

Aluminum Toxicity and Tolerance Mechanism in Cereals and Legumes - A Review

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Abstract Aluminum (Al), the third most abundant element overall, after silicon and oxygen, is found virtually in all food, air, soil and water. Under acidic conditions, Al is solubilized into $[\text{Al}(\text{H}_2\text{O})_6]^{3+}$, which is highly toxic to many plant species. Present paper reviewed Al toxicity and tolerance mechanism in agricultural plants with special reference to cereals and legumes. Even at micromolar concentrations, cell division in the root tip meristem in sensitive plants is quickly inhibited by Al^{3+} . Expressing the species-dependent manner of response, growth enhancement at low concentrations of Al^{3+} is also reported from some plants such as soybean. Plasma membrane can be identified as the primary target of Al toxicity, where production of higher reactive oxygen species and higher fatty acid peroxidation has been observed due to alteration of plasma membrane integrity. Though, toxicity and the mechanisms attributed to Al-resistance are extremely complex phenomena, exclusion is widely accepted as the key mechanism involved in detoxifying Al^{3+} . Exudation of chelating ligands, formation of pH barrier at the rhizosphere or at root apoplast, cell wall immobilization, selective permeability of the plasma membrane, and Al efflux have been proposed as the possible mechanisms for Al exclusion. Al-induced exudation in cereals and legumes is dominated by citrate, malate, and oxalate in varying degrees depending on the species and/or cultivar. Apart from sensitive cultivars, moderately tolerant or tolerant cultivars can also be distinguished from various kinds of cereals and legumes. However, reliable techniques for screening such resistant genotypes have not been developed for any economically important crops.

Keywords exudation · ligands · metabolism · tolerance · toxicity

Aluminum toxicity

In terms of relative abundance, aluminum (Al) is the third element after oxygen and silicon and the most abundant metal present in the earth's crust (Ma and Furukawa, 2003; Matsumoto and Motoda, 2012). It belongs to the non-essential category of metals, thus does not exert any known function in plant metabolism (Wang and Kao, 2004). However, the metal is considered to be a major growth-limiting factor particularly in acid soils (pH <5.0), which are estimated to be approximately 30–40% of arable lands in the world (Lilienfein et al., 2003). Depending on pH, Al exists in a number of different forms in the soil (Wang et al., 2006). Under acidic conditions, Al is solubilized into $[\text{Al}(\text{H}_2\text{O})_6]^{3+}$, generally referred to as Al^{3+} , which is highly toxic to many plant species (Éva Darkó et al., 2004). Despite the fact that many plants find it difficult to withstand against the Al toxicity, its most common forms i.e. oxides and aluminosilicates are harmless to plants (Ma and Furukawa, 2003; Wang and Kao, 2004).

In sensitive plants, cell division in the root tip meristem is quickly inhibited by Al^{3+} , thus root elongation is immediately affected (Gunsé et al., 2003; Doncheva et al., 2005; Meda and Furlani, 2005). This occurs because the apex of the root (root cap, meristem, and elongation zone) could accumulate comparatively higher amount of Al^{3+} than the other parts of the root (Zheng and Yang, 2005). Increased rigidity of the double helix of DNA caused by accumulated Al^{3+} results in poor cell division in root tip meristem (Meriga et al., 2010). In many plants, inhibition of root elongation has been reported within a few minutes even at micromolar concentrations of Al^{3+} (Matsumoto and Motoda, 2012), though enhanced root activity at low concentrations of Al^{3+} has also been reported in soybean (Yu et al., 2011). This might be due to Al-induced increasing activity of the apical meristem. In

