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Acid Tolerance Mechanisms in Soil Grown Plants

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ABSTRACT

Acid soil covers 30% of ice-free land in the world, mainly distributed in the tropical and subtropical regions where agriculture is the dominant business. Soil acidity, particularly aluminium (Al) and manganese (Mn) toxicity, often constitutes one of the critical constraints limiting crop production on these acid soils. Research on acid-tolerance mechanisms of soil grown plants will have important implication in facilitating soil and crop management in the tropical and subtropical regions. Soil becomes acidic due to natural soil acidification process. In acidic soils, Al toxicity is common due to solubilisation of Al^{3+} ion which is toxic for plants. The main symptom of Al^{3+} toxicity is the inhibition of root growth. After Al^{3+} toxicity, Mn toxicity ranks as the second major concern for plant growth in acid soils. Unlike Al, Mn is an essential plant nutrient and is toxic when taken up in excessive quantities by plants. In addition to Al and Mn toxicity, low pH also affects plant growth in highly acid soils. Low pH stress facilitates H^+ influx into root tissues resulting in poor plant growth. However, phosphorus (P) deficiency is also common in acid soils. Phosphorus leads to an Al-phosphate complex in acid soils that result in less P availability in these soils. Different Al tolerance mechanisms such as an increase in rhizosphere pH, plant tissue tolerance, exudation of organic acid and role of apoplast are discussed in this review. This review concludes that P may play an important role in Al tolerance. Thus, understanding acid tolerance mechanisms in soil grown plants has important implications for sustainable agriculture in the tropical and subtropical regions. This review suggests that introduction of Al-tolerant crops in acid soils will improve crop production in these soils.

Keywords: Organic acid exudation, Al and P interaction, apoplast, plant tissue tolerance.

INTRODUCTION

Soil acidity results in declining crop production all over the world (Samac and Tesfaye 2003). In the 1970s, there were about 3 billion hectares of acid soils in the world (Kochian *et al*. 2004). Twenty years later, a survey stated that this has increased to 4 billion hectares and importantly 178 million hectares were agricultural soils (Von Uexkull and Mutert 2004). Furthermore, it is now estimated that approximately 50% of the world's potentially arable lands are acidic (Kochian *et al*. 2004; Panda and Matsumoto 2007).

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Al becomes solubilised in low pH soils that results in increased activity of Al^{3+} ions (Hoekenga *et al.* 2003). This leads to a high concentration of soluble Al in acid soils which is toxic for plants and severely limits crop production (Delhaize and Ryan 1995; Foy 1988; Kochian *et al*. 2004; Pellet *et al*. 1996).

Little work has been done on acid-tolerance mechanisms on soil-grown plants (Ishikawa *et al.* 2000). Some studies on acid-tolerance mechanisms in solution culture show largely different results in soils (Ishikawa *et al.* 2000; Wenzl *et al.* 2001; Zheng *et al*. 2005).

Understanding soil chemistry and plant-soil interactions in acid soils is useful for making sound and cost-effective decisions to manage soil acidity. Thus, this review attempts to understand different issues like Al and phosphorus (P) chemistry in acid soils, Al and Mn toxicity effects on plant growth in acid soils, Al-tolerance mechanisms and a possible role of P in Al tolerance mechanisms.

THE CHEMISTRY OF SOIL ACIDITY

Soil Acidification Processes

Soil acidification is an ongoing natural process that can be accelerated by agricultural practices (Bolan *et al.* 1991). Soil acidification is mainly caused by the release of protons (H^+) during the transformation and cycling of carbon (C), nitrogen (N) and sulfur (S) in the soil-plant interfaces (Ulrich and Summer 1991). Thus, inputs of H^+ ions, changes in soil C, N and S can have adverse impacts when soils are unable to buffer against pH decrease (Mason *et al.* 1994). In the N and S cycles, mineralisation and oxidation of organic N and S produce H^+ ions. This H^+ is balanced by OH^- through uptake and assimilation of NO_3^--N and SO_4^{2-}-S by plants and microorganisms (Vries and Breeuwsma 1987). Leaching of SO_4^{2-} and NO_3^- with charge-balancing basic cations (Ca^{2+}, Mg^{2+}, K^+ or Na^+), rather than the H^+ ions generated during oxidation, results in permanent acidity remaining in the soil. This is reflected in a decrease in pH in soils with low pH buffer capacity (Breemen 1991).

