

Review



Recent Advances in Understanding Mechanisms of Plant Tolerance and Response to Aluminum Toxicity

Yunmin Wei, Rongrong Han, Yonghong Xie, Caode Jiang and Yongxiong Yu *

College of Animal Science and Technology, Southwest University, Chongqing 400715, China; weiym1024@163.com (Y.W.); 19891214rong@163.com (R.H.); Xieyh0128@163.com (Y.X.); jcdpjx@swu.edu.cn (C.J.) * Correspondence: yuyongxiong8@126.com; Tel.: +86-138-8360-8535

Abstract: Aluminum (Al) toxicity is a major environmental stress that inhibits plant growth and development. There has been impressive progress in recent years that has greatly increased our understanding of the nature of Al toxicity and its mechanisms of tolerance. This review describes the transcription factors (TFs) and plant hormones involved in the adaptation to Al stress. In particular, it discusses strategies to confer plant resistance to Al stress, such as transgenic breeding, as well as small molecules and plant growth-promoting rhizobacteria (PGPRs) to alleviate Al toxicity. This paper provides a theoretical basis for the enhancement of plant production in acidic soils.

Keywords: Al toxicity; Al tolerance mechanism; Al tolerance strategy



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1. Introduction

Aluminum (Al) is the third most abundant chemical element in the earth's crust. Al mainly exists as aluminosilicates and oxides with non-phytotoxicity in neutral or slightly acidic soils. In acidic conditions (pH < 5.0), the mineral form of Al dissolves to release the soluble Al³⁺ species, which can rapidly inhibit root elongation and further affect the uptake of water and nutrients, eventually resulting in nutritional deficiency and drought stress, which lead to severe loss of plant productivity [1,2]. Acidic soils occupy approximately 50% of potentially arable lands worldwide, most of which are distributed in Southwest Asia, Central Africa, and South America, as well as in Australia, eastern North America, and throughout Europe [3,4]. In recent decades, with an increasing intensity of human activities, especially an increase in acid deposition caused by global industrialization and the high-intensity utilization of agricultural soil have led to the continuous entry of a large amount of exogenous H⁺ into the soil, which has greatly accelerated the process of soil acidification, raising a huge threat to sustainable agricultural development and food security [5]. Liming can ameliorate Al toxicity by raising the soil pH, but it has little effect on the improvement of the underlying soil and hardens the soil structure [6]. The world's population is also growing rapidly and is anticipated to increase to 9.7 billion by 2050 [7]. Therefore, understanding Al-resistance mechanisms and the development of strategies to confer plant resistance for sustainable agricultural productivity remains imperative.

The research on Al stress has been updated rapidly in recent years, and a substantial number of new genes have been proven to be involved. For example, Snowden et al. cloned five *wali1–5* (wheat aluminum induced) genes from the root tips of Al-treated Warigal wheat (*Triticum aestivum*) [8]. Subsequently, Richards et al. cloned *wali6* and *wali7* in this variety of wheat [9]. However, there are limited reviews on Al stress. Furthermore, more and more evidence has confirmed the involvement and roles of Al in promoting plant growth, improving phosphorus efficiency, and alleviating H⁺, manganese, and iron toxicities in acidic conditions [10,11]. Additionally, Al stress confers plants tolerance to abiotic stresses by activating the stress-related genes and attracts the plant growth-promoting rhizobacteria (PGPRs) toward roots by inducing root exudates [10,12]. Therefore, more reviews on the progress of research on Al stress are needed. This paper comprehensively reviews recent

advances by studies on Al toxicity and tolerance in plants, thereby providing a theoretical basis for the cultivation of Al tolerant varieties.

2. Effects of Aluminum (Al) Stress in Plants

Al stress has become the main limiting factor with multifarious detrimental effects in plants (Figure 1). The Al³⁺ ion is a multivalent cation that rapidly and strongly binds to negatively charged sites in the root [13]. It has been reported that Al changes the properties of the cell wall (CW) and interferes with the transport of molecules across the cell membrane, influencing an array of intercellular processes [14]. The major target site of Al toxicity is the root apex, particularly the distal part of the transition zone [15]. Al binding of the root causes loss of Mg^{2+} , K^+ , and Ca^{2+} , as well as limits the availability of indispensable nutrients, especially phosphorus (P), magnesium (Mg), and molybdenum (Mo), therefore, impairing root growth [16,17]. Al also reduces expansion, stomatal closure, and net photosynthesis in leaves, and tends to bind with P to form insoluble complexes in acidic soil, thereby resulting in P deficiency for plant growth [18,19]. Likewise, Al stress decreases the phytoextraction capability from contaminated soils using hyperaccumulators [20]. Moreover, Al stress can cause the production of reactive oxygen species (ROS) and reactive nitrogen species (RNS), which trigger a series of free radical chain reactions, including the peroxidation of the cell membrane system, decrease in enzyme activities, decomposition of chlorophyll, and breakage of the DNA strand [21]. Recently, Al stress has been reported to disturb soil rhizobia by affecting the efficacy of nodulation and N-fixation in legume species, and therefore influences the balance of hormones in plant roots, which has been proposed to cause growth inhibition [22,23]. Intriguingly, Al³⁺ has been regarded as a beneficial element in the growth of some plants in acidic soil, and Al-induced growth enhancement in tea plants has been associated with the maintenance of DNA integrity in meristematic cells and increased uptake of nutrient elements [10,24,25].



Figure 1. Adverse detrimental effects of aluminum (Al) stress and their location in plants.

3. Al Tolerance Mechanisms in Plants

Plants thriving in acidic soil have adaptations, including external exclusion and internal tolerance, to detoxify Al [3,26]. External exclusion prevents Al from entering cells through Al-induced root exudation of organic compounds into the rhizosphere, decreasing the capacity of CWs to bind Al³⁺ and rhizosphere alkalization. Internal tolerance mainly includes the uptake and sequestration of Al in the vacuole and the improvement of antioxidant capacity inside cells [5,27]. Recently, various approaches have been used to

study the mechanisms of Al tolerance in plants. Transcriptome, proteome, metabolome, mutation breeding methodologies, and several Al-tolerant genes have been reported to be involved in the secretion of organic acids (OAs) for Al³⁺ chelation, CW modification for the reduction in Al content, pH increase in the rhizosphere, etc. (Table 1).

