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Review article

Aluminium toxicity in plants: a review

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Abstract – Aluminium toxicity and problems concerning tolerance and ecological performance are discussed briefly. Differential tolerance of plant genotypes to aluminium stress is a more promising approach to increase our understanding of aluminium tolerance in plants. Induction of Al tolerance and its characterization are also reviewed. The cytogenetic effects of aluminium on plants are discussed in depth. Efforts have been made to compare the relative sensitivity of various plant species including micro- and macro-flora to aluminium, and uptake and transport of aluminium are taken into account with phytotoxicity and their interactions with nutrients. Present knowledge concerning the physiology and biochemistry of aluminium with regard to phytotoxicity is discussed and offers some ways for increasing the Al tolerance. This review shows the complexity of the toxicity mechanisms of trace elements.

aluminium / phytotoxicity / tolerance / Al stress

Résumé – Toxicité de l'aluminium pour les plantes : mise au point. L'article fait le point sur la toxicité de l'aluminium, la tolérance des plantes à cet élément et leur performances écologiques. La tolérance au stress provoqué par l'aluminium varie d'un génotype de plante à l'autre et cette approche est prometteuse pour améliorer notre compréhension de la tolérance à l'aluminium. L'induction de la tolérance à l'aluminium et sa caractérisation sont également passées en revue. Les effets cytogénétiques de l'aluminium sur les plantes font l'objet d'une discussion approfondie. On compare la sensibilité relative à l'aluminium des diverses espèces de plantes, de la macroflore à la microflore. On traite de l'absorption et du transport de l'aluminium, ainsi que de sa phytotoxicité et de ses interactions avec les nutriments. La connaissance actuelle concernant la physiologie et la biochimie de l'aluminium en relation avec la phytotoxicité est discutée et offre certaines possibilités pour accroître la tolérance à l'aluminium. Cette mise au point montre la complexité des mécanismes liés à la toxicité des éléments traces.

aluminium / phytotoxicité / tolérance / article de synthèse

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1. Introduction

Metals occur naturally in soils which may be beneficial or toxic to the environment. Although excess of metals may produce some common effects on plants in general, there are many cases of specific effects of individual metals on different plants (i.e. both macro- and micro-flora). The biota requires some of these elements in trace quantities but may be sensitive to higher concentration of metal. Metal toxicity in plants has been reported by many workers [29–31, 38, 58–60, 75, 82]. Aluminium (Al) is not regarded as an essential nutrient, but low concentrations can sometimes increase plant growth or induce other desirable effects [61, 69, 75]. Aluminium toxicity is an important growth-limiting factor for plants in acid soils below pH 5.0 but can occur at pH levels as high as 5.5 in minespoils [3, 28, 37, 59, 60, 63, 64, 108, 163]. Generally, Al interferes with cell division in root tips and lateral roots, increases cell wall rigidity by cross linking pectins, reduces DNA replication by increasing the rigidity of the DNA double helix, fixes phosphorous in less available forms in soils and on root surfaces, decreases root respiration, interferes with enzyme activity governing sugar phosphorylation and the deposition of cell wall polysaccharides, and the uptake, transport, and also use of several essential nutrients (Ca, Mg, K, P and Fe) [64]. Excess Al even induces iron (Fe) deficiency symptoms in rice (*Oryza sativa* L.), sorghum and wheat [39, 69, 79]. Al is present in all soils, but Al toxicity is manifested only in acid conditions, in which the phytotoxic form Al^{3+} predominates. Recent progress in the study of toxic metals and their interactions with essential elements has greatly increased our understanding of the mechanism of toxicity at the biochemical level [1]. In this review, the salient features of aluminium toxicity and metabolism of different groups of flora and their interaction with essential elements, differential aluminium tolerance, aluminium uptake and transport, cytogenetic effect and biochemistry of aluminium phytotoxicity are elucidated, and their possible implications in the plant ecosystem are highlighted.

2. Aluminium toxicity

2.1. Effects on leaves

Aluminium toxicity is a potential growth-limiting factor for plants grown in acid soils in many parts of the world [59, 60, 62, 64, 66, 67, 76, 77]. The symptoms of aluminium toxicity are not easily identifiable. In plants, the foliar symptoms resemble those of phosphorous (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 Ca 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 [39, 69, 79].

