Effect of aluminum on the growth of sugar maple in solution culture

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The effect of aluminum (Al) on the growth of sugar maple (*Acer saccharum* Marsh.) was studied in two experiments in nutrient solution containing from 0 to 2000 μM Al at pH 4. Visible symptoms of injury to shoots or roots were not observed in either experiment. Reductions in seedling shoot size at the 1000, 1500, and 2000 μM concentrations were readily apparent; however, root biomass for these same concentrations did not differ significantly from the pH 4 controls. A plot of the relative total dry matter accumulation versus Al in solution showed that above 600 μM Al total seedling biomass declined exponentially. Of the mineral elements examined in these experiments, Ca was the most severely affected by increasing Al in solution. Even at 100 μM Al reductions in leaf, stem, and root Ca content were 17, 13, and 50% of the pH 4 controls, respectively. Some stimulation of growth and slightly higher P and K tissue concentrations were observed at low (100–500 μM) Al concentrations. At higher Al levels, P, K, and Mg were also reduced below the tissue content of the controls. The Al critical toxicity level for a 20% reduction in total seedling biomass was found to be 137 μg Al g dry weight^{-1} for newly expanded leaves.

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Les auteurs ont étudié l'effet de l'aluminium (Al) sur la croissance de l'érable à sucre (*Acer saccharum* Marsh.) dans deux expériences avec solution nutritive contenant de 0 à 2000 μM Al à pH 4. On n'a pas observé de lésions visibles aux pousses ni aux racines dans l'une ou l'autre expérience. Par contre, on a observé des réductions sensibles de la taille des semis cultivés à des concentrations de 1000, 1500 et 2000 μM Al; mais la biomasse de racine pour ces mêmes concentrations n'était pas significativement différente de celle des témoins à pH 4. En pointant l'accumulation totale relative de matière sèche versus la concentration de Al en solution, on a observé une diminution exponentielle de la biomasse des semis au-delà de 600 μM Al en solution. Parmi les éléments nutritifs examinés dans ces expériences. Ca fut le plus sévèrement affecté par l'augmentation de Al en solution. Même à 100 μM Al, les réductions de contenu en Ca des feuilles, de la tige et des racines furent réduites respectivement de 17, 13 et 50%, par rapport au témoin à pH 4. Aux faibles concentrations de Al (100–500 μM), on a observé une certaine stimulation de la croissance et des concentrations un peu plus élevées de P et K dans les tissus. Aux concentrations élevées de Al en solution, les teneurs en P, K et Mg des tissus furent également plus faibles que chez les témoins. Le niveau critique de toxicité de Al pour une réduction de 20% de la biomasse totale des semis s'élevait à 137 μg Al/g de poids sec des feuilles récemment formées.

[Traduit par la revue]

Introduction

Perturbations of forest ecosystems whether natural or anthropogenic may increase ecosystem stress (Smith 1984) and reduce tree vigor. If sufficiently severe or persistent, such stress may contribute to tree decline (Manion 1981). Sugar maple (*Acer saccharum* Marsh.) decline has been observed in northern hardwood stands and urban environments since the turn of the century (Westing 1966). In recent years, decline has been reported in a wide variety of sugar maple forests and has been accompanied by injury from insects and diseases (Allen 1985). This expansion of decline has been attributed by some to acidic deposition and (or) photochemical oxidants (Robitaille 1986; McLaughlin et al. 1985).

A potential effect of increased acidic deposition on forests is the solubilization and mobilization of aluminum caused by soil acidification and increased anion concentration (Cronan and Schofield 1979). Aluminum levels in affected soils may reach levels phytotoxic to some tree species (Pavan and Bingham 1982; Steiner et al. 1984; Thornton et al. 1986). No information is presently available on the Al sensitivity of sugar maple, leaving in question whether elevated soil Al levels can reduce sugar maple vigor and trigger decline. The objective of this study was to determine the effect of aluminum on root elongation, shoot growth, and nutrient content of sugar maple grown in solution culture.