Genes	Description	Plant Species	Functions	References
AhFRDL1	Ferric reductase defective-like 1 protein	Arachis hypogaea	Transport citrate	[28]
AtPrx64	Class III peroxidase	Arabidopsis thaliana	Peroxidase	[29]
AvSAMS1	S-adenosyl methionine synthetase	Andropogon virginicus	Alterations of methylation status	[30]
BoALMT1	Aluminum induced malate transporter	Brassica oleracea	Transport malate	[31]
BdMATE GmMATE75 GmMATE79 GmMATE87 GsMATE PtrMATE1 PtrMATE2 TaMATE1B	Multidrug and toxic compound extrusion	Brachypodium distachyon Glycine max Glycine max Glycine max Glycine soja Populus tomentosa Populus tomentosa Triticum aestivum	Transport citrate	[32] [33] [33] [34] [35] [35] [36]
FeSTAR1	Half-type ABC transporter	Fagopyrum esculentum	Affect cell wall hemicellulose metabolism	[37]
GmGRPL	Glycine-rich protein-like protein	Glycine max	Regulating the level of indole-3-acetic acid (IAA) and ethylene	[38]
GmIREG3	Iron regulated/ferroportin	Glycine max	Sequestrating Al into the vacuoles	[39]
GmME1 HtNHX1 HtNHX2	NADP-malic enzyme Sodium (potassium)/proton antiporters	Glycine max Helianthus tuberosus Helianthus tuberosus	NADP-malic enzyme activity Na+/H+ antiporter	[40] [41] [41]
HvABCB25	ATP binding cassette transporters	Hordeum vulgare	Vacuolar Al sequestration	[42]
MsCS	Citrate synthase	Medicago sativa	Citrate synthesis	[43]
MsPG	Polygalacturonase	Medicago sativa	increasing porosity and extensibility of cell walls	[44]
NtSUT1	Sucrose transporter	Nicotiana tabacum	Sucrose uptake	[45]
OsAUX3	Auxin carrier	Oryza sativa	Auxin influx carrier	[46]
VuAAE3	Acyl activating enzyme	Vigna umbellata	Oxalyl-CoA synthetase	[47]
VuFDH	Formate dehydrogenase	Vigna umbellata	Catalyze the oxidation of formate	[48]
ZjOMT	Methyltransferase	Zoysia japonica	Melatonin synthesis	[49]
ZmAT6	Aluminum tolerance protein	Zea mays	Scavenging reactive oxygen species	[50]
ZmPGP1	P-glycoprotein	Zea mays	Auxin efflux carrier	[51]

Table 1. Genes confirmed to be involved in Al tolerance in recent years.

3.1. External Exclusion Mechanisms

In the Al tolerance mechanism, plants can secrete OAs, such as citrate, malate, and oxalate, from roots under Al stress [3,26,52]. Accumulating evidence has shown that citrate is more dominant than malate and oxalate in response to Al stress [3]. Al-induced secretion of OAs is mediated through anion channels or transporters [53]. To date, Al-activated malate transporter (ALMT) and multidrug and toxic compound extrusion (MATE) have been identified [5,16,17,27]. Since Sasaki et al. identified TaALMT1 from wheat [54], it has been discovered that ALMT is involved in Al-induced secretion of malate to alleviate Al toxicity in *Arabidopsis* [55,56], barley (*Hordeum vulgare*) [57], rape (*Brassica napus*) [58,59], maize (*Zea mays*) [60], Yorkshire fog (*Holcus lanatus*) [61], Camelina (*Camelina sativa*) [62],

rubber tree (Hevea brasiliensis) [63], and cabbage (Brassica oleracea) [31], etc. Interestingly, TaALMT1 also plays a role in alkaline tolerance by promoting exudation of both malate and gamma-aminobutyric acid (GABA) in wheat. In addition, MATEs, which are well characterized as multidrug transporters, can transport various substrates, such as citrate, secondary metabolites, and plant hormones, through electrochemical cation gradients [64]. In recent years, MATE genes have been identified from various plant species, including Arabidopsis [65], cabbage [66], Brachypodium distachyon [32], eucalyptus (Eucalyptus camaldulensis) [67], buckwheat (Fagopyrum esculentum) [68], soybean (Glycine max) [33,69,70], Rubiaceae (Psychotria rubra) [71], sorghum (Sorghum bicolor) [72], rice bean (Vigna umbel*lata*) [73–76], maize [77,78], wheat [36], wild soybean (*Glycine soja*) [34], etc. The difference in cell location and Al-induced expression patterns of MATE transporters have been determined. For instance, *FeMATE1* localized on the plasma membrane (PM), is specifically expressed in roots, whereas FeMATE2 located on the Golgi membrane, is expressed in both the roots and the leaves [68]. Al stress could induce PtrMATE1 expression in 12 h, in contrast to the expression pattern of *PtrMATE2*, which occurred 24 h after Al³⁺ treatment [35]. VuMATE1 was expressed at 6 h after Al stress, whereas VuMATE2 was expressed at the early stage of Al stress [73,76]. However, most plants that adopt external exclusion need to protect the root tip from Al toxicity directly on the root surface and ensure the dynamic balance of plant essential nutrients [79]. Al is the most abundant metal element in the earth's crust; plants cannot alleviate all Al toxicity in acidic soil but can neutralize a portion around the root tip. Therefore, the first reaction of plants to Al toxicity is to prevent the Al³⁺ around the root tip from entering the root cells, which may be the main target of OAs [80].