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some cases, increased susceptibility to drought stress, lodging, and nutrient deficiencies are also reported from affected plants (Sun et al., 2010). The early signs of Al toxicity could be observed on the cells of the epidermis or outer cortex, which may be due to direct interaction of Al^{3+} with the plasma membrane (Barceló and Poschenrieder, 2002). Based on the results of several investigations, plasma membrane can be identified as the primary target of Al toxicity (Gunsé et al., 2003; Ahn and Matsumoto, 2006; Silva, 2012). According to Peixoto et al. (2001), production of higher reactive oxygen species and higher fatty acid peroxidation of the plasma membrane in Al-sensitive cultivars is due to deteriorated performance of affected plasma membrane. Therefore, growth reduction and alteration of plasma membrane integrity are the immediate consequences of binding of Al^{3+} to cell membrane components. Discovering another feature of Al toxicity, Sun et al. (2007; 2010) have reported that ethylene and auxin are also involved in inhibition of root elongation under Al stress. In summarizing, Tables 1 and 2 can be considered as the possible consequences of Al toxicity, which may vary depending on the species and the cultivar.

- Inhibition of cell division, root elongation and plant growth (Doncheva et al., 2005)
- Alteration of nutrient availability in the rhizosphere (Poschenrieder et al., 2008)
- Accumulation of certain metabolites (Peixoto et al., 2001; Amenós et al., 2009)
- Behavioral changes in many key enzymes (Zhou et al., 2009)
- Low P availability which can result in decreased photosynthetic efficiency and low dry matter production (Chaudhary et al., 2008)
- Increased susceptibility to drought stress, lodging, and nutrient deficiencies (Sun et al., 2010)
- High affinity of cationic Al for plant cell walls, membranes and metabolites is known to be the plants' quick response to Al toxicity (Kochian et al., 2005; Hiradate et al., 2007), which is often assessed with the use of different plant indicators such as inhibition of cell division and cell expansion (Ma et al., 2004; Horst et al., 2010), fine root development (Zobel and Kinraide, 2007), root elongation (Rangel et al., 2009), alteration of nutrient acquisition processes, and cell homeostasis (Purcino et al., 2003; Garzon et al., 2011), as well as changes in cytosolic Ca^{2+} , pH and K^+ levels, and plasma membrane polarization (Vanguelova et al., 2007; Bose et al., 2010), accumulation of callose (Hirano and Brunner, 2006), Al specific tissue staining (Tolrà et al., 2005), and lowering of species abundance (Poozesh et al., 2007).

Sensitivity and Tolerance

Al-sensitive and Al-resistant species/cultivars have been widely investigated and several studies revealed that Al phytotoxicity and the mechanisms attributed to Al-resistance are extremely complex

phenomena (Matsumoto, 2000; Ciamporová, 2002; Éva Darkó et al., 2004). In mitigating the adverse impacts of Al toxicity, plants use different strategies, of which exclusion is the widely accepted mechanism (Delhaize et al., 2007; Garzon et al., 2011). Exclusion is often proceeded with one or combination of following processes; exudation of chelating ligands, formation of pH barrier at the rhizosphere or at root apoplast, cell wall immobilization, selective permeability of the plasma membrane, and Al efflux (Éva Darkó et al., 2004; Wang et al., 2006; Delhaize et al., 2007; Tolra et al., 2009).

Among the above, exclusion of toxic Al^{3+} through chelating ligands is, however, the dominant detoxification mechanism for many plant species (Poschenrieder et al., 2005; Maron et al., 2010). In fulfilling this, organic acids such as citrate, malate, and oxalate are reported to be exuded at the rhizosphere and the apoplast (Ryan et al., 2001; Poschenrieder et al., 2005). In fact, exudation of malate, citrate and/or oxalate by root tips is recognized to be the key factor in Al-tolerance of many species due to their high affinity for binding of Al^{3+} (Kochian et al., 2005; Ryan et al., 2011). Elevation of pH at the surrounding environment is considered to be one of the other tolerance mechanisms, because high pH reduces the Al solubility, which leads the formation of less-toxic Al species, such as Al-hydroxides and Al-phosphates (Wang et al., 2006). Exudation of organic acids from roots is also encouraged by elevation of pH at rhizosphere. However, Garzon et al. (2011) elaborating their findings of the experiment carried out with two maize varieties reported that neither rhizosphere pH changes nor Al-tolerance were clearly related to Al-induced changes in exudation of organic acids into the rhizosphere. Formation of stable complex with ionic Al is known for some of these organic acids, thus, can prevent binding of Al^{3+} with extra- and intracellular substances of the root (Li et al., 2000). Chelation of Al^{3+} by other forms of ligands in the cytosol (Ma et al., 2001), Al compartmentation in the vacuole, and several other possible Al^{3+} protective mechanisms are also found in the literature (Éva Darkó et al., 2004; Delhaize et al., 2012).