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Material and methods

In an initial experiment (expt. 1), 23-day-old seedlings produced from seed obtained from F. W. Schumacher Co. (Sandwich, MA) were grown in solutions with Al concentrations of 0, 100, 300, 600, and 1500 μM adjusted to pH 4 and a 0 μM Al pH 5 control. In a second experiment (expt. 2), seed collected from a single tree near Truxton, NY, were utilized and in this experiment, 28-day-old seedlings were exposed to a range of Al concentrations up to 2000 μM (Table 1). Each treatment included five replicate 7.2-L pots containing four seedlings each in expt. 1 and 5 seedlings in 15.4-L pots in expt. 2. Seedlings were harvested after 45 days in both experiments.

Experiments were conducted in controlled environment growth chambers with a 16 h day (22°C) : 8 h night (12° C) photoperiod and a photosynthetic photon flux density of 300 μE m^{-2} s^{-1} from a combination of fluorescent and incandescent bulbs. The culture solution was that of Edwards et al. (1976), except that Ca, P, and Fe were lowered to 0.25, 0.04, and 0.01 mM, respectively. Solutions were changed weekly. After radicles emerged from the seed coat, the seedlings were transferred to a Styrofoam mat and floated in nutrient solution. Prior to subjecting seedlings to Al, seedlings were transferred to plastic pots containing nutrient solutions adjusted to pH 4. Seedlings were kept in pots 6–9 days before Al was added to minimize risk of shock (Schier 1985). After the acclimation period, Al was added as a mixture of $AlCl_3$ and $Al_2(SO_4)_3$ to avoid excessive additions of either anion. The Cl^- and SO_4^{2-} concentrations of all treatments were equalized by appropriate additions of NaCl and Na_2SO_4. The acidity of solutions was adjusted every 2 days with either 1 N HCl or 1 N NaOH. Nutrient solutions were changed weekly and Al levels were measured periodically to insure Al concentrations were close (±5%) to

TABLE 1. Effect of aluminum on the dry weight ($g\ plant^{-1}$) of sugar maple seedlings

Al concentration (μM)	Leaf	Stem	Roots
Experiment 1			
0, pH 4	1.78*a*	0.28*a*	0.52*a*
0, pH 5	2.11*a*	0.46*a*	0.59*a*
100	1.85*a*	0.35*a*	0.51*a*
300	1.81*a*	0.25*a*	0.51*a*
600	1.77*a*	0.31*a*	0.53*a*
1500	0.89*b*	0.10*b*	0.43*a*
Experiment 2*			
0, pH 4	2.50*a*	0.52*a*	0.63*a*
0, pH 4	2.45*a*	0.55*a*	0.81*a*
100	3.13*a*	0.72*b*	1.00*b*
500	3.22*a*	0.74*b*	1.04*b*
1000	1.52*b*	0.38*bc*	0.73*a*
2000	0.96*b*	0.26*c*	0.61*a*

NOTE: Means within columns followed by the same letter are not significantly different at $P = 0.05$.
*NaCl and Na_2SO_4 were added to balance Cl^- and SO_4^{2-} ions in the 2000 μM Al treatment.

TABLE 2. Effect of acidity on the growth of sugar maple seedlings

Growth parameter	pH 4	pH 5
Height growth (mm)	62	112*
Root elongation (mm)	136	182**
No. of leaves produced	8.5	10.7NS
Average leaf size (cm^2)	37.1	41.5NS
Mean leaf expansion rate (week 1 ($cm^2\ day^{-1}$))	2.60	2.72NS
Leaf DW production ($g\ plant^{-1}$)	1.79	2.11NS
Stem DW production ($g\ plant^{-1}$)	0.29	0.46NS
Root DW production ($g\ plant^{-1}$)	0.52	0.59NS

NOTE: Significance level of difference between acidity levels: *, $P = 0.10$; **, $P = 0.08$; NS, not significant. DW, dry weight.

desired levels. Aluminum speciation was also monitored during the experiment as described by Barnes (1975). No detectable difference in total or monomeric Al was observed, confirming that the Al present was primarily monomeric.