Other processes leading to permanent soil acidification include accumulation of organic N and nitrification of NH_4^+-based fertilizers. When uptake and assimilation of NH_4^+ or N_2 occur in plants, H^+ ions are excreted into the rhizosphere soil. These excreted H^+ ions are then separated from the rhizosphere soil and move to bulk soil, due to accumulation of organic N in the rhizosphere soil. This accumulation of organic N in rhizosphere soil occurs by the decarboxylation of organic acid anions. As more organic N accumulates in the rhizosphere soil, acidity increases, with a decrease in bulk soil pH (Williams 1980). Similarly, losses of N through NH_3 volatilisation or denitrification produce permanent soil acidity only when the N input is added in the form of NH_4^+ by the application of ammonium based fertilisers (Bolan and Hedley 2003).

Aluminium Chemistry in Acid Soils

The Al chemistry in acid soils is quite complex and its cations are partly responsible for soil acidity. The Al has a high ionic charge and a small crystalline radius, which confers it a level of reactivity that is unmatched by other soluble metals.

Al Behaviour in Soil

The forms of Al in the soil are complex. This is due to multiple Al compounds and its species that can be found in the soil solution or on soil solids. A simplified scheme of Al forms in soil can be shown as below:

Total Al = [Solid phase Al] + [Soil solution Al]
= [Lattice Al + Surface Al] + ["Al^{3+}" + AlL]

where, Lattice Al is structural Al and means that no direct or short-term influence on Al toxicity occurs other than as a potential source of Al; Surface Al represents a number of species on various surfaces; Al^{3+} represents phytotoxic forms of Al, and AlL means ligands that bind with Al (Ritchie 1995).

Many soluble and insoluble forms of Al exist in acid soils. Not all of these insoluble and soluble Al are harmful to plants. For example, Al exists in the form of insoluble aluminosilicate or oxide in acid soils that is non-toxic for plants. Similarly, soluble Al like polynuclear Al and low molecular-weight Al complexes are non-toxic for plants. In contrast, a soluble mononuclear form of Al, like Al^{3+}, is toxic for plants. This toxic Al^{3+} is usually exchangeable and bound closely with the cation exchange complex because of its high adsorption strength to soil particles (Kochain 1995).

Effect of pH on Al Species

Below pH 5, Al is the main source of H^+ due to dissociation of Al from clay minerals. Also, a soluble form of Al exists as octahydro-hexahydrated [$Al(H_2O)_6^{3+}$], frequently abbreviated to Al^{3+}.

Hydrolysis occurs when the charge/size ratio of the cation is sufficiently large to break the H-O links. The result is hydrate ionisation which produces hydrogen ions. Reactions (1), (2) and (3) are abbreviated and are as follows:

$$Al^{3+} + H_2O \longrightarrow Al(OH)^{2+} + H^+ \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

$$Al(OH)^{2+} + H_2O \longrightarrow Al(OH)_2^{+} + H^+ \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

$$Al(OH)^{+} + H_2O \longrightarrow Al(OH)_3 + H^+ \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3)$$

Each reaction releases H^+ and regenerates the Al^{3+} ions enabling further reaction (Serrano 2003). When the pH of a solution is raised above 5.0, the concentration of Al^{3+} decreases with increasing pH, and $Al(H_2O)_6^{3+}$ undergoes repeated deprotonations to form insoluble $Al(OH)_3$ at pH 7.0. In near neutral solutions, polynuclear forms of Al, contain more than one Al with the most important being triskaidekaaluminum, $AlO_4Al_{12}(OH)_{24}(H_2O)_{127+}$, referred to as

Al_{13}. At pH 7.4 (common pH in cytosol), $Al(OH)_4^-$, that is, aluminate ions are formed (Parker and Bertsch 1992).

