Specificity of Ion Uptake and Homeostasis Maintenance During Acid and Aluminium Stresses

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Abstract Low pH (proton toxicity) and aluminium toxicity coexist in acid soils, affecting plant growth worldwide. Decades of research concluded that proton and aluminium toxicity mechanisms are complex and remain unclear. Among the Al tolerance mechanisms, exudation of organic acid anions received considerable attention, leading to the identification of novel genes involved in organic acid anion metabolism and transport. As a downside, the major focus on exudation of organic acid anions has overshadowed research on other potential Al tolerance mechanisms (e.g. reduced cell wall binding, rhizosphere alkalisation, phosphate exudation, enhanced uptake of essential nutrients) that may be operating. In this work, the current knowledge on how proton and aluminium toxicity and tolerance mechanisms are operating when plants are exposed to acid soils is reviewed. Special emphasis has been given to the question of how uptake and homeostasis of hydrogen, potassium, phosphorus, calcium, and magnesium ions in plants are affected and regulated during low-pH and aluminium stresses. There is enough evidence to suggest that low-pH and combined low-pH/aluminium stresses differentially affect root tissues and, consequently, the rhizosphere. Less disturbed phosphorus, calcium, and magnesium uptake and homeostasis maintenance help plants to cope with low-pH and combined low-pH/aluminium stresses.

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1 Introduction

Acidic soils are formed mainly due to the weathering of acidic parent material and the leaching of basic cations by soil water. As a result, soils in high rainfall areas and older soils exhibit greater acidity. A number of other factors also contribute to soil acidification, including imbalances in the nitrogen, carbon, and sulphur cycles (Goulding et al. 1998; Mannion 1998); use of NH_4^+-forming fertilisers (Rowell and Wild 1985; Tang et al. 2000); atmospheric acidification (Vries and Breeuwsma 1987; Galloway 1989); nitrogen fixation by legumes (Bolan et al. 1991; Shen et al. 2004); and excessive uptake of cations by plants (Shen et al. 2004). Thus, soil acidification is a continuous process, which means the problem of acid soils is exacerbated over time in severity and extent (Rengel 2004).

In acidic soils, plant growth may be limited by various toxicities (H, Al, Mn) and deficiencies (NH_4-N, P, Ca, Mg, and MoO_4) (for references, see Kidd and Proctor 2001). Among these complex factors, aluminium (Al) toxicity received considerable attention because Al becomes increasingly soluble when the $pH_{(water)}$ decreases below 5 (Kochian 1995). In particular, activity of trivalent cationic $Al(H_2O)_6^{3+}$ (hereafter Al^{3+} for convenience) often peaks at around pH 4.2–4.3, severely affecting root growth in acid soils (Kinraide 1990, 1991, 1993; Matsumoto 2000; Taylor et al. 2000; Poschenrieder et al. 2008). Interestingly, low pH (H^+ toxicity) alone can affect growth in diverse plant species (Bose et al. 2010b). There are some low-pH soils (e.g. organic soils) where Al^{3+} ions are present in low concentration; thereby H^+ ions dominate the composition of the soil solution (Kidd and Proctor 2001). These H^+-ion-dominated soils account for a high proportion of acid soils around the globe. For instance, histosols occupy 200 million ha worldwide (Brady and Weil 1990). Hence, low-pH and combined low-pH/Al^{3+} stresses need to be separated in order to understand stress-specific toxicity and tolerance mechanisms in plants. In this chapter, the existing knowledge on how Al^{3+} and H^+ toxicity mechanisms are operating when plants are exposed to acid soils is reviewed. Special emphasis is placed on how Al^{3+} and H^+ toxicities specifically affect ion uptake and homeostasis regulation in plants.

2 Al^{3+} Toxicity in Plants

2.1 Inhibition of Root Growth by Al^{3+} Toxicity

An early symptom of Al^{3+} toxicity to plants is inhibition of root growth that becomes measurable within minutes of exposure to micromolar concentrations of Al^{3+} (see Delhaize and Ryan 1995; Rengel 2004 for references). Thus, roots have been the focus of research to decipher the mechanisms of Al^{3+} toxicity and tolerance in plants.

Root growth is a complex and dynamic phenomenon that involves a series of biochemical and physiological processes differing in various root tissues (Street 1966; Wang et al. 2006). Detailed investigations of the spatial sensitivity to Al^{3+} in different root zones revealed that the root apex (Ryan et al. 1993), particularly the distal elongation zone within the root apex (Sivaguru and Horst 1998; Kollmeier et al. 2000; Illes et al. 2006), is the primary site of Al^{3+} toxicity. The distal elongation zone (due to its specific architecture) has extraordinary capability to sense various environmental stimuli and act as a "plant command centre" to integrate sensory inputs into adaptive responses (Baluška et al. 2004). Accordingly, the distal elongation zone needs to be studied in detail for a greater understanding of the primary mechanisms of Al^{3+} toxicity and tolerance. However, Al^{3+} toxicity and tolerance studies on distal elongation zone are relatively rare. Some studies have shown that Al^{3+} also affects physiological and biochemical processes in other root zones, such as the root cap, meristem, elongation zone, and mature zone (Brady et al. 1993; Olivetti et al. 1995; Rengel 1996; Bose et al. 2010a, b, 2013).