Height growth, root elongation, leaf production, and leaf expansion rates were measured at weekly intervals. Root elongation and height growth were taken as the differences between initial and final root length and shoot length, respectively. Leaf area was determined by tallying leaf intercepts with a 1-cm^2 acetate grid overlay. Upon termination of the experiment, seedlings were rinsed with distilled, deionized water (DDW) and separated into leaves, stems, and roots. Roots were further rinsed for 1 min in 0.1 *M* $CaCl_2$, followed by a DDW rinse to remove surface-adsorbed Al. Plant material was oven-dried at 70°C and then weighed. Samples of leaf, stem, and root material from eight replicate seedlings per treatment were digested in nitric–perchloric acid (Johnson and Ulrich 1959). Al and P content of samples were determined colorimetrically (Thornton et al. 1985; Murphy and Riley 1962). Tissue content of Ca and Mg were analyzed by atomic absorption spectroscopy; K and Na were determined by flame emission spectroscopy. The accuracy of tissue analysis was confirmed by comparison with National Bureau of Standards reference material. Our recoveries ranged from 94 to 100% of the certified values.

Significance of treatment effects were evaluated by analysis of variance. Where appropriate, or of interest, either Duncan's new multiple-range test or Student's *t*-test were used to compare means.

Results

Seedling growth

The effect of Al on growth of sugar maple seedlings from the two experiments is shown in Table 1. Visible symptoms of Al injury to either shoots or roots was not observed in either experiment, but the reduction in shoot size at the 1000, 1500, and 2000 μM concentrations was readily apparent. The salt control in expt. 2 indicated that Cl^- or SO_4^{2-} did not significantly affect growth at the levels tested in this study. However, reduction of acidity from pH 4 to 5 improved height and growth of the seedlings (Table 2).

Aluminum significantly reduced dry matter accumulation in leaves and stems at concentrations above 1000 μM (Table 1). At low Al concentrations, stimulation of stem and root dry matter was observed in expt. 2. This stimulatory effect was not evident in expt. 1 (Table 1); however, since different seed sources were used in the two experiments the difference in response to low Al concentrations may have been a genetic component.

Since analysis of the data from the experiments revealed no significant difference in the relative total dry weight of seedlings (expressed as a percentage of pH 4 control seedlings) below 600 μM Al, we combined and normalized the data from the two experiments to establish the relationship between relative total dry matter accumulation and Al in solution (Fig. 1). The response curve had two segments: a zero slope at concentrations below 600 μM Al and an exponential decline in growth above 600 μM Al with increasing Al in solution. Relative total plant dry matter accumulation in the 1000, 1500, and 2000 μM Al treatments was decreased by 25, 44, and 54%, respectively.

The time dependency of shoot and root elongation is shown in Fig. 2. Shoot elongation appears nearly linear over the 6-week period, with a trend of increasing shoot elongation after the 2nd week. Shoot length of seedlings was reduced by all Al concentrations except 100 μM, where growth was stimulated (Fig. 2*a*). Above 1000 μM Al, height growth was reduced by 70–90% as compared with the controls.

The effect of Al on root elongation (Fig. 2*b*) was more complex. The change in slope of the curves for all treatments suggests an acceleration in the rate of elongation after the 3rd week. The largest increase was noted for the 500 and 1000 μM Al treatments; but, at higher concentrations, root elongation was reduced to that of the pH 4 controls.

Mean leaf expansion rates were calculated for weekly periods for individual leaves. Full expansion took approximately 3 weeks, regardless of treatment. Only the expansion rate during the 1st week was significantly affected by Al treatments. The 1500 μM treatment differed significantly from the pH 4 control ($F = 2.43$, $P = 0.036$); the mean expansion rate was reduced from 2.6 to 1.5 $cm^2\ day^{-1}$. Average leaf size in the 1500 μM treatment was also significantly reduced to 25.0 cm^2 compared with controls, which were 37.1 cm^2 ($F = 3.90$, $P = 0.002$). Other Al treatments did not significantly affect leaf size.

