

Molecular mechanisms of Al tolerance in gramineous plants

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Abstract

Background Aluminum (Al) toxicity has limited the productivity and expansion of cereal crops on acid soils; however, a number of plant species or cultivars have developed different strategies for detoxifying aluminum both internally and externally.

Scope This review focuses on recent progress on molecular mechanisms of Al tolerance in gramineous plants.

Conclusions A common mechanism in all gramineous plants is the secretion of organic acid anions (citrate and malate) from the roots. Genes belonging to ALMT (for Aluminum-activated malate transporter) and MATE (Multidrug and toxic compound extrusion) family involved in the secretion have been identified in several plant species; however, different plant species show different gene expression patterns including Al-induction, spatial and temporal expression, and tissue localization. Furthermore, the mechanisms regulating the gene expression also differ with plant species, which are achieved by increased tandem repeated element, increase of copy number, insertion of transposon, or

alteration of cis-acting element. In addition to these common Al exclusion mechanisms, rice as a highly Al-tolerant species has developed a number of other mechanisms for detoxification of Al. A transcription factor for Al tolerance ART1 identified in rice regulates at least 30 genes implicated in internal and external detoxification of Al. These multiple genes may contribute to the high Al tolerance of rice. In the future, regulation mechanisms of Al-tolerance genes need to be further investigated.

Keywords Aluminum · Anion transporter · Citrate · Gramineous plant · Malate · Tolerance

Introduction

The family Gramineae (also called Poaceae) includes many important crops such as rice (*Oryza sativa*), maize (*Zea mays*), wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*). The three most important cereals; rice, wheat and maize directly contribute more than half of all calories consumed by human beings (Awika 2011). Therefore, increasing the production of these cereal crops is a very important issue in terms of food security because the world population is predicted to increase by about two billions by 2050 (FAO 2011) and another one billion tones of cereals will be required to feed the increasing population every year.

Many cereal cultivars with potential high yield have been bred during decades, however, their genetic potential has been limited due to various stresses. For

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instance, acid soils are widely distributed around the world and these pose multiple abiotic stresses to plants. Acid soils cover 30–40 % of arable land and more than 50 % of potential arable land (von Uexküll and Mutert 1995), where important cereal crops are cultivated. Constraints to production on acid soils are caused by both deficiency of nutrients such as P, Ca and Mg and toxicity of metals such as Mn and Al, but Al toxicity has been considered as the major limiting factor.

Aluminum is the most abundant metal in soil and comprises about 8 % on the elemental basis. Most Al in soil (in the form of aluminum oxides) is insoluble; however, when soil pH drops, Al becomes more soluble. Soluble Al (mainly Al^{3+}) shows phytotoxicity, which rapidly inhibits root elongation at the micromolar level, subsequently affecting the uptake of water and nutrients (Kochian 1995; Ryan et al. 2001; Ma 2007). Aluminum inhibits both cell division and elongation of the roots, with a time- and Al concentration-dependent manner (Kochian 1995; Ma 2000). Exposure to a low Al concentration may only inhibit the cell elongation during a short-period. However, a prolonged treatment with a high Al concentration will inhibit both cell elongation and division. Intensive studies on the mechanism of Al toxicity have been made and many possibilities have been proposed (Horst 1995; Ma 2000; Kochian et al. 2005; Poschenrieder et al. 2008; Horst et al. 2010). It seems that Al targets multiple sites of the roots including cell wall, plasma membrane, mitochondrial and nucleus. Binding of Al to these components affects the function and integrity of the root cells. This is supported by a recent microarray analysis study: a short exposure to Al induced expression (both up and down) of a number of genes (Tsutsui et al. 2012). Interestingly, genes not only in the root tips, the site of Al toxicity, but also those in the mature root zone and above-ground part were also induced although more genes in the root tips were affected (Tsutsui et al. 2012).

On the other hand, there is a wide variation in Al tolerance between species and cultivars within a species. Intensive studies have also been made to understand how these Al-tolerant species or cultivars cope with Al toxicity. Physiological studies have revealed several mechanisms of Al tolerance in different plant species, which include organic acid anions secretion from the roots (Miyasaka et al. 1991; Delhaize et al. 1993; Pellet et al. 1995; Ma et al. 1997b), cell wall modification (Yang et al. 2008; Yang et al. 2011), alkalination of the rhizosphere (Degenhardt et al. 1998) and sequestration

of Al into vacuoles (Shen et al. 2002, 2003). A number of loci responsible for Al tolerance have also been identified in different gramineous plants (Wu et al. 2000; Ma et al. 2002; Nguyen et al. 2001, 2003; Ma et al. 2004; Magalhaes et al. 2004; Niedziela et al. 2013). Especially in the last decade, great progresses have been made in identification of genes involved in Al tolerance. In this review, we focus on recent progress on molecular mechanisms of Al tolerance in gramineous plants. For the progress made in other plant species, refer to recent review papers (e.g. Delhaize et al. 2012).