The transmembrane transport of OAs depends on the driving force formed by the proton electrochemical gradient on both sides of the PM, which provides continuous power for organic acid secretion [81,82]. Al stress increases the activity of PM H⁺-ATPase and inhibits the expression of VHA-a2, VHA-a3, and vacuolar proton pump activity, and therefore increases the proton gradient on both sides of the PM and promotes OAs secretion by AtALMT1 and AtMATE [83]. Al stress reduces the entry of OAs into vacuoles by inhibiting vacuolar proton pump activity and activating the PM transport system, which secretes large amounts of intracellular OAs to the apoplast. While OAs secretion is blocked, vacuolar proton pump activity is activated, indicating that intracellular Al tolerance may be an alternative [83]. Additionally, it is known that OAs secretion depends on the maintenance of internal concentrations of OAs. Zhou et al. identified a cytosolic NADP-malic enzyme, GmME1, which was implicated in the organic acid pool and confers higher Al resistance by increasing internal malate and citrate concentrations and their external efflux [40]. Recently, Sun et al. found that the level of the MsCS transcript was higher in Al tolerant cultivar as compared with the Al sensitive cultivar and the activity of citrate synthase (CS) affected Al resistance through citrate concentration and exudation in alfalfa cultivar [43]. These results suggest that OAs secretion can be regulated through the activation of OA transporters, PM H⁺-ATPase activity, and improvement of the internal OAs pool.

In addition to the secretion of OAs, the release of phenols has been verified to have the capacity to detoxify Al through chelating Al³⁺ ions. For example, Al and silicon (Si) trigger the release of catechol, catechins, and quercetin by root tips, which could potentially detoxify Al [84]. Ma et al. also found that phenolic compounds were involved in coping with Al toxicity in the Chinese fir by comparative transcriptome [85]. Chen et al. reported the enhancement of polyphenolic metabolism as an adaptive response to Al stress in lettuce roots [86]. Recently, the findings of Fu et al. indicated that Al-polyphenol complexes improved Al resistance in tea plants [87]. Therefore, a comprehensive exploration of the roles of phenolic compounds under Al stress might be an ideal target for genetic engineering in the future.

The CW is the first barrier for plants to resist external stress and has been recognized as the major target of Al toxicity; plants can alleviate Al stress by modifying the CW [88]. For example, OsSTAR1 interacts with OsSTAR2 to form an ATP-binding cassette (ABC) transporter complex, which is specifically responsible for transporting uridine diphosphate (UDP)-glucose and modifying CWs in rice [89]. Similarly, FeSTAR1 and FeSTAR2 also form an ABC transporter complex, which participates in Al tolerance through the CW matrix polysaccharide metabolism in buckwheat [37,90]. Recently, Fan et al. showed that abscisic acid (ABA) alleviation of Al toxicity in rice beans depends on ABI5-mediated CW modification and osmoregulation [91]. More recently, Liu et al. identified a 4-coumarate, which influences Al resistance through the modification the CW [46]. Moreover, pectin methylesterase (PME) plays an important role in Al tolerance by regulating the degree of pectin esterification in the CW, which converts highly methylated pectin into a negatively charged demethylation form, resulting in more Al³⁺ binding to pectin [92]. Overexpression of *OsPME14* accumulated the content of Al in the root tip CW and increased its sensitivity to Al in rice [93]. Furthermore, it was found that Al-tolerant varieties showed higher methylated pectin ratio and lower PME activity in rice, corn, and buckwheat [13,94,95]. Therefore, Al-resistant crop varieties can be cultivated by reducing the pectin content of plant root tips or increasing the degree of methylation of pectin.

Additionally, rhizosphere alkalization is one of Al tolerance mechanisms by reducing the solubility of Al [96]. For example, Yang et al. showed that elevated pH from 2.5 to 4.0, alleviates the Al-toxicity of *Citrus* by increasing root accumulation of malate and citrate [97,98]. Further experiment showed that raised pH alleviates Al-induced a decrease in total soluble protein level and an increase in electrolyte leakage in citrus leaves and roots by conferring the ability to maintain a balance between production and detoxification of ROS and methylglyoxal [92]. Moreover, Liu et al.'s study on wild barley showed that low pH and higher Al tolerance in XZ16 were associated with a higher ability of H⁺ uptake and rhizospheric alkalization [99]. Magnesium promotes the elevated root surface pH regulation in Populus, resulting in root surface alkalization in the transition zone, which alleviates the toxicity of high concentration Al [100].

3.2. Internal Tolerance Mechanisms

Internal tolerance mechanisms are mainly involved in Al detoxification, uptake, translocation, and accumulation of non-phytotoxic complexes of Al in the various organs [101,102]. For instance, buckwheat, hydrangea, and tea can accumulate a large amount of Al in the aboveground parts via transporting nontoxic Al complexes [103–105]. Several transporters have been reported to be involved in the absorption, sequestration, and transportation of Al from roots to aboveground parts in plants. In rice, OsNrat1, a PM-located transporter, belongs to the natural resistance-associated macrophage protein (Nramp) and has low similarity with other Nramp members, which specifically transports Al^{3+} rather than bivalent metals (Mn²⁺, Fe²⁺, and Cd²⁺) [102]. Bioinformatics suggest that the Ala-Ile-Ile-Thr element is the key determinant of Nrat1 for Al selectivity [106]. In Ara*bidopsis*, AtALS3 acts as an Al transporter to redistribute Al outside sensitive tissues [107]. Moreover, OsALS1, an ABC transporter located in the tonoplast, sequestrates Al^{3+} in the vacuole. The knockout of OsALS1 leads the high sensitivity of rice to Al stress [26]. FeALS1.1 and FeALS1.2, OsALS1 homologs, can also sequestrate Al³⁺ in the vacuoles and detoxify Al in the roots and leaves in buckwheat [108]. Likewise, the AvABCG1 transporter confers Al tolerance by accumulating Al³⁺ in specific areas of Andropogon virginicus [109]. HvABCB25 transports Al from the cytoplasm to the vacuoles for sequestration in barley [42]. In addition, HmPALT1 and HmVALT1 are involved in transporting Al in hydrangea (Hydrangea macrophylla) [105]. The mechanism of Al detoxification in plants is achieved by forming non-phytotoxic complexes of small molecular organic compounds with Al^{3+} [10,27,52]. NIP1;2, the closest homolog to HmPALT1, facilitates the transport of Al-malate from the CW to the symplast in *Arabidopsis* [110]. NIP1;2-mediated transport of Al-malate complex depends on Al-induced malate secretion mediated by AtALMT1. Therefore, the coordinated operation of the Al detoxification mechanism between external and internal parts of the plants is linked by NIP1;2 and AtALMT1.

