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STIMULATORY EFFECTS OF ALUMINUM ON GROWTH OF SUGAR MAPLE SEEDLINGS

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ABSTRACT

To determine the effect of aluminum (Al) on sugar maple (*Acer saccharum* Marsh.), seedlings were grown in sand irrigated with nutrient solution (pH 3.8) containing 0, 2.5, 5, 10, 20, or 40 mg L^{-1} Al. Seedling growth was enhanced at 2.5 and 5 mg L^{-1} Al. Although higher levels of Al reduced calcium (Ca) and magnesium (Mg) concentrations in leaves and caused root and foliar injury, no negative effects of Al on growth were observed.

INTRODUCTION

High concentrations of aluminum (Al) and manganese (Mn) in the soil solution of acidic mineral soils may inhibit plant growth. Previously, we

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investigated the response of newly germinated sugar maple (*Acer saccharum* Marsh.) seedlings to Mn,[1] because unusually high concentrations of foliar Mn ($>2000\,\mathrm{mg\,kg^{-1}}$) in seedlings and overstory trees suggested that Mn may have a role in sugar maple decline in northern Pennsylvania.[2] Seedling mortality was 90% at $40\,\mathrm{mg\,L^{-1}}$ and higher Mn. At lower Mn, seedling dry weight decreased with increasing Mn levels; root growth was inhibited more than shoot growth. Foliar concentrations of all mineral nutrients except phosphorus (P) were reduced by Mn. Symptoms of Mn toxicity included progressive chlorosis and necrosis of leaves, darkened root tips, and loosening of outer cortical cells in roots.[1]

Although foliar analyses did not implicate Al as strongly as Mn in sugar maple decline, we investigated the effect of Al on sugar maple seedlings because the high level of Al in the soil at the 0–5 cm soil depth ($348\,\mathrm{mg\,kg^{-1}}$) may have affected root growth.[2] Response of sugar maple seedlings to Al was examined by Thornton et al.[3] and Bertrand et al.[4] The latter found that $54\,\mathrm{mg\,L^{-1}}$ Al (only level tested) stimulated root growth. Thornton et al.[3] observed a significant reduction in leaf and stem dry weight at $27\,\mathrm{mg\,L^{-1}}$ and higher levels of Al, but no reduction in growth in the roots. At low Al levels in one of two experiments, Al stimulated the growth of stems and roots.

The objective of this study was to determine the effect of Al on the growth and mineral nutrition of sugar maple seedlings grown in sand irrigated with nutrient solution containing Al.

MATERIALS AND METHODS

Sugar maple seeds collected in Pennsylvania were purchased from the F. W. Schumacher Co. (Sandwich, MA). The seeds were surface sterilized with 0.07 M NaOCl, rinsed, and stratified at 2–4°C in plastic trays lined with moist blotting paper. After seven weeks, germinating seeds were planted in a moist vermiculite–peat moss (v : v, 1 : 1) medium in plastic flats and placed in a growth chamber with $500\,\mu\mathrm{E\,m^{-2}\,s^{-1}}$ light, 16 h-photoperiod, and 25 : 20°C (light–dark) temperature regime. After two weeks, seedlings were transplanted singly in acid-washed quartz sand in polyvinyl (PVC) containers (ID, 10.2 cm diam. × 26 cm height) and returned to the growth chamber.

An automated drip irrigation system fed the seedlings approximately 25 mL of a modified 0.1-strength Clark solution[5] with a pH of 3.8 three times per day. Composition of the nutrient solution (μM) was: 377 calcium (Ca); 724 potassium (K); 155 magnesium (Mg); 32 P; 1812 nitrate–nitrogen (NO_3–N); 557 ammonium–nitrogen (NH_4–N); 194 chloride (Cl); 182 sulfur (S); 4.5 iron (Fe); 1.8 Mn; 5.0 boron (B); 0.46 zinc (Zn); 0.12 copper (Cu); 0.16 molybdenum (Mo);

and 20 sodium (Na). Fresh solution was prepared every seven days. Two weeks after irrigation with the nutrient solution began, Al [$Al_2(SO_4) \cdot 18H_2O$] was added to the solution at 0, 2.5, 5, 10, 20 or 40 mg L^{-1} (0, 93, 185, 371, 741 or 1483 μM). The treatments were arranged in the growth chamber in 12 blocks of six Al levels.

Immediately after seedlings were harvested following 48 days of Al treatment, Al injury to leaves and roots was assessed visually. After the seedlings were separated into leaves, stem, and roots, the parts were oven dried at 70°C and weighed. Dried leaves from each seedling were ground to pass through a 20-mesh screen for mineral analysis. The analyses were done by the Analytical Laboratory of the Maine Agricultural and Forestry Experiment Station, Orono, ME.

Data were summarized and analyzed using the statistical routines of the SYSTAT computer program.[6] Analysis of variance was used to test for effects of Al treatment on growth and foliar concentration of mineral elements. If the effects of treatments were significant, the HYPOTHESIS command in SYSTAT's Multivariate General Linear Model was used to make Bonferroni pairwise comparisons between means.

RESULTS

Visual Symptoms

Fine roots of control seedlings were white or very light brown. At 2.5 mg L^{-1} Al, most roots were light brown. At 5 mg L^{-1} Al, roots were darker brown than at 2.5 mg L^{-1} and some thickening was observed. At 10 and 20 mg L^{-1} Al, necrotic root tips were common and, at 40 mg L^{-1} Al, necrosis had spread extensively along roots.

