Environmental Hazards of Aluminum to Plants, Invertebrates, Fish, and Wildlife

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I. Introduction

Aluminum (Al) is the third most common mineral and the most common metal in Earth's crust, accounting for approximately 8.1% of the crust by weight. Thus, it cannot be considered a contaminant in the usual sense of the word. However, despite its near omnipresence throughout the world, Al has been of major concern as a primary limiting factor to cultivated plants for several decades. In much of the world, Al severely restricts the growth and presence of plant species. Since the late 1970s, concern about Al toxicity has spread to natural habitats, most notably forests and aquatic communities. The primary impetus for this concern has been the increased awareness of the effects of anthropogenic acidification through mine drainage, acid deposition, and other sources. The toxicity of Al is intimately associated with pH in that the metal is soluble and biologically available in acidic (pH <5.5) soils and waters but relatively innocuous in circumneutral (pH 5.5–7.5) conditions. Forest die-offs and reduced survivorship or impaired reproduction of aquatic invertebrates, fish, and amphibians have been directly connected to Al toxicity. Indirect effects on birds and mammals also have been identified. The purpose of this review is to summarize the toxic effects of Al to populations and to evaluate the potential hazards to the communities in which these populations are found.

II. Sources and Environmental Chemistry of Aluminum

Although Al is ubiquitous in soils, it varies from 0.4% of total weight in carbonates to 9.4% in marine clays (Table 1). Across the United States, soils in Florida and parts of Georgia, Texas, Oklahoma, and Michigan are less than 2.0% Al, whereas portions of the Pacific Northwest, New England, Colorado, and Nevada have concentrations greater than 8.0%.

Aluminum can occur in many forms in soil. The metal occurs principally as tetrahedral and octahedral crystals of aluminosilicates. However, it may also combine with other substances to form amorphous or crystalline clays and sesquioxides, aluminum phosphates, or ionically bound organic compounds (Driscoll and Schecher 1990).

The biogeochemical cycling of the metal is complex (Driscoll and Schecher 1988). In the lithosphere, its primary reservoir, Al may be found as part of the mineral component of the soil or bound to charged soil and organic particles. Under circumneutral to slightly alkaline conditions (pH 6.0–8.0), Al has low solubility and is essentially biologically inactive. In alkaline soils and solutions (pH >8.0), the solubility of Al increases but its bioavailability is poorly known. Weathering or acidification to pH below 5.5 increases the dissolution kinetics of Al and places some of the metal into solution. Its dissolved form is most readily assimilated by living organisms.

Once in solution, Al may combine with several organic complexes, especially oxalic, humic, and fulvic acids. The metal may also combine

Table 1. Synoptic list of ambient aluminum levels in soil and water.

Source	Aluminum level	pH	Comments	References
Igneous rock	81,300 $mg \cdot kg^{-1}$		composite	1
Basalt	83,000 $mg \cdot kg^{-1}$		composite	1
Granite	67,000 $mg \cdot kg^{-1}$		composite	1
Sandstone	25,000 $mg \cdot kg^{-1}$		composite	1
Limestone	4000 $mg \cdot kg^{-1}$		composite	1
Shale	82,000 $mg \cdot kg^{-1}$		composite	1
Clay	86,000 $mg \cdot kg^{-1}$		composite	1
Marine clays	94,000 $mg \cdot kg^{-1}$		composite	2
Coal	10,000 $mg \cdot kg^{-1}$			2
Atmosphere	0.04–0.39 $\mu g \cdot m^{-3}$		median value	3
Precipitation	520–1,120 $\mu g \cdot L^{-1}$		median value	3
Snow	56–1,300 $\mu g \cdot L^{-1}$		median value	3
Adirondack lakes	4.3–21.9 $\mu g \cdot L^{-1}$	5.9–7.1	155 lakes sampled	4
Adirondack lakes	69.9–208 $\mu g \cdot L^{-1}$	4.7–5.1	179 acidic lakes	4
Maine lakes	18.9–472 $\mu g \cdot L^{-1}$	4.7–6.8	5 lakes	5
Florida	Median, 37.8 $\mu g \cdot L^{-1}$	4.9	260 Panhandle lakes	6
Florida	Median, 56.7 $\mu g \cdot L^{-1}$	6.4	845 northern lakes	6
Florida	Median, 40.5 $\mu g \cdot L^{-1}$	6.8	945 southern lakes	6
Florida	20–270 $\mu g \cdot L^{-1}$	4.4–5.6	14 acidic lakes	6
Wisconsin	35–172 $\mu g \cdot L^{-1}$	4.6–5.5	4 clearwater lakes	7
New Jersey	13–508 $\mu g \cdot L^{-1}$	3.6–6.2	6 acidified lakes	8
Ontario, Canada	73–1097 $\mu g \cdot L^{-1}$	4.0–5.6	7 lakes near smelter	9
Coal pile leachings	6–480 $\mu g \cdot L^{-1}$	6.6–4.8	above and below drainage	10
Kentucky stream	65–26,500 $\mu g \cdot L^{-1}$	8.5–2.6	above and below acid mine drainage	11