Phosphorous Chemistry in Acid Soils

Phosphorous chemistry in acid soils can be affected by some physico-chemical processes such as precipitation and specific adsorption and properties such as pH and interactions with other ions. These processes/properties are described below:

Precipitation

High levels of extractable Al in acid soils cause P deficiency which mainly occurs due to precipitation and formation of Al-phosphate complexes in acid soil solution (Sanchez *et al.* 1997). The initial precipitates of Al phosphates are amorphous and may show solubilities that are 10 to 100 times greater than the crystalline minerals (Veith and Sposito 1977). As a result, precipitated Al-P complex controls the level of P in acid soils (Lindsay 1979).

Specific Adsorption

In most acid soils, the major process that controls soil solution P concentration is the adsorption process. The adsorption process is regarded as the accumulation of P onto surfaces of soil particles (Sanyal and De Datta 1991). It describes the reaction of phosphate ions in soil solution at the surface of soil constituents, resulting in a chemical bond. The surfaces of Mn, Al and Fe oxides in acid soils play an important role in the P adsorption process (Wild 1950). The oxide surfaces may exhibit net negative, net positive, or net zero charge (Sanchez and Uehara 1980).

The adsorption of P in acid soils increases with the increase in extractable Al (Hall and Baker 1971; Robarge and Corey 1979). Ligand exchange reactions act as the principal mechanism by which P is adsorbed to variable-charge surfaces of Al. Initially, P is bound to the surface of adsorbents Al oxides and hydro-oxides by ligand exchange (Parfitt 1978). Adsorption occurs when P anions replace the hydroxyl groups on the surface of Al oxides and hydrous oxides (*Fig. 1*). Then, P becomes less available due to the molecular rearrangement of the adsorbed P. Furthermore, P ions which are adsorbed on the surface of the Al hydroxides are generally converted into crystalline Al phosphates (Dean 1949). The P converted to crystalline Al phosphate is considered completely unavailable for plant growth.

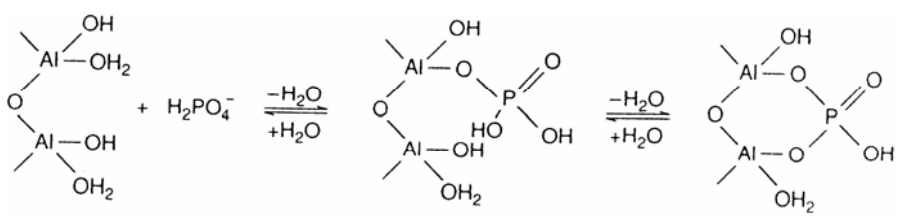
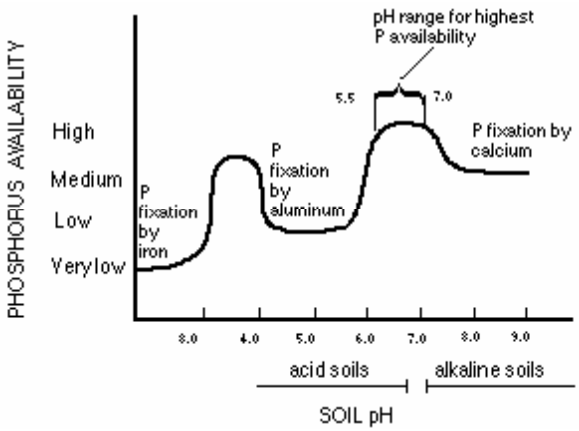


Fig. 1: Mechanism of P adsorption on Al oxide surface

Effect of pH on P Availability

Low P availability in acid soils is a major limiting factor for plant growth (Nian *et al.* 2009). Generally, P availability in soil is minimum in the pH range of 2 to 4 (Bowden *et al.* 1980). In low-pH soils, the formation of Al-phosphate decreases the concentration of P in the soil solution that is controlled by precipitation reactions (Pratt 1961). In addition, Schefe *et al.* (2007) reported that low soil pH reduces the availability of P also through increased P sorption reaction.