Interspecific and genotypic difference in Al tolerance in gramineous plants

There is a great variation in Al tolerance among gramineous species and cultivars within a species. In cereal crops, the Al tolerance usually follows rice, rye (*Secale cereale*) > oat (*Avena sativa*) > wheat > barley (Bona et al. 1993). However, due to root elongation rates and genotypic differences, it is difficult to directly compare Al tolerance between species.

Genotypic differences in Al tolerance has been reported in many species. In rice, usually japonica cultivars are more tolerant to Al than indica cultivars (Ma et al. 2002). A screening of barley germplasm also showed that there is a large genotypic difference in Al tolerance (Fig. 1; Ma et al. 1997a). Al-tolerant and -sensitive cultivars were also found in wheat, rye, maize and sorghum (*Sorghum bicolor*) (Rengel and Jurkic 1993; Ryan et al. 1995; Pinto-Carnide and Guedes-Pinto 1999; Pandey et al. 2007; Caniato et al. 2007). These variations have been providing materials for studying Al tolerance mechanisms and identifying Al-tolerance genes as described below.

Physiological mechanisms of Al tolerance in gramineous plants

Physiological studies have revealed that most gramineous species share a common mechanism of Al tolerance; that is secretion of organic acid anions from the roots in response to Al (Ma et al. 2001). However, they differ in the kind of organic acid anions, amount and secretion patterns. Rice (Ma et al. 2002), barley (Zhao et al. 2003), maize (Pellet et al. 1995) and sorghum (Magalhaes et al. 2007) only secrete citrate, but most Al tolerant wheat



Fig. 1 Genotypic difference in Al tolerance in barley. *Left*, three selected Al-tolerant cultivars with or without Al treatment; *Right*, three Al-sensitive cultivars

cultivars secrete malate although some cultivars also secrete citrate (Delhaize et al. 1993; Ryan et al. 2009). Rye (Li et al. 2000), oat (Zheng et al. 1998), triticale (*x Triticosecale Wittmark*) (Ma et al. 2000) and Yorkshire fog (*Holcus lanatus*) (Chen et al. 2013) secrete both citrate and malate. Both malate and citrate are able to chelate toxic Al, thereby detoxifying Al in the rhizosphere (Ma et al. 2001).

The amount of Al-induced secretion of organic acid anions also differs with plant species. Usually rye secretes more organic acid anions than wheat and barley (Zhao et al. 2003). Rice only secreted a small amount of citrate although this also contributes to Al tolerance (Ma et al. 2002; Yokosho et al. 2011).

There are two different patterns for organic acid anion secretion (Ma 2000; Ma et al. 2001). In barley and wheat (Pattern I), the secretion occurs immediately after the addition of Al; while in rye, sorghum, rice and maize (Pattern II), there is a delay between the secretion and exposure to Al. These differences are consistent with the expression patterns of Al-tolerance genes involved as described below.

Other physiological mechanisms have also been reported in gramineous plants. For examples, methylation of pectin to reduce Al binding to cell wall in rice (Yang et al. 2008); decreasing the ratio of phospholipids to Δ^5 -sterols in the plasma membrane to lower the negative binding site for Al binding in rice (Khan et al. 2009); Al activated exudation of phenolic compounds from maize roots for detoxification of Al in the rhizosphere (Kidd et al. 2001).

Al tolerance genes in gramineous plants

Al tolerance in barley (Ma et al. 2004; Furukawa et al. 2007), wheat (Aniol 1990), sorghum (Magalhaes et al. 2004, 2007) and oat (Nava et al. 2006) is largely controlled by a single dominant gene, while Al tolerance in maize (Pandey et al. 1994; Borrero et al. 1995; Ninamango-Cárdenas et al. 2003; Krill et al. 2010) and rice (Wu et al. 2000; Ma et al. 2002; Nguyen et al. 2001, 2003) is a quantitative trait controlled by multiple genes. Since the first Al-tolerance gene (*ALMT1*) was identified from wheat (Sasaki et al. 2004), a number of genes involved in Al tolerance have been identified by using different approaches in gramineous plants. Most of them are related to organic acid anion secretion although other Al-tolerance genes also have recently identified in rice.

