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Some Aspects of Aluminum Toxicity in Plants

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I. Abstract

Aluminum toxicity is a major factor in limiting growth in plants in most strongly acid soils. Toxic effects on plant growth have been attributed to several physiological and biochemical pathways, although the precise mechanism is still not fully understood. In general, root elongation is hampered through reduced mitotic activity induced by Al, with subsequent increase in susceptibility to drought. The initial site of uptake is usually the root cap and the mucilaginous secretion covering the epidermal cells. Al ions bind very specifically to the mucilage by exchange adsorption on the polyuronic acid, complexing with the pectic substances and by the formation of polyhydroxy forms, increasing the number of Al atoms per positive charge.

Toxicity has been suggested to be initiated at the sites of mucopolysaccharide synthesis. Al is absorbed on all Ca-binding sites on the cell surface. In the intact tissues, most of the Al is bound to the pectic substances of the cell wall and a part to the nucleic acids and cell membrane. Al is also reported to enter the plant by moving into meristematic cells via the cortex, bypassing the endodermal barrier. Being a polyvalent cation, it follows principally the apoplasmic pathway of transport through cortical cells, but may also enter the stele through the plasmalemma. Ultrastructural studies have shown the maximum accumulation to be in the epidermal and cortical cells.

The interaction of Al with different systems follows different pathways. The plasma membrane at the outer boundary of the root cell is a potential

target and its physical properties can be altered by Al through interaction with membrane-bound ATPase, lipids, carbohydrates and proteins. The Golgi apparatus has been suggested as the primary site of action, followed by damage to the plasmalemma.

Aluminum interferes with the uptake, transport and use of several essential elements, including Cu, Zn, Ca, Mg, Mn, K, P and Fe. Excess of Al reduces the uptake of certain elements and increases that of others, the patterns being dependent on the element, the plant part and species involved. A major factor is the pH concentration. At an acid pH, below 5.5, the antagonism between Ca and Al is probably the most important factor affecting Ca uptake by plants.

The molecular mechanism of tolerance of Al is as yet not clear. Tolerant plants reduce the absorption by the root or detoxify Al after absorption. Al tolerant plants may be grouped into those with higher Al concentrations in tops and those with less. In the latter, more Al is entrapped in roots. Uptake of Al may be reduced by binding to cell wall or to membrane lipid. Tolerance may be different in different species and seems to be controlled by one or more genes.

Absorption of Al in non-metabolic conditions is affected only slightly by temperature. Anaerobic conditions, like the presence of nitrogen and metabolic inhibitors, damage the endodermal membrane barrier, increasing the uptake and enhancing injurious effects.

Aluminum also causes morphological damage to plant parts. It affects photosynthesis by lowering chlorophyll content and reducing electron flow. Reduced respiratory activity might be due to reduced metabolic energy requirement. Protein synthesis is decreased probably due to effect on ribosome distribution at endoplasmic reticulum.

Aluminum is known to bind to DNA and nuclei. However, its penetrance to DNA of mitotically active centers is slow. On accumulating in roots, it initially inhibits mitotic activity, possibly through affecting the integrated control function of the root meristem.

Aluminum toxicity in acid soil is of special importance due to the destruction of components of forest ecosystems under specific conditions. It reduces biomass yield and tree growth and represses litter-degrading microflora.

Further information is required on the factors affecting membrane permeability, distribution and accumulation of Al in different plant parts and different species. Al tolerance may be studied with relation to the presence of different ligands, nitrogen metabolism (nitrate reductase and protein accumulation), nitrogen tolerance in relation to pH change and metal ion activities, the role of Ca and P and interference with water relations and litter degradation.

Zusammenfassung

Al giftig ist einer Wichtiger Umstand in Wachstum Begrezung im Pflanzen in meiste schwere Sauere Erde. Giftig Effekten an die Pflanze Wachstum haben zu vie physiologische und biokemiche Pfad beimessen, obgleich der genau Mechanismus jetzt nicht völlig verstanden hat. Allgem ein Wurzel Verlängerung ist durch leise mitotische Tätigkeit beim Al veranlass behindern wird mit Resultat Vergrößerung in der Dürre empfängung. Die anfängliche Lage Einfahrt ist allgemen die Wurzel-Kappe und die Schleim Absonderung daß die oberhaut Zelle verdeckt. Giftigkeit hat an die mucopolysaccharide Synthese Lage beginnen so vorschlagen werden. Al ion binden eben besonders an die Schleim beim Umtausch Adsorption an die polyuronic Saure, mit den pektiken Substanze Komplex gemacht werden und bei den polyhydroxy Form Bildüng und die Al atom per Positiv charge Nummer vermehern.

Al wird an alle Ca-binden Lage an die Zelle Fläche aufsaugen. In die unberührt Zelle meist des Al ist zu den pektiken Zelle Wand Substanze binden und ein Teil zu den Nucleic Saure und Zelle Membran. Al wird auch die Pflanze zu einfahren bei der Bewegung hinein meristematik Zelle *via* die Cortex, die endodermische Schranke passieren geanzeit. Wie es ein polyvalent Cation ist es folgt hauptsächlich den apoplasmiken Transport Pfad durch cortische Zelle, aberkann auch den Stele durch die Plasmalemma einfahren. Ultrastruktür Studiumen haben die Höchstmaß Anhäufung in der uberhaute und cortische Zelle gezeigt.

Der Al Gegenseitig Tätigkeit mit anderen System folgt andere Pfad. Die Plasmamembran, daß an die äußer Grenze auf die Wurzel Zelle ist, ist eine mögliche Scheibe. Sie physische Eigentum Kann beim Al durch Gegeuseitig Tätigkeit mit Membran bindet ATPase, Lipid, Carbohydrate und Protein sich veränderen. Der Golgi apparat hat as den haupten aktionen Zentrum mit Schaden zu Plasmalemma vorschlagen geworden.

Al einmischt sich mit der Einfahrt, Transport und Gebrauch auf mehrere wichtige Element, em schießlich auf Cu, Zn, Ca, Mg, Mn, K, P and Fe. Al übermaß vermindet sich der Reinfall auf sicher Element und vergrößt sich wie auf anderer, das Muster von die Element, die Pflanze Teile und Verwickelnte spezies abhängig sind. Ein wichtig Umstand ist die pH Konzentration. In Sauer pH, unter 5.5, der Widerstand zwischen Ca und Al ist vieleicht der meister wichtiger Umstand daß Pflanze Ca-Reinfall wirken auf.

Der molecular Mechanismus auf Al Duldsamkeit ist jetzt nicht klar. Duldsam Pflanze vermindet sich die Wachstum Aufsaugung oder Al nach Aufsaugung nicht giftig machen. Al-duldsam Pflanze konnen in zwei Gruppen geteilt werden mit höchste Al-Konzentration in oberstes Eude und mit kleiner. In der letztere, mehrere Al ist in die Wurzel einfangen

werden. Der Al Reinfall wird vieleicht bein Binden zur Zellewand oder zum Membran Lipid vermindern. Die Duldsamkeit wurde vieleicht im andere Spezies anders und bei ein oder mehre Gene Kontrolierten erscheinen.