At 2.5 mg L^{-1} Al, there were small chlorotic areas randomly throughout the leaves; some necrosis occurred at the margins of the areas. Chlorotic/necrotic patches, increasing proportions of which were necrotic, became larger with increasing Al levels.

Growth

Low concentrations of Al, 2.5 and 5 mg L^{-1}, increased seedling dry weight ($P < 0.001$) (Table 1). Higher concentrations of Al had no effect on growth. Relative to controls, mean increases in dry weight of leaves, stem, and roots by 2.5 and 5 mg L^{-1} Al were 42, 85, and 81%, respectively. The root/shoot ratio

Table 1. Effect of Al on Growth of Sugar Maple Seedlings

	Dry Weight (mg)				
Aluminum ($mg\,L^{-1}$)	Leaves	Stem	Roots	Total	Root/ Shoot Ratio
0	534ab[a]	94a	323a	952a	0.48a
	(250)[b]	(47)	(208)	(495)	(0.12)
2.5	733bc	171b	553b	1457b	0.61a
	(337)	(82)	(269)	(677)	(0.12)
5.0	784c	177b	616b	1574b	0.63a
	(254)	(60)	(221)	(519)	(0.08)
10.0	449a	106a	351a	906a	0.61a
	(168)	(39)	(171)	(362)	(0.15)
20.0	340a	85a	274a	698a	0.61a
	(124)	(30)	(131)	(273)	(0.13)
40.0	448a	105a	335a	889a	0.59a
	(129)	(35)	(144)	(299)	(0.10)
P level	<0.001	<0.001	<0.001	<0.001	0.130

[a]Component means within a column followed by different letters are significantly different at the 0.05 level.
[b]Standard deviation.

remained relatively constant (0.48 to 0.63) as the level of Al in the nutrient solution increased.

Mineral Elements

The concentration of Al in the leaves increased ($P < 0.001$) as the level of Al in the nutrient solution increased, initially becoming significantly different from the controls at $10\,mg\,L^{-1}$ (Table 2). Sand probably was the source of Al in the controls because Al added as a contaminant to the nutrient solution was less than $0.35\,mg\,L^{-1}$. Aluminum showed its greatest increases in concentration from 5 to $10\,mg\,L^{-1}$ Al (28%) and from 10 to $20\,mg\,L^{-1}$ Al (23%).

Aluminum significantly ($P < 0.001$) reduced foliar concentrations of P, Ca, and Mg, but not K (Table 2). Phosphorus was reduced by 44% relative to the controls at $2.5\,mg\,L^{-1}$ Al but showed no further decrease in concentration with increase in Al. Reductions in Ca and Mg were more gradual: 14 and 24% less than the controls, respectively, at $2.5\,mg\,L^{-1}$ Al, and 45% at $40\,mg\,L^{-1}$ Al (Table 2).

Table 2. Effect of Al on the Concentration ($mg\,kg^{-1}$) of Mineral Elements in Leaves of Sugar Maple Seedlings

Aluminum ($mg\,L^{-1}$)	Aluminum	Phosphorus	Potassium	Calcium	Magnesium
0	108a[a]	1777a	9236a	6607a	2295a
	(32)[b]	(314)	(1199)	(850)	(403)
2.5	107a	998b	8644a	5679b	1742b
	(24)	(352)	(2101)	(692)	(397)
5.0	122a	1044b	9207a	4638c	1503b
	(23)	(266)	(1193)	(789)	(428)
10.0	156b	1089b	7531a	4405cd	1436b
	(25)	(250)	(998)	(692)	(227)
20.0	192c	1025b	9545a	3845d	1464b
	(37)	(195)	(1680)	(640)	(171)
40.0	212c	933b	8556a	3023e	1036c
	(16)	(203)	(1236)	(391)	(183)
P level	<0.001	<0.001	0.115	<0.001	<0.001

[a]Component means within a column followed by different letters are significantly different at the 0.05 level.
[b]Standard deviation.

DISCUSSION

Significant increases in biomass at 2.5 and $5.0\,mg\,L^{-1}$ were the lone effect of Al on the growth of sugar maple seedlings. Thornton et al.[3] also found that the growth of sugar maple seedlings was enhanced by low levels of Al (2.7 and $13.5\,mg\,L^{-1}$). However, in contrast to our study, they found that growth was inhibited at high Al levels ($\geq 27\,mg\,L^{-1}$). Stimulation of growth by Al has been observed in other tree species: eucalyptus and radiata pine,[7] eastern white pine,[8] Douglas fir,[9] silver birch,[10] red spruce,[11] white spruce,[12] and northern red oak and American beech.[13] Explanations for Al enhancement of growth have ranged from suppression of fungal pathogens to stimulation of Fe and P uptake.[14] However, the one with the broadest applicability is that Al enhances growth by alleviating H ion toxicity.[15,16]

Although Al did not inhibit the growth of sugar maple seedlings, we observed root necrosis and foliar chlorosis at $10\,mg\,L^{-1}$ and higher Al and reduced foliar concentrations of P, Ca, and Mg with increasing Al levels. These effects are commonly observed expressions of Al toxicity and usually are associated with reductions in growth.[17] It is possible that similar reductions in growth would have been observed in this study following a longer period of Al treatment. However, in our study the phytotoxic effects of Al on sugar maple seedlings were not detrimental enough to overcome its stimulatory effects on growth.

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