The mature root zone is the longest, accounts for more than 90 % of root biomass, and is the principal area for nutrient absorption (Gahoonia and Nielsen 1998; Parker et al. 2000; Bibikova and Gilroy 2002). Taking K^+ as an example, 10 out of 15 K^+ transporters (KT/KUPs) are expressed in the mature zone (Ahn et al. 2004). Further, H^+, K^+ Ca^{2+}, and Mg^{2+} uptake at the mature zone is different to that at the root apex (Ferguson and Clarkson 1975, 1976; Kiegle et al. 2000; Newman 2001; Demidchik et al. 2002; Bose et al. 2010b; Guo et al. 2010; Bose et al. 2013). Interestingly, Al^{3+} concentration in the internal tissues of the mature zone is higher than in the cortex (Babourina and Rengel 2009) and cytosolic Ca signals propagate from mature zone to root cap during Al^{3+} stress (Rincon-Zachary et al. 2010). Because of this, the response of the mature zone to Al^{3+} might be different from that of the root apex. Indeed, H^+, K^+, and Mg^{2+} fluxes in response to Al^{3+} stress differ between mature root zone and elongation zone in Arabidopsis (Bose et al. 2010a, b, 2013). However, how these ion fluxes modulate the root growth during Al^{3+} stress remains to be elucidated.

2.2 Inhibition of Cell Division and Cell Elongation

Early work by Clarkson (1965) revealed that Al^{3+} toxicity strongly altered root development and pointed at the hampering of cell division by Al^{3+} ions as a primary cause of root growth inhibition. Indeed, (1) binding of Al to nucleic acids in root tips along with inhibition of cell division (Matsumoto et al. 1976; Morimura et al. 1978) and (2) reduction in the mitotic index along with different abnormalities such as chromosome bridges, breaks, sticky metaphases, nuclear dissolution, cell death, and in some cells chromosome duplication under Al^{3+} stress have been observed in maize and onion roots (De Campos and Viccini 2003). In contrast, Al^{3+}-induced stimulation of cell division was also reported under low concentrations of Al^{3+}, mainly in cell culture experiments. For example, cell cycle activity

was enhanced in the Al-tolerant cell culture line of Coffea arabica, whereas inhibition was observed in the Al-sensitive cell line (Valadez-Gonzalez et al. 2007).

The Al^{3+}-induced alterations of the cell cycle received considerable attention because (1) it has been well established that Al can enter the symplasm quite rapidly (Silva et al. 2000; Taylor et al. 2000; Babourina and Rengel 2009), and (2) Al^{3+} could alter the cell cycle through a signalling cascade without the need for Al to reach nuclei of meristematic cells (Poschenrieder et al. 2009). Further, Al^{3+} toxicity is not restricted to inhibition of root length. More detailed temporal and spatial study on the maize root cell patterning under Al^{3+} stress revealed that 5-min Al^{3+} exposure was sufficient to inhibit cell division in the proximal meristem zone and stimulate cell division in the distal elongation zone. Protrusion of an incipient lateral root was observed in the distal elongation zone after 180 min. These observations suggest a rapid change in the cell patterning events along the root axis upon a short-time Al^{3+} exposure (Doncheva et al. 2005).

Stiffening of cell walls and a consequent inhibition of root growth have been observed in response to Al^{3+} stress under different experimental conditions (Tabuchi and Matsumoto 2001; Ma et al. 2004; Jones et al. 2006). Indeed, large amounts of Al accumulate in the cell walls and intercellular spaces of root tips. For example, 85–99.9 % of Al was found in the apoplasm of root cells (Taylor et al. 2000; Ma 2007). Apart from precipitation of Al on the root surface and in intercellular spaces, binding of exchangeable Al to the negative charges of the pectin substances in the cell wall was also observed (Blamey 2001). In an in vitro study, Al treatment did not cause cell wall stiffening in dead root tips of maize (Ma et al. 2004), indicating that it is a biochemical process and not purely physical cross-linking between pectin material and Al^{3+}. This leads to the conclusion that Al binds to the newly formed cell wall material, which is required for cell elongation growth, thereby altering mechanical properties of cell wall and hampering cell elongation (Ma et al. 2004; Ma 2007). The cross-linking of other polar cell wall constituents, such as hydroxyproline-rich glycoproteins (HRGPs) by reactive oxygen species in combination with callose deposition, has been shown to inhibit cell elongation in Arabidopsis thaliana (De Cnodder et al. 2005).

2.3 *Production of Reactive Oxygen Species*

Reactive oxygen species (ROS) are natural by-products of aerobic respiration formed when oxygen is partially reduced. ROS can be toxic to plant cells or can act as signalling molecules depending on the circumstances (Scholz-Starke et al. 2005). ROS are essential for (1) root elongation because quenching of root ROS resulted in inhibition of root elongation in *Arabidopsis thaliana* (Demidchik et al. 2003), (2) regulation of hyperpolarisation-activated cation channels (HACC) present in the epidermis of the root elongation zone (Demidchik et al. 2003; Foreman et al. 2003), and (3) activation of a potassium outward-rectifying channel (KORC) and a non-selective cation channel (NSCC), which mediate, respectively,

K^+ efflux and Ca^{2+} influx in root hair tips of C3 and C4 plants (Demidchik et al. 2003).