Die Al Aufsaugung ist in nicht-metabolike Stellungen nur gering auf die Temperatur wirken. Anaerobike Stellungen, wie die Gegenwart nach N_2 und metabolik Hemmungen, schädigen die Endodermische Membran Barriere zur Reinfall und den schädlichen wirkungen sich vergrößern.

Al verursacht auch morphologischer Schaden an die Pflanze teile. Er wirk auf photosynthesis durch chlorophyll Gehalt und Elektron-Fluß leiser machen. Leiser Atmen Tätigkeit wurde vieleicht zur leisere metabolike Energy-Forderung. Protein Verbindung wurde vieleicht zur Wirkung an Ribosom Verteilung an Endoplasmik Reticulum Vermindern.

Al verbind DNA und Kern. Wie auch sein Eindringen ist langsam zu DNA von mitotiklich aktiv Zentrum. An Anhäufung in Wurzel, es verhindert anfänglich mitotike Tätigkeit, vieleicht auf die Wurzel Meristem einfügenlich Kontrol Function wirken.

Al Giftigkeit ist in sauere Erde auf spezial Wichtigkeit durch Wald Ekosystem Bestandteil Tötung unter spezifischen Stellungen. Es vermindert Biomass Ertrag, Pflanze Wachstum und Streu absetzenlich Microflora. Mehre Information hat über der Faktor daß Al Membran Durchlässigkeit, Verteilung und Anhaüfung in andere Pflanzeteile und anders spezies wirken auf gebraucht wird. Al-Duldsamkeit wird vieleicht in bezug auf andere Ligand, N_2 Metabolism (nitrate reductase und protein Anhäufung), N_2 Duldsamkeit in bezug auf pH veränderung und Metall ion Tätigkeit, die Rolle des Ca und P und Einmischung mit Wasser Erzählung und Streu-absetzung Studieren werden. (Translated by K. Talukder.)

Aluminum toxicity is probably the most important factor involved in limiting growth in plants in strongly acid soils and mine spoils (Carvalho et al., 1980; Foy, 1974, 1984; McLean, 1976; Silva, 1976), since it affects both depth and branching of roots (Foy, 1984). However, even with high levels of Al in soil, plant parts contain relatively low concentrations due to the poor solubility of the naturally occurring Al compounds (Elinder & Sjögren, 1986).

II. Uptake and Localization

The toxic consequences of Al on plant growth have been related to many symptoms, but the precise mechanism is poorly defined (Bennet et al., 1985a). Root elongation is hampered as a result of reduced mitotic activity (Clarkson, 1965). This effect is rapid and sites of uptake are possibly related to action (Jackson, 1967). A time course study of aluminum sulfate uptake by the primary root of *Zea mays* indicates the initial sites of uptake to be the root cap and the mucilaginous secretion covering the epidermal cells of the roots. Longer treatment (within 12 hours) resulted in the accumulation of appreciable quantities of the metal in the outer cortical cells, accompanied by gross morphological disorganization of the root apex and ultimately to disintegration of the outer cells. However, this severe cellular disorganization did not affect the inner cortical regions or the stele, indicating the protection afforded by the root cap. Removal of the root cap led to accumulation of Al in these regions as well, after prolonged exposure (Bennet et al., 1985b). Similar disturbances were recorded in *Triticum* (Hecht-Buchholz, 1983). The morphological changes induced by Al in roots include: decrease in the turgescence of epidermal cells of the tip (barley); occurrence of small depressions (oat, rice); destruction of epidermal and outer cortex cells (maize) and cross-sectional deep cracks in the inner cortex cells (pea) (Wagatsuma et al., 1987b).

Aluminum uptake has been regarded as a function of cell biochemistry (Bennet et al., 1985a, 1985b). Since the symptoms of Al toxicity are visible before the cells proximal to the cap/root junction actually receive the metal, toxicity may be initiated at the sites of mucopolysaccharide synthesis.

Al^{3+} is bound very specifically to the mucilage (Horst et al., 1982), partly by exchange adsorption on negative charges of the polyuronic acid (Wright & Northcote, 1974). After exposure for six hours, binding of Al in the mucilage is much higher than the corresponding decrease in the binding of other cations, possibly due to complexing of Al by the pectic substances (Schweiger, 1966) or the sugars (Angyal, 1973). The formation of polyhydroxy Al forms (Nair & Prenzel, 1978), increasing the number of Al atoms per positive charge, may also be a contributing factor (Horst et al., 1982). Removal of mucilage prior to the treatment with Al facilitates Al uptake in the root tissue.

Aluminum is absorbed according to a non-metabolic process in an exchangeable manner at all the Ca-binding sites on the cell surface. After having saturated a large portion of the absorption sites during a particular period (30 hours) Al cannot be absorbed until new absorption sites for it are produced by further root growth (Wagatsuma, 1983b).

In the intact tissues, the major part of Al is bound to the pectic substances in the cell walls and a part to the cell membrane and nucleic acids. However, when the cell membranes, which act as a barrier for the passive movement of Al, are destroyed or saturated, a large amount of the metal diffuses into the protoplast. It then binds to the various phosphate compounds and nucleic acid, accumulating largely in the roots. Since Al penetrates passively into the protoplast in the endodermal cells, it may even enter the central cylinder of the root, thus increasing its content in the plant top (Wagatsuma, 1983b).

III. Mode of Uptake

Transport pathways of ions through cortical cells may be symplasmic or apoplasmic. Al, being a polyvalent cation, may follow the apoplasmic pathway, but reports of its accumulation in nuclei (Aimi & Murakami, 1964; Huett & Menary, 1980; Ikeda et al., 1965; Matsumoto et al., 1976; McLean & Gilbert, 1927; Naidoo et al., 1978) indicate that some Al ions use the symplasmic one as well. Although Al passes through cortical cell walls via the apoplasmic pathway, it may enter the stele through plasmalemma, without suberin lamella at the endodermis (Wagatsuma, 1984).

In most plants, Al has been located in meristematic cells, mostly in the nucleus and cell wall (Clarkson & Sanderson, 1969; Henning, 1975; Matsumoto et al., 1976; Morimura et al., 1978; Naidoo et al., 1978; Rhue, 1976). However, no Al was observed in the meristem of *Zea mays* by Rasmussen (1968). It accumulates at high levels in epidermis, hypodermis, cortex and endodermis and a small amount in immature xylem (Wagatsuma, 1984).

Ultrastructural studies using electron microprobe, X-ray analyzer, scanning electron microscope and energy-dispersive X-ray analyzer showed that maximum accumulation of Al occurred in the epidermal and cortical cells. Relatively high levels were seen in the endodermal cell walls and cytoplasm, stelar tissues and cortical cytoplasm, while in some plant species some Al was observed in the xylem parenchyma cells. Al was observed to enter the plant by moving into meristematic cells and the symplasm via the cortex, hence bypassing the endodermal barrier (Huett & Menary, 1980; Matsumoto et al., 1976; Naidoo et al., 1978; Rasmussen, 1968).