Studies have showed that the transportation of other ions could also alleviate Al toxicity [19]. For example, Ca²⁺ serves as an essential second messenger to modulate

developmental plasticity in plants, which reduces the concentration of active Al and fixation of P under Al stress [111,112]. Treatment with higher Ca^{2+} concentration alleviates Al-induced inhibition of root growth, which is attributed to higher cytosolic Ca^{2+} concentrations through specific Ca^{2+} signatures triggering downstream responses [113]. Moreover, Mg^{2+} is involved in metabolism-activating enzymes such as CS and malate synthase by functioning as a cofactor for enzymes, thereby activating OA synthesis to alleviate Al toxicity [114]. Overexpression of AtMGT1 and OsMGT1 confers Al tolerance in plants by increasing the absorption of Mg and inhibiting potential targets of Al [115]. Li et al. showed that Mg promoted root growth and increased Al tolerance by modulating the production of nitric oxide in Arabidopsis [116]. Similarly, Kong et al. showed that the addition of Mg to the Al treatment solution alleviated Al-induced inhibition of root growth, suppressed Al uptake, and reduced hydrogen peroxide (H_2O_2) concentration in maize [99]. Furthermore, K⁺ efflux was related to Al tolerance by accompanying OA secretion [99]. Recently, Li et al. showed that ectopic expression of either *HtNHX1* or *HtNHX2*, from Jerusalem artichoke (Helianthus tuberosus), could enhance rice tolerance to Al stress and soil acidity by altering K^+ and H^+ fluxes and the CW structure [41]. In addition, the application of zinc has been shown to alleviate Al-induced damage via competing with Al and increasing the IAA content in alfalfa [46]. Sulfate supplementation activates short-term tolerance to Al toxicity in perennial ryegrass (Lolium perenne) roots by upregulating total superoxide dismutase (SOD) activity [117]. Further studies are required to investigate how the adjustment of the formula of fertilizer may alleviate Al toxicity.

Analogous to other abiotic stimuli, Al stress induces the overproduction of ROS and lipid peroxidation, resulting in serious cell damage and even cell death [118]. To protect plants from Al-triggered oxidative stress, plant tolerance to Al toxicity is enhanced by improving the activity of ROS-scavenging enzymes, reducing the production of ROS, and weakening lipid peroxidation [119]. For example, overexpression of WMnSOD1, an Alinduced SOD, increases oxidative resistance, and Al tolerance [120]. Overexpression of AtBCB and NtGDI1 ameliorates oxidative stress and confers a degree of resistance to Al stress [121]. Overexpression of AtPrx64 reduces the accumulation of ROS and Al, thereby promoting root growth [29]. Recently, ZmAT6, a chloroplast-located protein, has been shown to increase the expression level of the *ZmSOD* gene and improve the activity of antioxidant enzymes SOD in the antioxidant enzymatic system. In addition, the overexpression of *ZmAT6* in maize and *Arabidopsis* increased the activity of several enzymes within the antioxidant system, thereby enhancing Al toxicity tolerance [50]. Moreover, methyltransferase could reduce ROS, lipid peroxidation, and ion leakage, and overexpression of the *methyltransferase* gene can improve stress resistance of plants [122]. For example, overexpression of ZjOMT enhanced Al tolerance of Escherichia coli by increasing the content of melatonin [49]. In addition, a metabolic change is an internal tolerance mechanistic in response to Al stress [48]. Overexpression of VuFDH increased Al tolerance, which is likely due to their decreased Al-induced formate production in tobacco (Nicotiana tabacum) [48]. Likewise, VuAAE3 played a critical role in Al tolerance mechanisms via function as oxalyl-CoA synthetase [47].

4. Transcription Factors Are Involved in Adaptation to Al Stress

Transcription factors are protein complexes that regulate the transcription of genetic information from DNA to mRNA via specific binding to cis-acting elements in the promoters of target genes and acting downstream of signaling cascades in response to environmental stress [123]. The role of TFs in the Al signaling pathway has attracted significant attention since the first TF, sensitive to proton rhizotoxicity 1 (STOP1) and involved in Al tolerance, was identified. More TFs have also been identified to be involved in Al-induced signaling pathways (Table 2).

TFs	Categories	Plant Species	Functions	References
AtHB7 AtHB12	HD-Zip I transcription factor	Arabidopsis thaliana Arabidopsis thaliana	Regulate the capacity of the cell wall to bind Al	[124] [124]
AtWRKY47	WRKY transcription factor	Arabidopsis thaliana	Regulating genes responsible for cell wall modification	[125]
OsWRKY22		Oryza sativa	Activation of OsFRDL4 expression and enhancement of citrate secretion	[126]
CcSTOP1		Cajanus cajan	Regulate genes for OA transporters	[127]
GhSTOP1		Gossypium hirsutum L.	Regulate GhMATE and GhALMT1 expression	[128]
GmSTOP1a		Glycine max	Regulate the downstream Al or	[129]
GsGIS3	C2H2-type zinc finger	Glycine soja	low pH resistance genes Regulating Al-tolerance-related genes	[130]
HvATF1	uniscription factor	Hordeum vulgare L.	Regulating multiple downstream genes involved in Al resistance	[131]
NtSTOP1		Nicotiana tabacum	Activation of <i>NtMATE</i> expression	[132]
OsART2		Oryza sativa	Regulate at least four genes implicated in Al tolerance	[133]
SbSTOP1		Sorghum bicolor L.	Regulate SbMATE and SbSTAR2 expression	[134]
GsMAS1	MADS-box transcription factor	Glycine Soja	Accumulation of Al-activated citrate and malate	[135]
HvHOX9	Homeobox-leucine zipper transcription factor	Hordeum vulgare L.	Regulate the capacity of the cell wall to bind Al	[136]
MdMYC2	bHLH transcription factor	Malus domestica	Activation of ethylene biosynthesis	[137]
VuABI5	Basic-leucine zipper transcription factor	Vigna umbellata	Regulate genes involved cell wall modification and osmoregulation	[91]
VuNAR1	NAC-type transcription factor	Vigna umbellata	Regulate cell wall pectin metabolism	[138]