Genes involved in organic acid anion secretion

ALMT and MATE

Genes controlling efflux of malate and citrate from the roots have been identified in several gramineous plants. They belong to two different families; ALMT (for Aluminum-activated malate transporter) and MATE/AAC (for Multidrug and toxic compound extrusion/Aluminum activated citrate transporter) (Delhaize et al. 2012). TaALMT1 is a plasma membrane-localized protein with six transmembrane domains (Fig. 2c), which mediates the efflux of malate

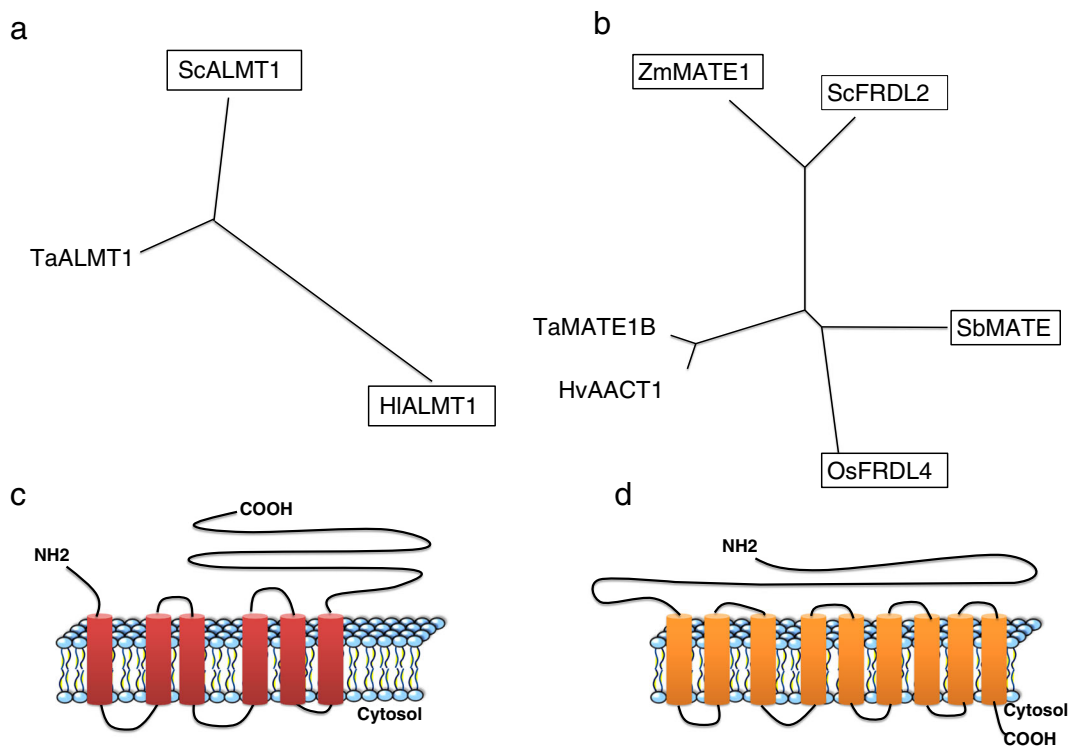


Fig. 2 Phylogenetic trees and secondary protein structure of ALMT and MATE/ACT in gramineous plants. Peptide sequence alignment was analyzed by Clustal W using default settings (<http://www.genome.jp/tools/clustalw/>). The phylogenetic tree of ALMT (a) and MATE/ACT (b) was constructed using the Tree View

program with the amino acid sequences. Frame marked genes are Al-inducible. The common membrane topology of ALMT (c) and MATE/ACT (d) is predicted by TMHMM server (<http://www.cbs.dtu.dk/services/TMHMM/>)

(Sasaki et al. 2004; Yamaguchi et al. 2005). Homologues of TaALMT1 have been identified in rye (ScALMT1, Collins et al. 2008), maize (ZmALMT1 and ZmALMT2, Piñeros et al. 2008; Ligaba et al. 2012), barley (HvALMT1, Gruber et al. 2010) and Yorkshire fog (HIALMT1, Chen et al. 2013) (Fig. 2a), but ZmALMT1, ZmALMT2 and HvALMT1 are not directly involved in the secretion of malate. On the other hand, MATE/ACT is also localized in the plasma membranes usually with nine transmembrane domains (Fig. 2d), but transports citrate (Furukawa et al. 2007). MATE genes have been identified in barley (HvAACT1, Furukawa et al. 2007), sorghum (SbMATE, Magalhaes et al. 2007), rye (ScFRDL2, Yokosho et al. 2010), maize (ZmMATE1, Maron et al. 2010), rice (OsFRDL4, Yokosho et al. 2011) and wheat (TaMATE1B, Tovkach et al. 2013) (Fig. 2b). These genes have been demonstrated to be involved in detoxification of Al toxicity in several species. Knockout or knockdown of these genes results in decreased Al tolerance. On the other hand, over-expression of these genes increases the

tolerance to Al toxicity in some cases (Delhaize et al. 2004, 2009; Pereira et al. 2010; Zhou et al. 2013). Interestingly, different species show distinct expression patterns, localization and regulation as detailed below.