The observation of epidermal penetration by Al, following prolonged exposure, does not agree with the earlier reports that Al was localized in the nuclei or root cap cells and that sensitive cultivars have more Al than the tolerant ones (Aimi & Murakami, 1964; Fleming & Foy, 1968; Ikeda et al., 1965).

The root cap is known to be involved in regulating the mitotic activity of the meristem (Clowes, 1972). Juniper (1972) proposed that the root cap has two integrated perception systems related to starch metabolism within its differentiating cells. The connection between Al toxicity and the biochemistry of the mucopolysaccharides indicates that the interference by Al could be directed along this pathway (Bennet et al., 1985a, 1985b). Al acts on differentiation of peripheral cap cells and increase in mean cap volume is due to interference by Al in mechanisms which control cell loss from the cap (Bennet et al., 1987).

IV. Interaction with Different Systems

A. INTERACTION WITH PLANT MEMBRANES

The plasma membrane at the outer boundary of the root cell is a potential target for Al action. Al ions may affect the membrane by increasing the permeability to non-electrolytes and decreasing its permeability to water and partiality for lipid permeators (Zhao et al., 1987). Electron microscopy has shown pronounced injuries of chloroplast membranes by 10 μM Al (Hampp & Schnabl, 1975) and restricted mobility of lipids (Caldwell & Haug, 1982). Increase in Al tolerance in the presence of divalent cations may be attributed to its reduced uptake at the plasma membrane (Aniol, 1983; Haug & Caldwell, 1985; Rhue, 1979) or to the higher resistance of the plasmalemma of root cells, as seen in barley (Henning, 1975; Hecht-Buchholz & Foy, 1981). Al may cause leakage of K from the plasmalemma, inducing passive Al permeation (Wagatsuma et al., 1987b).

Physical properties of the membranes can be altered by bound Al cations, since Al is very toxic to cells (Coughlin et al., 1983) and interacts with membrane bound ATPase, lipids, carbohydrates and proteins. The adsorption of Al^{3+} by *Saccharomyces cerevisiae* neutralizes the cell surface charge and allows the cells to adhere to glass and polycarbonate (Van Haecht et al., 1985).

Inhibition of membrane bound calmodulin-stimulated ATPase activity (probably Ca^{++}, Mg^{++} ATPase) was recorded upon application of Al to calmodulin at a molar ratio of 3:1 in root plasma membrane vesicles (Haug & Caldwell, 1985; Veltrup, 1983).

Aluminum ions are known to bind to phosphatidylserine (Blaustein, 1967) at the phosphodiester group. Al at concentrations as low as 10 mM produced pronounced lipid phase changes in the plasma membrane of *Thermoplasma acidophilum,* an archaebacterium (Vierstra & Haug, 1978).

Carbohydrate structures in membrane surfaces were additional binding sites for Al ions, which severely impaired the symbiotic relationship of soil bacteria, *Rhizobia,* with legumes (Andrew, 1978; Foy, 1984; Franco & Munns, 1982). Beryllium and Al greatly inhibited cap formation, i.e., antibody-induced redistribution of cell surface receptors on one pole of the cell in lymphocytes (Morita et al., 1982).

Interaction of Al with membrane protein is either through competition with Terbium (Tb^{3+}) for binding sites on the membrane proteins or through alteration of the structure of membrane bound proteins as seen in the inner epidermal cells of onion (Gomez-Lepe et al., 1979).

Molecular level information regarding the entry of Al through the plasma membrane is very meager. The likely mechanisms may involve (Haug & Caldwell, 1985):

(a) Permeation of electroneutral compounds such as $Al(OH)_3$ or $AlCl_3$, since the hydrophobic membrane core constitutes the primary barrier for charged molecular species (Haug, 1984).

(b) Association with inverted, micellar lipid configurations in non-bilayer membranes (Cullis & De Kruijff, 1979) or with naturally occurring carriers such as phospholipids or chelators. Preliminary experiments have shown phospholipids transporting Al ions from an aqueous to an organic phase (Haug, 1984).

Bennet et al. (1985b), however, do not confirm the plasmalemma as a primary site of Al action. The first effect noticed was on the Golgi apparatus, reducing the number of cisternae and secretory vesicles through biosynthesis of new membrane material destined for incorporation in the plasmalemma (Newcomb, 1980). Failure of the Golgi apparatus may, therefore, be expected to precede damage to the plasmalemma.

B. INTERACTION WITH MINERAL METABOLISM

The role of Al and its interaction with nutrient elements has for many years been a part of plant nutrient studies. The interaction of Al with other metals depends to a major extent on the concentration used. Al toxicity in wheat was prevented by increasing the concentrations of Ca, Mg, K or Na, either individually or collectively (Ali, 1973). These beneficial effects were probably due to a competitive reduction in Al-root contact or to a decrease in Al activity.

1. Calcium

Aluminum is found to reduce Ca uptake in different plants, thus reducing the retention of the latter in roots and tops (Fitter & Hay, 1981; Foy, 1974). These effects have been seen in almost all cultivated plants (Camargo, 1985), including rice (Alam, 1983), *Coffea arabica* (Pavan, 1982; Pavan & Bingham, 1982a, 1982b), *Manihot esculenta* (De Carvalho & Cesar, 1984), barley (Clarkson & Sanderson, 1971), potato (Lee, 1971), *Vigna unguiculata* (Mayz et al., 1984), *Lupinus, Vicia, Hordeum, Secale* (Horst & Göppel, 1986), *Acer* (Thornton et al., 1986a), *Gleditsia* leaf (Thornton et al., 1986b), and *Zea mays* stem (Gerzabek & Edelbauer, 1986).

The inhibitory effect of Al on Ca is independent of pH in *Sorghum* (Guerrier, 1982). Increased Ca concentration did not moderate the toxic effect of Al in *Rhizobium* (Munns et al., 1981). Ca is able to suppress Al toxicity only when present in considerably higher concentrations than Al in the medium (Wagatsuma, 1983b). It does not, however, affect the rate of uptake of Al, which was related to the activity of Al^{3+} in solution (Pavan, 1982).

Kinetic analysis shows that Al competitively inhibited Ca uptake by roots (Guerrier, 1978a, 1978b, 1978c, 1979). It is absorbed according to a non-metabolic process in an exchangeable manner at almost all the sites binding Ca on the cell surface (Wagatsuma, 1983b). On the other hand, Al treatment increased Ca in roots of *Gleditsia* (Thornton et al., 1986c).

Calcium treatment increased soil pH and ameliorated Al toxicity in peanut and cowpea (Chong et al., 1987). On the other hand, increase in Al concentration in soil decreased the absorption of Ca and P, with corresponding decrease in dry weight of roots and aerial parts (Costa et al., 1984).

2. *Manganese*

Aluminum treatment decreased the concentration of Mn in all parts of barley plants except stem, where more Mn concentration was recorded (Alam, 1981). However, in rice, Mn concentration decreased in plant tops but increased in roots with increasing Al, suggesting that Mn may compete effectively with Al for root absorption sites (Alam, 1983).

Twenty-five ppm Al reduced the uptake of Mn in maize (Mathan, 1980). Al up to 8 ppm reduced Mn content in both roots and tops of *Sorghum* (Cambraia et al., 1983b). Mn was decreased in rice plant tops (Nambiar, 1976), grain and straw but increased in roots following Al treatment (Sarkunan & Biddappa, 1982).