AtSTOP1, a C2H2-type zinc finger transcription factor, has been found to be critical for both proton and Al tolerance, which regulates the expression of downstream-STOP1 Alresistance genes (Figure 2). However, the expression of AtSTOP1 is unaffected by Al stress, which suggests that AtSTOP1 is modulated by Al at posttranscriptional or posttranslational levels. Zhang et al. showed that an F-box protein-encoding gene regulation of the Alactivated malate transporter expression 1 (RAE1) regulates the stability of STOP1 via the ubiquitin-26S proteasome pathway in Arabidopsis. This indicates that STOP1 is regulated at a posttranslational level [139]. Recently, Guo et al. showed that hyperrecombination protein 1 (HPR1) regulates nucleocytoplasmic STOP1 mRNA export to modulate the expression of STOP1 downstream genes and Al resistance of plants, highlighting that the regulation of STOP1 by HPR1 occurs at a posttranscriptional level [140]. More recently, Fang et al. showed that the SUMOylation of STOP1 is involved in the regulation of Al resistance [141]. In this study, STOP1 is mono-SUMOylated at K40, K212, or K395 sites; and blocking STOP1 SUMOylation reduced Al resistance through the reduction in STOP1 stability and the expression of STOP1-regulated genes. Moreover, the SUMO protease ESD4 specifically interacts with deSUMOylates STOP1, and mutation of ESD4 increases the SUMOylation of STOP1 and the expression of AtALMT1, which contribute to Al stress tolerance.



Figure 2. Model for regulation of STOP1 function and stability. RAE1, F-box protein-encoding gene regulation of AtALMT1 expression 1; HPR1, hyperrecombination protein 1; ESD4, SUMO protease; NPC, nuclear pore complex; STOP1-S, STOP1 SUMOylation.

The functions of STOP1-like proteins, including CcSTOP1 [127], GhSTOP1 [128], GmSTOP1 [129], NtSTOP1 [132], and SbSTOP1 [134], in other plant species, have been characterized, and proven to be essential for the expression of several Al-tolerance-related genes. For example, GmSTOP1 contributes to both Al resistance and H⁺ tolerance, and overexpression of *GmSTOP1a* increases the expression of *GmALMT1* and decreases Al accumulation in soybean hairy roots under Al stress [129]. AtSTOP1 and OsART1 are both central regulators involved in Al tolerance through the regulation of multiple downstream genes. However, the rice homolog (Al resistance transcription factor, OsART1) regulates only Al tolerance genes [142]. Furthermore, OsART2, a homolog of OsART1, has been shown to regulate Al tolerance independent of the OsART1-regulated pathway in rice and to play a supplementary role in Al tolerance [133]. HvATF1 (Al-tolerant transcription factor 1) is the closest homolog of AtSTOP1 and OsART1 and alleviates Al stress through regulating multiple genes in barley; this provides insights into the different molecular mechanisms of Al tolerance in plants [131]. Liu et al. also cloned a C2H2 zinc-finger protein, GsGIS3, which enhanced tolerance to Al toxicity by regulating Al-tolerance-related genes [130].

In Arabidopsis, two HD-Zip I TFs (AtHB7 and AtHB12) have been identified to specifically participate in Al resistance through a reversed genetic approach. Interestingly, AtHB7 and AtHB12 promote root growth through positive regulation of the cell number and cell length under normal conditions, while playing opposite roles by regulating the capacity of the CW to bind Al³⁺ under Al stress [124]. Recently, HvHOX9, a novel homeobox-leucine zipper transcription factor, was identified to play a critical role in Al tolerance in barley by decreasing root CW Al binding, increasing apoplastic pH in the root, and silencing of HvHOX9 which increased Al accumulation in root CW and decreased H⁺ influx after Al exposure [136]. Li et al. showed that WRKY47 was involved in altering Al distribution between the apoplast and symplast by regulating the genes responsible for CW modification, thereby improving Al tolerance [125]. Lou et al. reported that a NAC-type TF, VuNAR1, is involved in Al resistance in rice beans, and overexpression of VuNAR1 induced higher WAK1 expression and low pectin content via directly binding to the WAK1 promoter and regulating CW pectin metabolism [138]. Li et al. demonstrated that OsWRKY22 contributes to Al tolerance by functioning together with OsART1 in the positive regulation of OsFRDL4 expression and citrate secretion [126]. A MADS-box transcription factor, GsMAS1, presents

a constitutive expression pattern induced under Al stress. The overexpression of *GsMAS1* enhanced the tolerance to Al stress in *Arabidopsis* with larger values of the relative root length and higher proline accumulation as compared with those of wild type (WT) under Al stress through Al stress-related pathways [135]. These findings emphasize the need to study transcription factors involved in Al tolerance, which could help to understand the entire molecular network of Al tolerance in plants, elucidate the mechanism of plant Al tolerance, and lay a theoretical foundation for the cultivation of Al-tolerant varieties using modern molecular techniques.