The responses of plants to Al toxicity are highly variable within the species; more importantly, responses from different genotypes of a same species can also vary (Smith et al., 2011). Investigations on the toxicity and resistance mechanisms have often been performed taking physiological and genetic basis of resistance into consideration (Kochian et al., 2005; Godbold and Brunner, 2007). However, quantitative data needed to assess the magnitude of the physiological damage are still found to be scarce (Ruf and Brunner, 2003; Nagy et al., 2004; Hirano and Brunner, 2006; Vanguelova et al., 2007). Despite the fact that substantial attention is needed to be paid on the recovery mechanism from Al-induced injuries, information on the rehabilitation process is also lacking (Kikui et al., 2007; Motoda et al., 2010; 2011). In this context, Matsumoto and Motoda (2012), in reviewing Al toxicity recovery processes in root apices, have reported that at elevated concentrations of Al^{3+} , recovery is hardly noticeable, because root elongation stops completely, causing plants to begin dying. According to

Table 1 Varietal differences in three cereal crops in response to Al toxicity

Crop	Var./Culti.	Symptom/s	References
Maize (<i>Zea mays</i> L.)	Sikuani (tolerant)	No inhibition of root elongation No effects of Al on cytoplasmic Ca ²⁺ Increased vacuolar nitrate concentration Decreased vacuolar malate concentration	Garzon et al. (2011)
	Bakero (sensitive)	Significant inhibition of root elongation Decreased cytoplasmic Ca ²⁺ in root tips Increased vacuolar nitrate concentration Increased vacuolar malate concentration	
	ATP SR Yellow (tolerant)	Higher root elongation Less callose production	Gunsé et al. (2000)
	HS 701 B (sensitive)	Poor root elongation More callose production	
	Cateto (tolerant)	No inhibition of root elongation Roots accumulations of caffeic acid, catechol and catechin are high	Tolra et al. (2009)
	HS16 x 36 (sensitive)	Significant inhibition of root elongation Roots accumulations of caffeic acid, catechol and catechin are poor	
Wheat (<i>Triticum aestivum</i> L.)	Atlas 66 (tolerant)	Enhanced exudation of malic and citric acids High rhizosphere pH	Wang et al. (2006)
	Brevor (sensitive)	Accumulation of more Al in roots No exudation of organic acids Marked inhibition of root elongation	
	Scout 66 (sensitive)	Severe reduction in cellulose synthesis Marked inhibition of root elongation	Teraoka et al. (2002)
Rice (<i>Oryza sativa</i> L.)	Xiushui 132 (tolerant)	Slight growth inhibition Reduction in chlorophyll content Increased proline and malonaldehyde contents Increased peroxidase and superoxide dismutase activities	Guo et al. (2012)
	Yongyou 8 (sensitive)	Severe growth inhibition Severe reduction in chlorophyll content Significant increased in proline and malonaldehyde contents Significant increased in peroxidase and superoxide dismutase activities	
	Suraksha (tolerant)	Lesser reduction in root and shoot length	Meriga et al. (2010)
	Vikas (sensitive)	Higher reduction in root and shoot length Increased lipid peroxidation and higher activity of SOD and peroxidase	

Matsumoto and Motoda (2012), recovery and exudation of organic acids are of steps connected to each other. Exudation of organic acids begins with Al-induced stress. Recovery of injured roots begins to appear as a consequence of toxicity reduction by means of chelation. Once recovered, re-activated roots encounter toxic Al³⁺, which then forces the re-commencement of organic acids exudation. Under certain environmental conditions, inhibition of root elongation and the recovery process come into act simultaneously or may be as repeated steps, one following the other.