Aluminum injury led to accumulation of Mn in root tissues of potato (Lee, 1971). Al and Zn in combination increased Mn mobility in soil in soybean plants (Peneva & Stoyanov, 1982). Plants administered more than 4000 ppm Mn and 1000 ppm Al show less growth and other toxicity symptoms (Menten et al., 1981).

3. *Potassium*

Aluminum competes with K for root absorption site and depresses K uptake with consequent dose dependent decrease in K content in plant roots and tops (Alam, 1983). Similar reduction in K uptake was reported in tea (Sivasubramaniam & Talibudeen, 1971) and *Zea mays* (Gerzabek & Edelbauer, 1986). However, no effect on root K was found in *Gleditsia* and low Al increased uptake of K in *Acer* (Thornton et al., 1986a, 1986b, 1986c). Enhanced uptake of K was reported in *Zea mays* (Canal & Mielniczuk, 1983), in *Coffea arabica* (Pavan & Bingham, 1982b) and *Trifolium repens* (Lee & Pritchard, 1984).

Aluminum markedly affects K uptake at the zero NH_4^+ level in *Trifolium repens.* When present in the nutrient medium at 148 μM, Al causes an apparent K efflux which cannot be attributed directly to variation in pH changes. In the presence of NH_4^+ this effect is reversed (Lee & Pritchard, 1984).

4. *Magnesium*

Magnesium concentration and uptake decreased with increasing Al levels (1–10 ppm) in roots and tops of rice (Alam, 1983; Sarkunan & Biddappa, 1982), *Coffea arabica* (Pavan & Bingham, 1982b), *Manihot esculenta* (De Carvalho & Cesar, 1984), potato (Lee, 1971), *Zea mays* (Gerzabek & Edelbauer, 1986), *Lupinus, Secale, Vicia,* and *Hordeum* (Horst & Göppel, 1986).

Low concentration of Al elevated Mg in *Acer* (Thornton et al., 1986a) and *Gleditsia* (Thornton et al., 1986c) but higher ones reduced Mg level (Thornton et al., 1986c).

Earlier, Mg had been reported to counteract the adverse effect of Al toxicity in maize (Videl & Broyer, 1962).

5. *Iron*

Addition of 2 ppm Al to nutrient media increased the concentration of Fe in rice plant tops followed by a decrease. Roots accumulated Fe with increasing Al levels (up to 10 ppm) in rice (Alam, 1983) and potato (Lee, 1971). Treatment with Al reduced Fe in leaves and roots of *Zea mays* (Gerzabek & Edelbauer, 1986).

In oat plants, Al interferes with the reduction of Fe^{3+} to Fe^{2+}, a process essential for normal Fe metabolism. Fe-deficiency chlorosis was found to be a common symptom of Al toxicity in *Sorghum* and in rice (Clark et al., 1981; Furlani & Clark, 1981; IRRI, 1974).

6. *Aluminum*

Aluminum sulfate increased the concentration of Al in plant parts of barley and rice (Alam, 1981, 1983) and also in other crops (Lee, 1971; Pavan & Bingham, 1982a; Rorison, 1965). The content in leaves depended on the period of treatment and concentration of Al in the nutrient medium as seen in *Trifolium repens* (Lee & Pritchard, 1984) and *Anabaena cylindrica* (Pettersson et al., 1985). Al accumulation in *Lolium multiflorum* was enhanced in low pH (Ray & Robinson, 1984).

7. *Nitrogen*

Aluminum at concentrations 148 and 297 μM enhanced N concentration in both leaves and roots in *Trifolium repens* (Lee & Pritchard, 1984). Some reports are available of lowering of N concentration in aerial parts of *Vigna unguiculata* (Gomes et al., 1985; Mayz & Cartwright, 1984).

However, Al pretreatment (4×10^{-5} M) for 2 to 48 hours did not affect the root absorption of nitrate or ammonium by corn (Dovale et al., 1984) or N_2 fixation by nodulated *Stylosanthes* species at <100 μM (De Carvalho et al., 1982). In *Sorghum,* the amounts of total N accumulated and supplied to the aerial parts were drastically reduced in the presence of Al through effects on the root pressure (Gomes et al., 1985). However, other workers found that in the same species significantly higher amounts of amino acids accumulated in the Al treated plants (Cambraia et al., 1983a; Klimashevskii et al., 1970; Mosquim, 1977), possibly as a non-specific effect on N metabolism, mainly the proteins.

In cell sap, Al decreased the percentage of NO_3-N with a slight increase in the percentage of amino acid-N, indicating an interference with nitrate uptake as well as protein degradation (Gomes et al., 1985). Al possibly inhibits nitrate reductase (Foy & Fleming, 1982) and consequently, reduction and assimilation of N. The specific action of Al ions on nitrogenase activity is primarily responsible for the reduction in plant growth in the *Rhizobium–Pisum* symbiosis (Paulino et al., 1987). Increase in the free amino acid fraction might be the result of protein degradation (Possingham, 1956). The percentage of asparagine decreased but glutamine increased with Al level in the nutrient solution, indicating its interference in synthesis and/or interconversion of these amino acids (Bauer et al., 1977). NH_4-N nutrition increased the resistance to Al in spruce and beach seedlings (Van Praag et al., 1985).

8. *Copper*

Aluminum has to compete with Cu for the same binding sites at/or near the root surface (Hiatt et al., 1963). Al injury caused accumulation of Cu in root tissues of potato (Lee, 1971) and reduced Cu content in both roots and tops of *Sorghum* (Cambraia et al., 1983b).

9. *Phosphorus*

Aluminum precipitates P on the root surface, thus reducing its translocation to the tops (Clarkson, 1966; Hartwell & Pember, 1918; Helyar, 1978). The location of the interaction has been suggested to be either within the roots (Wright, 1943; Wright & Donahue, 1953), on the cell surface (Clarkson, 1966; Wallihan, 1948) or in the free space (Clarkson, 1966).

Decrease in P content in top was found to depend on Al concentration in rice (Alam, 1983), *Manihot* (De Carvalho & Cesar, 1984), *Acer* and *Gleditsia* (Thornton et al., 1986a, 1986b). Increasing Al concentration caused accumulation of P in the roots of various plant species (Mathan, 1980; Mugiwara et al., 1981; Thawornwong & Van Diest, 1974; Thornton et al., 1986c) but it was decreased in rice grains and straw concomitant with an increase in roots (Sarkunan & Biddappa, 1982). However, no effect on P metabolism was reported by Horst and Göppel (1986).

Pretreatment of *Sorghum* roots with Al decreased P uptake by 42% in Al-sensitive cultivars (Cambraia & Calbo, 1980). The disturbance of phosphate metabolism by Al^{3+} resulted in a marked decrease in the rate of sugar phosphorylation, probably effected by the inhibition of hexokinase (Clarkson, 1966). In yeast cells, Al inhibits the Mg-dependent enzyme hexokinase, responsible for sugar phosphorylation (Trapp, 1980). The formation of glucose-6-phosphate by the action of hexokinase on ATP apparently requires that the ATP first be combined with Mg. Since the affinity of Al for ATP is 40 times that of Mg, Al forms a highly stable Al–ATP complex, thus preventing the transfer of the terminal phosphoryl group to glucose by hexokinase (Foy, 1984).