The formation of ROS in response to Al^{3+} has been observed in many studies (Darko et al. 2004; Tamás et al. 2004; Babourina et al. 2006; Jones et al. 2006; Tahara et al. 2008), even though Al^{3+} is not a transition metal and therefore cannot catalyse redox reactions. However, Al^{3+} in combination with iron caused peroxidation of lipids in the plasma membrane of soybean (Cakmak and Horst 1991) and rice roots (Meriga et al. 2004) and cultured tobacco cells (Ono et al. 1995; Yamamoto et al. 1997). Further, Al^{3+} induced the expression of several genes encoding antioxidant enzymes such as glutathione S-transferase, peroxidase, and superoxide dismutase (SOD) in Arabidopsis thaliana (Richards et al. 1998; Ezaki et al. 2000), which established the significance of ROS production under Al^{3+} toxicity.

A number of hypotheses have been proposed for Al^{3+}-induced rapid production of ROS, including dysfunction of mitochondria (Yamamoto et al. 2002), formation of aluminium superoxide semi-reduced radicals (Exley 2004), and activation of oxidising enzymes (Šimonovicová et al. 2004a, b). However, time-dependent studies demonstrated that cell death and protein oxidation occurred several hours after the cessation of root growth (Boscolo et al. 2003; Šimonovicová et al. 2004b). For example, ROS production and loss of growth were observed after 12 h of Al exposure in tobacco (Yamamoto et al. 2002). Considering the time taken to produce ROS, it appears ROS production may not be the primary mechanism of Al^{3+} toxicity. Yamamoto et al. (2002) suggested that ROS production is not important for root growth inhibition, but rather important for callose biosynthesis. Indeed, cross-linking of ROS with hydroxyproline-rich glycoproteins (HRGPs) was accompanied by callose deposition and was shown to be an important mechanism for inhibition of cell elongation induced by the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) in *Arabidopsis thaliana* (De Cnodder et al. 2005).

2.4 Disturbance of Cytoskeleton

Cytoskeletal structures (microtubules and microfilaments) are pivotal for cell divisions and the elongation of growing roots (cf. Sivaguru et al. 1999, 2000; Kochian et al. 2005). Al-induced disturbance to organisation of microtubules and microfilaments in the root cells was well documented (e.g. Sivaguru et al. 1999, 2003; Amenos et al. 2009). Such Al-induced structural changes in the root cells might underlie morphological changes and structural malformations observed in Al-stressed roots (Kochian et al. 2005).

2.5 Changes in the Plasma Membrane Properties

As Al can enter the symplasm rather rapidly (Silva et al. 2000; Taylor et al. 2000; Babourina and Rengel 2009), Al^{3+} stress is likely to occur at the plasma membrane (Ahn and Matsumoto 2006). Al^{3+} has a strong affinity for the plasma membrane surface (560-fold stronger than Ca^{2+}) (Akeson et al. 1989). Yermiyahu et al. (1997) demonstrated that the surface charge of the plasma membrane vesicles isolated from the Al-sensitive wheat cv. Scout was 26 % lower than that of vesicles from the Al-tolerant cv. Atlas, allowing more Al to bind to the Scout vesicles, thereby causing greater Al toxicity compared with Atlas. Moreover, Ahn et al. (2001) reported that 50 μM Al neutralised the surface charge of the plasma membrane and caused a surface potential shift from −20 to +1 mV in squash roots. These results indicated that membrane surface charge regulated the accessibility of Al ions to cells. Indeed, strong correlation was observed between Al^{3+} toxicity and the concentration of adsorbed Al on the membrane surface, as calculated by Gouy–Chapman–Stern model (Kinraide et al. 1992; Kinraide 1994). Such binding of Al to the plasma membrane (1) alters its fluidity and structure (Chen et al. 1991) in addition to the surface potential (Kinraide 2001), (2) induces organic anion release (Ryan et al. 1995; Osawa and Matsumoto 2002), (3) blocks Ca^{2+} transport (Ding et al. 1993; Pineros and Tester 1993), and/or (4) inhibits H^+-ATPase activity (Ahn et al. 2002). These changes would alter the plasma membrane potential. However, there are contrasting results reported in the literature about Al^{3+} stress effects on the plasma membrane potential. For example, Al^{3+} stress induced depolarisation in intact roots of Al-sensitive wheat genotype Scout but not in Al-resistant genotype Atlas (Miyasaka et al. 1989). In some studies, Al^{3+} induced hyperpolarisation in Al-sensitive but not in Al-tolerant genotypes (Kinraide 1993; Lindberg and Strid 1997; Johnson et al. 2005; Wherrett et al. 2005). The reason for contradicting results may be plants either growing (for a few days) or just being conditioned (for a few hours) in the low-pH (≈4.5) medium before root cells were impaled with a measuring electrode (longer time in the low-pH medium may allow plants to recover from low-pH-induced depolarisation) (Kinraide 1993). Further research, especially on low-pH stress studied separately from Al^{3+} stress, is thus needed to understand Al^{3+}-specific changes in the plasma membrane potential.