References: (1) Goldschmidt 1958; (2) Freedman and Hutchinson 1986; (3) Havas 1986a,b; (4) Driscoll et al. 1991; (5) Kahl et al. 1991; (6) Pollman and Canfield 1991; (7) Cook and Jager 1991; (8) Sprenger et al. 1987; (9) Yan and Dillon 1984; (10) Tan and Coler 1986; (11) Short et al. 1990.

with inorganic molecules including sulfate (SO_4^{2-}), fluoride (F^-), phosphates (PO_3^{3-}), bicarbonates (HCO_3^-), or hydroxides (OH^-), depending on the relative concentrations of these anions. Biological activity and toxicity vary with composition. For example, Al sulfates are generally considered less toxic than hydroxide or organically bound Al (Driscoll and Schecher 1988). Aqueous Al (Al^{3+}), however, is more chemically and biologically active than that bound in soil or sediments.

The biological cycling of Al is considered unimportant to the overall balance of the metal. It is most likely not an essential element to life (National Academy of Sciences 1980) and is not stored in appreciable quantities within any tissue. Most ingested Al is rapidly excreted; it then reenters reservoirs in the lithosphere or hydrosphere.

The environmental chemistry of Al is essentially driven by pH, hence its toxicity is interwoven with that of hydrogen ion (H^+). Increased mobilization in acidic soils leads to a series of events including (1) greater availability to plants through increased concentrations in soil solutions; (2) general downward leaching in temperate podzolic soils with decreased concentrations in upper layers (i.e., A horizon) and concomitant increases in lower layers (B horizon); and (3) gradual removal from soil into streams and lakes of acidified watersheds. The bioavailability of Al is reduced in organically rich soils due to binding between cationic forms of Al and negatively charged organic molecules. High levels of phosphate in soils may also reduce bioavailability by precipitating $AlPO_4$. The cation-exchange capacity of soils, which is largely determined by calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), and sodium (Na^+) ions, also ameliorates the availability of Al through competition for binding sites on soil particles (Cronan and Schofield 1990).

Once in solution, Al can take several forms, depending on pH and, secondarily, on other constituents. Driscoll and Schecher (1990) presented a categorization of Al species that is widely used in the scientific literature. Total Al refers to all forms, dissolved and undissolved, in water. Dissolved, or monomeric Al, can be separated into organically bound (nonlabile) and labile (Al^{3+}), with Al^{3+} possibly combining with one of the anions mentioned previously. The concentration of the labile form increases with acidity. Aluminum concentrations in streams and lakes impacted by acidification tend to follow seasonal trends, with the greatest levels in early spring following snowmelt (Herrmann et al. 1989; Sprenger et al. 1987).

The greatest concern for Al toxicity is associated with anthropogenic acidification of watersheds. Numerous studies have found that concentrations of the more toxic monomeric species increase in soil and water with acidification. For example, in circumneutral, oligotrophic waters Al concentrations range from 0.2 to 20 $\mu g \cdot L^{-1}$ but may reach 1,000 $\mu g \cdot L^{-1}$ in some acidified lakes (Havas 1986a). However, dissolved Al levels may naturally exceed 10,000 $\mu g \cdot L^{-1}$ in acidic bogs (see Table 1).