Cereals and Legumes

Cereals, belong to family Poaceae, are economically the most important crops in the world, because they are the staple food sources in many nations (León-Ruiz et al., 2011). Due to widespread distribution and the diversified genetic base, cereals can now be found in all continents, regardless of latitude, soil, and climate. Cultivation of cereals in different scales under different cropping systems is found almost everywhere, in particular, with the introduction of genetically modified and enhanced varieties of

Table 2 Varietal differences in three legume crops in response to Al toxicity

Crop	Var./Culti.	Symptom/s	References
Soybean (<i>G. max</i> L.)	Zhechun 2 (tolerant)	Severe reduction in root length and volume Decreased root activity Increased plasma membrane permeability Disorganized cytoplasm of root tip cells	Yu et al. (2011)
	Zhechun 3 (sensitive)	Severe reduction in root length and volume Marked decreased in root activity Marked increased in plasma membrane permeability Disorganized cytoplasm of root tip cells	
	Zhechun 2 (tolerant)	Increased inhibition of root elongation Dose-dependent pectin methylesterase activity in the root tip	Cai et al. (2011)
	Huachun 18 (sensitive)	Significantly increased inhibition of root elongation Dose-independent pectin methylesterase activity in the root tip	
Pea (<i>P. sativum</i> L.)	Rachana (tolerant)	Significantly reduced seed germination and seedling growth Increased lipid peroxidation High content of superoxide dismutase, catalase, ascorbate peroxidase, guaiacol peroxidase, ascorbic acid and non protein thiol in root tips	Singh et al. (2011)
	Arkil (sensitive)	Significantly reduced seed germination and seedling growth Significantly increased lipid peroxidation Low content of superoxide dismutase, catalase, ascorbate peroxidase, guaiacol peroxidase, ascorbic acid and non protein thiol in root tips	
Common bean (<i>P. vulgaris</i> L.)	Preto and Carioca (tolerant)	Slight inhibition of root elongation	Gunsé et al. (2003)
	Contender and Superba (sensitive)	Severe inhibition of root elongation	
	Andean (tolerant)	Slight reductions in the elongation rate of the primary roots, total root length and specific root length	Blair et al. (2009)
	Mesoamerican (sensitive)	Higher reductions in the elongation rate of the primary roots, total root length and specific root length	
	Quimbaya (tolerant)	Severe inhibition of root elongation with substantial recovery High content of cell wall pectin	Rangel et al. (2009)
	VAX-1 (sensitive)	Severe inhibition of root elongation with no recovery Low content of cell wall pectin	

specific species and better-adapted hybrids (Damialis and Konstantinou, 2011). Recent study showed that over the first decade of the 21st century, leading cereal crops (maize, wheat, and rice) have contributed 80–90% of world grain production, and almost 40% of calorie intake of the world population (Van Wyk, 2005). Cereals are the only group of crops with cultivation that exceeds 20% of global land area or 61% of the total cultivated land. Wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), rice (*Oryza sativa* L.), barley (*Hordeum* spp.), millet (Small-grained cereals that include a large number of different botanical species), and rye (*Secale cereal* L.) are considered to be dominant cereal crops.

Legumes (family-Fabaceae) are the third largest family of angiosperms after Orchidaceae and Asteraceae. There are about

20,000 species belong to family Fabaceae (Doyle and Luckow, 2003), and the family has a significant agricultural importance, because some key legumes such as soybean (*Glycine max* L.), pea (*Pisum sativum* L.), common bean (*Phaseolus vulgaris* L.), mungbean (*Vigna radiate* L.), peanut (*Arachis hypogaeae* L.), pigeon pea (*Cajanus cajan* L.), and cowpea (*Vigna unguiculata* L.) are cultivated on 12–15% of the arable land throughout the world (Graham and Vance, 2003). Legumes also bring remarkable additional benefits, in particular their capacity to fix atmospheric nitrogen through mutualistic interactions with rhizobial soil bacteria. As to how cereals and legumes response to Al toxicity is discussed below with major emphasis given to the key economically important species.