Our recent study involving Arabidopsis wild type (Col-0) clearly separated low-pH stress from combined low-pH/Al^{3+} stresses. The low-pH treatment induced plasma membrane depolarisation, which was significantly diminished ($P \leq 0.05$) when combined stresses (low-pH/Al^{3+}) were imposed (Bose et al. 2010b). Further, Al-tolerant alr104 and the wild type had depolarised plasma membranes for the entire 30-min measurement period under combined low-pH/Al^{3+} treatment, whereas in the Al-sensitive mutants (als3 and als5), initial depolarisation to around −60 mV became hyperpolarisation at −110 mV after 20 min (Bose et al. 2010a). Thus, the ability of plants to maintain plasma membrane depolarisation during Al stress is critical for Al tolerance.

2.6 *Inhibition of Nutrient Uptake*

Long-term exposure to Al^{3+} (from hours to days) results in a deficiency of one or more nutrients, such as Ca, Mg, NH_4-N, P, K, and B (cf. Mugwira et al. 1980; Grimme 1983; Foy 1988; Keltjens 1988; Rengel and Robinson 1989; Rengel 1990; Rengel and Elliott 1992; Keltjens and Tan 1993; Lenoble et al. 1996; Mariano and Keltjens 2005). These deficiencies may be due to (1) direct inhibition of uptake system and/or (2) Al^{3+}-induced impairment of root growth and a consequent decrease in the nutrient-absorbing surface area (Clarkson 1985). The latter cause of deficiency is common after prolonged exposure to Al^{3+} (hours to days), whereby root growth reduction is associated with decreased nutrient accumulation (see Rengel 1992 for references). Therefore, long-term Al^{3+} exposure studies may not provide information about specific Al^{3+} effects on nutrient uptake. Further complication with long-term studies is that Al^{3+} may inhibit root growth without reducing nutrient uptake. For example, root growth inhibition under Al^{3+} was observed in Norway spruce, small birch, and wheat without reduction in Ca^{2+} and/or Mg^{2+} uptake (Göransson and Eldhuset 1995; Ryan et al. 1997; Godbold and Jentschke 1998). Hence, short-term Al^{3+} exposure studies involving direct measurements of ion fluxes are essential for understanding immediate Al^{3+} effects on nutrient uptake.

2.6.1 Calcium Uptake

The interaction between Al^{3+} toxicity and Ca^{2+} uptake received considerable attention because symptoms of severe Al^{3+} toxicity resemble Ca^{2+} deficiency in plants (see Foy 1988; Rengel and Elliott 1992 for references), and exogenous application of relatively high (millimolar) concentrations of Ca^{2+} alleviated Al^{3+} toxicity in many plant species (Brady et al. 1993; Keltjens and Tan 1993; Kinraide et al. 2004). Thus, the capacity of genotypes to maintain Ca^{2+} influx from low-pH environments may contribute to low-pH tolerance. Indeed, low-pH-tolerant Arabidopsis mutants (alr104 and als5) (Bose et al. 2010a) recorded higher Ca^{2+} influx in the distal elongation zone than the wild type and als3 mutant in the low-pH treatment (Bose et al., unpublished results). However, the combined low-pH/50 μM Al stress caused Ca^{2+} efflux from both distal elongation and mature root zones within a minute in all four genotypes (Col-0, als3, als5, and alr104). Such an initial Al-induced Ca^{2+} efflux is likely to have been due to extensive displacement of apoplastic Ca^{2+} by Al ions.

Al^{3+} might inhibit Ca^{2+} influx into intact root cells (Huang et al. 1992; Ryan and Kochian 1993), protoplasts (Rengel and Elliott 1992; Rengel 1994), and the membrane vesicles (Huang et al. 1996; White 1998) through binding of Al^{3+} on the plasma membrane surface (Akeson et al. 1989). Such binding of Al^{3+} to the plasma membrane surface may block Ca^{2+}-permeable channels in the plasma membrane. Indeed, both the hyperpolarisation-activated Ca^{2+}-permeable channels (Ding et al. 1993; Kiegle et al. 2000; Very and Davies 2000) and depolarisation-activated

Ca^{2+} channels (Rengel et al. 1995; Pineros and Tester 1997) are sensitive to Al, but Ca^{2+} influx inhibition was higher in the former (87 ± 7 %) (Kiegle et al. 2000) than the latter (only 44 %) (Rengel and Zhang 2003). During Al stress, Ca^{2+} fluxes in the distal root elongation of Al-tolerant genotypes (wild type and alr104) recovered to show net influx after the initial Al-induced Ca^{2+} efflux, but Ca^{2+} influx in Al-sensitive genotypes (als3 and als5) remained inhibited. Given that combined low-pH/50 μM Al stress caused less depolarisation and eventual hyperpolarisation of E_m in the Al-sensitive mutants (als3 and als5), it may be suggested that Al^{3+} stress inhibited hyperpolarisation-activated Ca^{2+}-permeable channels in Al-sensitive mutants (Bose et al. unpublished results).

