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Aluminum and Phosphorus Interactions in Mycorrhizal and Nonmycorrhizal Highbush Blueberry Plantlets

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Abstract. Aluminum (Al) and phosphorus (P) interactions were investigated in mycorrhizal (M) and nonmycorrhizal (NM) highbush blueberry (*Vaccinium corymbosum* L.) plantlets in a factorial experiment. The toxic effects of Al on highbush blueberry were characterized by decreased shoot, root, and total plant dry mass. Many of the negative effects of Al on plant root, shoot, and total dry matter production were reversed by foliar P and N application, indicating P or N uptake were limited by high Al concentration. However, Al-mediated growth reduction in P-stressed plants indicated that the restriction of P uptake by high Al may not have been the only mechanism for Al toxicity in this experiment. Root Al and P concentration were negatively correlated in NM but not M plantlets, suggesting mycorrhizal infection may alter P uptake processes. Al uptake was also affected by mycorrhizal infection, with more Al accumulating in M plantlet roots and leaves. Correlations among foliar ion concentrations were also affected by mycorrhizal fungal infection.

In field experiments, high levels of Al in the soil have been shown to be a limiting factor for rabbiteye blueberry plants (Patten et al., 1988; Peterson et al., 1987). Korcak (1989) also found that the shoot fresh mass of highbush blueberry plants was decreased by high Al concentrations in solution culture. Because blueberries in nature are found in acid soils where Al ions can accumulate to toxic levels, it might be assumed that they are relatively tolerant to Al ions. However, native populations of *Vaccinium* are most often found in soils that have low Al and/or high levels of organic matter that binds active forms of Al. When produced commercially in mineral soils, highbush blueberry plants grow best when organic matter is incorporated into the soil before planting and when organic mulches are used (Gough et al., 1977; Goulart et al., 1995). These organic amendments and mulches may mediate fluctuations in soil moisture and temperature and also bind active forms of Al that are released when the mineral soils are acidified before planting.

The toxic effects of Al are largely associated with Al interference in P metabolism and with Al binding to root cell pectins, which stops root elongation and affects root growth (Foy, 1983). The presence of Al often results in the precipitation of P in the root cell walls and/or the intracellular space (Rasmussen, 1968). The P translocation is limited because of nonmetabolic $AlPO_4$ accumulation in the root cell (Cumming and Weinstein, 1990a; Cumming et al., 1986). However, an ectomycorrhizal symbiont can prevent $AlPO_4$ accumulation by reducing Al movement toward the root surface and by solubilizing $AlPO_4$ precipitates in the rhizosphere, thus minimizing Al-induced P localization (Cumming and Weinstein, 1990a, 1990b). Therefore, ectomycorrhizal infection can alleviate Al-mediated P deficiency as well as interact directly with the P nutrition of the host. It is uncertain whether a similar mechanism exists in mycorrhizal blueberry plants.

In ericaceous plants, mycorrhizal infection is important for host plant acquisition of N and P (Read and Stribley, 1973). It is assumed that the acid phosphatases produced by mycorrhizal fungi release inorganic P from organic esters, which releases P for subsequent uptake by the host (Mitchell and Read, 1981; Pearson and Read, 1975). The activity of these acid phosphatases is only slightly affected by Al concentrations as high as 200 mM (Shaw and Read, 1989). We hypothesize that mycorrhizal infection in blueberry plants alters root P and other nutrient uptake processes under high Al concentrations.

The detrimental effects of excess Al to mycorrhizal (M) and nonmycorrhizal (NM) highbush blueberry plantlets were determined in a previous study (W.Q. Yang, B.L. Goulart, and K. Demchak, unpublished data). Toxicity symptoms were characterized by reduced shoot and root growth and interference in nutrient uptake. Plantlet uptake of P and N was reduced by high concentrations of Al, suggesting that high Al concentration primarily limits the ability of roots to acquire P and N in highbush blueberry plantlets.