2.2. Effects on roots

Aluminium does not affect the seed germination but helps in new root development and seedling establishment [146]. Root growth inhibition was detected 2–4 days after the initiation of seed germination [22]. Vanpraag and Weissen [187] reported that plant species and ecotypes growing on acid soils had become very resistant to the inhibitory effects of aluminium on root absorption and growth in course of time and phenological evolution. The major Al toxicity symptom observed in plants is inhibition of root growth [22, 50, 75, 120, 130, 166, 181, 182]. The roots exhibit greater signs of cellular damage than other parts of the plant [162, 192]. Al toxicity could be observed in the root system particularly in root-tips and in lateral roots; lateral roots become thickened and turn brown [115, 163]. The root system as a whole is corraloid in appearance with many stubby lateral roots but lacks fine branching [75]. The toxicity appears to be determined by the availability of certain monomeric species of Al to the plant roots [14, 24]. Losses of phytoactive, monomeric Al can occur by polymerization of Al as the pH and the Al concentrations rise [8, 9, 24] to make complex formation or chelation with phosphate and organic acids [14, 24]. Kinraide et al. [114] demonstrated rapid assay for aluminium phytotoxicity at submicromolar concentrations of Al to *Trifolium pratense*. Wagatsuma et al. [192] noted the role of aluminium on root cells of various crops. They reported that the cells of the epidermis and outer cortex 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. They also reported that in the case of peas, the roots were elongated due to a low level of Al treatment. Aluminium 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 Ca content was almost constant. Bennet et al. [18] reported that an anisotropic growth response of cortical cells with 20-h root exposure to Al were associated with the collapse of the conducting tissue of the stele and disintegration of the outer cells of the root.

2.3. Effects on plant physiology and morphology

Aluminium is one of the most abundant elements in the earth's crust, and toxic for many plants when the concentration is greater than 2–3 ppm with a soil pH < 5.5 [13]. A significant correlation between low pH and high Al concentration has also been shown in acidified freshwater, where this metal may reach levels of 0.3–1.6 mM [51] and cause serious metabolic derangement in some hydrophytes [150]. In general, young seedlings are more susceptible to Al than older plants [184]. So far as physiology is concerned, Al has been shown to: interfere with cell division in plant roots; fix phosphorous 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, P) and water supply to plants [57, 62, 64, 143]; alters cell-wall Donnan free space [45, 105], the plasma membrane [136], membrane transport proteins [34, 180] and regulates the activity of many enzymes [44, 90, 173, 186] and metabolic pathway for repair mechanism [154]. Trim [185] reported that Al is known to form strong complexes to precipitate nucleic acids. Soileau and Engelstad [175] and Soileau et al. [176] indicated that chemical factors were more important than physical factors in limiting cotton root growth in an acid (pH 4.4) fragipan soil. 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 [62, 108]. Dickson [51] reported that there was a significant correlation between low pH and high aluminium concentration in fresh water, and metal may reach levels of 0.3–1.6 mM. It also causes serious metabolic derangement in some hydrophytes [150]. Berggren and Fiskesjo [23] reported aluminium toxicity in *Allium cepa* with reference to root growth and morphology. Further, Severi [169] analyzed the aluminium toxicity in *Lemna minor* with reference to citrate and cytokinin metabolism. Physiological mechanisms due to Al toxicity have been focussed on field crops and other herbaceous plants [75]. Plieth et al. [152] reported that low pH elevation in cytosolic calcium were inhibited by aluminium as a potential mechanism for aluminium 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 aluminium. They also suggested that a primary toxic effect of aluminium might impair calcium-mediated plant defence responses against low pH.