Different expression pattern and localization

The expression pattern of ALMT and MATE differs with plant species in terms of induction, spatial and temporal expression. The expression of TaALMT1 (Sasaki et al. 2004), and HvAACT1 (Furukawa et al. 2007), is not induced by Al, whereas that of ScALMT1 (Collins et al. 2008), ScFRDL2 (Yokosho et al. 2010), SbMATE (Magalhaes et al. 2007), OsFRDL4 (Yokosho et al. 2011) and HIALMT1 (Chen et al. 2013) is up-regulated by Al (Fig. 2a, b). Furthermore, the expression of ScALMT1 and OsFRDL4 is up-regulated within hours upon exposure to Al, while that of SbMATE requires few

days to be induced (Collins et al. 2008; Yokosho et al. 2011; Magalhaes et al. 2007). These expression patterns are consistent with secretions patterns of organic acid anions as described above. Rapid secretion in Pattern I species does not require gene induction, while gene induction is required for the delayed secretion in Pattern II species.

Most *ALMT* and *MATE/AACT* genes are expressed in the root tips. For example, *TaALMT1* is highly expressed in the root tips (0–5 mm; Sasaki et al. 2004). High expression of *HvAACT1* is also observed in the first 3 mm of barley roots (Fujii et al. 2012). Since root tips are the target site of Al toxicity (Ryan et al. 1993), high expression in this position can efficiently detoxify Al externally. However, some *MATE* genes are also expressed in the mature root zones. For example, similar expression level of *OsFRDL4* was found in both the root tips and mature zones (Yokosho et al. 2011). In an Al-tolerant cultivar of wheat (Carazinho), higher expression of *TaMATE1B* was found in the basal root region than in the root tips (Tovkach et al. 2013). There are two possibilities for the expression of *MATE* in the basal root zones. One is that citrate is also secreted from this region to prevent toxic Al into the cells. The other is that these genes may play different role in the mature root zone. This is demonstrated by a recent study showing that *HvAACT1* in the mature root region is involved in translocation of Fe from the roots to the shoots (Fujii et al. 2012).

The tissue and cellular localization was only investigated in a limited number of species. In barley, *HvAACT1* is localized in the epidermal cells (Furukawa et al. 2007). In rice, *OsFRDL4* is expressed in all rice root cells (Yokosho et al. 2011). Recently, *SbMATE* in sorghum was found to be localized in the epidermal and outer cell cortical cell layers of the DTZ (Sivaguru et al. 2013). The difference in the tissue localization may be associated with the root structures of different plant species.

Regulation mechanism of *ALMT* and *MATE* gene expression

The expression level of *ALMT* and *MATE/AACT* is higher in Al-tolerant cultivars than in Al-sensitive cultivars, indicating that the Al tolerance is regulated by the expression level. Recently, a few studies have revealed the mechanisms regulating the expression of *ALMT* and

MATE/AACT. They include increased tandem repeated element, increase of copy number, insertion of transposon, and alteration of cis-acting element (Fig. 3, Delhaize et al. 2012). The wheat *TaALMT1* promoter is highly polymorphic with eight different alleles described to date. These alleles comprise of single nucleotide polymorphisms (SNPs) and perfect tandem repeats of various sizes. The high expression level of *ALMT1* is associated with tandem repeated elements in the promoter region in most Al-tolerant lines (Fig. 3a, Sasaki et al. 2006; Ryan et al. 2010). In sorghum, tourist-like miniature inverted repeat transposable elements (MITEs) occur upstream of the *SbMATE* gene and the number of these repeats is broadly correlated with the level of *SbMATE* expression (Fig. 3a, Magalhaes et al. 2007). In rye, the high Al tolerance in Al-tolerant genotype is attributed to the increased genomic copy number of *ScALMT1* (Fig. 3b, Collins et al. 2008). Al-tolerant genotypes of rye have five *ScALMT1* genes clustered together on chromosome 7R, of which two are highly expressed in the root tip, whereas only two copies in the sensitive genotype, of which only one are highly expressed in the root tip (Collins et al. 2008). Recently, Maron et al. (2013) also found that Al-tolerant cultivars of maize have three copies of *ZmMATE1* in the genome, which are identical and part of a tandem triplication (Fig. 3b). This copy number is associated with both gene expression and Al tolerance (Maron et al. 2013). On the other hand, transposon insertion was found to regulate the expression level in barley and some wheat cultivars (Fig. 3c). In barley, a 1-kb insertion (CACTA-like transposon) was found in the 5' untranslated region (UTR) of the *HvAACT1* coding region of Al-tolerant cultivars. This insertion functions as a promoter, which enhances and alters the tissue localization of *HvAACT1* (Fujii et al. 2012). Recently, an 11.1-kb transposon-like element (a Sukkula-like transposon) located 25 bp upstream of the start codon was also found to extend *TaMATE1B* expression to the root apex of Al-tolerant wheat cultivar Carazinho, which secretes citrate constitutively (Tovkach et al. 2013). In an accession of Yorkshire fog well adopted in acid soil, the high expression of *HIALMT1* is achieved by increasing the number of cis-acting elements of ART1 in the promoter region (Fig. 3d, Chen et al. 2013). ART1 is a transcription factor for Al tolerance as described below. These findings indicate the expression of *ALMT1* and *MATE1* is regulated by different ways depending on plant species.