This study compared the growth response and ion content in M and NM highbush blueberry plantlets grown at different Al and P levels. The specific objectives were to 1) evaluate the effect of mycorrhizal infection on Al and P ion concentration and content, 2) evaluate the effect of Al solution concentration on P nutrition in M and NM plants, and 3) determine if the growth reduction caused by Al is due to limited P and N uptake.

Materials and Methods

Tissue-cultured 'Elliot' highbush blueberry (*Vaccinium corymbosum*) shoots were planted in 7-cm-deep plastic flats (52 × 37 cm) filled with triple-washed sand (Silica Co.) and covered with 0.2-mm polyethylene plastic tents that were supported by 15-cm plastic pot stakes. Humidity was maintained within these chambers by periodically misting with distilled water. The flats were kept at 25 °C under 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation (PAR) for 16 h daily. When the root system was developed, plantlets were watered with a nutrient solution (pH 4.5) containing the following nutrients (in mM): 1.25 N (as NH_4), 0.15 P, 0.5 K, 0.5 Mg, 0.25 Ca, 1.4 S, 0.5 Cl, and (in μM) 44.8 Fe (as FeEDTA), 17.1 B, 5.0 Mn, 0.5 Zn, 0.005 Cu, and 0.01 Mo once a

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week until plants reached a height of 10 to 15 cm. At this time, plantlets with well developed root systems were inoculated with mycorrhizal fungi.

Due to the difficulties of inoculating tissue-cultured blueberry (*Vaccinium corymbosum*) plants in sand or other media with known ericoid mycorrhizal fungi in a preexperiment, the soil from a native lowbush blueberry (*Vaccinium angustifolium* L.) site in the Little Flat nature area of Rothrock State Forest, Pa. (40°25' long., 78°00' lat.) was used as the inoculum. To inoculate, plantlets were grown in this Leetonia extremely stony loamy sand soil (Spodosol) for 8 weeks at an ambient temperature of 25 °C and a daylength of 16 h with 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR. Three ericoid mycorrhizal fungi were subsequently isolated from lowbush blueberry roots growing in this soil. Fungi were identified to genera as *Hymenoscyphus, Oidiodendron,* and *Scytalidium* by Yolande Dalpé at the Center for Land and Biological Resource Research, Ottawa, Ont., Canada. Nonmycorrhizal control plantlets were grown in the same soil, which had been air dried and autoclaved at 105 °C for 90 min. At week 9, samples of plant roots were washed, cleared, and stained and examined for mycorrhizal infection using a grid-line intersect technique (Giovannetti and Mosse, 1980) modified to determine percentage of cells infected. Inoculated plantlets had an infection level of 15% to 25%, while uninoculated control plantlets remained uninfected.

The M and NM plantlets were then washed using dilute H_2SO_4 solution (pH 4.5) to remove organic debris and sand particles associated with roots and transplanted into 4-inch square pots filled with silica sand. Silica sand (R.J. Glass, Inc., Duncansville, Pa.) was acid washed with 0.5 N H_2SO_4 to remove preexisting nutrients. The medium was flushed with distilled water until medium pH reached 4.5. Plantlets were then watered with the treatment solution by an automated trickle irrigation system, which delivered 70 mL per plant twice daily. The treatment solution (pH 4.5) contained the following nutrients (in mM): 2.5 N (as NH_4), 1 K, 1 Mg, 0.5 Ca, 2.8 S, 1 Cl, and (in μM) 89.5 Fe (as FeEDTA), 34.2 B, 10.0 Mn, 0.99 Zn, 0.01 Cu, and 0.02 Mo. Treatments were arranged in a randomized complete block in a 2 × 2 × 3 factorial design with eight replications. Plantlets were grouped into blocks by fresh mass so that plants in each block had similar fresh mass. Treatment factors consisted of two mycorrhizal statuses (M and NM plants), two Al levels in solution (0 and 600 μM), and three P treatments (0 and 300 μM P in solution, and 0 P in solution plus a foliar 1700 ppm P and 500 ppm N application). For Al [as $Al_2(SO_4)_3$] and P (as NaH_2PO_4) treatments, the nutrient solution was supplemented by each Al and P combination with solution pH adjusted to 4.5 using 0.1 N NaOH. Phosphorus concentration in the treatment solution was determined to be 289 and 97 μM for 0 and 600 μM Al treatment by Murphy and Riley's method (Murphy and Riley, 1962). Two weeks after solution treatments began, foliar P and N were applied with commercial ammonium polyphosphate (APP) once every 10 d to the foliar P-treatment plants. The spray solution contained diluted APP (1:200) plus 5 mL Tween 20/L. Element concentrations of the foliar solution were analyzed by The Pennsylvania State Agricultural Analytical Services Laboratory. Elemental concentrations were (in ppm) 500 N, 1700 P, 361 K, 0.9 Ca, 3.4 Mg, 5.4 Al, 11 Fe, 0.5 Mn, and 1 Zn. Root medium and nontreatment plants were protected from contamination during foliar P and N application.