Maize (*Z. mays* L.)

Maize, a widely known food crop, is gaining worldwide attention as a source of biofuel as well. When exposed to Al, responses differ among different maize varieties, thus sensitive and moderately tolerant varieties can be distinguished (Meda and Furlani, 2005). Exclusion as the dominant defense mechanism against the Al toxicity in maize is often discussed. Kidd et al. (2001) reported that as in many other crops, Al-resistance in maize (Var. Sikuan) is attributed to exudation of strong Al chelating agents such as malate and citrate. However, Garzon et al. (2011) reported that Al-induced enhancement of root exudation of citrate was hardly detected in maize (Var. Sikuan and Bakero). Based on their findings, where a weak correlation between organic acid exudation and Al-tolerance has been observed, other contributors may also come into play a substantial role in Al-tolerance of maize as reported previously by Piñeros et al. (2005) and Tolra et al. (2009). Tolra et al. (2009) investigated Al-induced pattern of phenolic compounds of two maize varieties and concluded that, in addition to Al exclusion from the roots, higher contents of phenolic substances with a high antioxidant and antiradical activities also contribute to Al-tolerance in maize. Liu et al. (2009) also confirmed the Al-induced root tip exudation of flavonoid type phenolics in maize. However, due to high affinity for H^+ , phenolics gain lower recognition compared to organic acids in acidic soils. Kidd et al. (2001) reported that Al-induced exudation of flavonoid-type phenolics could also be contributed to silicon-mediated amelioration of Al toxicity in maize. However, even in highly tolerant varieties, Al manages to gain access into the cells as observed by Gaume et al. (2001). Therefore, once Al^{3+} has managed to enter the symplast, internal detoxification by means of chelation and/or sequestration to less sensitive compartments is equally important (Tolra et al., 2005; Klug and Horst, 2010). As reported by Tolra et al. (2009), compounds bearing catecholate moieties are also strong ligands for Al^{3+} . Detoxification of Al^{3+} , which has already surpassed the exclusion barrier, is done by these catecholate moieties. Poschenrieder et al. (2005) used callose and haematoxylin staining as indicators for Al toxicity and reported that 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) by binding Al^{3+} can protect the root tips of sensitive maize plants against Al toxicity *in vitro*. Root growth inhibition similar to many other crop species has also been reported in maize (Kochian, 2004; Li et al., 2004). As recorded in several studies, Al^{3+} possess the ability to bind to carboxyl and phosphoryl groups of the cell wall and the plasma membrane, thus specific changes in the lipid composition of the plasma membrane could also contribute in maintaining root growth under Al stress (da Silva et al., 2006). In addition to root exudation, contribution from phenolic compounds to the defense mechanism in maize is considered to be encouraging findings. Though reliable screening techniques are yet to be developed, reports available on tolerant cultivars are also important.

Wheat (*T. aestivum* L.)

In the case of Wheat, a leading staple food crop in the world, Al-induced inhibition of root elongation is widely known (Teraoka et al., 2002; Zakir et al., 2003). The stress can alter the ultrastructure of root cells (Xiao et al., 2003; Li et al., 2006). Alteration of the physical dimensions of the root apex in wheat has come to appear due to shortening of the root elongation zone while increasing in the diameter of the cells on the outer cortex, which ultimately results in ruptures of the epidermis (Motoda et al., 2010). Structural alterations in similar nature have also been reported in maize. As reported by Matsumoto and Motoda (2012), the rigidity of the cell wall increases with the inhibition of root elongation under Al stress. Among the defense mechanisms, concentration-dependent efflux of malate from root tips is reported in wheat also (Zhang et al., 2001), though capacity to release malate varies with the cultivar. Osawa and Matsumoto (2001) have suggested that protein phosphorylation is involved in the Al-responsive malate efflux in the wheat root apex. Darkó et al. (2004) investigated the formation of reactive oxygen species induced by Al stress in sensitive genotype and in tolerant lines developed by *in vitro* microspore selection. The roots of tolerant plants were found to accumulate less Al^{3+} and reactive oxygen species than sensitive plants. They concluded that among the superoxide dismutase, ascorbate peroxidase (APX), catalase (Cat), and glutathione-S-transferase (GST) enzymes induced by Al stress, catalase and GST may play an important role in the detoxification of reactive oxygen species in Al-tolerant wheat plants. Two wheat cultivars, Darab (Al-sensitive) and Maroon (Al-tolerant) grown on hydroponic solution were used in assessing growth of wheat seedlings under Al stress (Nasr et al., 2011). Results revealed that, for fresh weight of root, fresh weight of shoot, dry weight of shoot and length of root, Al concentrations and their interaction with cultivar were highly significant. They have further reported that application of malate or citrate is effective in diluting the Al toxicity in wheat seedlings. Among cereals, wheat has been employed extensively in exploring many aspects related to Al toxicity, enabling genetic engineering to engage in producing wheat cultivars with greater resistance. Therefore, continuous production of wheat even in acidic soils would be ensured in due course.