As the above Ca^{2+} influx inhibition following Al^{3+} exposure precedes root growth inhibition (Huang et al. 1992; Ryan and Kochian 1993), it could be one of potential primary causes of Al^{3+} phytotoxicity (Rengel 1992; Rengel and Zhang 2003). However, further studies revealed that low concentration of Al^{3+} can inhibit root growth without affecting Ca^{2+} influx, and addition of ameliorating cations (Mg^{2+} and Na^{+}) improved root growth, even though the net Ca^{2+} influx remained inhibited (Ryan and Kochian 1993; Ryan et al. 1997). Similarly, Al^{3+} caused root hair growth inhibition without affecting Ca^{2+} influx in *Limnobium stoloniferum* (Jones et al. 1995). Poor correlation between Al-induced Ca^{2+} influx inhibition and elongation growth of Chara (Reid et al. 1995) indicated that Al-induced inhibition of Ca^{2+} influx alone cannot be a critical factor in triggering Al toxicity in plants. However, prolonged inhibition of Ca^{2+} influx into Al-treated root cells disrupts Ca nutrition, which in turn exacerbates Al toxicity in plants (Rengel and Zhang 2003).

2.6.2 Magnesium Uptake

Mg^{2+} is unique among the major biological cations due to the largest hydrated radius (0.428 nm), the smallest ionic radius (0.072 nm), and the highest charge density. Because it binds water molecules 3–4 orders of magnitude more tightly than do other cations, Mg^{2+} often interacts with other molecules while maintaining its hydration sphere (Maguire and Cowan 2002). As a result, Mg^{2+} binds quite weakly to the negatively charged groups in the root cell wall, so the excess cations like H^{+} and Al^{3+} present in acid soils can inhibit Mg^{2+} loading in the apoplasm and uptake across the plasma membrane (Marschner 1991, 1995).

Al^{3+}-induced inhibition of Mg^{2+} uptake has been observed in diverse plant species (Grimme 1983; Keltjens 1988; Rengel and Robinson 1989; Rengel 1990). Al^{3+} might cause Mg^{2+} uptake inhibition through competitive interactions between Al^{3+} and plasma membrane transporters for Mg^{2+} (Rengel and Robinson 1989; Rengel 1990) because (1) Al and Mg have similar hydrated ionic radii, and (2) plants preferentially take up heavy isotope ^{26}Mg (the daughter nuclei of ^{27}Al) from a mix of Mg^{2+} isotopes in nutrient solutions and store it in tissues (reviewed in Bose et al. 2011a). This might be true because *Arabidopsis thaliana* magnesium transporters (AtMGT1 and AtMGT10) are highly sensitive to Al^{3+}, providing potential molecular targets for Al^{3+} toxicity in plants (Li et al. 2001). On the

contrary, overexpression of Mg^{2+} transporter genes in yeast (MacDiarmid and Gardner 1998), *Nicotiana benthamiana* (Deng et al. 2006), and rice (Chen et al. 2012) conferred Al tolerance by potentially alleviating Al-induced magnesium deficiency (Chen and Ma 2013), but these studies did not provide sufficient evidence of enhanced magnesium uptake and an increase in intracellular Mg^{2+} concentration in the presence of Al^{3+} ions. This issue has been addressed by measuring Mg^{2+} uptake using Mg^{2+}-selective microelectrodes and fluorescent dye in Arabidopsis roots during short-term (0–60 min) exposure to Al^{3+} stress (Bose et al. 2013). The results showed that enhanced Mg^{2+} uptake and increased intracellular free Mg^{2+} concentration correlated with an improved capacity of Arabidopsis genotypes to cope with low-pH and combined low-pH/Al stresses (Bose et al. 2013).

2.6.3 Potassium Uptake

K^+ is essential for cell division through polymerisation of actin (Alberts et al. 1994) and turgor-dependent cell elongation caused by accumulation of K^+ in the vacuole (Frensch 1997; Dolan and Davies 2004; Sano et al. 2007). However, there is no causal relationship between Al^{3+} toxicity and K^+ nutrition in plants because Al^{3+} induced either inhibition (Matsumoto and Yamaya 1986; Nichol et al. 1993) or an increase in K^+ uptake (Lee and Pritchard 1984; Lindberg 1990; Tanoi et al. 2005). The reason for increased K^+ uptake under Al^{3+} stress may be a decrease in net K^+ efflux rather than an increase in uptake (Horst et al. 1992; Olivetti et al. 1995; Sasaki et al. 1995). Several patch clamp studies demonstrated that Al ions decrease the open probability of K^+ inward-rectifying channels through internal blocking (Gassmann and Schroeder 1994; Liu and Luan 2001). In contrast, Al induced or maintained K^+ efflux in Al-tolerant wheat genotypes together with enhanced malate release (Ryan et al. 1995; Osawa and Matsumoto 2002; Wherrett et al. 2005), probably to balance charges created by exudation of weak organic acid anions (Ryan et al. 1995; Matsumoto 2000; Ma et al. 2001; Osawa and Matsumoto 2002; Wherrett et al. 2005). This notion is also confirmed in Arabidopsis thaliana wherein Al-tolerant genotypes (alr104 and Col-0) showed greater K^+ efflux than Al-sensitive genotypes (*als3* and *als5*) during Al^{3+} stress (Bose et al. 2010a).