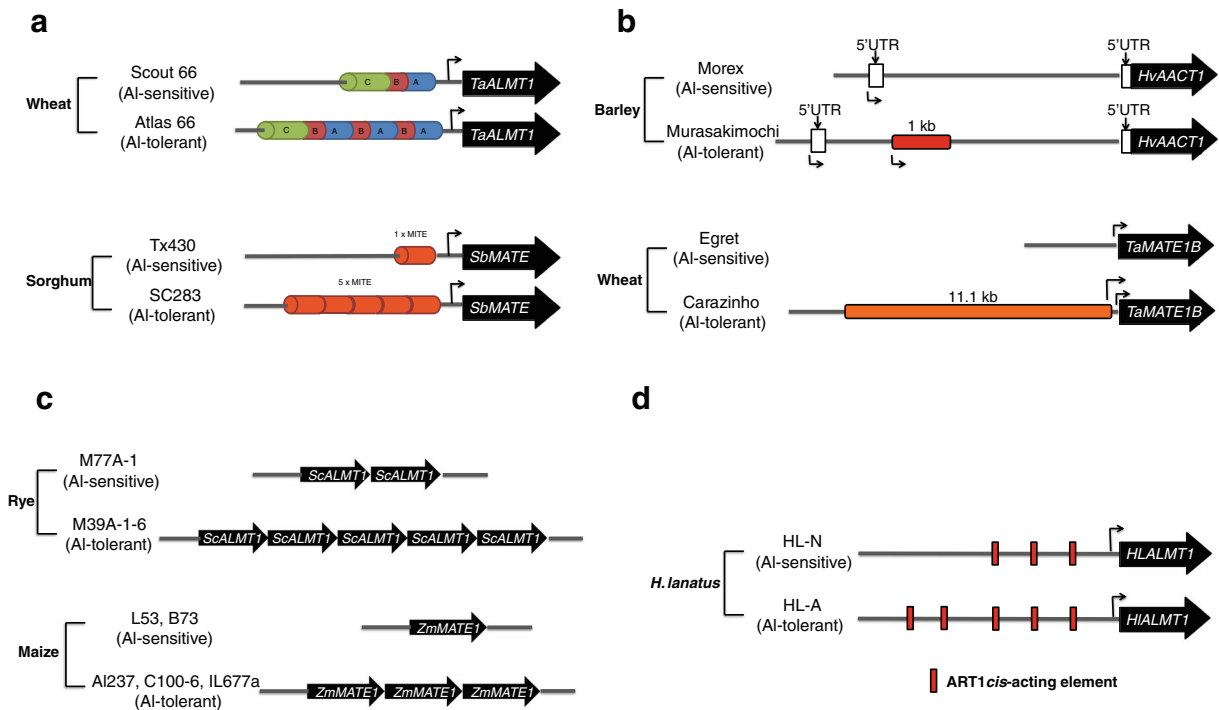


Fig. 3 Different regulation mechanisms of Al-tolerance genes involved in organic acid anion secretion in gramineous plants. The high gene expression level is achieved by increase of tandem

repeated element (a), insertion of transposon (b), increase of copy number (c), or alteration of *cis*-acting element (d). Modified according to Delhaize et al. (2012)

Interestingly, in barley, the 1-kb insertion was only detected in some accessions cultivated in acid soil area including Japan, China and Korea, but not in wild barley (Fujii et al. 2012). Three-copy alleles of *ZmMATE1* were only found in three cultivars of maize, which share the same geographical origin, in regions of acid soils of the South American tropics (Maron et al. 2013), but not in teosinte (*Zea luxurians*). The difference in the number of *cis*-acting elements in Yorkshire fog seems to have occurred over 150 years due to single nucleotide substitutions although this is also a possibility that these SNPs are the result of selection of various alleles on the acidic plots (Chen et al. 2013). These findings suggest that the regulatory mechanism of the gene expression was developed as a result of adaptation to acid soil during relatively short term as proposed by Ryan and Delhaize (2010).