Rice (*O. sativa* L.)

Rice is basically considered to be an Al-tolerant crop, although the response is largely dependent upon the cultivar of concern (Guo et al., 2012). Meriga et al. (2010) investigated the effect of Al on seedlings of two rice cultivars (Vikas and Suraksha) under different pH regimes and reported that as pH reduces, reduction in plant growth, accumulation of Al^{3+} in roots, lipid peroxidation, and activity of superoxide dismutase (SOD) and peroxidase were

more pronounced in Vikas, the sensitive cultivar. Furthermore, they have observed an increasing resistant with the age of the seedlings even in sensitive cultivar. Increased activity of SOD, one of the most effective anti-oxidative enzymes, which prevents cellular damage, has been reported previously (Sharma and Dubey, 2007) also in rice seedlings in response to Al toxicity. Hydroponic experiments conducted by Guo et al. (2012) to assess the Al toxicity and P deficiency in two rice genotypes (Yongyou 8 and Xiushui 132) also revealed growth inhibition along with reduced chlorophyll content, increased proline and malonaldehyde contents, and increased peroxidase and superoxide dismutase activities in roots. Their findings can of course be considered as re-confirmation of previous findings (Ismail, 2005; Sarker and Karmoker, 2011) with some other crops such as mungbean, carrot, radish, and lentil seedlings. Based on the results of higher proline content in Al-tolerant genotype over the sensitive cultivar, Guo et al. (2012) suggested that the difference between the cultivars in response to Al toxicity could be assessed based on proline content. Well documented Al-induced inhibition of root elongation is also reported in rice (Kikui et al., 2005). Kuo and Kao (2003) and Tewari et al. (2004) reported an increased malonaldehyde (MDA) content in rice seedlings under Al and P starvation stress. Confirming these previous reports, Guo et al. (2012) observed similar response pattern indicating that lipid peroxidation occurred as a result of reactive oxygen species (ROS) formation induced by high level Al toxicity. Reports with tolerant cultivars draw key attention in the field of Al toxicity to rice. Distinguishing such cultivars based on higher proline content is further encouraging.

Soybean (*G max L.*)

Soybean, an important source of high quality but inexpensive protein (40%) and oil (20%) is grown in over 90 million ha throughout the world. Yu et al. (2011) studied the effect of Al on the root growth and cell ultrastructure of two soybean genotypes (Zhechun 2 and 3 respectively Al-resistant and -sensitive) and observed significant reduction in root biomass at higher concentration (90 mg/L) of Al³⁺ with a slight difference between two genotypes. However, root activity of sensitive variety was significantly lower than that of resistant. Furthermore, they have observed alterations in the cellular organization, mitochondria, vacuoles, and nuclei physiology with marked varietal differences as well as reduced root elongation and development when Al concentration in the solution was increased. Confirming the earlier findings (Kollmeier et al., 2000), root tip and prolongation zone have been identified by Yu et al. (2011) also as the locations, which underwent sever difficulties resulting immediate toxicity symptoms. Most importantly, they have stressed that under low concentrations (depending on the variety of soybean, 10–30 mg/L), Al could enhance root activity, maintain high respiration metabolism, and strengthen the absorption abilities of water and minerals, which is in agreement with Li et al. (2004). Growth enhancement in legumes under low