Before applying any treatments, plantlet fresh mass, canopy volume, root volume, canopy and root density (evaluated subjectively from 1 to 5, 1 = sparse, 5 = dense), and basal shoot and lateral numbers were recorded for each plantlet. Canopy and root volume (cm^3) were estimated using the formula for a cylinder ($\pi r^2 H$), where r = the average radius of canopy or root system (using the average of two perpendicular measurements per plantlet), H = canopy or root system height. Root measurements were taken immediately after sand was shaken from the roots. This was possible because the roots retained their spacial conformation after sand removal. A relative canopy or root volume was developed by multiplying canopy or root density by canopy or root volume.

Plantlets were grown in pots under 25 °C, 16 h daylength, and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR for 8 weeks. All pots were flushed once every 10 d with distilled water adjusted to pH 4.5 with 1 N H_2SO_4 to remove residual ions in the media. At harvest, relative canopy and root volume were determined by the same protocol used for the initial data collection. A small fraction of roots from each plantlet was sampled and stained with trypan blue to examine the level of mycorrhizal infection using a modified grid-line intersect technique (Giovannetti and Mosse, 1980). After shoot and lateral numbers were recorded, plantlets were divided into shoots and roots, fresh mass was recorded, and plantlet materials were dried for 72 h in a drying oven at 60 °C. Shoot and root dry mass were then recorded. Total plantlet dry mass and root : shoot ratio were calculated. Within each treatment combination, plantlet leaves from replications 1, 2 and 3, replications 4, 5 and 6, and replications 7 and 8 were pooled to three replications and ground to pass through a 20-mesh screen. Leaf Kjeldahl N concentration was analyzed by Kjeldahl's method and the concentrations of other foliar ions including P, K, Ca, Mg, Mn, Fe, Cu, B, Al, and Zn by inductively coupled plasma atomic emission (ICP) spectrophotometry. Tissue ion analysis was performed by The Pennsylvania State Univ. Agricultural Analytical Services Laboratory. Shoot ion content was estimated by multiplying leaf ion concentration by shoot (including leaves) dry mass. Root tissue was ashed for 12 h

Table 1. Analysis of variance significance and interactions for growth parameters of highbush blueberry plantlets in a three-way factorial experiment (M × Al × P).[z]

Effect	df	Total dry mass (g)	Shoot dry mass (g)	Root dry mass (g)	Root to shoot ratio	Shoot no.	Lateral shoot no.	Relative root vol (cm^3)	Relative canopy vol (cm^3)	Mycorrhizal infection (%)
M	1	NS	NS	***	***	**	NS	NS	NS	***
Al	1	***	***	***	***	NS	***	NS	***	NS
M × Al	1	NS	NS	NS	NS	NS	NS	NS	NS	NS
P	2	***	***	**	***	NS	***	*	**	NS
M × P	2	NS	NS	NS	NS	NS	NS	NS	NS	NS
Al × P	2	***	***	NS	***	NS	***	NS	***	NS
M × Al × P	2	NS	NS	NS	NS	NS	NS	NS	NS	NS