The fixation of P depends on soil pH (Hsu 1964). The fixation onto colloidal iron (Fe) surfaces beginning at very low pH levels, usually below 4, is the dominant P fixation process in soils (Kanwar and Grewal 1990; Naidu *et al.* 1990). There is a relationship between soil pH and P fixation. Soil pH below 5.5 affects solubility of P in soils characterised by cracking clays, where Al and Fe dominate. The P fixation with Al is more commonly seen from pH 4.5 to 6 and results in substantial lock-up of P, while in less acid-to-neutral pH soils, calcium (Ca) phosphate is the more commonly encountered inorganic form of P. Above pH level 7.0, Ca is the dominant ion and fixation is less permanent. The fixation of P in acid, neutral and alkaline soils due to Fe, Al and Ca is shown in *Fig. 2*.



(Source : CSIRO 2006)

Fig. 2: The fixation and availability of P is affected by soil pH

Interaction between Soluble Al and P Availability in Acid Soils

The addition of soluble phosphates to acid soils reduces the soluble Al (Brown *et al.* 1950; Hartwell and Pember 1918). Soluble P increases when soils turn from acid to neutral. This could be due to high amounts of Al available in acid soils as compared to neutral soils that help to increase P availability in neutral soils (Holford 1997). In contrast, the soluble P decreases in highly acid soils due to availability of soluble Al. The Al phosphate forms surface coatings on particles of Al compounds that would have otherwise dissolved in highly acid soil. Thus the interaction of Al and P in acid soils reduces the soluble Al (Pratt 1961).

In many acid soils, P is concentrated at the surface of the soil while a high concentration of phytotoxic Al is found in the subsoil. Crops growing on such

soils are exposed to various concentrations of P and Al at different depths in the soil profile. Therefore, surface applied P interacts little with Al in subsoils (McLaughlin and James 1991).

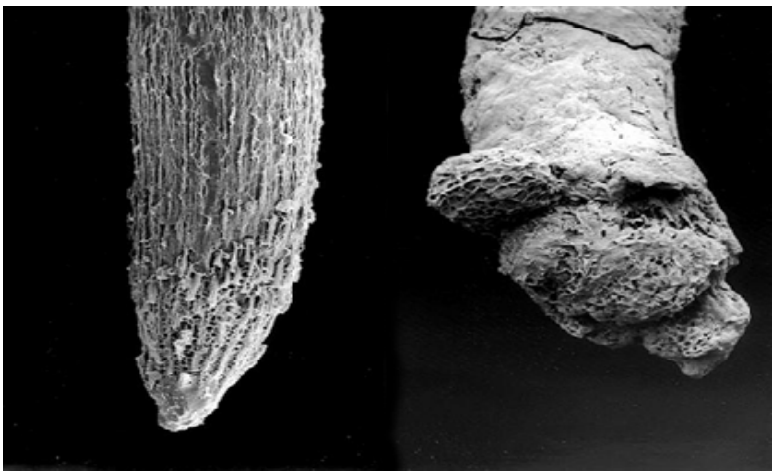
IMPACT OF SOIL ACIDITY ON PLANT GROWTH

In acid soils, plant growth can be limited by various toxicities like Al^{3+}, Mn^{2+} and H^{+} (Kidd and Proctor 2001). These toxic effects on plant growth are described further in the following sections.

Al Toxicity

Al toxicity is one of the principal factors that limits plant growth in acid soils (Foy 1988; Panda *et al.* 2009). The primary symptom of Al toxicity is the inhibition of root growth that can occur within 3 hours in solution culture experiments (Ownby and Popham 1989). Plant roots become thickened, stubby and distorted due to the inhibition of growth (Helyar 1998). Similarly, toxic levels of Al in the soil solution affect root cell division and the ability of the root to elongate. This results in a reduction in root growth and branching (Gazey and Davies 2009).