pH is of particular important, because the growth of rhizobia with which soybean is known to have deep symbiotic relationship could be badly affected by the acidic environment. Rhizobial growth is considered to be optimum at pH between 6.0 and 7.0 (Hungria and Vargas, 2000) and as of previous reports (Ying et al., 2005), number of nitrogen-fixing bacteria also decreases with the increase of Al concentration. In addition to the well known toxicity response, growth enhancement at low concentrations of Al³⁺, alterations in the cellular organization and potential threat to the associated bacteria etc., could be considered as important findings of the researches with Al toxicity to soybean.

Pea (*P. sativum L.*)

Pea, a source of high quality protein in human diet and animal feed, is grown for its seeds. Matsumoto and Motoda (2012) elaborating the process of recovery form of pea roots exposed to Al and reported that injuries come into appear more intensively in closely located cells in the region of Al uptake, where unique structural alterations begin to appear quickly. According to them, it takes only a few seconds to reach the metal to the cell wall of epidermal cells, whereas time taken for reaching other root tissues was about one hour. Therefore, starting from epidermal cells, Al-induced injuries could be observed in outer cortex, middle cortex, inner cortex and style as reported previously by Ciamporova (2002). Singh et al. (2011) studied the morphological and biochemical characteristics of two pea varieties (Arkil and Rachana) under Al stress in soil and observed remarkably reduced seed germination and seedling growth in both the varieties. Furthermore, Rachana, the tolerant variety increased the activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaicol peroxidase (GPX), ascorbic acid (AsA) and non protein thiol (NPSH) markedly compared to those of Arkil, the sensitive variety. Enhanced production of reactive oxygen species, a common feature of Al toxicity has been reported in Pea also. As of the reports so far published, moderately tolerant cultivars such as Rachana have been identified and available for further studies.

Common bean (*P. vulgaris L.*)

Common bean is considered to be the second important food legume, in particular, in developing countries. Investigations conducted with soybean, pea and common bean have been used, in part, to answer the much debated question; whether the initial toxicity display of Al is on inhibition of cell elongation or cell division. It is the present understanding that in legumes, cell elongation and cell division are both inhibited; however, responses due to inhibition of cell division are largely irreversible (Barcelo and Pochenrieder, 2002). Rangel et al. (2005) observed a positive correlation between Al-induced callose formation and inhibition of root elongation and Al contents in the root apices of common

bean. Though some genotypes such as Andean and Mesoamerican have been found to display greater performance under acidic soil conditions, Rangel et al. (2005) suggested having more investigations in order to understand genotypic differences in response to Al toxicity and to develop quick screening techniques for Al resistance. Not like for other key legume species, literature on Al toxicity in common bean is still lacking in many aspects. Therefore, further investigations are needed, in particular, to distinguish varietal differences in response to Al toxicity.

Conclusion

Though the focused areas of this review have been investigated over the years, contradictory reports such as inhibition, as well as growth enhancement at low concentration of Al^{3+} are often found. This might be due to species-dependent manner of response and/or differences in experimental material and methodology used. In addition, the vast majority of the investigations have been aimed at elucidating the effect of Al on a particular parameter of the plant; thus comprehensive understanding on as to how Al affects overall performance of plants has yet to be elucidated. It is necessary to conduct, more studies under field conditions to understand the process of recovery from Al toxicity, because findings of such investigations would have undeniable practical significance. Due to little attention so far paid on the recovery process, development of appropriate agronomic practices to ensure speedy recovery from Al toxicity is also found to be lacking. Development of reliable screening techniques for resistant genotypes would be another area to be worked on. However, taking the species-dependent nature of response into consideration, a series of researches are needed to identify dependable parameters for use in such screening methods.

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