[z]M = mycorrhizal status, Al = aluminum level, P = phosphorus treatment.
NS,*,**,***Nonsignificant or significant at $P = 0.05$, 0.01, or 0.001, respectively.

in a muffle furnace at 496 °C. Root P and Al concentrations were determined by Murphy and Riley's method (Murphy and Riley, 1962) and the aluminon method (Cabrera et al., 1981; Chenery, 1948), respectively.

Data for mycorrhizal infection level were square root transformed before analysis. Covariance analysis was used account for the variation among individual experimental units. The covariates were initial plant mass and initial relative canopy and root volumes. Simple correlation analysis was used to investigate relationships between root Al and P concentrations and among leaf ion concentrations. All data analyses were performed using SAS procedures (SAS Institute, Cary, N.C.).

Results

Plant growth

There were no M × Al, M × P, or M × Al × P interactions for any of the growth parameters. However, the Al × P interaction was significant for the most of these parameters (Table 1). Therefore, data presentation reflects the main M effect for all of the growth parameters, the main Al and P effects for those growth parameters that were not affected by Al × P interactions, as well as the Al × P interactions.

There were no differences in total plantlet dry mass, shoot dry mass, relative root and canopy volume, and lateral shoot number between M and NM treatments (Table 2). However, M plantlets had more shoots than NM plantlets. The M plantlets also had a higher root : shoot ratio because of their increased root dry mass than NM plantlets (Table 2). Level of infection on M plantlets decreased from 15% to 25% to an average of 5% after 8 weeks. However, the level of infection was greater ($p < 0.001$) in M plants than in NM plantlets (Table 2).

Root dry mass, shoot number, and relative root volume were not subject to Al × P interactions. Shoot number also was not affected by Al or P treatments (Table 1). High Al decreased root dry mass compared to the Al control but had no significant effect on relative root volume (data not shown). The root dry mass and relative root volume were greater in the 0 mM P than in the 300 mM P treatment (data not shown). Further, foliar P and N application increased root dry mass and relative root volume compared to the 300 μM P treatment (data not shown). There was no difference in root dry mass and relative root volume between foliar P and N application and 0 μM P treatment.

Interactions between Al and P occurred in all other growth related parameters. For the 0 and 300 mM P treatments, Al decreased plantlet canopy and lateral development and shoot dry mass. As a result, total plantlet dry mass was also reduced. However, this reduction was reversed by foliar P and N application. In response to P stress, plantlet growth was stunted, as evidenced by the smaller canopy, fewer laterals, and less shoot and total dry mass (Table 2).

Plantlet root : shoot ratios exhibited complex patterns in response to an Al × P interaction (Table 2). Plantlets under P stress (0 μM P) had higher root : shoot ratios than nonstressed plants (300 μM P). High Al in solution increased root : shoot ratio; however, this increase was reversed by foliar P and N application. Changes in root : shoot ratio were in concurrence with the shoot and root growth responses to toxic Al levels and/or P stress.

Tissue analysis

There were no M × Al × P interactions for any of the tissue ion concentrations or shoot ion contents. Therefore, only significant main effects and first-order interactions are presented throughout the text.

Tissue Al and P. Having 0 μM P in solution decreased leaf P concentration and content compared to 300 μM P in solution or P and N spray treatment (Table 3). Foliar P and N application had the highest leaf P content among P treatments and increased leaf P concentration to a level comparable to the 300 μM P treatment (Table 3).

There was a significant M × Al interaction for root and leaf Al concentration. Both M and NM plantlet leaf Al concentration increased with increasing Al level in solution (Table 3). After 8 weeks exposure to Al, leaf Al concentration was higher in M than

Table 2. Main effect of mycorrhizal (M) infection and interaction between Al and P on highbush blueberry plantlet growth.

