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REVIEW ARTICLE

Effect of Aluminum Toxicity and Genetic Control Mechanisms in Crops: A Review

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ABSTRACT

Aluminum (Al) toxicity is one of the major factors constraining crop production on 67% of the total acid soil area in the world. Al toxicity restricts root growth and affects nutrient and water absorption with resultant stunted growth and reduced grain and biomass yield of crops. Cereals occupy about half of the world's cropland area and, therefore, take a lion share of the global Al toxicity constraint. Al toxicity is more serious in tropical environments, where the soil is highly resistant to improvement by lime application. In addition, in these environments, the use of adequate lime and organic fertilizer sources is constrained by various technological and socioeconomic constraints. Studies on genetic control of Al toxicity are active areas of research for most of the globally important cereals. Development and use of Al-tolerant crop varieties are economically feasible and an environmentally friendly management option that can complement other non-genetic management options. This paper introduces the importance of soil acidity and effect of Al toxicity on plant growth and development and yield.

Key words: Aluminum toxicity, genetic control, soil acidity

INTRODUCTION

Soil acidity is one of the most important factors that affect crop production worldwide. Acid soils (pH <5.5 in surface layer) constitute 3950 million ha or 30% of the world's total ice-free land or about 40% of the arable land. In Africa, 22% or 659 million ha of the total 3.01 billion ha land area has soil acidity problem. Al toxicity is the single most important contributing factor constraining crop production on 67% of the total acid soil area in the world (Eswaran *et al*., 1997). Aluminum is the most abundant metal and the third most common element in the earth's crust (Delhaize and Ryan, 1995; Vitorello *et al*., 2005). In soils, it mostly exists as structural constituent of primary and secondary minerals, especially of the aluminum silicates. Nonetheless, despite its abundance, Al is not known to be used in any living organisms.[1-10]

As the soil gets acidic, the silicon will be leached leaving aluminum in the solid forms as aluminum oxyhydroxides, such as boehmite and gibbsite. These forms release the phytotoxic aluminum species. Al^{+3} also known as Al(H2O)_6^{+3} into the soil solution (Abebe, 2007). Even though there are several forms of aluminum species in the soil, Al^{+3} and monomeric Al-hydroxyl species (AlOH^{+2} and Al(OH)^{2+}) are the most phototoxic ones (Miyasaka *et al*., 2007). The trivalent Al^{+3} is dominant in soil solutions when the soil pH is <5. The most common and immediate toxic effect of Al^{+3} in plants is inhibition of root growth which happens within few hours after exposure to micromolar concentrations of aluminum (Barcelo and Poschenrieder, 2002). Root inhibition could be exhibited on primary and lateral root apexes, and such roots become thick and develop brown color (Vitorello *et al*., 2005; Wang *et al*., 2006; Miyasaka *et al*., 2007). The yield loss associated with Al toxicity varies depending on soil Al saturation, the crop species, and the specific

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variety used. For instance, Al-tolerant maize variety gave 61% higher grain yield than Al-sensitive variety and with lime treatment, the yield increment of 208 and 82% was obtained for Al-sensitive and Al-tolerant varieties of maize, respectively.[11-25]

Applications of lime, manure compost, and use of tolerant crop species or varieties are the most common methods used to overcome the impact of Al toxicity. Nevertheless, in the context of tropical Africa, utilization of lime, manure, and other organic fertilizer sources have their own technical and/or socioeconomic constraints. Lime has been extensively used to ameliorate acid soils of temperate areas. In these areas, soil acidity develops mainly as a consequence of heavy use of chemical fertilizers and environmental pollution (Rao *et al*., 1993). In tropics, several experimental reports also indicate significant yield increment with application of lime (The *et al*., 2006). However, the highly acidic soils of this region have strong buffering capacity against amendment by lime. Such soils demand heavy dose and need deeper incorporation to ameliorate the subsurface acidity.[26-39]