Primary toxic effects of Al are localized to the distal transition zone in the root tip (Sivaguru and Horst 1998). The root tip appears to be a critical site for Al toxicity (Ryan *et al.* 1993). The root tips are deformed and brittle under Al toxicity (*Fig. 3*). The root tip i.e., root cap, meristem and elongation zones are highly sensitive to Al and accumulate Al easily. Greater physiological damage occurs



(Source: Delhaize and Ryan 1995)

Fig. 3: Healthy root tip (left) compared to a root tip affected by Al toxicity (right). Photograph taken for healthy root tip on Al-tolerant (ET8) and affected root tip on Al-sensitive (ES8) wheat genotypes that differ at the Alt1 locus. The seedlings were grown for 4 days in a solution that contained 5 µM $AlCl_3$ in 200 µM $CaCl_2$ at pH 4.3

within meristematic and root cap cells, as well as a disruption of dictyosomes and their secretory function (Poschenrieder *et al.* 2008).

A number of mechanisms may cause Al-induced root injury, including Al interactions within the cell wall, the plasma membrane or the root **s**ymplasm (Horst 1995; Kochian 1995; Marschner 1991; Taylor 1988). Al may interact with the cell wall and be absorbed in the root cell wall by the negative charges (Wagatsuma 1983b). The cell wall and the cell membrane probably function as an important barrier to the passive movement of Al into the symplasm (Wagatsuma 1983a). Thus, a large amount of Al is bound to the plasma membrane, and the plasma membrane is eventually destroyed by Al (Wagatsuma 1989).

The toxic effects of Al on shoots are generally not easily identifiable. The shoots of Al- toxic plants appear typically P deficient. The Al toxicity shows overall stunting, small, dark green leaves and late maturity, purpling of stems, leaves and leaf veins, yellowing and death of leaf tips (Bouma *et al.* 1981). This Al toxicity is due to Al dislocation of the plant P metabolism. The occasional observation of yellow spots or pale flecking of the leaves of grasses or cereals may reflect the effects of Al toxicity on other metabolic processes (Helyar 1998). In some cases, Al toxicity induces calcium (Ca) deficiency or reduces Ca transport (curling or rolling of young leaves and collapse of growing points or petioles). Excess Al even induces iron (Fe) deficiency symptoms in rice (*Oryza sativa* L.), wheat (*Triticum aestivum*) and sorghum (*Sorghum bicolor* L.) (Furlani and Clark 1981). But in most cases, Al toxicity in shoots is associated with cellular modifications in leaves, reduced stomata opening, decreased photosynthetic activity, chlorosis and foliar necrosis (Vitorello *et al.* 2005).

Mn Toxicity

Although Al is generally the major toxic metal in acid soils, Mn toxicity can occur in acid soils (Delhaize *et al.* 2004). Mn toxicity is possibly the second most important metal toxicity in acid soils after Al (Foy *et al.* 1973). Unlike Al, Mn is an essential plant nutrient, but is toxic when taken up in excessive quantities. Its toxicity is common at pH level as high as 5.6. In addition, Mn toxicity may be more important than Al toxicity in limiting crop production, in some acid mineral soils (Sumner *et al.* 1991).

The Mn toxicity symptoms in plants are localized at the morphological level, with the effect being pronounced in shoots. Shoot growth becomes stunted and necrotic lesions appear due to Mn toxicity. Also, toxic effects of Mn include crinkling or cupping of shoots and splotches of chlorotic tissue (Alam *et al.* 2000). The physiological mechanism of Mn toxicity and tolerance is still poorly understood. Horst *et al*. (1999) suggested that Mn-induced oxidative stress is a cause of Mn toxicity. Later, Fecht-Christoffers *et al.* (2007) proposed that shoot apoplast was the most important compartment for development of Mn toxicity and tolerance. They also suggested that more detailed studies with emphasis on very early stages of Mn toxicity and a comparison of Mn-sensitive and Mn-tolerance for shoot are required.