	Total dry mass (g)	Shoot dry mass (g)	Root dry mass (g)	Root to shoot ratio	Shoot no.	Lateral shoot no.	Relative root vol (cm^3)	Relative canopy vol (cm^3)	Infection level (%)
Main M effect[z]									
M	4.90	3.95	1.07	0.28	3.11	4.74	205	9722	5.21
NM	5.22	4.21	0.89	0.22	1.67	3.67	204	8680	0.01
p (F) [y]	0.12	0.15	<0.05	<0.001	<0.01	0.91	0.91	0.12	<0.001
Al × P interaction									
0 μM P									
0 μM Al	5.12	4.00	NA[z]	0.276	NA	3.89	NA	10195	NA
600 μM Al	3.77	2.84	NA	0.328	NA	1.06	NA	4756	NA
300 μM P									
0 μM Al	6.51	5.60	NA	0.160	NA	8.54	NA	13372	NA
600 μM Al	3.93	3.05	NA	0.282	NA	3.06	NA	7498	NA
Foliar P/N application[x]									
0 μM Al	5.35	4.30	NA	0.246	NA	4.81	NA	9477	NA
600 μM Al	5.67	4.69	NA	0.206	NA	5.96	NA	9907	NA
LSD (0.05)[w]	0.46	0.41	NA	0.038	NA	1.53	NA	2437	NA

[z]M = mycorrhizal, NM = nonmycorrhizal, NA = not applicable, because Al and P responses did not interact.
[y]p (F) values indicate significance level.
[x]Foliar P/N application was 5 mL of ammonium polyphosphate plus 5 mL of Tween 20/L, resulting in a concentration of 1700 $mg \cdot L^{-1}$ P and 500 $mg \cdot L^{-1}$ N.
[w]LSD (0.05) = least significant difference for mean comparison within each column for Al and P interaction, n = 16.

Table 3. P effect and mycorrhizal (M) × Al interaction on highbush blueberry plantlet tissue Al and P concentration and content.

		Leaf P concn (%)	Shoot P content (mg/shoot)
Main P effect			
0 μM P		0.053	1.46
300 μM P		0.118	3.23
Foliar P/N application[z]		0.118	4.04
LSD (0.05) [y]		0.015	0.61
	Root Al ($mg \cdot g^{-1}$)	Leaf Al ($mg \cdot g^{-1}$)	Shoot P content (mg/shoot)
M × Al interaction[x]			
0 μM Al			
M	12.55	0.056	2.84
NM	6.46	0.045	3.66
600 mM Al			
M	22.01	0.107	2.69
NM	4.09	0.091	2.46
LSD (0.05)[w]	10.32	0.011	0.70

[z]Foliar P/N application was 5 mL of ammonium polyphosphate plus 5 mL of tween 20/L, resulting in a concentration of 1700 $mg \cdot L^{-1}$ P and 500 $mg \cdot L^{-1}$ N.
[y]LSD (0.05) = least significant difference for mean comparison within each variable.
For P effect, n = 12.
[x]M = mycorrhizal, NM = nonmycorrhizal.
[w]LSD (0.05) = least significant difference for mean comparison within each variable. For root, n = 24; for leaf and shoot, n = 9.

in NM plantlets, as was root Al concentration. Further, a significant increase in root Al concentration occurred in M but not NM roots at 600 μM Al (Table 3). Shoot P content was also affected by the M × Al interaction, with P content of NM shoots decreased by high Al while that of M plantlets was not (Table 3).

There were significant M × P and Al × P interactions for root P concentration (Table 4). Root P concentration was increased by P foliar application compared to 0 μM P in solution regardless of the Al levels (Table 4). High Al level in solution, however, decreased root P concentration only with 300 μM P. Root P concentration did not differ in M and NM roots in the 0 μM P treatment. The M roots accumulated more P than NM roots when P was supplied in solution. The greatest effect of foliar feeding P and N was an increase in root P concentration in M and NM roots and a significant increase in NM root P concentration compared to M root P concentration.