Mechanism of Al-induced activation

Heterologous expression analysis showed that most ALMT and MATE proteins require external Al to

activate their function. However, the mechanism underlying Al activation is still poorly understood. Motoda et al. (2007) reported that ALMT1 protein contains six transmembrane domains with the amino and carboxyl termini located on the extracellular side of the plasma membrane. Furuichi et al. (2010) found that three main residues (Glu274, Asp275 and Glu284) in the C-terminal domain of *TaALMT1* are involved in the Al-activation response by directly binding Al. However, a recent study showed that the N-domain, which is predicted to form the conductive pathway, can mediate organic anion transport in the absence of the C-domain (Ligaba et al. 2013). Furthermore, it was found that both the N- and C-domains are involved in Al-mediated enhancement of transport activity. It is argued that the C-terminal half is, at least in part, oriented towards the intracellular space, and is thus incapable of direct interaction with extracellular Al (Dreyer et al. 2012; Mumm et al. 2013). In addition, a recent comprehensive phylogenetic analysis showed that these three residues are highly conserved throughout the entire ALMT family, in which some members do not show Al-activation. Information of crystal structure of ALMT1 will be

required in order to understand the interaction between Al and the proteins. Although MATE activity was also activated by Al (Furukawa et al. 2007; Yokosho et al. 2011), there is no study on the underlying mechanism.

ART1-mediated high Al tolerance in rice

Among the small grain cereal crops, rice is characterized by superior Al tolerance (Ma et al. 2002). Genetic analysis has shown that Al tolerance in rice is controlled by multiple genes and a number of loci associated with Al tolerance have been detected (Wu et al. 2000; Ma et al. 2002; Nguyen et al. 2001, 2003). By using mutant approach, a transcription factor for Al tolerance, ART1 (Al resistance transcription factor 1) has been identified (Yamaji et al. 2009). ART1 is a C₂H₂ zinc-finger protein, which is a homolog of STOP1. In *Arabidopsis thaliana*, STOP1 regulates the expression of *AtMATE1* and *AtALMT1* (Liu et al. 2009; Sawaki et al. 2009). ART1 binds to the core cis-acting element [GGN(T/g/a/C)V(C/A/g)S(C/G)] that is present in the promoter of ART1 downstream genes (Tsutsui et al. 2011). ART1 regulates at least 31 genes (Yamaji et al. 2009). Functional analysis of some of ART1 downstream genes showed that they are involved in detoxification of Al both externally and internally. Although the expression and localization of ART1 is not induced by Al, the expression of downstream genes is up-regulated by Al within hours (Yamaji et al. 2009). All the proteins encoded are localized at all root cells (Huang et al. 2009, 2012; Xia et al. 2010, 2013; Yokosho et al. 2011; Chen et al. 2012), but play different roles in Al detoxification (Fig. 4). *STAR1* and *STAR2* encode an ATP-binding domain and a membrane-binding domain, respectively, of a bacterial type ABC transporter (Huang et al. 2009). The STAR1-STAR2 complex localized at the vesicles transports UDP-glucose, which may be involved in cell wall modification, resulting in decreased Al accumulation in the cell wall. Four genes (*OsFRDL4*, *OsCDT3*, *OsMGT1* and *OsNrat1*) all encode plasma-membrane-localized proteins, which are involved in Al tolerance. *OsFRDL4* described above is responsible for the secretion of citrate in response to Al (Yokosho et al. 2011). Compared with other ART1-regulated genes, the up-regulation of *OsFRDL4* by Al is the greatest. *OsCDT3*, encoding a small cysteine-rich peptide shows binding activity with Al, thereby preventing Al entering into the root cells (Xia et al. 2013). On the other hand,

OsMGT1 functions as a Mg transporter (Chen et al. 2012), and up-regulation of *OsMGT1* could alleviate internal Al toxicity by enhancing Mg uptake. The involvement of Mg transporter in Al tolerance was also reported in yeast (*ALR1* or *ALR2*) and Arabidopsis (*AtMGT1*) (MacDiarmid and Gardner 1998; Deng et al. 2006). *Nrat1*, a member of Nramp family, transports trivalent Al (Xia et al. 2010), which is required for sequestration of Al into the vacuoles for final detoxification. Vacuolar sequestration of Al is mediated by *OsALS1*, a half-size ABC transporter localized at the tonoplast (Huang et al. 2012). Knockout of any gene described above results in increased Al sensitivity, but at different extent. Among these genes examined, *OsFRDL4* showed a good correlation between the expression and Al tolerance (Yokosho et al. 2011). Variation of *Nrat1* explained 40 % of Al tolerance in aus subpopulation from *Indica* varietal group (Famoso et al. 2011). These findings suggest that these two genes may be responsible for genotypic difference in Al tolerance. By contrast, there is no correlation between the expression of *STAR1*, *STAR2*, *OsMGT1*, *OsCDT3*, *OsALS1* and Al tolerance, suggesting that they are involved in basic detoxification of Al in rice. Therefore, the high Al tolerance in rice is achieved by multiple genes involved in both internal and external detoxification.