Low pH

In addition to Al and Mn toxicity, plants shows other effects when grown in highly acid soils (Kinraide *et al.* 1992). There is evidence that low pH can directly inhibit root growth (Yang *et al*. 2005a). Low pH stress facilitates H^+ influx into root tissues that result in poor plant growth (Rangel *et al.* 2005). Thus, it is imperative to understand H^+ toxicity mechanisms in plants in order to develop plants that are more tolerant to H^+ stress in acid soils. At a low pH, the H^+ ions themselves are of sufficient concentration to be toxic to some plants, mainly by damaging the root membranes. Low pH activates rapid H^+ influx that depolarises the plasma membrane potential and causes cytoplasmic acidification (Babourina *et al.* 2001). Short-term root responses to low pH exhibited similar responses in mature and distal elongation zones in terms of H^+ flux. Thus, low pH affects root tissues which might contribute to the differential mechanisms of plant adaptation to acid soils (Bose *et al.* 2010).

Species or Genotypic Variation in Response to Soil Acidity

Tolerance to soil acidity varies across plant species and between genotypes of a same species. Some plant genotypes or species have evolved mechanisms to tolerate Al stress (Fukuda *et al.* 2007). For example, Hede *et al.* (2001) showed that wheat varieties collected from acid-soil regions are more likely to be Al tolerant than those collected from regions with natural or basic soils. Thus, the differences in Al tolerance among species and between genotypes are important to develop varieties that are suitable for cultivation in acid soils (Yang *et al.* 2005b).

MECHANISMS OF AL TOLERANCE

Mechanisms of Al tolerance mainly involve exudation of organic acid anions, changes in rhizosphere pH and plant tissue tolerance to Al.

Exudation of Organic Acid Anions

Exudations of organic acid anions from plant roots play a central role in Al tolerance mechanisms. More than twelve Al-tolerant plant species are known to exude organic acid anions from their roots in response to Al treatment (Ryan and Delhaize 2001). Although many types of organic acid anions are found in root cells, only one or two specific organic acid anions are exuded in response to Al treatments from Al-tolerant plant species (Ma *et al*. 1997b). Citrate, oxalate and malate are some of the commonly released organic acid anions (Ma *et al.* 2001). Citrate exudates from Al-tolerant cultivars of maize (*Zea mays*) (Pellet *et al.* 1995), oxalate exudates from Al-tolerant buckwheat (*Fogopyrum esculentum*) (Ma *et al.* 1997a) and malate exudates from of Al-tolerant wheat genotypes (Delhaize *et al.,* 1993). These exuded organic acid anions are able to form stable complexes with Al (Guo *et al*. 2007) and protect the root apex from Al toxicity damage (Delhaize *et al*. 2004).

Anion channels are responsible for exudation of organic acid anion (Kollmeier *et al*. 2001). An anion channel is a membrane-bound transport protein that allows

the passive flow of anions down their electrochemical gradient. One patch-clamp study on protoplasts prepared from wheat roots showed that Al^{3+} activates an anion channel in the plasma membrane which is permeable to malate (Ryan *et al.* 1997). When this response was compared in a pair of near-isogenic wheat lines that differed in Al tolerance at a single genetic locus, Al^{3+} was found to activate anion channels that were both larger and more frequent in the protoplast of the Al-tolerant genotype than of the Al-sensitive genotype (Zhang *et al.* 2004). Other studies also showed that Al-tolerant maize exudated citrate in response to Al treatment by the activation of an anion channel on the plasma membrane (Pineros and Kochian 2001).

Increase in Rhizosphere pH

Rhizosphere pH has a positive effect on Al tolerance (Wang *et al*. 2006). Elevated rhizosphere pH reduces the toxicity and solubility of Al (Foy *et al.* 1965). Likewise, Ohno *et al*. (2003) postulated that OH^- and H^+ are transported across the plasma membrane in the root tips of wheat to maintain rhizosphere pH, and to alter rooting Al species by changing the plasma membrane charge positively and reject external Al. For example, Wang *et al*. (2006) found that an Al-induced increase in rhizosphere pH occurs in Al-tolerant wheat cultivar, *Atlas 66,* compared to Al-sensitive wheat cultivar, *Brevor.* They conducted a solution culture experiment under a controlled environment condition for a period of 14 days. They explained that Al-induced organic acid anions exude to the rhizosphere, which made wheat root tips positively charged. Then the root tips can exclude Al^{3+} and have an attraction for OH^- and thus tolerate Al. On the contrary, the cultivar Brevor does not. This difference may relate to their genotypic tolerance to Al.