5. Plant Hormones Involved in Adaptation to Al Stress

Plant hormones play an important role in the internal tolerance mechanisms [23,143]. For example, TAA1 regulates auxin biosynthesis in the root apex transition zone (TZ) in Arabidopsis, which mediates Al-induced inhibition of root elongation [144]. Subsequently, flavin monooxygenase-like proteins (YUCCA), which act downstream of TAA1, have been reported; they regulate auxin accumulation in the root apex TZ in response to Al stress, thereby controlling root growth [145,146]. The synergistic effect of auxin and cytokinin in response to Al stress in Arabidopsis has been described; Al stress induces the expression of the key gene of cytokinin synthesis by mediating Al-induced auxin signaling, eventually leading to the accumulation of cytokinin and inhibiting root growth in the root apex TZ [147]. Moreover, miR393 is involved in Al-induced root growth inhibition by regulating auxin signaling in barley [148]. Exogenous IAA treatment could promote the secretion of H⁺ in the plant rhizosphere, balance the level of H⁺ in internal and external cells, and reduce Al content in pectin by reducing the content of pectin and PME activity in the root tip. This reduces Al accumulation in the CW [149,150]. Wang et al. investigated an auxin influx carrier, OsAUX3, which is involved in root growth in response to Al stress by affecting acropetal auxin transport in rice [46]. Similarly, Zhang et al. found that an auxin efflux carrier, ZmPGP1, was involved in root growth inhibition in maize under Al stress [44]. The Al tolerance of OsAUX3 knockdown lines and zmpgp1 mutants was significantly higher than that of WT but auxin accumulation had an opposite trend in root tips. These findings show that auxin may play different roles in Al-induced root growth inhibition in different plants.

Melatonin is universally distributed in plants, and it plays important roles in various physiological and biochemical processes [151]. Recent studies have shown that melatonin ameliorates Al toxicity by scavenging ROS and secreting OAs. For example, melatonin enhanced the activities of antioxidant enzymes and increased the exudation of malate and citrate in soybean [152]. Moreover, melatonin interferes with nitric oxide (NO)-mediated reduction in cell division cycle progression and the quiescent center cellular activity, which subsequently alleviates Al-induced root growth inhibition [153]. Furthermore, melatonin confers Al tolerance by decreasing Al binding in the CWs. In wheat seedlings, melatonin augments antioxidants and induces antioxidant enzymes to control ROS and also enhances the exclusion of Al from the root apex by altering CW polysaccharides [154]. Therefore, melatonin ameliorates Al toxicity by building a defense line in response to Al stress, which suggests that applying exogenous melatonin or enhancing melatonin biosynthesis may be an effective strategy for enhanceing plant Al resistance.

Ethylene mediated Al-induced inhibition of root growth has also been confirmed using mutants defective in ethylene signaling [155]. An et al. found that MdMYC2 negatively regulates Al tolerance through upregulating the expression of ethylene-responsive genes by binding to the promoter of *MdERF3* (positive regulator of ethylene biosynthesis) [137]. The synergistic action of auxin and ethylene mediates Al-induced inhibition of root growth [143,155]. Moreover, Chen et al. showed that *GmGRPL* conferred Al tolerance in *Arabidopsis* through regulation of the level of IAA and ethylene and improvement of antioxidant activity [38]. Similarly, overexpression of the *GsERF* gene enhanced Al tolerance of *Arabidopsis* through an ethylene-mediated pathway [156]. In addition, ABA was involved in regulating Al tolerance [157]. For example, ABA was involved in the early tol-

erance mechanism in buckwheat seedlings by increasing the levels of ROS and activities of catalase (CAT) and ascorbate peroxidase (APX) [158]. Recently, Fan et al. showed that ABA alleviation of Al toxicity in rice beans depends on ABI5-mediated CW modification and osmoregulation [91]. These findings indicate that plants respond to Al stress by regulating the distribution and levels of various plant hormones.

6. Small Molecules to Alleviate Al Toxicity

Al toxicity is a major limiting abiotic factor for plant growth and productivity in acidic soils. In the past few decades, various strategies have been used to alleviate Al toxicity. Interestingly, the use of small molecules to alleviate Al toxicity has been confirmed. Among these, there are many reports about Si, boron (B), and polyamines (PA).

Silicon is the second most abundant element in the earth's crust after oxygen and has versatile functions in plant biology, especially in plant defense and tolerance to both biotic and abiotic stressors [159]. Si ameliorates the effects on Al toxicity in maize [160], Norway spruce [161], rice [106,162,163], ryegrass [164], soybean [94], sorghum [165], and wheat [166]. For example, Si treatment was shown to increase the growth of plant shoots grown in the presence of Al without influencing the root growth in upland rice [163]. In ryegrass, Si-mediate the alleviation of Al toxicity by the modulation of Al/Si uptake and antioxidant performance [164]. In soybean and sorghum, Si reduces Al toxicity through the formation of Al-Si complexes in mucigel and outer cellular tissues, thereby decreasing the binding of Al to the CW [165]. These results suggest that the alleviation of Al toxicity by Si is an effective strategy of Al detoxification for improving plant tolerance in acid soils.

Boron is an essential microelement for plant growth and is involved in alleviating Al toxicity. This has been identified in many plant species, including citrus [167–169], common bean [170], pea [171–173], rapeseed [174], sunflower [175], and wheat [176]. Li et al. reported that pretreatment with B promoted polar auxin transport driven by the auxin efflux transporter, PIN2, led to the downstream regulation of the PM-H⁺-ATPase, resulting in elevated root surface pH, which is essential to decrease Al accumulation in this Al-targeted apical root zone [173]. Moreover, pretreatment with B significantly increased the activity of APX, peroxidase (POD), and CAT, therefore, increasing the elimination rate of H₂O₂ in rice roots [177]. Furthermore, Yan et al. revealed that B pretreatment improved root growth by weakening Al binding to alkali-soluble pectin, and reduced Al fixation on the CW reduced Al accumulation, resulting in the alleviation of Al toxicity [178]. Therefore, the application of B in nutrient solutions significantly increases root growth by alleviating Al toxicity, emphasizing the feasibility of this method.

Polyamines are important signaling molecules in the ROS regulation under Al stress. The application of putrescine could protect plant roots against Al-induced oxidative stress by maintaining the antioxidant capacity in wheat [179,180]. Putrescine could reduce the Al content in the CW by inhibiting the production of ethylene, therefore, alleviating the inhibition of the root growth in wheat and rice [181,182]. Likewise, the application of spermidine alleviates the adverse effects of Al toxicity by improving the antioxidant system, as has been demonstrated in rice and mung bean [183,184]. These findings show that the application of polyamines or improvement of endogenous polyamine content is an effective strategy for plants to adapt to acidic soil.