2.6.4 Phosphorus Uptake

Apart from causing direct toxicity to roots, Al^{3+} ions also exacerbate P deficiency by binding with P to form sparingly soluble Al–P complexes that are not plant available (Haynes and Mokolobate 2001). Hence, even in acidic soils that have relatively high total concentration of P, availability of P is limiting (Kochian et al. 2004; Fukuda et al. 2007). Selection of genotypes for either P efficiency or Al tolerance independently may be unsuccessful because these two soil constraints occur jointly in acidic soils (Foy 1988; Yan et al. 1995). For example, Al-tolerant

soybean genotype 416937 selected under controlled conditions was found to be sensitive to acid soils in the field (Ritchey and Carter 1993; Ferrufino et al. 2000). In contrast, an Al-sensitive soybean genotype was found to be relatively tolerant to acid soils (e.g. Foy et al. 1992). These discrepancies might be due to failure in the selection process to account for interactions between Al and P that normally occur in acid soils. Thus, a thorough understanding of the Al–P interactions is essential for improving the productivity of crops in acid soils.

Generally, plants may respond to both Al toxicity and P deficiency by exuding organic acid anions (Lopez-Bucio et al. 2000; Haynes and Mokolobate 2001; Shen et al. 2002). Exudation of low-molecular-weight organic acid anions (e.g. citrate, malate) in the rooting media is advantageous because organic acid anions can (1) protect plants from Al toxicity by forming non-phytotoxic Al-organic anion complexes and (2) enhance P availability and thus improve plant P uptake by chelating Al from the Al–P complexes, thus liberating P for plant uptake (Subbarao et al. 1997; Ishikawa et al. 2002).

The signal perception of Al toxicity or P deficiency and translocation of this signal into activation of organic acid synthesis and exudation are pivotal for P nutrition and Al tolerance in acid soils. Proteomic (Fukuda et al. 2007) and transcriptomic (Wasaki et al. 2003) analysis of rice roots grown in Al-toxic and P-deficient low-pH solution revealed that (1) modifications of root protein expression were similar under Al toxicity and P deficiency, and (2) carbon supply to the tri-carboxylic acid (TCA) cycle to produce organic acids was maintained by enhancing glycolysis. Indeed, P-efficient genotypes were able to enhance Al tolerance in acid soils by stimulated exudation of different Al-chelating organic acid anions in soybean (Liao et al. 2006), cowpea (Jemo et al. 2007), and barley (Delhaize et al. 2009). Interestingly, Liao et al. (2006) found that Al toxicity induced citrate exudation, P deficiency triggered oxalate exudation, and malate release was induced by either Al toxicity or P deficiency in soybean. In contrast, Ligaba et al. (2004) reported that citrate exudation was enhanced by P deficiency but not by Al toxicity in purple lupin. These controversial results clearly suggest that there are important differences in how Al toxicity and P deficiency may effect organic anion exudation, which is of huge importance when these two environmental stresses occur together as they regularly do in acid soils.

3 Disturbance of Ion Homeostasis

The maintenance of optimal concentrations of inorganic ions such as H^+, K^+, Ca^{2+}, and Mg^{2+} (ionic homeostasis) inside plant cells and organelles is pivotal for the functioning of biopolymers (Andreev 2001). Ion homeostasis in plants is regulated by controlled flux of ions across the plasma membrane and the endomembranes in addition to storage in organelles (Bose et al. 2011a). Entry of Al ions into the cytoplasm (Silva et al. 2000; Babourina and Rengel 2009) may affect homeostasis of various ions inside the cell.

3.1 H^+ Homeostasis

The change of pH (ΔpH) between the cytoplasm and the apoplasm is the major driving force for the translocation of ions in plant cells. Under no stress, the pH is 7.3–7.6 in the cytoplasm, 4.5–5.9 in vacuoles, ~7 in mitochondria, 7.2–7.8 in chloroplasts, and ~5.5 in the apoplast (Kurkdjian and Guern 1989; Bose et al. 2011a, b). Thus, cytoplasm is less acidic when compared to vacuoles and the apoplast. This pH difference is regulated by proton pumps (H^+-ATPase and H^+-PPase) located at the plasma membrane and the tonoplast, driving H^+ from the cytoplasm to either the apoplast or the vacuole (Marty 1999). Hence, disturbance in H^+-ATPase activity by environmental stresses would affect cytoplasmic pH regulation. Indeed, transient changes in cytoplasmic pH are pivotal for the signal cascades to elicit defence mechanisms or developmental processes in response to a variety of environmental stimuli (Roos et al. 2006). The low-pH treatment caused net H^+ influx into the root tissue and caused intracellular acidification (Gerendas et al. 1990; Plieth et al. 1999; Babourina and Rengel 2009; Bose et al. 2010b). Further, genes controlling cytoplasmic pH were downregulated in the low-pH-hypersensitive Arabidopsis stop1 mutant (Iuchi et al. 2007; Sawaki et al. 2009). Thus, cytoplasmic acidification may be responsible for poor root growth in the treatments with low pH only. Interestingly, low-pH tolerance of als5 and alr104 mutants coincided with high H^+ influx, suggesting that aforementioned mutants may possess effective mechanisms to prevent cytoplasmic acidification despite high H^+ influx from the external environment; in contrast, such mechanisms would be absent/ineffective in the low-pH-sensitive mutant (als3) (Bose et al. 2010a).