3. Differential aluminium tolerance in plants

3.1. Existence of differential tolerance

The phenomenon of metal tolerance in plants has attracted the interest of plant ecologists and physiologists as well as evolutionary biologists [10]. Development of metal tolerance is one way to reduce the harmful effects of excessive exposure to metal ions [186]. Plant species and varieties vary widely in tolerance to excess Al in the growth medium [59, 60, 72, 121]. Aluminium toxicity and differential Al tolerance in various plant groups were reported in some studies [4, 63, 88, 159, 163, 181]. Differential aluminium tolerance to different wheat cultivars were reported by Foy et al. [73]; Slootmaker [174]; Konazak et al. [121]; Aniol and Kaczkowski [7]; Aniol [5]. Aniol [6] analysed Al tolerance in wheat by breeding. Since tolerance is genetically determined, selection is possible for better Al tolerance in wheat. In several species, these differences are genetically controlled [156]. Closely related genotypes are valuable tools for studying the physiological mechanisms of toxicity or tolerance. Root length in response to Al stress has been used to assess Al tolerance of sorghum genotypes [79, 147], wheat [113], soybean [89], rice [172] and many other temperate legumes [11, 12, 25, 26, 54, 55, 128]. Differential tolerances of *Amaranthus tricolor* to high levels of aluminium in acid soils was reported by Foy and Campbell [70]. Foy [66] tested and screened out ten barley (*Hordeum vulgare* L.) cultivars for Al tolerance by growing them for 25 days in the greenhouse in pots containing acid soil and Al-toxic Tatum subsoil. He also reported that relative shoot dry weights averaged 28.6% for tolerant and 14.1% for sensitive cultivar groups. At pH 4.4, Al concentrations were nearly three times higher in shoots of sensitive cultivars as in those of the tolerant group; these differences were reduced or absent at pH 5.7. Foy [67] also tested fifteen Durum wheat (*Triticum durum* Desf.) cultivars for aluminium tolerance at pH 5.7. Concentrations of aluminium and phosphorous were significantly higher in shoots of sensitive lines as compared to the tolerant ones grown in acid soils. Foy et al. [72] first demonstrated that an Al-tolerant cultivar of *Triticum aestivum* was able to increase pH in nutrient solutions comparatively to an Al-sensitive cultivar when both were tested with or without aluminium. They also demonstrated the effects due to variations of pH of the soil on plant growth. A good relationship between Al and pH of the growth medium was reported in *Triticum aestivum* [56, 68, 69], *Secale cereale* [139, 140]. Taylor and Foy [183] reported the cultivar tolerance, expressed both as the root and shoot tolerance index, was negatively correlated with the negative log of the mean hydrogen ion concentration. Wood et al. [200] concluded that rhizobium multiplication and nodule function were the most susceptible aspect of the symbiotic relationship to excess Al. Moreover, the concentration of salts or ionic strength of the nutrient solution affected the critical level for tolerance to aluminium [131]. Spehar [177] selected aluminium tolerant soybean genotypes in hydroponic experiments. Subsequently, Ma et al. [127] conducted rapid hydroponic screening method for aluminium tolerance in 600 barley lines from various regions of the world. They also indicated that most lines were sensitive to Al, but ninety lines showed intermediate tolerance. Krizek et al. [124] tested two cultivars of *Coleus blumei* in nutrient solution containing 0 to 24 mg/l aluminium and on an acid Al-toxic Tatum subsoil under greenhouse conditions. Significant inhibitory effects of Al stress on shoot growth were generally observed in solution culture at 8 mg/l Al or higher concentration, while inhibition of root growth in solution culture was generally observed at 16 mg/l Al or higher levels. Rout et al. (unpublished data) tested eight cultivars of mung bean (*Vigna radiata* L.) and six cultivars of rice (*Oryza sativa* L.) in nutrient solution containing Al (0, 6, 12, 24, 48 and 96 mM) to assess Al tolerance in terms of root and shoot tolerance index and total biomass production. They noted that root decreased in mung bean cvs. K-851, PDM-116 and LGG-407 and rice cvs. Subhadra, Sankar by 15.20, 18.10 and 20.11 and 16.04 and 21.32 percent respectively in the presence of Al as compared to their respective controls, while in “TARM-1” and “Dhauli” of mung bean and “Rudra” and “Khandagiri” of rice, the root length was reduced by 30.12 and 42.22 and 29.41 and 34.61 percent respectively. In the rest of the cultivars the effects on root growth were intermediate. They concluded that “K-851”, “PDM-116” and “LGG-407” of mung bean and “Sankar” and “Subhadra” of rice were tolerant to Al having RTI values 97.09, 94.06, 90.19 and 98.95 and 91.17 respectively. Root and shoot biomass production were in accordance with root length; "K-851" had 11.49 percent increase in root biomass as compared to the control. The cultivars PDM-116 and LGG-407 showed 18.78 and 20.98 percent increase in root biomass respectively. Cultivars like Dhauli, TARM-22, TARM-1, TARM-21 and TARM-26 of mung bean were sensitive to Al toxicity showing 36.43 to 56.45 percent reductions in the root biomass as compared to the respective controls. Cultivars such as K-851, LGG-407 and PDM-116 of mung bean and Sankar and Subhadra showed an increase in the shoot/root biomass ratio in the presence of Al compared to their control.