P, OAs, biochar, etc. reduce the effect of Al toxicity. The addition of P relieves Al toxicity by increasing the carbohydrate content and relieving the inhibition of protein synthesis [185]. The application of malate has also been shown to alleviate Al toxicity in *Pinus massoniana* seedlings [186]. The application of biochar increases the pH value, water holding capacity, and available nutrients in acidic soil, and also improves soil texture and aggregation, therefore, relieving the plants [187]. Lin et al. showed that biochar alleviates Al toxicity in achieving cabbage productivity [188]. Xia et al. reported that biochar mitigates the Al toxicity of maize, which contributes to the improvement of soil quality and enhancement of nitrogen use efficiency in acidic soil [189]. These results show that the ability of small molecules to alleviate Al toxicity is a strategy in the acidic

soil. However, further studies are needed to ascertain promising and sustainable small molecules for ameliorating Al toxicity.

7. Plant Growth-Promoting Rhizobacteria (PGPRs) Alleviate Al Toxicity

Plant growth-promoting rhizobacteria are known to exert beneficial effects on plant growth and health [190,191]. Several studies have reported the application of PGPR mitigated Al toxicity in acidic soil (Table 3). For example, inoculation with Pseudomonas fluorescens 002 decreased the impact of Al toxicity in maize roots and increased the root lengths and numbers [192]. Similarly, P. plecoglossicida Pp20 conferred maize root tolerance to Al toxicity by producing the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase and IAA [193]. The authors further reported that Bacillus toyonensis Bt04 reduced Al accumulation and lipid peroxidation in maize seedlings, promoted maize growth, and enhanced root development [194]. Moreover, inoculation of B. megaterium CAM12 and Pantoea agglomerans CAH6 improves Vigna radiata growth and reduces Al uptake in plants [195]. The subsequent experiment revealed that Rhodotorula mucilaginosa CAM4 reduced Al accumulation and conferred Al tolerance to Lactuca sativa [196]. Furthermore, Al-resistant PGPR induced a higher expression level of Al-stress related genes, exudation of OAs, and production of polysaccharides, thereby alleviating Al toxicity [197-199]. Additionally, *Rhizobium panacihumi* DCY116^T was used as a potential PGPR, which produced higher proline, phenolic, sugar contents, and related gene expressions, to induce ROS scavenging activity in Al-stressed seedlings [200]. These studies support the application of PGPR to improve plant growth in acidic soils, by functioning as a biofertilizer for healthy and safe crop production.

Table 3. Plant growth-promoting rhizobacteria (PGPRs) alleviate Al toxicity.

Strains	Function	Target Plant	Effect of Aluminum Imposed on Plant	References
Bacillus megaterium CAM12	Produce siderophore	Vigna radiata	Reduced Al uptake	[195]
Bacillus sp. PSB16	Produce OAs and polysaccharides	Oryza sativa	Chelated the Al, increased solution pH, and enhanced rice growth	[197]
Bacillus toyonensis Bt04	Produce auxin and cytokinin	Zea mays	Reduced Al accumulation in the young maize roots, promotes maize growth, and enhances root development	[194]
Burkholderia ginsengiterrae N11–2	Produce auxins and siderophores and phosphate solubilization	Arabidopsis thaliana and Panax ginseng	Showed the higher expression level of Al-stress related genes and higher biomass and higher chlorophyll content	[198]
Burkholderia seminalis ASB21	Produce OAs and polysaccharides	Oryza sativa	Chelated the Al, increased solution pH, and enhanced rice growth	[197]
Burkholderia thailandensis ASB7	Produce OAs and polysaccharides	Oryza sativa	Chelated the Al, increased solution pH, and enhanced rice growth	[197]
Chryseobacterium polytrichastri N10	Produce auxins and siderophores and phosphate solubilization	Arabidopsis thaliana and Panax ginseng	Showed the higher expression level of Al-stress related genes and higher biomass and higher chlorophyll content	[198]
Enterobacter sp. RJAL6	Secrete oxalate, citrate, succinate and siderophores	Lolium perenne	Promote ryegrass growth by forming Al-siderophore complexes	[199]
Klebsiella sp. RC3	Secrete oxalate, malate, citrate, succinate and siderophores	Lolium perenne	Promote ryegrass growth by forming Al-siderophore complexes	[199]
Klebsiella sp. RCJ4	Secrete malate, citrate, succinate and siderophores	Lolium perenne	Promote ryegrass growth by forming Al-siderophore complexes	[199]

Strains	Function	Target Plant	Effect of Aluminum Imposed on Plant	References
Pantoea agglomerans CAH6	Produce siderophore	Vigna radiata	Reduced Al uptake	[195]
Pseudomonas fragi N8	Produce auxins and siderophores and phosphate solubilization	Arabidopsis thaliana and Panax ginseng	Showed the higher expression level of Al-stress related genes and higher biomass and higher chlorophyll content	[198]
Pseudomonas plecoglossicida Pp20	Produce ACC deaminase and IAA	Zea mays	Increased in lengths of seminal roots and root dry mass	[193]
Pseudomonas simiae N3	Produce auxins and siderophores and phosphate solubilization	Arabidopsis thaliana and Panax ginseng	Showed the higher expression level of Al-stress related genes and higher biomass and higher chlorophyll content	[198]
Stenotrophomonas maltophilla Sb16	Produce OAs and polysaccharides	Oryza sativa	Chelated the Al, increased solution pH, and enhanced rice growth	[197]
Pseudomonas fluorescens 002	Releases IAA	Zea mays	increased primary, lateral, and seminal root lengths and numbers, as well as root dry mass	[182]
Rhodotorula mucilaginosa CAM4	Bioaccumulation of Al	Lactuca sativa	Reduce proline and MDA contents, and enhance accumulation of antioxidant enzymes	[196]
Rhizobium panacihumi DCY116 ^T	Produce IAA	Panax ginseng	Produced higher proline, phenolic, sugar contents and related gene expressions to induce ROS scavenging activity	[200]
Stenotrophomonas sp. RC5,	Secrete malate, citrate, succinate and siderophores	Lolium perenne	Promote ryegrass growth by forming Al-siderophore complexes	[199]
Serratia sp. RCJ6	Secrete malate, citrate and succinate	Lolium perenne	Promote ryegrass growth by forming Al-siderophore complexes	[199]

Table 3. Cont.