Most of resource poor farmers in the tropics, however, are constrained by unavailability of transport high cost of this bulky dose (Rao *et al*., 1993). In addition, since lime incorporation to the subsoil is hardly possible, even when surface soil is neutralized; difficulty of ameliorating the subsoil restricts root growth of plants to surface soil and makes them vulnerable to drought (Little, 1989; Foy, 1992). Runoff pollution and adverse effects of lime on rotation crops are also other side effects of lime application (Wang *et al*., 2006). The use of organic matter seems an applicable strategy to resource poor farmers of the tropics who cannot afford purchase of large volume of lime and fertilizers. However, regular and high-volume application of manure and compost to the highly acidic soils is limited by competing uses of organic matter sources for fuel, animal feed, and construction (Schlede,1989). On contrary, in the tropics, the use of acid-forming fertilizers on cultivated land and expansion of crop production to forest inhabited areas accelerate development of the soil acidity and Al toxicity.[40-44]

Cereals, the predominant stable food crops of the world population, are cultivated roughly on the half of the world's crop land (Dyson, 1999). By the year 2025, the world's farmers are expected to produce about 3 billion tons cereals to feed the human population of the around 8 billion, and this requires an average world cereal yield of about 4 metric tons per hectare (Dyson, 1999). The current average cereal yields in Africa are below 1 ton/ha (Langyintuo, 2011). The use of tolerant crop varieties is considered to be the best complement to non-genetic management option for combating Al toxicity problem (Rao *et al*., 1993). This paper attempts to review the effect of Al toxicity and genetic control mechanism in crops. Therefore, the objective of the paper was to understand basic information on Al toxicity and genetic control in crops.

LITERATURE REVIEW

Effect of al toxicity on plant growth and development

Effects on leaves

Aluminum toxicity is potential growth liming factor for plants grown in acid soils in many parts of the world (Foy, 1974). The symptoms of aluminum toxicity are not easily identifiable. In plants, the foliar symptoms resemble those of phosphorus (P) deficiency (overall stunting, small, dark green leaves and late maturity, purpling of stems, leaves and leaf veins, yellowing, and death of leaf tips). In some cases, Al toxicity appears as an induced calcium (Ca) deficiency or reduced calcium transport problem (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.), sorghum, and wheat (Clark *et al*., 1981).[45-49]

Effects on roots

Aluminum does not affect the seed germination, but helps in new root development and seedling establishment (Nosko *et al*., 1988). Root growth inhibition was detected 2–4 days after the initiation of seed germination (Bennet *et al*., 1991). Vanpraag and Weissen *et al*. (1985) reported that plant species and ecotypes growing on acid soils had become very resistant to the inhibitory effects of aluminum on root absorption and growth in course time and phonological evolution. The major Al toxicity symptom observed in plants is inhibition of root growth (Bennet *et al*., 1991). The roots exhibit greater signs of cellular damage than other parts of the plant (Rincon and Gonzales, 1992). Al toxicity could be observed in the root system particularly in root tips and in lateral roots; lateral roots become thickened and turn brown (Kinraide, 1985). The root system as a whole is coralloid in appearance with many stubby lateral roots, but lacks fine branching (Foy *et al*., 1978). The toxicity appears to be determined by the availability of certain monomeric species of Al to the plant roots (Bartlett and Reigo, 1972).[50-54]

Losses of photoactive, monomeric Al can occur by polymerization of Al as the pH and the Al concentration rises to make complex formation or chelation with phosphate and organic acids (Bartlett and Reigo, 1972). Kinde *et al*. (1985) demonstrated rapid assay for aluminum phytotoxicity at submicromolar concentration of Al to *Trifolium pratense*. Wagatsuma *et al*. (1987) noted the role of aluminum on root cells of various crops. They reported that the cells of the epidermis and outer of maize (Al sensitive) in the portion approximately 1 cm from the root tip were damaged and the walls of these cells were abnormal and partially detached in barley (a plant highly sensitive to Al); more pronounced abnormality and detachment of the cell walls involved almost the whole cortex, and few cortex cells remained alive in oats (Al tolerant) after 6 days exposure to the Al treatment.

Aluminum was absorbed in large amounts in the tip portion of the root. In the tip portion, the K content decreased with the increase of the Al content, but the calcium content was almost constant. Bennet *et al*. (1985) reported that an anisotropic growth response of cortical cells with 20 h root exposure to Al was associated with the collapse of the conducting tissue of the stele and disintegration of the outer cells of the root.[55-59]

Effect on plant morphology and physiology

Aluminum is one of the most abundant elements in the earth's crust and toxic for many plants when the concentration is >2–3 ppm with a soil pH <5.5 (Balsberg, 1990). A significant correlation between low pH and high Al concentration has also been shown in acidified fresh water, where this metal may reach levels of 0.3–1.6 mM (Dickson, 1978) and cause serious metabolic derangement in some hydrophytes (150). In general, young seedlings are more susceptible to Al than older plants (Thawornwong and Diest, 1974). So far as, physiology is concerned.