C. INTERACTION WITH CALMODULIN

During the interactions of Al with plant cells, the root plasma membrane (Hampp & Schnabl, 1975; Vierstra & Haug, 1978) and cytosolic-calcium regulating proteins are potential targets (Foy et al., 1978; Haug & Caldwell, 1985). Al binds stoichiometrically and cooperatively to calmodulin (Siegel & Haug, 1983a), a key cytosolic protein for Ca regulation in plant and animal cells (Cheung, 1982; Klee & Vanaman, 1982). The pronounced structural changes induced lead to the inhibition of Ca and calmodulin-dependent enzymes, cyclic nucleotide phosphodiesterase and membrane bound ATPase activity (Siegel & Haug, 1983a, 1983b). Micromolar levels of Al induced a helix-coil transition in calmodulin (Siegel & Haug, 1983a), accompanied by pronounced thermodynamic alterations and enhanced its hydrophobic surface exposure.

The binding of Al to calmodulin seems to be specific regarding the differences in charge, the crystal and ionic radii (Nightingale, 1959) and thermodynamic binding characteristics (Siegel et al., 1983; Tanokura & Yamada, 1983). Al is speculated to exclude Ca from its binding sites (Hanson, 1984). The two ions compete for binding sites on phosphatidylserine membranes (Deleers, 1985). However, Kinraide and Parker (1987) suggest that instead of displacing Ca from critical sites, Al occupies other sites from which it can be displaced by cations, e.g., calmodulin.

Presence of certain organic acids like citrate in sufficient concentrations may enable the plant cell to detoxify Al entering the cell, possibly by protecting calmodulin from Al injury, allowing unimpaired signaling or amplification of Ca changes by the regulatory protein. Humiferous substances in soil are rich in carboxylate ligands, which are potential binding sites for Al chelation (Haug, 1984) and thus they generally improve crop production.

V. Absorption of Aluminum in Non-metabolic Conditions

A. EFFECT OF LOW TEMPERATURE

Aluminum uptake by excised cucumber, buckwheat and rice roots at 30°C was higher than at 2°C up to about 20 minutes. There was little increase thereafter, suggesting that most of it may be adsorbed by Donnan free space (Wagatsuma, 1983a). However, effects of low temperature on Al uptake in barley, cabbage and kikuyu grass roots were negligible (Clarkson, 1967; Huett & Menary, 1979).

B. EFFECT OF METABOLIC INHIBITORS

Most inhibitors increase Al uptake (Huett & Menary, 1979), suggesting an energy-dependent transport. They might act on the root cell membrane by injuring it or causing structural changes (Wagatsuma, 1983a).

C. EFFECT OF N_2 GAS

Nitrogen irreversibly injured the membranes of the cells of the cortex endodermis which are regarded as the barriers (Wagatsuma, 1983a).

Thus, if the metabolic or structural function of the roots is impaired, roots may be injured by large amounts of Al and finally may suffer from Al toxicity appreciably. Therefore, to minimize Al toxicity, the maintenance of the physiological function of the roots and the improvement of the root environment, i.e., aerobic conditions may be required.

VI. Tolerance of Aluminum

Since drought (Boyer, 1982) and aluminum (Foy et al., 1978) represent severe, partially interrelated environmental stress factors, development of aluminum-tolerant crop cultivars with deep root penetration is of paramount importance. No systematic efforts have been undertaken to incorporate traits of Al tolerance into crop production (Reid, 1979; Rhue, 1979), possibly due to lack of information on molecular processes involved and on adequate screening techniques for Al tolerance (Haug & Caldwell, 1985).

A. MECHANISMS

Various hypotheses have been formulated to explain the mechanism of plant tolerance to Al. The exact physiological mechanism remains unknown, probably due to varied effects of the element in plants (Cambraia et al., 1983a). Tolerance may be different in different species and varieties and seems to be controlled by more than one gene (Foy, 1984; Foy et al., 1978). A specific tolerance mechanism seems to be controlled by a dominant gene (Reid, 1979). Tolerance in maize appears to be controlled at a single locus by a multiple allele series (Rhue, 1979). A single dominant gene for Al tolerance in wheat was also postulated by Kerridge and Kronstad (1968).

Tolerant plants must either be able to reduce the absorption by the roots or to detoxify Al after absorption (Foy & Fleming, 1978). Both mechanisms can operate in the same plant. In *Sorghum,* tolerant cultivars adsorb more Al in the free spaces of the root system than the sensitive ones. However, an appreciable amount penetrates the cell, indicating an internal mechanism as well (Calbo & Cambraia, 1980). In oats, buckwheat, hydrangea and blueberry, tolerance may be due to exclusion of Al ions by the plasmalemma in root cells (Wagatsuma et al., 1987a).

The considerable differences in Ca, Mg and P concentrations of the roots between Al-tolerant rye and lupin do not suggest a common physiological mechanism (Horst & Göppel, 1986), though the differences in tolerance have been related to Ca- and Mg-absorbing ability of the roots (Saneoka et al., 1986).

Wheat tolerance to Al is a relative rather than an absolute characteristic, depending on temperature as well (Camargo, 1983). There is a possible role of the synthesis of inducible Al-binding protein in the mechanism of Al tolerance (Aniol, 1984).

Foy (1984), after reviewing the literature, suggested many ways of tolerance among crop cultivars, which have been briefly discussed below.

1. pH Changes in Root Zones

Some tolerant cultivars of wheat, barley, rice, pea and maize (inbreds) increase the pH of the nutrient solutions and thus decrease the solubility and toxicity of Al by precipitation (Foy et al., 1978). Differential Al tolerance has in some cases been attributed to the differences in the pH caused by the difference in the absorption of cations and anions (Foy et al., 1965, 1967, 1969, 1974; Mugiwara et al., 1976; Rhue & Grogan, 1977).

2. Uptake and Distribution

Aluminum-tolerant plants may be grouped according to where aluminum accumulates within their tissues. In one group, tolerance apparently involves an exclusion mechanism as in some cultivars of wheat, barley, soybean, snapbean and triticale (Foy, 1974; Klimashevskii et al., 1976; Mugiwara et al., 1981).

In a second group plants show less Al in plant tops and more in roots, such as in azalea, cranberry, rice, triticale, rye, alfalfa clones, wheat, barley and potato (Foy et al., 1978), tomato genotypes (Baumgartner et al., 1976), populations of paper birch (Steiner et al., 1980) and kikuyu grass, compared with Al-sensitive cabbage and lettuce (Huett & Menary, 1980).

In a third group, tolerance is directly associated with accumulation in tops. Such plants show high internal tolerance. Examples are tea, certain Hawaiian grasses, pine trees, mangrove (Foy et al., 1978), flowering dogwood (Crum & Franzmeir, 1980), river birch (Bartuska & Ungar, 1980) and mouse ear cress (Tingey et al., 1982).