3.2. Mechanisms involved in Al tolerance

Al tolerance or the ability of a cultivar to survive in a relatively high pH in the growth medium has been demonstrated in *Triticum aestivum* [56, 68, 69], a *Secale cereale* [139, 140] and *Pisum sativum* [117, 118]. The mechanisms of aluminium tolerance in *Triticum aestivum* has also been reported by Taylor and Foy [183]. Sivaguru and Paliwal [170] tested tolerance of twenty two rice cultivars to Al toxicity in nutrient solution at pH 4.1, out of which, six cultivars showed significant changes in their expression in the presence of Al compared to the control on the basis of root tolerance index (RTI), shoot tolerance index (STI) and relative growth reduction in shoots and root. Further, they also reported the mechanism of aluminium tolerance on the basis of mineral uptake and utilization. The tolerant cultivars efficiently took up and utilized Ca and P in the presence of aluminium. The susceptible (Al-sensitive) and intermediate cultivars exhibited less Ca and P uptake and utilization [171]. Clune and Copeland [43] tested the effects of Al on roots of Canola (*Brassica napus* var. Napus) seedlings grown in nutrient solution at pH 4.5. They indicated that the nutrient solution having Al at concentrations below 40 mM stimulated root growth of Canola seedlings, increasing both the size and number of central cap cells. At higher concentration of Al above 60 mM, root growth was strongly inhibited with cellular damage in peripheral root cap cells.

4. Cytogenetic effects of aluminium

4.1. Al tolerant genes

The toxic effects of aluminium on plants first take place in the roots, and the mechanisms have been reported [2, 16, 17, 41, 132, 192]. Al tolerance in certain barley populations is controlled by one major, dominant gene [156]. Al tolerance is controlled by a single gene in certain wheat populations [112]. Iorezeski and Ohm [102] reported the occurrence of different Al-tolerant genes in the two wheat cultivars IAS-58 and Norteno. Subsequently, Campbell and Lafever [35, 36] stated that Al tolerance in wheat was not simply inherited and that the expression of Al tolerance was additive with high values of heritability. Rhue et al. [161] reported that in the case of diploid *Zea mays*, Al tolerance is controlled at a single locus by a multiple allelic series. In diploid *Hordeum vulgare*, Al tolerance is controlled by a single dominant gene, located on chromosome-4 [179]. Al tolerance in barley, however, is expressed at a much lower level of Al concentration in the medium as compared to wheat, and it might be that only one subcellular compartment is involved in Al tolerance in barley [179].

4.2. Effect of Al on nuclear activity

Foy [64] reported that aluminum interfered with cell division in root tips and lateral roots, increased cell wall rigidity by cross-linking pectins, and reduced DNA replication by increasing the rigidity of the double helix. Minocha et al. [137] reported that the application of aluminium (0.2–1.0 mM) inhibited cell division and cell viability. They also reported that aluminium treatment resulted in a severe inhibition of DNA synthesis within 16 h–24 h. Matsumoto et al. [134] suggested that the binding of Al to DNA was a potential cause for inhibition of cell division. Bennet et al. [18] reported that nuclear changes were obtained with a low level of Al due to chromatin condensation of the nucleus and an increase in size and frequency of vacuoles in the nucleoli. They also considered ultrastructural features as possible indicators of increased nuclear activity involving RNA synthesis [107]. Aluminium interfered in the function of the Golgi apparatus in the peripheral cap cells of intact roots and the quiescent centre [16–20] and in mitotic activity [40] and DNA synthesis [194]. Bennet et al. [21] reported significant alterations in cell volume of the root cap and disruption of golgi apparatus activity in the peripheral cap cells at the lowest Al concentration (0.5 mg/l). Aluminium treatment also resulted in a redistribution of amyloplasts to the proximal halves of central cap cells as well as alterations in the linear arrangement of these cells and rapid efflux of H^+. Frantzios et al. [78] reported that Al affected the mechanisms controlling the organization of the microtubule cytoskeleton, as well as tubulin polymerization and which induced the delay of the microtubule disassembly during mitosis, resulting in the persistence of preprophase microtubule bands in the late prophase cells and a disturbance in the shortening of kinetochore microtubule bundles in anaphase cells. They also indicated that Al affected the disorder of chromosome movements carried out by the mitotic spindle. After prolonged Al treatments chromatin condensation was inhibited. The microtubule cytoskeleton was a target site of Al toxicity in mitotic root-tip cells of *Triticum turgidum* as observed by Frantzios et al. [78].