OTHER FOLIAR NUTRIENTS. No M × Al and M × P interactions were observed for N, K, Ca, Mg, Mn, Fe, Cu, B, and Zn in leaf concentration or shoot content. The M main effect was significant for some of these ions in leaf concentration. Leaf N, Ca, Mg, and Mn concentrations were higher in M than NM plantlets (data not shown). Leaf K and B concentrations tended to be higher in M plantlets ($P = 0.13$ and 0.12, respectively). There were no differences between M and NM plantlets in shoot N, K, Ca, Mg, Mn, Fe, Cu, B, and Zn content (data not shown). Leaf N, Ca, and Fe were at concentrations considered deficient in field plantings, while other nutrients were within an adequate range.

There was a significant Al × P interaction for N, K, and Al ion concentrations and shoot contents. In 0 or 300 μM P treatment plantlets, high Al level in solution decreased leaf N concentration and shoot content but increased leaf K concentration (Table 5). Foliar P and N application increased leaf N concentration and shoot N content at 600 μM Al. Under 0 μM Al, leaf N concentration was increased by adding P in solution but there was no difference in shoot N content. Leaf Al concentration and content increased with increased Al level in solution regardless of P level or application method.

Table 4. Interactions among Al and P, and mycorrhizal (M) infection and P on highbush blueberry plantlet root P concentration.

	Root P concn (%)		Root P concn (%)
Al × P interaction		M × P interaction [z]	
0 μM P		0 μM P	
0 μM Al	1.36	M	1.15
600 μM Al	1.29	NM	1.50
300 μM P		300 μM P	
0 μM Al	4.53	M	4.51
600 μM Al	3.67	NM	3.68
Foliar P/N application[y]		Foliar P/N application	
0 μM Al	4.01	M	3.56
600 μM Al	4.41	NM	4.84
LSD (0.05)[x]	0.63	LSD (0.05)[x]	0.63

[z]M = mycorrhizal, NM = nonmycorrhizal.
[y]Foliar P/N application was 5 mL of ammonium polyphosphate plus 5 mL of Tween 20/L, resulting in a concentration of 1700 $mg \cdot L^{-1}$ P and 500 $mg \cdot L^{-1}$ N.
[x]LSD (0.05) = least significant difference for comparisons among interaction means (n = 16).

Table 5. Highbush blueberry plantlet leaf N, K, and Al concentration and shoot content as affected by Al × P interaction.

	Leaf concn			Shoot content		
	N (%)	K (%)	Al ($\mu g \cdot g^{-1}$)	N (mg/shoot)	K (mg/shoot)	Al (mg/shoot)
Al × P interaction						
0 μM P						
0 μM Al	1.36	0.74	75	45.6	14.7	0.15
600 μM Al	1.20	0.85	103	25.0	17.6	0.21
300 μM P						
0 μM Al	1.75	0.60	37	57.6	19.6	0.12
600 μM Al	1.40	0.81	97	32.2	18.7	0.22
Foliar P/N application[z]						
0 μM Al	1.55	0.83	40	53.4	28.4	0.14
600 μM Al	1.58	0.82	97	56.6	29.4	0.34
LSD (0.05) [y]	0.09	0.07	42	15.1	6.4	0.057

[z]Foliar P/N application was 5 mL of ammonium polyphosphate plus 5 mL of Tween 20/L, resulting in a concentration of 1700 $mg \cdot L^{-1}$ P and 500 $mg \cdot L^{-1}$ N.
[y]LSD (0.05) = least significant difference for comparison among interaction means (n = 6).

The Al main effect was dramatic especially for shoot ion content. Higher Al level in solution did not affect leaf Ca, Mg, or micronutrient concentrations except for Mn, but did decrease the shoot content of Ca, Mg, Mn, Fe, Cu, B, and Zn (Table 6).