In tolerant tea plants, Al is bound to cell walls of epidermal and mesophyll cells and thereby prevented from reaching critical metabolic sites within the cells (Memon et al., 1981).

In barley cultivars, tolerant varieties exclude Al actively outside the plasmalemma of the root cells. It may polymerize and/or react with P to precipitate out Al. Consequently in such cultivars, the Al content may be low in the root protoplasts, high in the whole root tissue and the contents of Ca or other nutrients may be high in the roots (Wagatsuma & Yamasaku, 1985).

3. Nitrogen Nutrition

Part of N metabolism may also be involved in the mechanism of tolerance as discussed earlier. The superior tolerance of some species may be related to their abilities to use NO_3-N in the presence of NH_4-N and to increase the pH of the growth medium or rhizosphere (Dodge & Hiatt, 1974; Foy & Fleming, 1978; Foy et al., 1978) or to nitrate reductase activity (Foy & Fleming, 1982). The synthesis of some unknown specific protein has been suggested as related to Al tolerance (Klimashevskii et al., 1970). Mesdag et al. (1970) found high protein in the wheat grain of tolerant varieties but no such relationship was observed in 55 spring wheat varieties (Aniol & Kaczkowski, 1979).

4. Calcium Nutrition

Calcium is well known for its ability to relieve Al toxicity (Alva et al., 1986). In wheat seedlings the order of effectiveness of different cations was found to be Ca^{2+} Mg^{2+} Sr^{2+} K^{+} Na^{+}, the effectivity depended on the competition between the cation and Al for external binding sites (Kinraide & Parker, 1987).

Aluminum tolerance in certain cultivars of wheat, barley, soybean and snapbean has been associated with the ability to resist Al-induced Ca deficiency (Foy et al., 1978). In tolerant barley cultivars the uptake of Ca or other cations is less inhibited leading to a consequent increase in their contents (Wagatsuma & Yamasaku, 1985).

5. *Phosphorus Nutrition*

In many plants, Al tolerance appears to be closely related to P use efficiency, such as toleration of lower P levels in maize (Foy et al., 1978), absorption and use of P in presence of Al (Klimashevskii et al., 1979), lower P requirement in tomato (Baumgartner et al., 1976), absorbance of more P per unit of root length in soybean (Sartain, 1974).

6. *Aluminum and Plant Membranes*

Tolerance of Al was related to higher Al stress of plasmalemma in *Spirogyra* (Hofler, 1958) and in barley cultivars (Hecht-Buchholz & Foy, 1981).

Exclusion of Al by plasma membrane was not found in wheat varieties (Aniol, 1983; Caldwell & Haug, 1982; Niedziela & Aniol, 1983) and in *Vicia, Lupinus, Hordeum* and *Secale* (Horst & Göppel, 1986).

7. *Interaction of Aluminum with Magnesium, Silicon and Potassium*

Aluminum tolerance has been associated with greater uptake of K and Mg in potato cultivars and with greater Mg uptake in maize inbred lines (Foy, 1984). Certain Al-tolerant rice cultivars accumulate high levels of Si in the epidermal cells of their leaves. Silicon is known to reduce the toxicity of Mn in barley leaves and could play a similar role in detoxifying Al (Foy et al.,1978).

8. *Aluminum Water Relationships*

Aluminum-sensitive barley varieties are more sensitive to aluminum induced water stress than aluminum-tolerant varieties (Krizek & Foy, 1981).

9. *Organic Aluminum Complexes*

Organic acids may form soluble complexes with Al to eliminate its toxicity (Barlett & Riego, 1972; Foy et al., 1978; Jayman & Sivasubramaniam, 1975; Jones, 1961). This capacity is directly related to the relative positions of OH/COOH groups on the main carbon chains, favoring the formation of stable 5- or 6-bond ring structures with Al (Hue et al., 1986).

In tea plants high Al tolerance was attributed to chelation (and detoxification) of Al by organic acids and phenols (Sivasubramaniam & Talibudeen, 1972). Substantially higher concentrations of citric acid were found in tolerant varieties of pea, maize and barley (Klimashevskii & Chernysheva, 1980). Fifty-five percent more accumulation of organic acids occurred in tolerant cultivars of *Sorghum* (Cambraia et al., 1983a). However, another report gives a low intracellular chelating capacity of organic acids for the trivalent element in *Sorghum* (Guerrier, 1982).

A possible detoxification mechanism seems to consist of protecting calmodulin from Al injury, allowing unimpaired signaling or amplification of Ca changes by the regulatory protein (Caldwell & Haug, 1982).

VII. Beneficial Effects of Aluminum

Although aluminum is a non-essential metal, low concentrations are sometimes reported to be beneficial to many plants such as rice (Howeler & Cadavid, 1976), tropical legumes (Andrew et al., 1973), eucalyptus (Mullette, 1975), tea (Matsumoto et al., 1979), peach (Edwards et al., 1976), sugar beet (Kesar et al., 1975), maize inbreds (Clark, 1977) and wheat (Foy & Fleming, 1978).

The mechanism of beneficial effects may be different for different plant genotypes and possible explanations include (Foy, 1984):

(i) Increasing the solubility and availability of Fe in calcareous soils (through hydrolysis of Al and lowering of pH).

(ii) Correcting or preventing Fe deficiency.

(iii) Blocking negatively charged sites on cell walls and thereby promoting P uptake (Mullette, 1975).

(iv) Correcting or preventing P toxicity (Clark, 1977).

(v) Altering the distribution of growth regulator in roots of peach seedlings (Edwards et al., 1976).

(vi) Preventing toxicities of Cu (Liebig et al., 1942) and Mn (Rees & Sidrak, 1961).

(vii) Serving as a fungicide (Ko & Hora, 1972; Lewis, 1973; Muchovej et al., 1980).

(viii) Reducing undesirable top growth in N-rich nursery stock (Borkenhagen & Iyer, 1972).

VIII. Toxic Symptoms

Cationic Al has been implicated as early as 1918 in root growth retardation in barley and rye plants grown on acidic soil (Hartwell & Pember, 1918). Since then, the attention of plant ecologists has been focused on Al as an important factor preventing the growth of calcicole and non-calcifuge species in acid soils (Clarkson, 1963; Clymo, 1962; Hackett, 1964; Rorison, 1960).

A. ON MORPHOLOGY

1. On Roots

Aluminum was found to induce similar abnormalities in the root systems in a wide variety of species. These include dwarfing of roots (Kerridge et al., 1971), reduction or inhibition of the growth of main axis of root with consequent dwarfism, thickening and mottling (Alam, 1981); initiation of numerous lateral roots, the growth of which is subsequently reduced (Horst & Göppel, 1986). These abnormalities frequently give rise to root systems resembling coralloid mycorrhiza (Clarkson, 1965) and reduced root elongation and branching as in *Gleditsia* (Thornton et al., 1986b). Al injured roots are characteristically stubby and brittle. Root-tips and lateral root become thickened and brown (Foy, 1984).