Al has been shown to interfere with cell division in plant roots; fix phosphorus in less available forms in the soil and in or on plant roots; decrease root respiration; interfere with certain enzymes governing the deposition of polysaccharides in cell walls; increase cell wall rigidity (cross-linking pectins) and interfere with the uptake, transport and with some essential nutrients (Ca, Mg, K, and P) and water supply to plants (Fleming *et al*., 1974); alters cell wall Donnan free space (450), the plasma membrane transport proteins (Caldwell, 1989); and regulates the activity of many enzymes (Copeland and DeLima, 1995) and metabolic pathway for repair mechanism (Plucinska and Ziegler, 1995). Trim (1985) reported that Al is known to form strong complexes to precipitate nucleic acids. Soileau and Engelstad (1969) and Soileau *et al*. (1969) indicated that chemical factors were more important than physical factors in limiting cotton root growth in an acid (pH 4.4) fragipan soil.[60]

Al becomes soluble or exchangeable and also toxic depending on the soil pH and many other factors including the predominant clay minerals, organic matter levels, concentrations of other cations, anions, and total salts and the plant species (Foy, 1984). Dickson (1978) reported that there was a significant correlation between low pH and high aluminum concentration in fresh water, and metal may reach levels of 0.3–1.6 mM. It also causes serious metabolic derangement in some hydrophytes (Plieth *et al*., 1985). Berggren and Fiskessjo (1987) reported aluminum toxicity in *Allium cepa* with reference to root growth and morphology. Further, Severi (199) analyzed the aluminum toxicity in *Lemna minor* with reference to citrate and cytokinin metabolism. Physiological mechanisms due to Al toxicity have been focused on field crops and other herbaceous plants (Foy *et al*., 1978). Plieth *et al*. (1999) reported that low pH elevation in cytosolic calcium was inhibited by aluminum toxicity. They observed that plant roots responded to external low pH by a sustained elevation in cytosolic free calcium concentration Ca^{+2} (C) in the presence of aluminum. They also suggested that a primary toxic effect of aluminum might impair calcium-mediated plant defense responses against low pH.

Factors affecting Al toxicity

Al toxicity is affected by many factors such as pH, concentration of Al, temperature, and concentration of cations and anions in culture solution. A pH of 5.0 or above will reduce Al solubility (Reid *et al*., 1971), thus reducing Al toxicity. Root elongation depended critically on the concentration of Ca^{+2}, whether in the presence or absence of Al, with at least 0.2 mmol/L Ca^{+2} being essential for optimum growth (Kinraide *et al*., 1985). The concentration of Ca^{+2} greatly influences the Al toxicity at a given pH and Al concentration. As the Ca^{+2} concentration approached 1 mmol/L, the inhibition by 1 micromole/L Al was nearly eliminated (Kinraide *et al*., 1985). Increased concentrations of basic cations in solution of the root rhizosphere, particularly calcium, have been shown to ameliorate Al toxicity (Brady *et al*., 1993). Mg^{+2} at concentration of 0.5 mmol/L can also alleviate Al toxicity as did Ca^{+2} (Kinraide *et al*., 1985). Application of NH_4Cl to a soil with a high exchangeable Al significantly reduced barley seedling emergence, shoot and root weights, spike numbers/m^2, and grain numbers/spike, whereas $NaNO_3$ significantly increased all these parameters. At harvesting, soil analysis showed that NH_4Cl significantly reduced soil pH and increased soil Al and Mn contents and this was confirmed by tissue analysis of shoot and roots (Stange *et al*., 1995). $NH_4^+N^-$ induced release of H^+ from the roots particularly while $NO_3^-N^-$ significantly increased pH by release of OH^- (Borie *et al*., 1994). Adding excess P in nutrient solution will precipitate and detoxify Al (Kinraide *et al*., 1985).