Mineral nutrition

The concentration of mineral elements of sugar maple seedlings is shown in Fig. 3. Tissue samples from both experiments were used to develop Al response curves. Decreasing the acidity from pH 4 to 5 had no significant effect on

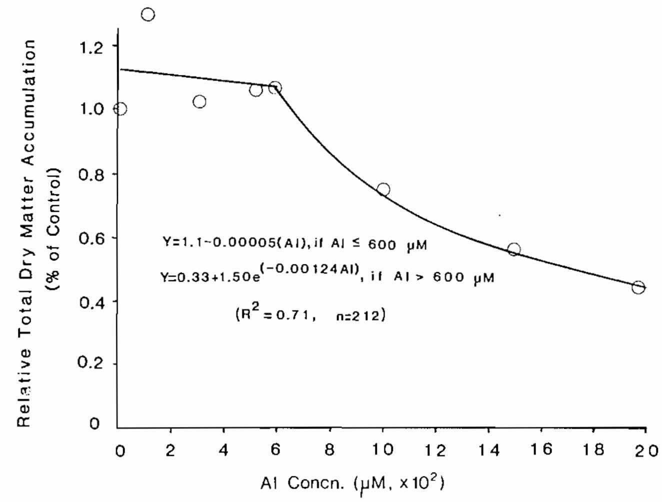

FIG. 1. Relationship of relative total dry matter accumulation of sugar maple and Al in solution (composite of data from expts. 1 and 2).

elemental content of nutrients in leaf, stem, or roots of maple seedlings (data not included).

Root concentrations of Al were 15 times greater than that of shoot tissue. Leaf and stem Al contents were linearly related to Al in solution, while a quadratic relationship exists for root Al content (Fig. 3*a*). As a function of Al in solution, the P and K content of all plant components were best described by parabolic response curves (Figs. 3*d* and 3*e*). The root and stem Mg content also showed a parabolic relationship to Al concentration, but leaf Mg content was best fit as an exponential (Fig. 3*c*). At the highest Al treatment, 2000 μ*M*, the leaf contents of P, K, and Mg were reduced by 66, 16, and 50% as compared with those of the pH 4 controls, respectively. Reductions of similar magnitude were measured in roots.

The Ca content of maple seedlings was significantly reduced by Al in solution (Fig. 3*b*). Even at the lowest Al concentration studied (100 μM), reductions in leaf, stem, and root Ca content were 17, 13, and 50% as compared with the pH 4 controls, respectively. Calcium content of shoots approached an asymptote as Al concentration in solution reached 1000 μ*M*; however, the Ca content of roots continued to decline exponentially past 1000 μ*M* Al (Fig. 3*b*).

A linear trend of decreasing Na content of maple seedlings with increasing Al was observed (Fig. 3*f*). This trend was expected since less Na (both as NaCl and $Na_2(SO)_4$) was added to the higher Al treatments to balance Cl^- and SO_4^{2-} additions from the Al salts.

In an attempt to establish the relationship between seedling growth and foliar Al levels, we plotted plant dry weight accumulation in relation to Al content of leaves (Fig. 4). This relationship has been used to establish Al critical toxicity levels (CTLs) for other tree seedlings (Worku et al. 1982; Thornton et al. 1986). We selected a 20% reduction in plant dry weight as the basis for establishing the Al CTL since this value closely corresponds to a statistically significant reduction in weight over that of the controls. The Al CTL was strongly influenced by the age of the leaf material sampled. Old leaves (the lower two or three leaves) had Al CTLs approximately 3 times greater than newly expanded leaves with Al contents of 338 and 137 μg g^{-1}, respectively.

Discussion

At pH 4, the growth of sugar maple is stimulated by 100 and 500 μ*M* aluminum concentrations. Such stimulation has been