Modulation of cytosolic pH by combined low-pH/Al^{3+} stress can act as a secondary messenger to activate/inactivate transporters and enzymes and, in turn, regulate synthesis of organic acid anions and their subsequent release. An increase in intracellular pH (from ≈5.7 under control pH $5.5_{[water]}$) towards pH ≈ 6.5 following a combined low-pH/100 μM Al stress was observed in Arabidopsis wild type (Bose et al. 2010b). This rise in intracellular pH would favour deprotonation of organic acids inside the cytoplasm (Davies 1986) and potentially their anion exudation into the rhizosphere. Though Al^{3+} decreased the H^+-ATPase activity in the plasma membrane vesicles prepared from Al-treated seedlings of barley (Matsumoto 1988; Matsumoto et al. 1992), wheat (Sasaki et al. 1995), and squash (Ahn et al. 2001, 2002), inhibition of H^+-ATPase activity appears to be dependent on Al^{3+} concentration. For example, Al^{3+} concentrations lower than the threshold Al^{3+} phytotoxicity caused upregulation of H^+-ATPase, whereas phytoxic Al^{3+} concentrations resulted in H^+-ATPase inhibition in maize (Facanha and Okorokova-Facanha 2002) and soybean roots (Shen et al. 2005). In addition, cytoplasmic pH may also vary depending on the Al^{3+} concentrations used. Thus, more work is needed to understand Al^{3+} concentration's influence on the cytoplasmic pH homeostasis.

3.2 Ca^{2+} Homeostasis

Being the secondary messenger, free cytosolic Ca^{2+} activities are pivotal for transduction of hormonal and environmental signals to the responsive elements of cellular metabolism (see Rengel and Zhang 2003; Bose et al. 2011b for references). Free cytosolic Ca^{2+} activities in plant cells are usually maintained in the 100–200 nM concentration range (Bush 1995; Webb et al. 1996). However, Ca^{2+} activities in the cell wall (apoplasm) and other internal organelles (e.g. vacuoles and endoplasmic reticulum) are higher than the cytosolic Ca^{2+} by 3–4 orders of magnitude (Clarkson 1984; DuPont et al. 1990; Evans et al. 1991; Bose et al. 2011b). Low concentrations of cytosolic Ca^{2+} are maintained by ATP-dependent Ca^{2+} pumps and Ca^{2+} exchangers (CaX) in the plasma membrane and the endomembranes via (1) sequestration into different organelles and (2) pumping Ca^{2+} into the apoplasm (Evans et al. 1991; Hirschi 2001; Miedema et al. 2001; Bose et al. 2011b).

Al^{3+} affects the Ca^{2+} homeostasis maintenance in three ways. Firstly, Ca^{2+} is essential for cross-linking the pectic materials in the cell wall. Aluminium displaces pectin-bound Ca^{2+} because Al has a higher affinity for pectic material than Ca^{2+} (Blamey 2001), and overexpression of pectin methylesterase enzyme in *Solanum tuberosum* resulted in severe Al toxicity (Schmohl et al. 2000). In fact, between 90 % (Reid et al. 1995) and 99.99 % (Taylor et al. 2000) of cell-wall-bound Ca^{2+} is displaced by Al^{3+} in Chara internodal cells. In *Arabidopsis thaliana* roots, initial Al-induced Ca^{2+} efflux was higher in the Al-sensitive genotypes (*als3* and *als5*) than in the wild type and Al-tolerant alr104 mutant, suggesting extensive displacement of apoplastic Ca^{2+} by Al ions in the Al-sensitive mutants (Bose et al. unpublished results). Hence, displacement of Ca^{2+} by Al^{3+} would severely alter the physical properties of the cell wall, including extensibility, rigidity, and permeability (Reid et al. 1995; Tabuchi and Matsumoto 2001; Jones et al. 2006; Horst et al. 2007), thereby detrimentally affecting cell division and elongation. However, contradicting results were observed in onion root tips where the particle-induced X-ray emission technique indicated that Ca^{2+} in the root tips was not displaced by Al (Schofield et al. 1998). These discrepancies might be due to different experimental systems and environmental conditions. Secondly, Al^{3+} inhibits the Ca^{2+} influx (reviewed in Sect. 6.1). Thirdly, Al disturbs cytosolic Ca^{2+} activity, thereby affecting the signal transduction pathways involved in root growth. However, a disagreement exists in the literature about Al effects on cytosolic Ca^{2+} homeostasis and its involvement in Al toxicity.

In many plant species, Al^{3+} toxicity caused elevation of cytoplasmic Ca^{2+} activity, with such elevation being higher in Al-sensitive than Al-tolerant genotypes of the same species (Jones et al. 1998a; Zhang and Rengel 1999; Ma et al. 2002; Rengel and Zhang 2003). This cytosolic Ca^{2+} rise would play a major role in the expression of Al^{3+} toxicity because the cell-responsive elements may stop responding to transient rises in cytosolic Ca^{2+} caused by a variety of signals (Rengel and Zhang 2003). For example, an increase in cytosolic Ca^{2+} caused closure of