Genetic control of Al tolerance in crop plants

Studies on genetic control of Al toxicity are active areas of research for most of the globally important cereals. In wheat, earlier reports presumed that Al toxicity in wheat is controlled at least by two major loci (Didier *et al*., 1996). The two genes proposed were genes that encode for malate and phosphate exudation to the rhizosphere (Didier *et al*., 1996). A major aluminum tolerance gene in wheat, ALMT1 latter renamed as TaTAALM1, is known to confer an Al-activated efflux of malate from root apices (Sasaki *et al*., 2004). This gene is mapped to chromosome 4DL using "Chinese spring" deletion lines. Absence or loss of this gene resulted in loss of Al tolerance and malate exudation (Raman *et al*., 2005a). Hence, it was suggested that Al tolerance in diverse range of wheat genotypes to be primarily controlled by TaALMT1 located at Alt_{BH} (Raman *et al*., 2005a).

Very recently, with discovery of a new mechanism of Al tolerance that involves efflux of citrate in root apices of Brazilian wheat cultivars, another gene that resides on chromosome 4 BL has been identified (Ryan *et al*., 2009). They also indicated that the citrate efflux is controlled by single gene which could explain 50% of the phenotypic variation in citrate efflux. In addition, Navacode *et al*. (2009) located two major Al tolerance quantitative trait loci (QTL) on chromosome arm 4 DL and 3 BL which could, respectively, explain 49 and 31% of the phenotypic variance present in the population of "Chinese Spring" wheat cultivar. These findings indicated that the trait is controlled by major and minor genes in wheat. In barley, Echart *et al*. (2002) indicated that the F2 generation analyzed with hematoxylin staining followed the Mendel's segregation ratio 3:1 for Al toxicity tolerant to susceptible plants, revealing the fact that the trait is controlled by single dominant gene. It is generally agreed that Al tolerance in barley is conditioned by the *Alp locus* which is located on the long arm of chromosome 4 H. This locus is associated with Al-induced efflux citrate from root apices of tolerant barley varieties (Wang *et al*., 2006). A gene encoding a multidrug and toxic compound extrusion protein is proposed as a candidate gene for Al tolerance in barley (Wang *et al*., 2007). In addition, QTL that could explain 50% of the phenotypic variation are also associated with the same chromosomal location (Jian Feng *et al*., 2004).

Similarly, Raman *et al*. (2005b) identified QTL for root elongation under aluminum stress on 3 H, 4 H, 5 H, and 6 H chromosomal locations. Alike other cereals, aluminum tolerance in rye is effected by efflux of organic acids. Segregation ratio of 3:1 (tolerant to sensitive) was found in three F2 populations analyzed indicating the fact that the trait is controlled by single dominant locus (Matos *et al*., 2005). So far, four independent loci Alt1, Alt2, Alt3, and Alt4 located on chromosome arms 6 RS, 3 RS, 4 RL, and 7 RS, are known to confer aluminum toxicity tolerance in this crop (Matos *et al*., 2007).

Specifically, the Alt4 locus contains cluster of genes homologues to the single copy Al-activated malate transporter (TaALMT1) (Collins *et al*., 2008). Tolerant and sensitive rye genotypes contain five and two genes of the clusters at the locus, respectively. Out of these, two ScALMT1-M39.2 and one ScALMT1-M77 genes are highly expressed in the root tip (Collins *et al*., 2008). In rice, root growth under Al stressed condition is controlled by several QTL genes. Two-three QTLs of largest effect, however, are identified to explain phenotypic variation for Al tolerance (Ma *et al*., 2002a). A recent study identified two genes STAR1 and STAR2 which function as bacterial-type ATP binding cassette transporter to control Al tolerance in rice (Hang *et al*., 2009). The mechanism, however, is not yet clear enough.

CONCLUSION

Aluminum toxicity is an important growth-limiting factor for plants in many acid soils, particularly in pH of 5.0 or below. Aluminum toxicity in plants is often clearly identifiable through morphological and physiological symptoms. Differential tolerances to Al toxicity almost certainly involve differences in the structure and function of roots. Aluminum interferes with cell division in roots, decreases root respiration, and uptake and use of water and nutrients, particularly calcium and phosphorus and metabolic pathway. Other promising approaches to studying metal toxicity in tolerant and sensitive plant genotypes are to determine the metal uptake and transportation in various plant parts, the mechanisms behind the interaction with mineral nutrients, specific genes responsible for tolerance, levels and kinds of organic and amino acids which act as metal chelators and detoxifies, level and forms of enzymes, and changes in root permeabilities to ions and molecules and its mechanisms.

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