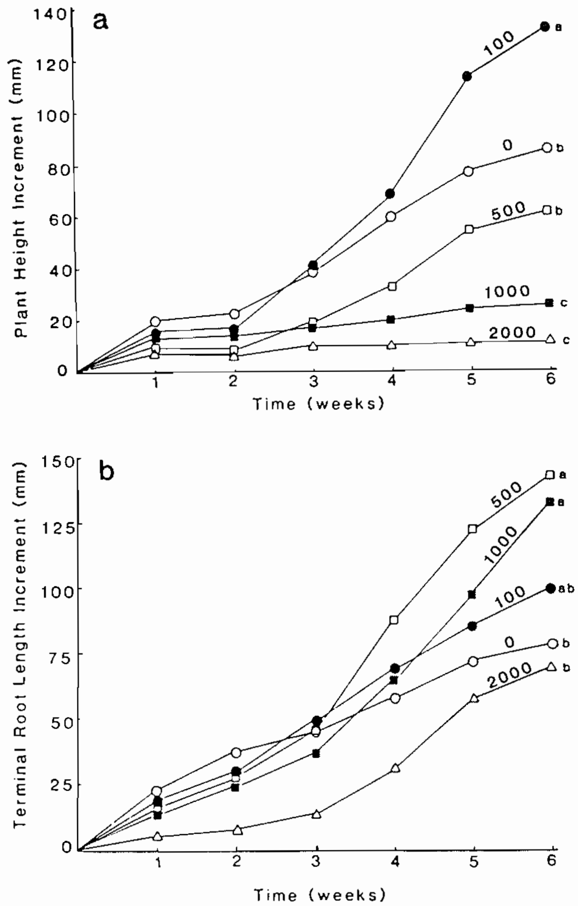

FIG. 2. Effect of Al concentration (micromolar) on (*a*) mean height and (*b*) mean root growth increment of sugar maple seedlings over time for expt. 2. Means (n = 20) followed by the same letter are not significantly different at P = 0.05 for the week 6 values.

observed for other tree species (Schier 1985; Hutchinson 1985; Thornton et al. 1986). Injurious effects of high H^+ ion concentration can be reduced in the presence of polyvalent cations including Al (Viets 1944; Fawzy et al. 1954). Since root elongation was significantly greater at pH 5 than at pH 4 (Table 2), the observed stimulation at 100 and 500 μ*M* Al may be related to a polyvalent cation effect. Other tree species at comparable Al levels have shown similar increases in root growth (Edwards et al. 1976).

The parabolic shape of maple shoot growth response function suggests that Al has at least two effects on growth. At high acidity (pH 4), Al may act as a polyvalent cation and protect against H^+ ion damage to the root. At higher Al concentrations, the inhibitory effects override the stimulatory effects and growth declines compared with maximum growth rates. At the highest Al concentration (2000 μ*M*), growth was reduced by over 50% compared with the maximum growth achieved in the 100 and 500 μ*M* Al treatments. Thus, it is difficult to ascertain the actual Al sensitivity of sugar maple seedlings from shoot growth alone.

Interpretation of the relative total dry weight response of seedlings (Fig. 1) is clearer than the growth response of shoots. Above 600 μ*M* there was an exponential decline in biomass with increasing Al. Height growth of seedlings followed a pattern similar to shoot biomass, except at 100 μ*M*, where there was a significant stimulation in growth. Similar reports of increased shoot growth with Al have been reported for red