Tissue Tolerance

There is evidence that Al tolerance is associated with plant tissue tolerance to Al. Some plant species that can accumulate Al to high levels in the shoot appear to be the mechanisms of internal Al detoxification (Kochian *et al.* 2004). For example, buckwheat accumulates Al as high as 15000 mg kg^{-1} in leaves when grown on an acid soil (Ma 2000). Likewise, Silva *et al.* (2010) found that the Al-tolerant wheat genotype, *Barbela* 7/72, has the ability to accumulate more Al in the shoots than the Al-sensitive wheat genotype, *Anahuac*. Similarly, Zhang and Taylor (1988) reported that Al-tolerant wheat cultivars accumulate more Al in its root than Al-sensitive wheat cultivar.

Rincon and Gonzales (1992) stated that part of the mechanisms for plant tissue Al tolerance in wheat is metabolism-dependent. Poschenrieder *et al.* (2008) speculated that the accumulation of Al in shoot occurs in cell wall or in leaf vacuoles. Likewise, Haridasan *et al.* (1986) suggested that high shoot Al accumulation implies xylem transport of soluble Al complexes and the accumulation of Al in the shoot apoplast. This accumulation of the toxic Al ions in the individual cells accompanied by their disintegration may allow the surrounding tissue to survive under Al-stress conditions (Ciamporova 2002).

Role of Apoplast in Al Tolerance

Cell walls and intercellular spaces, the apoplast, are the first compartments of the root that contact with the potentially toxic Al species present in the soil solution (Poschenrieder *et al*. 2008). Many studies have shown that most of the Al that accumulates in roots corresponds to Al in this apoplastic space (Heim *et al.* 1999). This root apoplast plays a major role both in perception of Al toxicity and expression of Al tolerance mechanism (Horst 1995). Al accumulates predominantly in the root apoplast where it binds to the pectin matrix of the cell wall with its negative charges (Schmohl and Horst 2002). This suggests that the strong bindings of Al to the pectic matrix of the cell wall that is not desorbable by 50 mM $BaCl_2$ is the main factor for Al tolerance (Wang *et al*. 2004). Likewise, Eticha *et al*. (2005) found that differences in cell wall pectin and its degree of methylation contribute to genotypic differences in Al tolerance in maize in addition to the release of organic acid anions discussed above. In addition, Horst *et al*. (2010) recently speculated that the modification of the binding properties of the root apoplast contributes to Al tolerance.

Role of P on Al Tolerance Mechanisms

As discussed above, P forms insoluble compounds with soluble Al. Thus, application of P to acid soils reduces the availability of extractable Al. Furthermore, P may improve plant Al tolerance by alleviating Al toxicity in the plant.

P and Al Reactions in Acid Soils

The most common Al and P reaction in acid soils is precipitation (Iyamuremye and Dick 1996). The Al and P react within acid soil solution and precipitate as insoluble Al-phosphate (Wright 1989), thus reducing the bio-availability of Al in soil solution. This precipitation process is prominent when excess Al is available in acid soil (Gallardo *et al*. 1995). Therefore, the precipitation and formation of a non-toxic Al-P complex within the soil solution results in the reduction of extractable Al in acid soil (Nakagawa *et al.* 2003).

Role of P on Al Tolerance Mechanisms in Plants

Although P nutrition plays a major role in Al-tolerance, the mechanisms are still poorly understood. Several mechanisms exist that enable plants to tolerate Al in the presence of P. These include utilization of P as a nutrient, immobilization of Al by P in the root tissue, complexation and precipitation of Al by P in the root and Al-P interactions in the root apoplast.