The most extensive source of acidification in natural waterways is wet and dry acid deposition. Principal sources of this deposition include industrial and automotive emission. During the 1980s, an extensive effort was expended on determining the extent and effects of acid deposition in North America (NAPAP 1991). It was estimated that, within most of the U.S., 20% of both streams and lakes could be considered acidic or threatened with acidification. Not all of these waterways are becoming acidified by anthropogenic processes, but many streams and lakes, especially in the northeastern part of the country and southern Canada, are affected by acid deposition. Many waters with pH below 5.5 have elevated levels of Al.

Surface mining can be an important factor in Al contamination of water because of the acidity associated with mining and because deeper soil horizons with higher metal concentrations are exposed to weathering and leaching. For example, river water pH dropped from 8.5 just above an acid mine inflow to a Kentucky river to 2.6 just below the inflow. Total Al levels increased from 65 $\mu g \cdot L^{-1}$ above to 26,500 $\mu g \cdot L^{-1}$ below the inflow. At 2.4 km below the inflow, pH returned to 8.3 and total Al was 219 $\mu g \cdot L^{-1}$ (Short et al. 1990).

Leachate from a coal pile that abutted a Massachusetts stream decreased pH in the stream from 6.6 to 4.8 and increased total Al from 6 $\mu g \cdot L^{-1}$ to 480 $\mu g \cdot L^{-1}$ (Tan and Coler 1986). Concentration of the monomeric form was positively correlated to acidity among 1977 spoil banks produced by surface mining of coal in Illinois (Haynes and Klimstra 1975). Spoil banks with pH below 3.1 had Al to 1920 $mg \cdot kg^{-1}$ ($\bar{x}$ = 525 $mg \cdot kg^{-1}$), those with pH 4.1–5.0 to 480 $mg \cdot kg^{-1}$ ($\bar{x}$ = 13.6 $mg \cdot kg^{-1}$), and those with pH above 8.0, $\bar{x}$ = 2.4 $mg \cdot kg^{-1}$ Al.

Other perturbations of soil or sediments can also increase concentrations of toxic Al. Extensive logging in an experimental forest decreased the pH of a nearby stream from 5.4 to 4.6 and increased labile Al more than sixfold from 27 $\mu g \cdot L^{-1}$ to 1620 $\mu g \cdot L^{-1}$ (Lawrence et al. 1987); levels remained elevated for more than 8 mon following removal of the trees. Alum [$Al_2(SO_4)_3$] used to precipitate particulates from wastewater can increase aqueous Al when discharged into acidic streams.

III. Effects on Plants

Aluminum has been recognized as a major limiting factor for plants in acid soils for over 50 years, and numerous original and summary papers have been written about the metal's phytotoxic effects in terrestrial and aquatic ecosystems (e.g., Crowder 1991; Fageria et al. 1988; Havas 1986b; Taylor 1988). Elevated levels in acidic soils, sediments, and water can alter the species composition of primary producers, reduce their vigor, and raise Al concentrations in wildlife foods.

A. Aquatic Plants

It is difficult to generalize about the toxic effects of Al in aquatic plants or other organisms because comparisons among studies are confounded by differences in experimental design, water chemistry, and physical characteristics. Studies vary from whole-lake or *in situ* experiments that examine toxicity under actual conditions to more rigidly controlled mesocosm or laboratory toxicity tests. Field studies are particularly difficult to compare because of differences in pH and concentrations of organic ligands or other cations. Controlled mesocosm studies present a more accurate analysis of the direct toxic effects of Al, but their simplified environments may produce results that cannot be directly applied to ponds and lakes. The most reliable information comes from a combination of both types of sources, but such studies are rare.

Aquatic plants apparently can tolerate higher levels of Al and acidity than aquatic invertebrates, amphibians, or fish. For example, several species of algae have been reported at pH less than 3.0 and dissolved Al above 100 $mg \cdot L^{-1}$ (Table 2) (Havas 1986b). *Charcium* spp., *Euglena mutabilis*, and *Pinnularia acoricola* survive at Al levels of 2500 $mg \cdot L^{-1}$ or greater.