5. Effect of aluminium on metabolism

In general, many plant species are resistant or can be tolerant to certain amounts of metals. This is probably achieved through trapping of these metals with metal-binding proteins. Many of the biochemical effects of Al on plants are probably associated with the alteration of root membrane structure and function [91]. Plant membranes are visualized as arrangements of semi fluid proteins and lipids. Aluminium can bind either proteins or lipids, depending on pH and other conditions. Vierstra and Haug [189] found that Al decreased lipid fluidity in membranes of *Termoplasma acidophilium*. Gomez-Lepe et al. [83] found Al in the cell membrane proteins on the inner epidermal cells of onion. Foy and Fleming [69] reported that chlorosis seemed to be due to Al-induced interference in the uptake and/or use of iron, copper and potassium. Under Al stress in nutrient solution, the Al-sensitive cultivar was characterized by chlorosis, decreased Fe concentrations in tops, decreased Ca and Mg in both shoots and roots, a tendency towards accumulation of P, Al and Fe in roots, and reduced Mn in tops. Gallagher et al. [81] noted that nitrate reductase activity was higher in Al tolerant cultivars grown in nutrient solution having aluminium. Al toxicity was also closely related to nitrogen metabolism [69]. Aluminium (100 μM) was found to inhibit the influx of the cations of calcium (69%), ammonium (40%) and potassium (13%) and enhance the influx of the anions of nitrate (44%) and phosphate (17%). Aluminium interfered with the binding of the cations in the cell wall by the same order of magnitude as their respective influxes whereas phosphate binding was strongly enhanced [144]. They also reported that aluminium was bound to the plasma membrane phospholipids, forming a positively charged layer that influenced ion movement to the binding sites of the transport proteins. Huang et al. [96, 97] suggested that Al^{3+} induced inhibition of ion fluxes, particularly Ca^{2+} which played an important role in mechanisms of Al^{3+} toxicity due to binding of cations or screening of the negative charges on the plasma membrane, thus reducing the activity of Al^{3+} close to the cell surface. Ryan et al. [165] showed that only the meristem was sensitive to Al^{3+}. Miyasaka et al. [138] found that there was a net K^+ efflux and H^+ influx at the root apex (first 1 cm), whereas in the rest of the root these fluxes were reversed. In general, aluminium adversely affected several physiological activities producing a severe physiological stress which increased peroxidase activity [149]. Increased peroxidase activity might be linked to a decreased growth rate, as found in plants after treatment with aluminium [32]. Aluminium effectively interfered with the metabolism of cell wall polysaccharides and calcium-producing fissures in the case of *Lemna minor* [75, 98, 168]. Severi [169] reported that the presence of aluminium had the tendency to decrease the multiplication rate of *Lemna minor* L. with significantly increased guaiacol peroxidase activity. Schier and McQuattie [167] compared the application of nitrogen to Al toxicity in non-mycorrhizal and ectomycorrhizal pitch pine (*Pinus rigida* Mill) seedlings. They observed that the application of nitrate or ammonium had no significant effect to Al toxicity in non-mycorrhizal seedlings. Symptoms like thick and stunted roots of ectomycorrhizal pitch pine seedlings was obtained at ambient N levels due to Al toxicity. Al toxicity at ambient ammonium – N was reduced by elevating the level of NO_3 – N or NH_4 – N.

6. Aluminium uptake and transport

Although aluminium is not recognized as an essential element for plant growth, it may, nevertheless, fulfill some fundamental role in the physiology of plants adapted to acid environments with a high concentration of soluble Al [86]. Some plants have the ability to accumulate enormous amounts of Al in their foliage without any evidence of injury or toxicity. Jackson [103] concluded that correlations between Al contents in the foliage of crop plants and Al toxicity were more the exception than the rule. He also stated that toxic effects of Al may result from excess Al in the growth medium with little or no change in the Al contents in the foliage.

6.1. Aluminium accumulation in tolerant plants

Aluminium-tolerant plants may be grouped according to Al accumulates within their tissues [75]. In one group, Al concentrations in the shoots are not consistently different from those of Al-sensitive plants, but in the root Al concentrations are lower in certain tolerant cultivars of wheat, barley, soybean and pea [59, 60, 119]. In such cases, Al tolerance apparently involves an exclusion mechanism. In a second group of plants, Al tolerance is associated with less Al in plant shoots, entrapment of more Al in roots or both in wheat, barley and potato [75] and grass and cabbage [99]. In a third group, Al tolerance is directly associated with Al accumulation by the tops; such plants have high internal tolerance to Al particularly pine trees, tea and mangroves [75].

6.2. Aluminium uptake at root level

Henning [92] reported that much of the Al absorbed by wheat roots penetrated the boundary between root apex and root cap and accumulated in the nuclei and cytoplasm of cells adjacent to this zone. Some Al passed through the epidermis and cortex, but considerable amounts were retained in cortical cells. Although the endodermis seemed to prevent movement of Al into the central cylinder. He suggested that some Al might have bypassed the epidermis by entering the root apex and passing through meristematic cells of the central cylinder.