2. *On Stem*

Decrease in shoot growth was observed after Al treatment in rice (Fagria, 1982), in coffee (Pavan & Bingham, 1982a, 1982b), in barley (Alam, 1981), in *Manihot esculenta* (De Carvalho & Cesar, 1984), and in *Gleditsia* (Thornton et al., 1986b, 1986c).

3. *On Leaf*

Younger leaves become small, curled along the margin and chlorotic, while older leaves show a marginal chlorosis which progresses to the center of leaf in coffee plant (Pavan & Bingham, 1982a). Similar chlorotic effect with subsequent lethality was found in rice (Miyazawa et al., 1981).

Aluminum reduces significantly the yield in rice at >24 ppm (Sarkunan et al., 1984), at >100 ppm (Miyazawa et al., 1981) and in peanut (Blamey, 1983). Yield of *Cajanus cajan* increased with increasing soil pH, decreasing exchangeable Al content and increasing exchangeable Al:Ca ratio (Abruna et al., 1984). Al decreases dry weight of tops and roots, length of roots and plant height in rice (Fagria, 1982).

Plants with more than 4000 ppm Mn and 1000 ppm Al show lower growth, shortening of internodes, development of lateral buds, small crinkled leaves with downward capping, chlorosis, necrotic spots, delayed and reduced blossoming and pod filling (Menten et al., 1981). In some plants the foliar symptoms resemble those of P deficiency (overall stunting, small, dark green leaves and late maturity, purpling of stem, leaf veins, yellowing of leaf tips) and in others Ca deficiency, like curling or rolling of young leaf and a collapse of the growing point or petioles (Foy, 1984).

B. ON CHLOROPHYLL AND PHOTOSYNTHESIS

Chlorophyll a and phycocyanin were decreased in *Anabaena cylindrica* following Al treatment. This was accompanied by ultrastructural changes such as accumulation of cyanophycin granules and degradation of thylakoids (Pettersson et al., 1985). Similar reduction in quantity of chlorophyll pigments was reported in rice (Sarkunan et al., 1984) and buckwheat

(Sung & Kwon, 1980). In rice the ratio between chlorophyll a and b also declined, accompanied by a marked decrease in gross photosynthesis and photosynthetic rate (Sarkunan et al., 1984). In isolated spheroplasts of *Cyanobacterium synechococchus* and chloroplasts of *Beta vulgaris* Al^{3+} stimulated photosystem II, catalyzed electron flow and O_2 evolution and suppressed photosystem I mediated electron transport (Wavare et al., 1983).

C. ON RESPIRATION

In rice, the total respiratory rate decreased with increased supply of Al, following reduction of the soluble carbohydrates, including reducing sugars which formed the substrate for respiration (Sarkunan et al., 1984). Treatment for 2 hours reduced respiration in peripheral cap cells, epidermal cells of root apex and quiescent center in maize. Within 12 hours only isolated respiratory activity remained. Al also inhibits the metabolic activity of apex cells immediately (Bennet et al., 1985b).

Aluminum does not have any effect on mitochondria. Reduced respiration following Al treatment seems to reflect a decline in energy requirement rather than a direct consequence. Reduced mitotic activity could not be related to reduced respiration (Bennet et al., 1985b; Clarkson, 1969).

D. OTHER PHYSIOLOGICAL EFFECTS

Other physiological activities were affected adversely by Al resulting in a serious physiological stress (Sarkunan et al., 1984).

Excess Al in most plants interferes with cell division, decreases root respiration, interferes with certain enzymes governing the deposition of polysaccharides in cell walls, increases cell wall rigidity and interferes with uptake, transport and use of several elements and water (Barber, 1974). Al also decreases protein and RNA content in rice (Sarkunan et al., 1984) and high bond energy P in pea (Dedov & Klimashevskii, 1976). Thus, the availability of energy compounds like ATP for metabolism becomes limited.

Root-tip, main root, main stem and the proximal stems show an enhancement of peroxidase and polyphenol oxidase activity in *Pisum* seedlings (Henry et al., 1981).

Soluble sugar increased in *Sorghum* when treated with Al up to 2 ppm and then remained nearly constant (Cambraia et al., 1983a). The increase was due to reduction in photorespiration (Rodrigues, 1979), hexose phosphorylation (Clarkson, 1966) and cell wall polysaccharide synthesis (Huck, 1972). *Brachiaria* and *Cenchrus,* two pasture grasses, show a decrease in root cation exchange capacity when given 1.5 ppm Al (Fernandes et al., 1984).

E. EFFECTS ON CELL DIVISION AND CHROMOSOMES

There are very few reports about the cytotoxicity of aluminum salts on plants (Sharma & Talukder, 1987).

In the secondary roots of *Vigna unguiculata,* cell division was drastically reduced after 5 hours of Al treatment and completely inhibited within 10 hours, to restart after 18 hours. Inhibition was due to an accumulation of Al in the root-tip and did not involve any nutrient deficiency. This recovery, even with continuous supply of Al, was considered as an adaptive mechanism (Horst et al., 1983).

Though found in DNA and nuclei of meristematic cells (Morimura et al., 1978; Naidoo et al., 1978), Al was detected in the root cap initials only after 12 hours and a longer period is needed to reach the quiescent center and mitotically active cells of the root meristem (Bennet et al., 1985). Thus, the action of Al on mitoses may be indirect, through the integrated control function of the root meristem.

In *Vicia faba* aluminum chloride and sulfate at 0.1, 0.05, 0.01, 0.001 and 0.0001 M concentrations after 24 hours of incubation induced mitodepression, irreversible at higher concentration. Chromosomal aberrations (fragmentation and bridges in anaphase or telophase), micronuclei, binuclear cells and inhibited elongation of roots were also recorded. Aluminum chloride was clastogenic while Al sulfate disturbed spindle formation. The former was a stronger inhibitor of mitosis (Wojciechowska & Kocik, 1983).

Chronic treatment of *Allium sativum* bulbs with 10^3, 10^2, 10 and 1 ppm of aluminum sulfate led to a dose and time dependent decrease in mitotic index and enhancement of abnormal cells. Acute treatment of *Pisum sativum* seeds showed a similar effect (Roy, unpubl.).

Aluminum in concentrations of 0.02–1.85 mM and exposure times of 2 hours to 48 hours inhibited DNA synthesis and depressed [^{3}H] thymidine uptake in wheat (Ulmer, 1979; Wallace & Anderson, 1984).

Earlier studies indicated that nucleic acids might provide many adsorption sites for Al which may upset DNA replication (McLean & Gilbert, 1927; Naidoo et al., 1978). In barley cells, division was stopped by Al treatment but DNA synthesis continued. However, the synthesized DNA has an unusual base composition and is metabolically labile (Sampson et al., 1965).

The effect of Al on cell division has been frequently associated with DNA synthesis (Clarkson, 1967; Morimura et al., 1978; Naidoo et al., 1978), which concept is in accord with the location of Al in the nuclei of meristematic cells (Matsumoto et al., 1976; Morimura et al., 1978; Naidoo et al., 1978). In *Pisum,* Al is bound preferentially with DNA and once bound is not easily dissociated in vivo. Al was suggested to increase the melting temperature (T_m) of DNA by binding phosphate and stabilized the DNA helix which would lead to limited template activity. Primal binding site of Al^{3+} is the phosphorus group in DNA (Matsumoto et al., 1976). The binding of Al to DNA may even be altered by histones thus influencing the template activity. It may explain the adverse effect on cell division reported by Clarkson (1965, 1969).