The species compositions of algae typically change with reduced pH or elevated Al. Often, dominant species change and overall species richness decreases. For example, Havens and DeCosta (1987) compared algal communities in polyethylene mesocosms filled with lake water under three treatments: acidification to pH 4.5 (Ac), acidification with 300 $\mu g \cdot L^{-1}$ total Al (Ac + Al), and control (pH 7.0). Algal responses in both the Ac and Ac + Al treatments were similar. *Euglena* spp., *Chlorella vulgaris, Dinobryon divergens*, and *Arachnochloris minor* diminished or disappeared in both treatments as pH decreased, and dissolved Al increased to 180 $\mu g \cdot L^{-1}$. In contrast, *Chlamydomonas mucicola* and *Peridinum inconspicuum* increased in density with declining pH. The authors concluded that acid-tolerant species of algae were also likely to be Al tolerant.

In general, overall algal density declines and diatom and chrysophyte communities are replaced by dinoflagellates and chlamydomonads with elevated Al. Filamentous green algae, especially *Mougoetia*, however, may increase in biomass (Havens and Heath 1990). Under a regimen of slow acidification of mesocosms (pH drop from 8.5 to 4.5 and Al increase from

Table 2. Algae species that can live at aqueous Al levels greater than 1000 $\mu g \cdot L^{-1}$.[a]

Species	Al level ($\mu g \cdot L^{-1}$)
Chlamydomonas acidophila	810
Chlamydomonas applanata	1570
Characium sp.	2500
Cryptomonas sp.	600
Euglena mutabilis	3130
Eunotia arcus	212
Eunotia glacialis	800
Hormidium rivulare	411
Lepocinclis ovum	400
Migrathomnion strictissium	169
Nitschia communis	800
Nitschia elliptica	411
Nitschia subcapitellata	325
Pinnularia acoricola	2500
Ulothrix zonata	138
Zygongonium ericetorum	411

[a]After Havas 1986a,b.

below detection limits to 180 $\mu g \cdot L^{-1}$), filamentous blue-green algae, particularly *Aphanizomenon flos-aquae*, was replaced by cryptophytes, chrysophytes, and nanochlorophytes. *Peridinium inconspicuum*, *Cryptomonas erosa*, and *Chlamydomonas globosa* predominated early during acidification but subsequently were replaced by *Closterium* spp. The addition of Al did not alter the final outcome of the experiment but caused some of the changes to occur earlier than acidification alone.

Pillsbury and Kingston (1990) demonstrated an effect of Al beyond that of acidification alone. Their treatments consisted of lake water (pH 5.7) with 50, 100, or 200 $\mu g \cdot L^{-1}$ Al, untreated lake water (pH 5.7), and water acidified to pH 4.7 without Al addition. The diatom *Asterionella ralfsii* dominated in the lake water and acid treatment but decreased with the addition of 50 $\mu g \cdot L^{-1}$ Al and nearly disappeared at 100 $\mu g \cdot L^{-1}$; various desmid species showed similar patterns. Population levels of *Peridinum limbarum, Dinobryon bavaricum,* and *Elaklothrix* spp. declined with the addition of 200 $\mu g \cdot L^{-1}$ Al.

Aluminum may bind with phosphorus (P) and reduce its availability to primary producers. Nalewajko and Paul (1985) observed a greater precipitation of both elements at pH 6.1 and 6.9 than at pH 4.5 and that precipitation of P increased with increasing levels of Al. Phosphorus uptake by phytoplankton was suppressed at the higher pHs with the addition of Al. Additional P resulted in greater uptake of P at pH 6.9 but not at 6.1 or 4.5. At all three pH levels, the addition of Al decreased photosynthetic rates of algae.

Elevated H^+, reduced Ca, and reduced P may interact with Al under acidic conditions to influence plant growth. As a result, it is difficult to discriminate between the direct toxic effects of Al and those of factors associated with reduced pH. For example, Jackson and Charles (1988) investigated relationships between presence and absence of floating-leaved and submersed macrophytes and water chemistry in 29 lakes in the Adirondack mountains. The pH of these lakes ranged from 4.5 to 7.8 and Al levels from 5 to 673 $\mu g \cdot L^{-1}$. Total Al, soluble Al, alkalinity, Ca, Mg, Na, conductivity, and elevation were important in predicting the presence or absence of plant species. However, these factors were also highly correlated with pH. A gradient in species composition corresponded to pH, and the authors concluded that acidity was the principal factor limiting plant distribution, whereas Al was only secondary.