Wallace and Rommey [195] reported that threshold concentrations of Al toxicity were 30 mg/kg in soybean leaves and 20 mg/kg in rice roots. Malavolta et al. [129] stated that Al toxicity in sorghum was associated with 640 mg/kg of Al in lower leaves and 1220 mg/kg in upper leaves. Duncan [52] found that sorghum genotypes were tolerant to low soil pH (and probably Al), and contained lower concentrations of Al, Fe and Mn than those that were more sensitive. Wagatsuma [190] reported the mechanism of Al uptake by plant roots in relation to non-metabolic conditions. Under normal conditions, Al was absorbed in an exchangeable manner at almost all the Ca existing sites on the cell walls of roots. The metabolic inhibitors like chloroform gas and 2,4-dinitrophenol (DNP) increased the Al uptake by roots significantly. Further, Wagatsuma [191] also noted the characterization of absorption sites for aluminium in the roots of *Cucurbita pepo*, *Vicia faba*, *Glycine max*, *Lycopersicon esculentum* and *Pisum sativum*. Among the plant species, Al content in the roots was positively correlated with the cation exchange capacity (CEC) of the dry root powder. Al content of the dry root powder was considerably higher than that of the excised roots which were treated with Al. He also indicated that in most of the cases Al was bound to the pectic substances in the cell walls but a part of Al entered the protoplast and combined with nucleic acids and acid soluble phosphates. A higher concentration of Al was found in nuclei and other cell compartments of root tissue in tolerant wheat genotypes than in sensitive genotypes, and tolerant plants survived accumulating higher Al in cellular components than sensitive genotypes of *Cucurbita pepo, Vicia faba, Glycine max, Lycopersicon esculentum* and *Pisum sativum* [133, 141, 145] and Lotus species [25].

6.3. Aluminium and nutrient uptake

Bennet et al. [16] noted the aluminium toxicity in *Zea mays* and observed nutrient disorders involving the uptake and transport of P, K, Ca and Mg. Phosphorous transport between roots and shoots diminished with increased Al concentration in roots. Aluminium changed the Ca and Mg concentrations in plants which were primarily connected in the uptake and transportation. The positive correlation of P and Al in roots of sorghum was reported [147]. Poor plant growth with Al toxicity was a result of phosphorous starvation [126]. Wagatsuma et al. [193] reported that the concentration of Al was high in the roots and generally low in the tops. In sensitive plants, Al was considerably deposited in the root-tips; the root elongation was retarded and finally the top growth inhibited. Nalewajko and Paul [142] demonstrated that the addition of Al (250 $\mu g \cdot l^{-1}$) significantly decreased the microbial phosphate uptake in water samples from two Canadian lakes. Pettersson et al. [151] indicated that aluminium exerted toxic effect in *Anabaena cylindrica* causing phosphate starvation. Husaini and Rai [100] observed a pH-altered reduction in uptake and assimilation of nitrate and phosphate in the cyanobacterium *Nostoc linckia* under aluminium stress. Further, Husaini et al. [101] reported that a pH-dependent inhibition of Mg^{2+} and Ca^{2+} - ATPase activities of *Nostoc linckia* and *Chlorella vulgaris* exposed to either $AlCl_3$ or $AlCl_3$ + NaF. DeGraaf et al. [49] analysed the aluminium toxicity and tolerance in three heathland species on the basis of Al accumulation and growth rate. They reported that Al concentrations increased with increasing Al concentrations in the nutrient solution in all the three heathland species (*Arnica montana, Cirsium dissectum* and *C. vulgaris*). Application of Al for 1 h to individual 1 mm section of root apex only inhibited root elongation. Aluminium-induced prominent alterations in both the microtubular and the actin cytoskeleton were found especially in the apical 1–2 mm zone using monoclonal antibodies as reported by Horst et al. [94]. They also indicated that NaCl- adapted plants with higher pectin content accumulated more Al in their root apices and these were more Al-sensitive indicating more severe inhibition of root elongation and enhanced callose induction by Al.

7. Phytotoxicity and its interactions with nutrients

Ideally, each metal causing phytotoxicity would cause some characteristic symptoms that would allow its diagnosis, further, these symptoms would be apparent before substantial economic or ecological damages occurred [93] or alter both the natural and man-made ecosystem [186]. The most general symptoms are stunting, curling of young leaves, death of leaf tip, chlorosis, inhibition of root growth and indication of calcium and phosphorous deficiency [57].