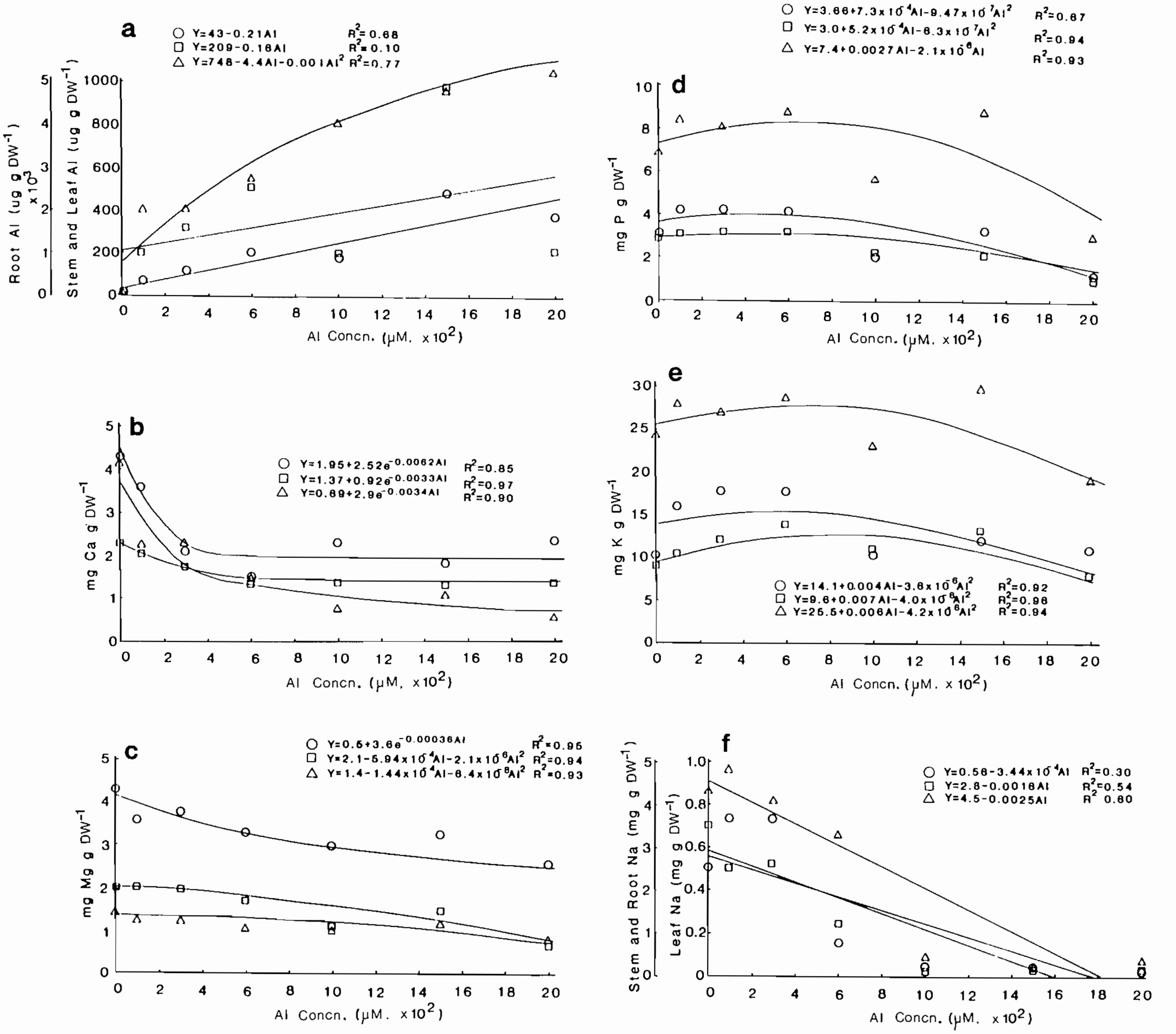

FIG. 3. Mineral content of sugar maple tissues (dry weight, DW) in relationship to Al concentration in solution (composite of data from expts. 1 and 2). (*a*) Aluminum content of leaves, stems, and roots. (*b*) Calcium content of leaves, stems, and roots. (*c*) Magnesium content of leaves, stems, and roots. (*d*) Phosphorus content of leaves, stems, and roots. (*e*) Potassium content of leaves, stems, and roots. (*f*) sodium content of leaves, stems, and roots. ○, leaves; □, stems; △, roots.

spruce, jack pine, and American beech (Schier 1985; Hutchinson 1985; F. C. Thornton, unpublished).

Unlike some other tree species (Edwards et al. 1976; Pavan and Bingham 1982; Thornton et al. 1986), no symptoms of root or shoot injury were observed in these experiments. Even at Al concentrations where significant reductions in shoot biomass occurred, differences in root appearance and morphology in Al treatments were not distinguishable from controls. Whereas shoot growth proceeded at a nearly constant rate, root elongation in the 500 and 1000 μM treatments was accelerated substantially after the 3rd week. This may be due to the cyclic pattern of root growth of sugar maple (Wood and Hanover 1980) or physiological adaptation.