plasmodesmata (Holdaway-Clarke et al. 2000) and inhibited plasmodesmata-mediated cell-to-cell transport in Al-sensitive wheat roots (Sivaguru et al. 2000). A good correlation was observed between Al-induced cytosolic Ca^{2+} rise (within 30 min) and root growth inhibition in wheat genotypes (Zhang and Rengel 1999), leading to the hypothesis that disruption of Ca^{2+} homeostasis may be the primary cause of Al^{3+} toxicity (Rengel and Zhang 2003). However, in a recent study on Arabidopsis, an Al-induced cytoplasmic Ca^{2+} rise started in the mature (least Al-sensitive) root zone (in 48 s) and proceeded towards the root cap (in 100 s). Moreover, a Ca^{2+} rise did not differ among Al-resistant, Al-sensitive, and the wild-type Arabidopsis roots (Rincon-Zachary et al. 2010). Similarly, a lack of correlation between Al-induced growth inhibition and alteration in cytosolic Ca^{2+} in the root hairs of Arabidopsis thaliana wild-type, sensitive, and tolerant genotypes (Jones et al. 1998a) indicated that alteration in cytosolic Ca^{2+} may not be responsible for growth inhibition. In some studies, such as in tobacco cell cultures, Al decreased the cytosolic Ca^{2+} concentration along with growth inhibition (Jones et al. 1998b). More detailed comparison (Plieth et al. 1999) of low-pH and combined low-pH/Al^{3+} effects on cytosolic Ca^{2+} dynamics using *Arabidopsis thaliana* indicated that intact roots responded to low pH by a sustained elevation of cytosolic Ca^{2+}. However, this low-pH-mediated elevation in cytosolic Ca^{2+} activity was abolished in the presence of Al, suggesting that Ca^{2+}-mediated protection mechanism against low pH is irreversibly inhibited by Al (Plieth et al. 1999). More information, especially during the first few seconds of low-pH and Al^{3+} stress, is clearly needed to resolve many discrepancies in the literature.

3.3 Mg^{2+} Homeostasis

Al^{3+} and Mg^{2+} ions have similar hydrated radii; hence, Al^{3+} ions compete with Mg^{2+} ions for apoplastic binding, uptake via Mg^{2+}-permeable cation channels and transporters, and binding with enzymes, ATP, and anions (reviewed in Bose et al. 2011a). As a result, Mg^{2+} transport and metabolism under Al^{3+} stress might be impaired in all the compartments of the cell (Bose et al. 2011a). However, little information is available on how Al^{3+} stress modulates the cytosolic free Mg^{2+} concentration. To shed light on this issue, intracellular free Mg^{2+} concentrations were measured in the epidermal root cells of Arabidopsis genotypes using an Mg^{2+}-selective fluorescence dye (Magnesium Green^{TM}). Under control conditions (pH 5.45), free cytosolic Mg^{2+} concentrations were in the range of 0.8–1.4 mM. The Al-resistant mutant alr104 recorded the highest intracellular Mg^{2+} concentration followed by als5 ~ wild type > als3. The low-pH (4.2) stress did not alter the free cytosolic Mg^{2+} concentration, whereas combined low-pH/50 mM Al stress raised the intracellular Mg^{2+} concentration in all genotypes tested but to a different extent. The Al-tolerant genotypes (wild-type Col-0 and *alr104* mutant) recorded a higher intracellular Mg^{2+} concentration than the Al-sensitive mutants (*als3* and *als5*) (Bose et al. 2013). The ability of Al-tolerant genotypes (Col-0 and alr104) to

maintain the influx of Mg^{2+} ions into the root tissue from the external medium is the primary reason for enhanced intracellular Mg^{2+} concentration in these genotypes.

Elevated intracellular Mg^{2+} might play a pivotal role in the maintenance of H^+-ATPase activity, acid phosphatase activity, organic acid synthesis and metabolism, cytosolic Ca^{2+} dynamics, and reactive oxygen species homeostasis during Al^{3+} stress (Bose et al. 2011a; Chen and Ma 2013). Interestingly, exposure of Arabidopsis wild-type (Col-0) roots to Al concentrations higher than 50 μM (i.e. 100 and 500 μM $AlCl_3$ treatments, pH 4.2) decreased the intracellular Mg^{2+} concentration in a dose-dependent manner. This decline is explained by the decreased Mg^{2+} influx, or increased efflux, at 500 μM Al^{3+}, caused by Al inhibition of the plasma membrane cation channels (Bose et al. 2013). Above observations suggest that the efficacy of phytotoxic Al to block Mg^{2+} transport through cation channels is concentration and genotype dependent. More work is needed to identify threshold Al^{3+} concentration for different crop species.

4 Conclusions

Low-pH and combined low-pH/Al^{3+} stresses differentially affect uptake and homeostasis of hydrogen, phosphorus, potassium, calcium, and magnesium. Plants with a superior capacity to take up hydrogen at the same time preventing cytoplasmic acidification along with enhanced uptake of phosphorus, calcium, and magnesium ions perform well under low-pH and combined low-pH/Al^{3+} stresses. In the case of potassium, enhanced uptake may help plants resist low-pH stress, whereas an enhanced potassium loss to balance charges with the organic acid anion exudation is the preferred strategy to combat the combined low-pH/Al^{3+} stress. Breeding for enhanced nutrition of phosphorus, calcium, and magnesium under Al^{3+} stress may be both possible and desirable approach to improve crop growth in acid soils.

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