Ormerod et al. (1987a) found that Al levels in aquatic plants correlated inversely with pH among 85 stream sampling sites in Wales. The range in mean pH among these sites was 4.9–6.2 and that of mean filterable Al was 48–227 $\mu g \cdot L^{-1}$. Acidity, followed by Al^{3+}, correlated negatively to the presence or absence of aquatic macrophytes. When pH was removed from the analysis, Al became the dominant water-quality characteristic. In contrast, Catling et al. (1986) found that Al was not important in determining species distributions of aquatic macrophytes in 20 lakes of Kejimkujik National Park, Nova Scotia. Levels ranged from 35 to 250 $\mu g \cdot L^{-1}$ for Al and 4.4 to 6.0 for pH.

Because aqueous Al is frequently negatively correlated with pH (Sprenger and McIntosh 1989), many plants that grow in acidic conditions are probably Al tolerant. This generalization is supported by studies on algae reported earlier. Therefore, certain species such as *Eriocaulon septangulare, Lobelia dortmana, Eleocharis acicularis, Sphagnum* spp., and *Scirpus subterminalis* (Table 3) may be considered Al tolerant. A few species that grow well under acidic conditions (e.g., *Potamogeton confervoides, Nuphar microphyllum, Isoetes acadiensis, I. macrospora*) (Catling et al. 1986) actually may be stimulated by Al. Alternatively, these species may simply be tolerant and better able to compete with sensitive species under acidic conditions.

B. Forest Species

Declines in forest vigor and die-backs of some stands have been observed in Germany, central Europe, Scandinavia, U.S., and Canada during the past 30 years (Krahl-Urban et al. 1990). Over 50% of the forests in Germany have declined, particularly the southern fir forests. Beech, oak, pine, and spruce forests have also been affected. In North America, die-backs or reduced growth are obvious at high elevation in red spruce (*Picea rubens*) of the Appalachian mountains, balsam (*Abies balsamea*) and Fraser firs (*A. fraseri*) in New England and Canada, loblolly (*Pinus taeda*) and slash pine (*P. elliottii*) in commercial forests of the southeast, and sugar maples (*Acer saccharum*) in eastern U.S. and southeastern Canada. In spruce-fir forests, signs of these declines include reduced growth of trees, needle discoloration and loss, crown thinning, apical bud die-back, and branch and tree mortality; 26%–37% of some stands may consist of dead trees (Adams and Eagar 1992).

Several species of conifers grown in Al-enriched solutions in laboratories experience reduced root growth rates. For example, growth significantly declined at pH 3.8 in red and white spruce (*Picea glauba*) at 50 $mg \cdot L^{-1}$ Al, jack pine (*Pinus banksiana*) at 40 $mg \cdot L^{-1}$, and white pine (*Pinus strobus*) at 80 $mg \cdot L^{-1}$ (Hutchinson et al. 1986). At 1.3 $mg \cdot L^{-1}$ Al and pH range 3.2–4.6, white spruce seedlings had shorter roots, less root mass, and lower root : shoot ratios than controls (Nosko et al. 1988). In European birch (*Betula pendula*) and Norway spruce (*Picea abies*), 2.7 $mg \cdot L^{-1}$ Al reduced root elongation, whereas 13.5 $mg \cdot L^{-1}$ Al was required before Scotch pine (*Pinus sylvestris*) showed effects (Eldhuset et al. 1987). Other toxic levels of Al included 3 $mg \cdot L^{-1}$ (pH 3.9) in *Populus* hybrids (Steiner et al. 1984), 3 $mg \cdot L^{-1}$ (pH unreported) in peach (*Prunus persica*) (Baes and McLaughlin 1987), and 27 $mg \cdot L^{-1}$ in sugar maple (Thornton et al. 1986). When exposed to 2.7 $mg \cdot L^{-1}$ Al (pH 4.2–5.4) for 8 wk, dry mass of beech (*Fagus sylvatica*) leaves, roots, and stems were 21%–44% lower than controls (Bengtsson et al. 1988). At pH 3.8, shoot growth of balsam fir was reduced by 24% when

Table 3. Partial list of aquatic plants that are presumably enhanced by, tolerant of, or highly sensitive to acidity and elevated levels of aluminum.[a]