8. Transgenic Approaches Manipulating Al-Tolerant Genes

Transgenic breeding is a promising tool for abiotic stress improvement in crops, which can create new and significant sources of resistance with rapid multiplication potentials [201]. In the previous decade, numerous studies were conducted to develop Al-tolerant crop cultivars through the manipulation of Al-tolerant genes, mainly concentrating on the secretion of OAs, Al sequestration, and defense system.

Al-induced OAs secretion is an important mechanism for controlling the degree of resistance to Al toxicity in most plant species [5,17,27]. Therefore, increasing OAs secretion is a research hotspot in the cultivation of Al-tolerant plant varieties. However, this is mainly achieved through the genetic transformation of enzymes related to OAs metabolism and OAs channel proteins. To date, ALMT and MATE have been identified to confer Al tolerance through the secretion of malate and citrate. Particularly, heterologous expression of ALMT or MATE confers Al-induced malate or citrate secretion and enhances their Al tolerance in transgenic plants. For example, GmMATE13, GmMATE47, GmMATE75, GmMATE79, and GmMATE87 have a citrate transport activity; and overexpression of these genes have enhanced the tolerance of transgenic plants to Al toxicity in Arabidopsis [70,202]. Recently, AhFRDL1, a citrate transporter gene from peanut (Arachis hypogaea) that is induced by both iron (Fe)-deficiency and Al stress, participated in both root-to-shoot Fe translocation and Al tolerance. Overexpression of AhFRDL1 in Fe-efficient varieties contributed to higher levels of Al tolerance and Fe translocation by promoting citrate secretion [28]. Additionally, the secretion of OAs is related to the maintenance of internal concentrations of OAs and the activity of PM H⁺-ATPase [43,81]. Therefore, the combined

transformation of these multiple genes should be considered and explored for sustainable applications in the future.

The compartmentalization and detoxification of vacuoles is an important internal tolerance mechanism in plants [131,203,204]. Al transporters in the PM and tonoplast play an important role and the genetic transformation of these transporters can significantly improve the Al tolerance of plants. For example, overexpression of *HvABCB25* significantly improves Al tolerance and reduces Al accumulation of root tip cytoplasm in Tibetan wild barley [42]. FeIREG1, an IREG transporter located in the tonoplast in buckwheat, plays an important role in detoxification by sequestrating Al into vacuoles. Overexpression of *FeIREG1* enhances Al tolerance in *Arabidopsis* [203]. In soybean, the function of GmIREG3 is similar to that of FeIREG1, and overexpression of *GmIREG3* enhances Al tolerance in *Arabidopsis* [39]. In rice, Al transporter OsNrat1 and OsALS1 cooperate to detoxify Al. Overexpression of *OsNrat1* enhances Al tolerance in *Arabidopsis* [101]. In other plants, *OsNrat1* homologous genes, including *ZmNrat1* [205] and *SbNrat1* [206], have also been reported to be involved in transporting Al. To the best of our knowledge, the co-genetic transformation of Al transporters in the PM and tonoplast has not been reported. Hence, their transformation into Al-sensitive plants to enhance Al tolerance is necessary.

Plants improve stress resistance by regulating the expression of tolerant genes. The transformation of these genes can effectively improve Al tolerance of plants [201]. For example, *AvSAMS1* is a multiple tolerance gene and transgenic *Arabidopsis* showed a higher tolerance to Al stress than Col-0 ecotype and also higher tolerance to other metal stresses [30]. In addition, the DNA damage response (DDR) pathway maintains the genome integrity under adverse conditions that affect DNA replication. The inhibition of root growth regulated by DDR regulators in response to Al toxicity pinpoints DNA as a primary target of internalized Al and also offers new strategies for obtaining Al-resistant crops. Due to the highly conserved nature and function of the DDR, identified *Arabidopsis* mutations may be easily mimicked in orthologous crop genes using the latest developments in the CRISPR/Cas9 field [4], which provides useful insight into the genetic basis for a new Al detoxification mechanism for improving plant tolerance to Al stress in acid soils.

9. Conclusions and Future Perspectives

Al stress is considered to be an important factor limiting plant growth in acidic soil, but other minerals present in the soil can interact with Al [10]. This review covers the current knowledge about Al resistance genes and the adaptive mechanisms of various crops under Al stress. However, studies investigating the effect of Al interactions with other restricting factors are scarce. These studies are imperative for developing plant varieties in acidic soils.

The sensing of Al stress by plants and the transduction of the Al signal to activate various downstream Al-tolerant strategies are fundamental frontier issues in plant sciences. Studies have shown that signaling cascades of Al-induced citrate exudation comprised heterotrimeric G-proteins, phospholipase C, inositol triphosphate, diacylglycerol, Ca²⁺, and protein kinases [2,6]. However, there are limited reports on Al transmembrane signal transduction. The Al receptor has not yet been identified, which is the most important topic in plant Al stress research. Currently, salt and H₂O₂ sensors have been found using Ca²⁺ imaging-based forward genetic screens, which inspires the identification of Al receptor [207,208]. Future work should focus on the identification of early Al-sensing components using genetic and biochemical approaches.

The rapid development of whole-genome sequencing and genome editing technology provides more opportunities to reveal the mechanisms of Al tolerance and identify novel Al-tolerant genes, which make it possible to cultivate Al-tolerant plant varieties using modern biotechnology. Al tolerance in plants is a multi-level, multi-pathway, and multigene control process. However, the improvement of Al tolerance of transgenic plants is concentrated on one single gene. Therefore, the development of multiple Al tolerance genes is critical to enhancing the Al tolerance of plants in acidic soils through molecular and conventional breeding.

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