A homolog of rice ART1 was also identified in Yorkshire fog (Chen et al. 2013). Similar to rice ART1, *HIART1* interacts with the promoter region of *HIALMT1*, suggesting that rice and Yorkshire fog share a similar regulatory pathway. Recently, an ART1 homolog in wheat, *TaSTOP1*, was cloned (Garcia-Oliveira et al. 2013). The expression of *TaSTOP1* is also not induced by Al, but the role of this gene in Al tolerance remains to be investigated further since *TaALMT1* is expressed constitutively.

In addition to ART1, recently *ASR5* (Abscisic acid, stress and ripening) was reported to be involved in Al tolerance in rice (Arenhart et al. 2013a). *ASR5* is localized in both the nucleus and the cytoplasm and acts as a transcription factor, which may regulate the expression of different genes that collectively protect rice cells from Al-induced stress responses. Furthermore, *ASR5* protein could bind *STAR1* promoter (Arenhart et al. 2013b). However, knockdown of this gene not only resulted in decreased Al tolerance, but also decreased tolerance to other stress such as drought and morphologic changes (Arenhart et al. 2013a). This raises a question whether *ASR5* is involved in Al tolerance directly.

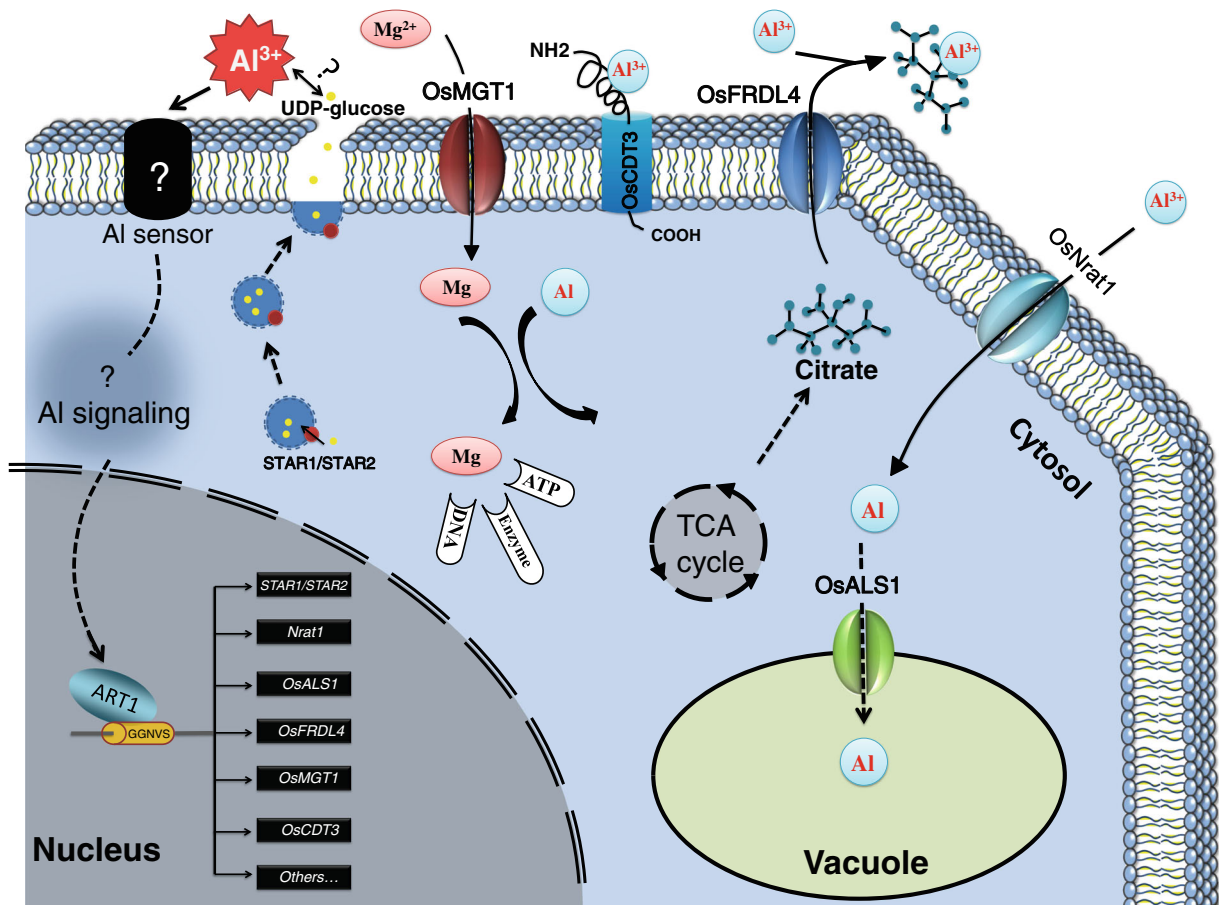


Fig. 4 ART1-mediated Al tolerance in rice. STAR1/STAR2, UDP-glucose transporter; Nr1, plasma membrane-localized Al transporter; OsALS1, tonoplast-localized Al transporter;