Correlation analyses. Root Al concentration was negatively correlated with root P concentration in NM plantlets ($r = -0.4291$, $P = 0.04$) but not in M plants ($r = -0.172$, $P = 0.43$). Correlations among foliar nutrient concentrations exhibited very complex patterns in M and NM plantlets (data not shown). Most importantly, there was a positive correlation between leaf N and P concentration ($r = 0.741$, $P = 0.006$ for M plantlet; $r = 0.721$, $P = 0.008$ for NM plantlet) and a negative correlation between leaf N and Al concentration ($r = -0.749$, $P = 0.005$ for M plantlet; $r = -0.689$, $P = 0.013$ for NM plantlet).

Discussion

It is evident that high-Al treatment reduced the growth of highbush blueberry. This growth reduction by high Al is largely due to its detrimental effect on nutrient uptake. Plantlets exposed to high Al have a lower shoot nutrient content than those unexposed. Poor plant growth induced by high Al is characterized by decreased root, shoot, and total dry mass; decreased lateral shoot number; and restricted canopy development. As suggested by Foy (1983), these negative growth responses to high Al were secondary effects following the primary action of Al on the root systems. The secondary effects led to a higher root : shoot ratio in blueberry plantlets. It was also possible that the effect of Al on plant growth responses was caused by different P availability rather than Al effect alone. In fact, foliar P and N application reversed most of the negative plant growth responses to high Al, indicating that P was deficient under high Al treatment. However, root growth as determined by dry matter production was reduced by high Al, particularly under foliar applied P and N treatment, indicating that the mechanism for Al toxicity was root growth inhibition and at least in part, by limiting P and N uptake in the rhizosphere.

It is evident that decreased blueberry root growth as determined by dry matter production reflects that root growth was disrupted by high Al. This was also demonstrated in other studies for cotton and wheat (Foy et al., 1967; Huang et al., 1992). In contrast, relative root volume was not affected by Al treatment, suggesting that the effect of Al on the root system could be obscured by root response to P deficiency.

When P was deficient (0 μM P), plantlets had larger relative root volume and more root growth and had a higher root to : shoot ratio than those under sufficient P supply (300 μM P). This suggests that plantlets sensed and responded to P stress by allocating more resources to roots. Such response may be similar to P stress elicited changes in root branching pattern and total root length in barley (Drew, 1975). Further, a decrease in plantlet growth under P stress and toxic Al level suggested that another mechanism might also be responsible for the growth reduction by high Al. For example, Al could simply reduce plant growth by limiting water and other nutrient uptake (Foy, 1983). Indeed, leaf N concentration of

Table 6. Effect of Al treatment on highbush blueberry plantlet leaf concentration and shoot content.

	Leaf concn						
	Ca (%)	Mg (%)	Mn ($\mu g \cdot g^{-1}$)	Fe ($\mu g \cdot g^{-1}$)	Cu ($\mu g \cdot g^{-1}$)	B ($\mu g \cdot g^{-1}$)	Zn ($\mu g \cdot g^{-1}$)
0 μM Al	0.332	0.217	130	46	6.1	70	15.2
600 μM Al	0.317	0.213	119	44	5.7	66	14.9
p (F)[z]	0.08	0.51	<0.05	0.32	0.16	0.07	0.66
	Shoot content						
	(mg/shoot)	(mg/shoot)	(μg/shoot)	(μg/shoot)	(μg/shoot)	(μg/shoot)	(μg/shoot)
0 μM Al	11.1	7.3	433	150	21	221	51
600 μM Al	8.2	5.7	306	122	16	181	39
p (F)[z]	<0.01	<0.01	<0.01	<0.05	<0.05	<0.05	<0.01

[z]p(F) values indicate significance level.

blueberry plantlets in 0 and 300 mM P was reduced as a result of high Al. This toxic effect of Al was also suggested by the negative correlation between leaf Al and N concentration.

