initial stage of domestication of the *japonica* subspecies. A similar pattern exists for maize. In a diversity panel of almost 200 maize inbreds, founders and teosinte, only two inbred lines possessed multiple copies of *ZmMATE1*, indicating that it is a rare allele (Maron *et al.*, 2013). Both of those lines were resistant to Al stress and shared similar geographic origins in tropical South American where acid soils are prevalent.

The tandem repeats described upstream of the *TaALMT1* gene in wheat could not be detected in 29 accessions of *Aegilops tauschii*, the D genome donor of hexaploid wheat. This also suggests that those mutations occurred after hybridization of the diploid and tetraploid ancestors (Ryan *et al.*, 2010). Similarly, wheat genotypes with the *Sukkula*-like TE upstream of *TaMATE1B* have only been detected in a few older Portuguese landraces and cultivars from Brazil (Tovkach *et al.*, 2013; Garcia-Oliveira *et al.*, 2014; Pereira *et al.*, 2015; Aguilera *et al.*, 2016). It is proposed that the Portuguese immigrants introduced these varieties to Brazil and the selection pressure posed by the highly Al-toxic soils in Brazil increased the frequency of the *TaMATE1B* allele with the TE insertion (Aguilera *et al.*, 2016).

In sorghum, the Al-resistant alleles of *SbMATE* in the $Alt_{SB}$ locus are rare and non-randomly distributed across the range of species diversity (Caniato *et al.*, 2011). A large analysis of the haplotype network indicated that Al resistance likely had a single and recent origin (Caniato *et al.*, 2014). Resistance was most prevalent in *guinea*-type accessions and material from West and South/East Africa (Caniato *et al.*, 2011). The mutations to *SbMATE* associated with Al resistance possibly appeared after the initial migration from the origin of domestication and after the *guinea* race differentiated from the progenitor *bicolor* types (Caniato *et al.*, 2011).

## Concluding remarks

TE activity can generate genetic changes in all living organisms containing these elements. Occasionally the TE-induced mutations result in beneficial changes that will facilitate adaptation to biotic and abiotic stresses. The first suggestions that TE-induced mutations contributed to Al resistance in plants were reported in wheat and sorghum. Similar roles have now been proposed in many other species. Most of these TEs are inserted upstream of OA transporter genes where they increase gene expression in the root apices. This increases organic anion release from those cells and protects the growing tissues from Al toxicity. TEs can also enhance expression by duplicating sequences or increasing gene copy number. However, not all TE insertions are beneficial. Those that reduce the expression of a key gene, affect splicing patterns, or alter protein function can decrease tolerance to acid soils. These might be underrepresented in any germplasm analysis because the greater sensitivity to Al would often be selected against in both wild and domesticated accessions.

TEs are an important factor in cereal domestication. Their activity near OA transporter genes appears to have had a major impact on the evolution of Al resistance in acid soils in many major crops species. These changes likely facilitated their selection and wider distribution to regions with acidic soils. There remains much to learn about the impact of TEs on plant adaptation to stress. Further characterization of the sequences flanking *ALMT* and *MATE* genes, together with expression studies and analysis of *cis*-acting elements, will provide further insights into the genetics of this important trait.

## Supplementary data

Supplementary data are available at *JXB* online.

Table S1. Putative *cis* elements detected at the 1023-bp insertion (*CACTA*-like transposon) upstream of *HvAACT1* that may be associated with altered gene expression in comparison with the allele not containing the insertion.

Table S2. Putative *cis* elements detected at the first 1 kb of the MRL insertion upstream of *HvAACT1* (bases −6601 to 7600 upstream of the first ATG) that may be associated with altered gene expression in comparison with the allele not containing the insertion.

Table S3. Putative *cis* elements detected at the first 2.3 kb upstream of *TaMATE1B* (containing the *Sukkula*-like transposon insertion) that may be associated with altered gene expression in comparison with the allele not containing the insertion.

Table S4. Putative *cis* elements detected at one MITE insertion upstream of *SbMATE* that may be associated with altered gene expression in comparison to the allele not containing the insertion.

Table S5. Putative *cis* elements detected at the 1.2 kb solo LTR upstream of *OsFRDL4* that may be associated with altered gene expression in comparison with the allele not containing the insertion.

Fig. S1. Putative *cis*-acting elements of ART1/STOP1 and WRKY22 manually detected in the transposon insertions upstream of *HvAACT1*, *TaMATE1B*, *SbMATE*, and *OsFRDL4*.

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## Author contributions

JFP performed the *in silico* analysis and illustrated the artwork. JFP and PRR contributed to the discussion and wrote the manuscript.

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