Root Ca and Mg contents declined with increasing Al in solution (Figs. 3*b* and 3*c*). Root Mg content declined gradually over the range of concentration studied while root Ca content declined exponentially between 0 and 600 μM Al. The large decrease in root Ca may have resulted from competition between Ca and Al at the root surface binding and uptake sites. Similar findings have been reported for wheat (Johnson and Jackson 1954). The significant decrease in leaf Ca and Mg content with increasing an Al concentration is consistent with findings from other studies of tree seedling response to elevated Al (Edwards et al. 1976; Schier 1985; Pavan and Bingham 1982; Thornton et al. 1986). The pattern of decline was similar for roots and might be related to decreased uptake and translocation combined with some dilution of nutrient content caused by slightly better seedling growth. Reductions in Mg and Ca content at low Al concentrations are not associated with any growth reductions. Interpretation of the composition data is, at present, uncertain since critical deficiency levels for essential nutrients for sugar maple are not available. Such information is essential if Al toxicity and nutrient deficiency effects are to be unequivocally differentiated.

In an attempt to relate Al content of leaves to seedling growth, we have used the concept of critical toxicity level. We chose to

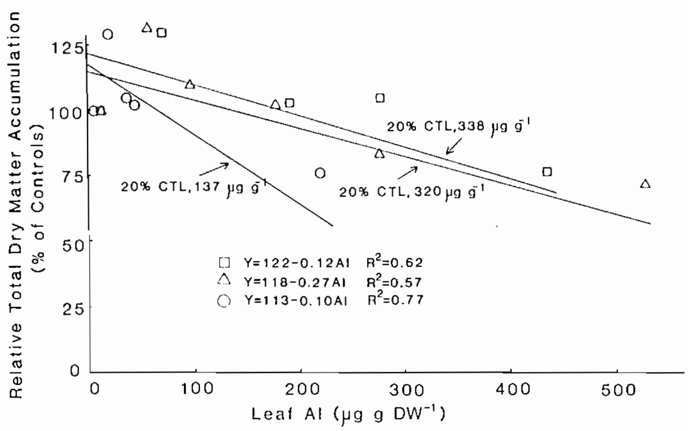

FIG. 4. Relationship of relative total dry matter accumulation of sugar maple seedlings and Al content of leaves (dry weight, DW). ○, newly expanded leaves; □, old leaves; △, composite of all seedling leaf material. Data points are means of eight replicate seedlings.

establish our Al CTL with a 20% reduction in total dry matter accumulation as it closely corresponded to the significant reduction of 25% at 1000 μ*M* as predicted from our regression equation (Fig. 1). Leaf Al CTL for young and old leaves was 137 and 338 $\mu g\ g^{-1}$, respectively (Fig. 4). The Al CTL estimated for young leaves in the present study is similar to values reported for coniferous species. Studies with red spruce, black spruce, white pine, and jack pine have reported reductions of 22, 38, 22, and 11% in total dry weight of seedlings associated with shoot contents of Al of 161, 125, 136, and 100 μg Al g^{-1}, respectively (Hutchinson 1985). Worku et al. (1982) suggested that 200 μg Al g^{-1} in leaf samples of several citrus varieties grown in a pot study represented the Al toxicity threshold. The Al CTL for honey locust (*Gleditsia triacanthos* L.), a woody legume, has been shown to be approximately 3 times lower with 20% reductions in growth associated with a leaf Al content of 40 $\mu g\ g^{-1}$ (Thornton et al. 1986). The importance of proper sampling designs in assessing nutrient deficiencies and toxicities is also well exemplified in the CTL curves developed for the various leaves (Fig. 4). The predictive power of the regression increased 22% by careful sampling of young leaves rather than a composite sample of all leaf material and Al CTL associated with a 20% reduction in growth was also reduced 250%, from 336 to 137 μg Al g^{-1}.

The Al CTL defined for young maple leaves in this study adequately predicts the sensitivity of maple seedlings to Al in solution culture, but we caution using this value to predict Al sensitivity for maple grown in soil since it has not been etablished whether the critical Al concentration is independent of other variables.

In conclusion, these experiments demonstrate that sugar maple growth can be significantly reduced at solution Al concentrations above 600 μ*M*. However, Al reduced Ca and, to a lesser degree, Mg contents at 100 μ*M*. Thus, under conditions of nutrient stress, Al could affect tree growth and vigor. Such soil solution Al concentrations may be found in soils supporting hardwood stands (Sharpe et al. 1984) and, therefore, it could be anticipated that in some instances, Al may impair the growth of sugar maple.

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