Most of the vegetative growth parameters increased with either P supplied in solution or via foliar applications. In particular, foliar P and N application ameliorated Al-induced P deficiency and increased most plantlet growth parameters under Al or P stress. Further, root P concentration was affected by foliar P and N application, Al, and mycorrhizal status. Foliar P and N application increased root P concentration only in NM plantlets when P uptake was restricted by high Al or P stress. These results suggested that foliar applied P and N has been translocated down the root system to offset the low root P levels caused by P stress. Foliar P and N application also increased leaf N concentration. The reasons for the increase in leaf N may be 2-fold. First, the APP spray solution contained some N as a foliar N feeding source. Second, translocation of P down to the roots may have a synergistic effect on root N uptake.

Although M plantlets did not differ in total plant dry mass from NM plantlets, root growth was stimulated by mycorrhizal infection. The M plantlets also developed more shoots and laterals. These changes in growth pattern by ericoid mycorrhizal infection may be due to improved host nutrient uptake and may also involve host hormonal responses. Ericoid mycorrhizal fungi have been demonstrated to synthesize auxin in culture (Gay and Debaud, 1986). Their associations with blueberry plants could alter the host hormonal balance, perhaps the cytokinin : auxin ratio, and result in changes in shoot branching pattern.

The M plantlets did not take up more P than NM plantlets. One explanation was that there was no organic P source available. Second, there were no conditions (e.g., depletion zone) that limited P uptake in the sand culture system. Another possibility is that ericoid mycorrhizae have less vegetative hyphae outside root cells than inside (Read, 1985). Such limited external hyphal networks may be not as effective as those in other mycorrhizal symbioses to enhance P uptake of the host roots. However, the processes of governing P uptake under Al exposure was affected by ericoid mycorrhizae. Specifically, NM root P was negatively correlated with NM root Al, indicating Al reduced root P uptake through the binding of P in rhizosphere or damaging root P uptake processes (Cumming et al., 1986). In contrast, root P and Al levels were not correlated in M plantlets, suggesting that the binding between P and Al in the roots may not occur in mycorrhizal roots.

The fact that there was more Al in M than NM roots supports the hypothesis that M roots accumulate more Al than NM roots. Similar results have also been reported in ecto- and endomycorrhizal infected plants (Eeckhaoudt et al., 1992; Maddox and Soileau, 1991). But leaf Al concentration revealed that Al was readily transported into leaf tissues of M and NM plantlets, with leaf Al concentration higher in M plantlets than NM plantlets. These results suggested that excess Al ions, like excess heavy metals such as Zn and Cu (Bradley et al., 1982), could be seized by vegetative hyphal coils in ericoid mycorrhizal root cells. However, Al sequestration may effectively impede Al transport into leaves for only a limited time. Once Al binding and accumulation sites in M roots are fully occupied, excessive Al then may be transported into leaves of M plantlets. Alternatively, mycorrhizal cells could degenerate within 7 weeks post infection (Duddridge and Read, 1982), and Al seized in the hyphal coils could be released and transported into leaf tissue. In 8 weeks, it is reasonable to assume that the degeneration of mycorrhizal cells could have occurred, especially since mycorrhizal infection level had decreased from 15% to 25% to an average of 5% by the end of experiment. Therefore, processes governing Al uptake and transport in blueberry plantlets were altered by ericoid mycorrhizal infection.

Although M infection altered P and Al uptake processes as well as foliar ion correlations, the total dry mass of M plantlets was not differ from that of NM plantlets when both were treated with high Al. This indicates that high Al is toxic to M and NM plantlets. The potential of M infection for the mediation of Al toxicity in highbush blueberry is uncertain. However, the growth reduction of both M and NM plantlet by 600 μM Al can be overcome with foliar APP application, which could possibly provide a useful means for correcting this nutritional disorder in highbush blueberries growing in acidified mineral soils.

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