Aluminum fixed in cytoplasm was probably bound to RNA and membranes and could interfere with protein and energy production (Naidoo et al., 1978). Al probably accumulated by ionic exchange onto esteric P in the nucleic acids and membrane lipids (Naidoo et al., 1978).

Aluminum does not interfere directly with spindle formation or chromatid separation (Clarkson, 1965). Due to the ease of binding between Al^{3+} and P, Al may destabilize the DNA (Matsumoto et al., 1976).

Aluminum also caused an abnormal distribution of ribosomes on the endoplasmic reticulum of barley root cells, thus interfering with protein synthesis (McLean, 1980). $AlCl_3$ increased the firmness and decreased the solubility of protein/casein fibers in broad bean (Schmandke et al., 1979). Aluminum was also believed to form coordination complexes with carboxyl and sulfhydryl groups of the protein, resulting in a cross-linkage (Foy, 1984).

Inhibition in cell division was reported within 5–6 hours of Al treatment (Clarkson, 1965; Horst et al., 1983; Sampson et al., 1965). However, it takes a longer time for Al to reach the mitotically active nuclei in *Zea mays,* suggesting that Al acts indirectly on mitosis through the integrated control function of the root. Control must operate at two levels: on the function of the Golgi apparatus of the peripheral cap and on communication with mitotically active cell populations. Al^{3+} may also disrupt the electric field, guiding the directional and selective flow of secretory vesicles in the Golgi apparatus (Giulian & Diacumakes, 1976; Morrè, 1977).

Control through communication with mitotically active cell populations can be achieved either through alteration of hormone gradients within the root meristems as a consequence of damage to the endoplasmic reticulum, which is a hormone-binding site (Raven & Rubery, 1982) or through the release of hydrolyzing enzymes contained in the Golgi apparatus after being damaged by Al.

IX. Aluminum Toxicity as Related to Forest Ecosystems

Disturbances in the ecosystems, whether natural or man-made, often enhance ecosystem stress and reduce tree vigor (Smith, 1981, 1984, 1985). SO_2 and nitrogen oxides, together with HCl and other compounds, mix in the atmosphere with oxygen and water vapor to form solutions of mineral acids. These substances are deposited on the soil as acid rain, snow or fog (Klein, 1985). In North America, acid precipitation in the range of pH 2.3 to 5.0 has been shown to leach essential nutrients, particularly base cations, like K, Ca and Mg from the leaves of sugar maple, yellow birch and white spruce. In West Germany, foliar leaching has been associated with the compensatory mechanism of increased uptake of nutrients from the soil (Bartuska et al., 1985). Acid deposition was found to accelerate the normal soil acidification process, with consequent leaching of essential nutrients from the soil (Ulrich et al., 1981).

A potential effect of increased acid deposition in forests is the solubilization and mobilization of Al through increased anion concentration (Bache, 1985; Crenan & Schofield, 1979).

Aluminum activity in soil is determined by the soil pH and amount of exchangeable Al present. The toxicity induced is particularly severe below pH 5.0 but has been reported even at pH 5.5 (Peterson & Girling, 1981). In highly acidic soils, Al hydroxysulfate (Al $OHSO_4$) may exist as an intermediate product, buffering proton concentration. It is ultimately dissolved at low pH to produce Al and SO_4 as soil percolates (Khanna et al., 1987).

The high level of Al induced by acid deposition has been suggested to be a major cause of tree decline and dieback (Klein, 1982; McLaughlin, 1985). In general, monomeric soil Al concentration depends on acidity and may become high enough to cause phytotoxicity into some trees below pH 4.0 (Pavan & Bingham, 1982a, 1982b), with adverse effects on the Ca and P levels. Hydroponic studies with the honeylocust (*Gleditsia triacanthos* L.) seedlings have shown that treatment with Al significantly lowered the concentrations of Ca and Mg in the young leaves. Leaf size, production, expansion rate and plant height were also reduced (Thornton et al., 1986a). Other trees, found to be sufficiently Al-sensitive to be affected by the levels of Al found in acid soils, include conifers (Hutchinson, 1985), sugar maple (Thornton et al., 1986b) and poplar hybrids (Steiner et al., 1984). A similar sensitivity has been reported in clover (Wright & Wright, 1987). Though earlier Al tolerance in trees was suggested to be higher than in field crops (McCormick & Steiner, 1978), yet further studies have shown high sensitivity in certain trees as well (Thornton et al., 1986c).

However, the relationship between soil acidification, Al content and tree decline is also affected by several factors, including the site and the tree species. Thin soils with restricted root zones are more vulnerable than richer, deeper soils with high concentrations of Ca and K. Melting of the spring snow leads to release of Al and other metals into the soil and consequent periodic increase in acidity. In fact, 1 to 2 mg per liter of Al soil solution could damage root systems. Amounts recorded have been much higher than this threshold, reaching 6 mg of Al per liter under beech and 15 mg under spruce forests (Matzner & Ulrich, 1981). The threshold for root damage in forests in Norway is much higher (80 to 160 mg Al per liter, Bartuska et al., 1985). These differences have been attributed to site-specific higher levels of Ca. Thus, soil acidification and Al toxicity appear to be major problems in the middle to higher elevation spruce-fir forests of central Europe growing on mineral soils with poor felling capacities (Ulrich et al., 1980). Acid rain poses a less harmful prospect in the higher elevation forests in the eastern USA, found mostly on organic soils (Friedland et al., 1984; McCormick, 1985).

A significant decline in the density of maples, beech and red spruce, along with loss of biomass recorded in the mature forest of Camels Hump Mountain in northern Vermont, USA, has been associated with air pollution, including acid deposition (Vogelmann et al., 1985). Toxic heavy metals are present in the precipitation (Scherbatskoy & Bliss, 1983), increasing the soil burden of metals, including mobilized Al at a pH close to 3.3 in melting snow (Friedland et al., 1984).

A further effect of acidic conditions is reduction of microbial respiration and CO_2 evolution from litter. Reduction in litter decomposition may be due to repression of litter-degrading microflora by precipitation acidity and increased availability of metals like Al in the soil (Moloney et al., 1983). The foliar leaching by acidic solution has been attributed to cation exchange (Scherbatskoy & Klein, 1983).

Nitrification in soils was not affected by acidic treatment; NO_3-N percolates increased when acidic simulated rain was supplemented by ammonium and nitrate ions (Like & Klein, 1985).

Nitrogen availability is a limiting factor in natural forests. For example, red spruce needs high nitrogen for best growth but acidity and soluble metals in the root environment are unlikely to be important factors in nitrogen transformation in roots (Yandow & Klein, 1986). At pH 3.0, Zn and Al repressed nitrate reductase induction.

Thus, with progressively increasing environmental metal load and consequent acid rain, soil acidification is enhanced, albeit periodically, and Al plays a major role in the loss of specific tree species as well as lower total vegetational cover at specific sites.

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