Enhanced species[b]	Tolerant species[c]	Sensitive species[d]
Eleocharis smallii	*Brassenia schreiberi*	*Arthrodesmus indentatus*
Isoetes acadiensis	*Drepanocladus fluitans*	*Arthrodesmus octocornus*
Isoetes macrospora	*Drepanocladus exannulatus*	*Arthrodesmus quiriferus*
Nuphar microphyllum	*Elatine minima*	*Asterionella falfsii*
Potamogeton confervoides	*Eleocharis acicularis*	*Ceratophyllum demersum*
Scirpus subterminalis	*Eleocharis robbinsii*	*Chara vulgaris*
	Eriocaulon septangulare	*Elodea canadensis*
	Fontinalis spp.	*Elodea nuttallii*
	Gratiola aurea	*Elodea occidentalis*
	Hyscomium armoricanum	*Isoetes tuckermanni*
	Isoetes muricata	*Lemna minor*
	Juncus peliocarpus	*Myriophyllum verticillatum*
	Lobelia dortmanna	*Potamogeton amplifolius*
	Mougeotia sp.	*Potamogeton epihydrus*
	Myriophyllum farwellii	*Potamogeton gramineus*
	M. tenellum	*Potamogeton perfoliatus*
	Najas flexilis	*Potamogeton praelongus*
	Nardia compressa	*Potamogeton robbinsii*
	Nuphar variegatum	*Potamogeton spirillus*
	Nuphar luteum	*Sparganium fluctuans*
	Nymphoides cordata	*Spirodela polyrhiza*
	Oedogonium sp.	*Staurastrum arachnae*
	Peridinum limbatum	*Staurastrum longipes*
	Pontederia cordata	*Staurastrum pentacerum*
	Rhacomitrium aciculare	*Utricularia gibba*
	Sagittaria angustifolium	*Utricularia intermedia*
	Sagittaria graminea	*Vallisneria americana*
	Scapania undulata	
	Sphagnum sp.	
	Utricularia gemniscapa	
	Utricularia purpurea	
	Utricularia resupenata	
	Utricularia vulgaris	

[a]After Wile and Miller 1983; Roberts et al. 1985; Catling et al. 1986; Ormerod et al. 1987b; Jackson and Charles 1988; Pillsbury and Kingston 1990.

[b]Enhanced species were found only in low-pH waters with presumably elevated levels of Al (see text) or had growth increased with Al additions.

[c]Tolerant species are found in waters with pH 4.9 or lower, where Al levels are presumably higher than in circumneutral waters (see text).

[d]Sensitive species were only found in waters with pH above 6.8, where Al is reputedly nontoxic.

seedlings were kept in a nutrient solution containing 200 mg·L^{-1} Al at pH 3.8 for 32 d, and 50 mg·L^{-1} significantly reduced root growth of both balsam fir and red spruce (Schier 1985).

Studies have shown that very low levels of Al may enhance growth, although the mechanism is unknown. For example, red spruce, balsam fir (Schier 1985), and sugar maples (Thornton et al. 1986) appear to increase shoot growth when exposed to the metal compared to plants grown in solutions with no Al.

Aluminum appears to alter the uptake of several ions by tree roots. When exposed to 2.7 mg·L^{-1}, beech seedlings experienced an 80% decline in Ca and Mg in all plant parts compared to controls, and at 27 mg·L^{-1} Al, Ca dropped 90% (Bengtsson et al. 1988). Rengel (1992) suggested that Ca : Al molar ratios were important in determining Al toxicity in that ratios less than 1 were likely to be more toxic than higher ratios.

Phosphorus uptake increased at lower exposure levels but decreased when plants were exposed to 27 mg·L^{-1} Al. Potassium uptake increased at both levels. In the same experiment, seedlings exposed to a soil solution from the A horizon of an acidic forest soil with 5 mg·L^{-1} total Al, 0.5 mg·L^{-1} labile Al, and pH 3.7 did not differ from controls in ion uptake. However, when exposed to a solution taken from the B horizon with a labile Al concentration of 11 mg·L^{-1} and similar pH, seedlings lost Ca and Mg and gained P at a rate similar to that of 27 mg·L^{-1} Al in solution.