7.1. Al interference with Ca, Mg and P

The beneficial effects of Ca on plants grown under conditions of Al toxicity have been recognized for a long time [116, 157, 202]: inhibition of root growth and disturbance in root structure, particularly cell wall loosening and secretory activity due to the deficiency or reduction of Ca transport [95, 122, 157, 158, 178, 188, 203] and disruption of cellular Ca^{2+} homeostasis [96, 97]. Al interference with the uptake, transport and utilization efficiency of most of the mineral elements have been well documented [135]. Huang et al. [96, 97]

reported that net calcium influx at the root apex was strongly inhibited by Al^{3+}. Furthermore, Ca^{2+} flux was affected to a greater extent than the fluxes of other ions. Nichol and Oliveira [143] noted that Al^{3+} reduced Ca^{2+} influx in barley (*Hordeum vulgare*). Callose deposition at the root apex was a major symptom of Al toxicity [144]. Increased synthesis of callose was always associated with increased cytosolic calcium [201]. Rhue and Grogan [160] reported that increasing the Ca concentrations in nutrient solutions decreased the Al tolerance differences among corn inbred lines. Aluminium markedly increased the redox potential of root tissues, decreased contents of high bond energy phosphorous, and increased contents of mineral P in the root of peas [48].

DeGraaf et al. [49] reported the interaction of Al with minerals by using various plant species. High Al concentrations in nutrient solution influenced the uptake of minerals; uptake of divalent cations particularly Ca and Mg was often disturbed by Al [50, 75]. Aluminium interference with P uptake might result in P deficiency in plants grown on acid soils or in nutrient solutions [71, 104]. Decrease in Ca concentrations in soybean tops and roots were associated with Al toxicity [74] and Mg concentrations declined in sorghum with high Al concentrations [147]. Clarkson and Sanderson [42] reported that Ca uptake was primarily concerned with surface reactions involving the charge on the Al^{3+} ion. In addition to declined plant growth, Al stress typically decreased the concentration of several mineral elements, especially Ca, Mg and P [67]. Krizek and Foy [123] reported that Al stress in Tatum subsoil decreased P and Ca in both Al-tolerant Dayton and Al-sensitive Kearney barley cultivars grown under both low and adequate soil moisture status. Al, P and Fe usually got accumulated in roots, but not in shoots of Al-injured plants, and Al stress induced deficiencies of both P and Fe [64, 65]. Aluminium injury was associated with the displacement of Ca and Mg from the roots by Al [84] and with the decreased uptake by Ca, Mg and P from deeper soil zones by beech and other trees [15, 196, 197]. Wheeler and Dodd [198] reported that there was variation in chemical concentrations and physical symptoms of monocotyledons and dicotyledons by Al toxicity. Keltjens and Tan [111] reported that Mg was more effective than Ca in alleviating Al stress in monocotyledons whereas the reverse occurred for the dicotyledons. Blair and Taylor [27] reported the nature of interaction between aluminium and manganese on growth and metal accumulation in *Triticum aestivum*. They also indicated that accumulation of Mn in roots and shoots decreased significantly with increasing Al supply. Zhang et al. [202] reported the interaction between Al and Ca on pollen germination and tube growth of Australian species Geraldton wax flower (*Chamelaucium uncinatum*). They noted that pollen germination was inhibited by micromolar concentrations of trivalent cations like Al^{3+}, La^{3+} and Gd^{3+}. Exposure of the growing pollen tubes to micromolar concentrations of Al^{3+} concentration and a millimolar concentration Ca^{2+} chelator (ethyleneglycol-bis (beta-aminoethyl ether) –N, N'- tetraacetic acid) led to rapid tip bursting. The Al^{3+} treated pollen tube bursting was reduced significantly by increasing either the solution pH from 4.5 to 6.0 or Ca^{2+} from 0.25 to 5 mM.

7.2. Al interference with NO_3^- and NH_4^+

It is well established that Al interferes with mineral nutrition, particularly the nitrate nutrition of plants [33]. Rufty et al. [164] showed that NO_3^- uptake by soybean decreased when Al concentration in solution increased from 10 to 50 μM. Keltjens [109] indicated that Al increased ammonium uptake and H^+ release in Al-sensitive sorghum cultivars. Grauer and Horst [85] observed that nitrate uptake in lupin, which increased the pH in the root environment, paradoxically aggravated the depressive effect of Al on root growth. Keltjens [109] noted that Al stimulated NH_4^+ uptake with both Al-tolerant and Al-sensitive sorghum cultivars. Kinraide [115] showed that root cells of wheat plants cultivated in the presence of a toxic concentration of Al (100 μM) maintained a normal membrane electrical potential since the membrane potential was largely determined by active H^+ excretion and K^+ transport. Calba and Jaillard [33] reported that Al reduced Cl^- and NO_3^- uptake in maize. Rufty et al. [164] showed that NO_3^- uptake decreased with Al concentration in solution between 10 and 50 µM. Most of the authors reported that disturbance of mineral nutrition was most often accompanied by increased H^+ release in sorghum [80], maize [53], wheat [56, 183] and soybean [164].