Plants enhance their ability to acquire P when they suffer Al toxicity (Akinrinde *et al.* 2006). Plants develop mechanisms to utilize P efficiently and to detoxify Al simultaneously to survive in Al-toxic acid soils. Plants that survive under Al-stress conditions appear to stimulate P uptake, enabling survival in Al-toxic acid soil (Watanabe and Osaki 2001).

The P nutrition may affect tolerance to Al through changes in cation-anion balance within plants (McLaughlin and James 1991). The nutrient uptake pattern,

that is, total cation and anion uptake was influenced by both Al and P. Excess cation uptake tended to increase with decreasing P supply and at a high Al stress. This causes Al-induced changes in root morphology and rises to higher root proton efflux density that may make plans tolerant to Al (Tan and Keltjens 1990).

Immobilization of Al by P within the root tissue is one of the Al-tolerance mechanisms in plants. Zheng *et al.* (2005) found that the concentrations of P and Al in the roots of Al-tolerant cultivar, *Jiangxi*, were higher than the Al-sensitive, *Shanxi* cultivar. They also found that more Al had localized in the cell walls of *Jiangxi* than the *Shanxi* cultivar. They suggested that immobilization of Al in the root with P may contribute to the genotypic differences in buckwheat. Similarly, Gaume *et al.* (2001) stated that P deficiency symptoms in plants suffering from Al toxicity are due to the immobilization of Al by P on or within the root tissue.

Insoluble Al-P precipitates can accumulate on the root surface and in the cell wall, or in the root cells and are generally not toxic to plants (Taylor 1991). Jemo *et al.* (2007) found that Al-tolerant cowpea genotype, IT89KD-319 maintained higher P uptake in the presence of Al relative to the Al-sensitive genotype, IT89KD-349. Similarly, IT89KD-319 accumulates higher Al than IT89KD-349. They also found that Al accumulation in roots of IT89KD-319 significantly increased with P application. They conducted a solution-culture experiment under controlled climatic conditions for a period of 8 days. They postulated that Al, in the presence of P, forms insoluble complexes (Al-P) precipitating and accumulating at the surface or inside plants root, thus reducing Al toxicity. Zheng *et al.* (2005) also speculated that the formation of Al-P complexes in the cell wall, and especially in soluble compounds like $AlPO_4$, might be helpful in retarding the uptake of Al into the cytosol. Thus, P may be involved in Al-tolerance mechanisms through precipitation and formation of Al-P complex in roots.

The tolerance of Al may not only occur through Al complexation and possible precipitation of Al in the roots, but also through Al-P interactions in the root apoplast or even at the root cell plasma membrane. An earlier study conducted by McCormick and Borden (1972) found that Al-PO_4 reaction occurs at the root surface. They also suggested that adsorption reaction between Al and P occurred along the cell wall or membrane. In addition, Zheng *et al*. (2005) also speculated that Al and P interaction may occur in the root apoplast of Al-tolerant buckwheat (Zheng *et al*. 2005).

CONCLUDING REMARKS AND RESEARCH GAPS

Soil acidity is characterized by low pH, Al toxicity, Mn toxicity and P deficiency. At low pH, Al becomes solubilized in soil solution and Al^{3+} activity is high. This Al^{3+} primarily decreases root proliferation of plants that result in poor root systems and less nutrient uptake than plants grown without Al-toxic condition. This decreases final yields for the plants grown in Al-toxic acid soil. Therefore, introduction of acid-tolerant crops is necessary for optimal crop production in acid soils.

Plant genotypic characteristics are involved in plant tolerance to Al (Kochian *et. al.* 2004). There are generally three classes of Al tolerance mechanisms such as exudation of organic acid anions, increase in rhizosphere pH and plant tissue tolerance to Al. Phosphorous appears to play a role in improving Al-tolerance in plants. However, little is known about the mechanisms by which P alleviates Al toxicity. Furthermore, the majority of previous studies have used solution culture; this review urges soil-grown plants and near-isogenic lines to study the interactions between P and Al in an attempt to improve understanding of Al-tolerance in plants.

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