Probably by competing for binding sites, Al can decrease the uptake of Cd and other heavy metals under acidic conditions. A solution with 2.7 mg·L^{-1} Al decreased Cd uptake of *Pinus abies* by 40%, and 13 mg·L^{-1} Al depressed Cd uptake by 86%. Cadmium uptake could be further depressed by increasing Ca levels. Aluminum depressed concentrations of several minerals in the needles and roots of red spruce and balsam fir (Schier 1985). For spruce roots, the ranking of least to most affected minerals was P < K < Cu < Mg < Ca = Zn = Fe < Mn, whereas the order in fir was P < Cu = Zn < K = Ca = Mn < Mg < Fe.

C. Cultivated Plants

Aluminum is widely recognized as one of the most important limiting factors to crop production in soils with a pH below 5.5 (Taylor 1988). A casual examination of bibliographic compilation sources shows that one to seven new scientific papers on Al toxicity in crop plants appear each week. Many reviews (e.g., Fageria et al. 1988; Foy 1988; Parker et al. 1989; Taylor 1988) have appeared. A complete review of this literature is beyond this paper, but some of this extensive bank may be useful in understanding Al toxicity to plants.

High levels are particularly a problem in tropical soils (e.g., oxisols, utisols, and inceptisols) (Fageria et al. 1988), and up to 50% of the world's nonirrigated croplands or 40% of all arable lands may be affected negatively (Taylor 1988). Approximately 1 billion ha in the tropics and 470 million ha in temperate regions are susceptible (Fageria et al. 1988).

Several species of crop plants have cultivars or ecotypes that differ in their tolerance to Al phytotoxicity. Among these are rice (*Oryza sativa*), corn (*Zea mays*), wheat (*Triticum aestivum*), oats (*Avena sativa*), kaffir (*Sorghum bicolor*), sugarcane (*Saccharum officinarium*), rye grass (*Lolium* spp.), canary grass (*Phalaris aquatica*), rye (*Secale cereale*), bluestem grass (*Bothriochloa* spp.), barley (*Hordeum vulgare*), amaranthus (*Amaranthus* spp.), lima beans (*Phaseolus vulgaris*), soybean (*Glycine max*), string beans (*Centrosema* spp.), lespedeza (*Lespedeza cuneata*), alfalfa (*Medicago sativa*), tomato (*Lycopersicon esculentum*), tobacco (*Nicotiana tabacum*), sweet potato (*Ipomoea batatas*), and sunflower (*Helianthus annuus*) (Fageria et al. 1988; Foy 1988).

Taylor (1988) summarized possible mechanisms for differences among crop plant sensitivities. Some of these mechanisms may also pertain to forest species, but there have not been sufficient studies to make generalizations. A brief synopsis of each mechanism is provided here:

1. Differences in the ability to assimilate Al: Some tolerant cultivars of wheat tend to transport less Al across cell membranes than sensitive varieties.
2. Detoxification of Al after assimilation: Tolerant varieties of tea (*Camellia sinensis*) and other species produce relatively large concentrations of organic compounds such as oxalate and citrate, which complex with Al and reduce its toxicity.
3. High rate of root growth: Because Al tends to inhibit root elongation, cultivars that have greater rates of root growth may overcome some of the toxic effects.
4. Higher cellular respiration: Greater rates of respiration may alter the uptake of cations, including Al, and make them less toxic.
5. Local enhancement of pH: The roots of some cultivars of corn, barley, wheat, and rice release buffers that increase local pH and may reduce the solubility of Al. There is some speculation as to whether this mechanism occurs only in monocotyledons or in dicotyledons as well.
6. Reduced protoplasm viscosity: Aluminum tends to increase the viscosity of protoplasm and reduce overall permeability of salts. Cultivars with thinner cytoplasm may be less inhibited.
7. Partitioning of Al: Cultivars can be separated into one of three groups based on their tendency to partition Al into roots or shoots. One group (represented by wheat, barley, soybean, and snap bean) tends to exclude it from entering roots. Another group (e.g., azalea [*Azalea* sp.], cranberry [*Vaccinium oxycoccus*], rice, and triticale) concentrates the metal in roots and transports little of it to shoots. A third group (including tea, some pines, shadscale [*Atriplex hastata*], and mangrove [*Rhizophora* sp.]) selectively partitions Al into shoots.