8. Biochemistry of Al phytotoxicity

To evaluate meaningful biochemical effects of toxic metals, one must examine conditions (different metals and their concentrations) which are phytotoxic in nature [47]. Aluminium toxicity is strongly influenced by acid soils (pH 5.0) but can occur at pH levels as high as 5.5 [59, 60]. Woolhouse [199] noted that aluminium inhibited the activities of ATPase in plants. He also found that the ATPase activity of cell wall preparations from roots of an acid soil ecotype of *Agrostis tenuis* was inhibited less by Al than that of a preparation from a calcareous soil ecotype of the same species. He also suggested that structural changes in these enzymes might be responsible for differential Al tolerance of the ecotypes. Foy and Fleming [69] reported that under Al stress in nutrient solutions, the Al-sensitive cultivar was characterized by chlorosis, decreased Fe concentrations in tops, decreased Ca and Mg in both tops and roots, a tendency toward accumulation of P, Al and Fe in roots, and reduced Mn in tops. Aluminium induced changes in the uptake of most macroelement cations by plant roots, including reductions in the uptake of calcium [42, 106], magnesium [99, 125] and potassium [46]. Foy and Fleming [69] found negative effects of Al on the nitrate reductase activity (NRA), the first enzyme involved in the NO_3^- assimilation in plants. Further, Keltjens and vanUlden [110] compared the effect of Al on nitrogen uptake, nitrate reductase activity and protein release in two sorghum cultivars differing in Al tolerance. Prolonged Al stress induced an enhancement of lipid peroxidation [169] and caused formation of highly toxic oxygen free radicals [32]. An increase in the activities of superoxide dismutase and peroxidase and a decrease of catalase activity indicates the presence of an antioxidant scavenging system in Al-treated roots [32]. Plucinska and Karolewski [153] reported a significant decrease of the anabolic reduction charge (ARC: $NADPH/(NADP^+ + NADPH)$) and an increase of the redox status ($NAD(P)H/NAD(P)^+$), catabolic reduction charge (CRC: $NADH/(NAD^+ + NADH)$) and phosphorylation capacity expressed as $NADPH^+/NAD^+$ ratio in the presence of 4.0 mM Al treatment in hydroponic culture of Scots Pine seedlings. Subsequently, Plucinska and Ziegler [154] indicated that the longer exposure to Al ions led to a drastic decrease in AdN (total adenylate) and ATP pool-levels with a corresponding rise in ADP and AMP content and great depression both in ATP/ADP and AEC (adenylate energy charge) and inhibition of metabolic activity [155]. Pavlovkin and Mistrik [148] studied the effect of Al on the electrical membrane potential (Em) of outer cortex root cells of 3-day-old maize seedlings. They indicated that Em values of root cells ranged between –115 and – 146 mV. The membrane potential was rapidly and significantly depolarized by Al. The depolarization was concentration-dependent and reached the maximum at 150 mM Al. The extent of membrane depolarization by 100 mM Al decreased continuously from the apex to the base of the root. Both the P-ATPase activator fusicoccin and glucose diminished the depolarizing effect of Al on electrical membrane potential. The roots exposed to Al retarded K^+ efflux from root tip segments and had no effect on K^+ efflux from segments of the root base as reported by Pavlovkin and Mistrik [148]. Gunse et al. [87] tested two maize (*Zea mays*) cultivars on root growth by using Al and the role of ethylene metabolism. They suggested that Al-resistant genes were not constitutively expressed in the absence of Al in the growing medium, but activated upon exposure to Al. Enhanced ethylene formation does not seem to play a role either in the Al-induced inhibition of root elongation or in the induction of the resistance mechanism.

9. Conclusion

Aluminium toxicity is an important growth-limiting factor for plants in many acid soils, particularly in pH of 5.0 or below. Aluminium toxicity in plants is often clearly identifiable through morphological and physiological symptoms. Differential tolerances to Al toxicity almost certainly involves differences in the structure and function of roots. Aluminium interferes with cell division in roots, decreases root respiration and uptake and use of water and nutrients, particularly calcium and phosphorous 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 mechanism behind the interaction with mineral nutrients, specific genes responsible for tolerance, levels and kinds of organic and aminoacids which act as metal chelators and detoxifiers, level and forms of enzymes, and changes in root permeabilities to ions and molecules and its mechanisms.

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