OsFRDL4, citrate transporter; OsMGT1, magnesium transporter; OsCDT3, 53-amino acid peptide rich in cysteine

Manipulation of Al-tolerance genes

Identification of Al-tolerance genes makes it possible to introduce these genes into Al-sensitive species and cultivars, thereby producing transgenic crops with high Al tolerance. Several attempts have been made, mainly by enhancing organic acid anion secretion. Secretion of organic acid anions from the roots involves synthesis and transport processes. Since organic acids such as malate and citrate are common cellular components with high turnover rates and only a small part of organic acids are secreted in response to Al, the synthesis process is unlikely a limiting factor for secretion of organic acid anions (Ryan et al. 2011). However, several studies have shown that over-expression of genes encoding organic acid synthesis also resulted in increased citrate secretion and Al tolerance (Anoop et al. 2003; de la Fuente et al. 1997; Koyama et al. 2000; Tesfaye et al. 2001),

although the same result was not observed in another study (Delhaize et al. 2001). By contrast, over-expression of genes involved in secretion of organic acids has successfully improved the Al tolerance. Over-expression of *TaALMT1* in barley, wheat and Arabidopsis resulted in enhanced secretion of malate and Al tolerance (Delhaize et al. 2004; Pereira et al. 2010; Ryan et al. 2011). Introduction of *MATE* genes also resulted in increased citrate secretion and Al tolerance in tobacco (*Nicotiana tabacum*) and Arabidopsis (Furukawa et al. 2007; Magalhaes et al. 2007). Recently, it was also found to be effective to increase Al tolerance in barley and wheat by over-expressing *HvAACT1* (Zhou et al. 2013). However, it seems that there is a limit to increase Al tolerance by manipulating these genes. For example, transgenic barley carrying *HvAACT1* showed lower Al tolerance compared with Al-tolerant barley cultivar, Dayton (Zhou et al. 2013).

These findings suggest that there is still potential to enhance Al tolerance by introducing multiple genes rather than a single gene and genes involved in the regulations.

Prospective

Great progresses have been made in understanding molecular mechanism of Al tolerance in gramineous plants during the last decade. It becomes clear that species having multiple Al-tolerance genes like rice is more tolerant to Al than species having single tolerance gene like barley. For the single Al-tolerance gene such as *ALMT* and *MATE/AACT*, the expression level determines the Al tolerance. Although the mechanisms regulating the expression level of *ALMT* and *MATE/AACT* have been elucidated in some species as described above, the whole picture on how these genes are regulated in different species and cultivars, remains to be further investigated in detail. Recently, Melo et al. (2013) found that introduction of *SbMATE* into different background resulted in different expression level and Al tolerance, suggesting that *SbMATE* expression is regulated at multiple levels. It seems that both *cis*- and *trans*-acting elements are involved in regulating *SbMATE* expression.

The transcription factor ART1 plays a central role in Al tolerance in rice and Yorkshire fog (Yamaji et al. 2009; Chen et al. 2013). However, the upstream pathway is still unknown. The expression and localization of ART1 is unaffected by Al (Yamaji et al. 2009), therefore, there must be a process for activation of ART1. It will be interesting to identify ART1-interacting proteins in future. On the other hand, although eight downstream genes of ART1 have been functionally characterized, the role of remaining genes is unknown. Functional characterization of these genes will extend our understanding on high Al tolerance in rice. It will also be interesting to examine whether ART1-mediated Al tolerance is also present in other gramineous species such as barley and wheat, and why some genes such as *HvAACT1* and *TaALMT1* are not induced by Al. Famoso et al. (2011) detected 46 candidate genes for Al tolerance in rice by GWA (Genome-wide association) analysis. Identification of these QTL genes will provide new insight into molecular mechanisms underlying genotypic difference in Al tolerance.

For breeding Al-tolerant species and cultivars, in addition to transgenic approaches as described above,

other approaches such as marker-assisted selection (MAS), genomic selection will also be useful. Introduction of multiple Al-tolerance genes rather than a single gene will be more effective to improve Al tolerance and therefore increase crop production on acid soils.

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