

## The effect of aluminium and media on the growth of mycorrhizal and nonmycorrhizal highbush blueberry plantlets

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### Abstract

A factorial experiment was conducted to determine the effect of aluminium (0 and 600  $\mu\text{M}$ ) and media (sand, and 1:1 sand:soil) on mycorrhizal (M) and non-mycorrhizal (NM) highbush blueberry plantlets. There were no differences in nutrient uptake and total plant dry weight between M and NM plantlets. However, more root growth, as determined by dry weight, was observed in M than NM plantlets. The plantlets growing in sand had more dry weight than did those in the soil medium. Although the root growth and shoot growth were reduced by the 600  $\mu\text{M}$  Al treatment, the direct effect of Al on plantlet growth was not clear due to Al and P interactions. Plant nutrient uptake was reduced by high concentrations of Al, suggesting that high Al concentration limited the ability of roots to acquire most of the nutrients. Mycorrhizal cortical cell infection levels of 15–20% were maintained in the roots in soil medium but decreased to about 5% over the 6 weeks of the experiment in the sand medium. Although M plantlets accumulated more Al in their roots, Al was readily transported to the leaf tissues of M and NM plantlets.

### Introduction

Blueberry plants require acid soil for optimum growth (Korcak, 1989a). In low pH soils, soluble aluminium (Al) is considered to be the most growth limiting factor for most plants (Adams, 1981). Because organic mulch is often used when growing highbush blueberry in upland mineral soils, the toxic effect of Al may be minimized by the complexation of soluble Al by organic acids. The growth of rabbiteye blueberry increased with mulching, which resulted in a uniform root distribution from the plant crown outward (Spiers, 1986). Peterson et al. (1987) reported that rabbiteye blueberry with a pre-plant sawdust amendment had better growth with soil acidification by aluminium sulfate and elemental sulfur than plants without amendment. Elimination of organic mulch in mineral soil significantly decreased rabbiteye and highbush blueberry growth (Goulart et al., 1995; Patten et al., 1988). In addition, the shoot fresh weight of highbush blueberry plants was also reduced by high Al in solution culture (Korcak, 1989b). This strongly implies that excess Al is

detrimental to highbush blueberry growth. It is possible that the release of Al ions from acidification of mineral soils reduces plant growth while the addition of mulch binds active forms of Al, reducing the toxic effect. This is of fundamental interest as the increase in highbush blueberry production, coincident with the increased need to preserve the wetlands where blueberries are typically produced, makes it more important to produce highbush blueberries on mineral ("upland") soils.

Blueberry plants are mycorrhizal under natural and commercial field conditions (Boyer et al., 1982; Goulart et al., 1993; Jacobs et al., 1982). Mycorrhizal associations in ericaceous plants enable them to assimilate various N-containing compounds and increase plant growth (Bajwa and Read, 1986; Stribley and Read, 1974, 1980). Alterations of nutrient uptake ability by mycorrhizal infection may be of great importance for plants to access nutrients, particularly under low nutrient conditions (Read and Stribley, 1973).

Mycorrhizal symbiosis may increase resistance of the host plants to metal toxicities. Plants with ericoid mycorrhizal infection outgrew the nonmycor-

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rhizal controls when both M and NM plants were exposed to relatively high Cu and Zn concentrations (Bradley et al., 1982). Mycorrhizae may alleviate metal toxicity by sequestering the toxic metals in the fungal hyphae to exclude them from host metabolism (Dosskey and Adriano, 1991). In a similar scenario, excess Al could be excluded by mycorrhizal infection in highbush blueberries grown in acid soils.

To test this hypothesis, an experiment was undertaken to investigate

- 1) the effect of high Al on the growth and nutrient uptake of highbush blueberry grown in sand and a soil/sand (1:1) medium, and
- 2) the role of mycorrhizae in nutrient uptake and plant growth in relation to Al toxicity.

## Materials and methods

Tissue cultured 'Elliot' blueberry (*Vaccinium corymbosum* L.) shoots were rooted in sand under high humidity when they were 6 weeks old. After 9 months, plants were about 10 to 15 cm tall with a well-developed root system. They were then transferred into nonsterile soil<sup>1</sup> from Little Flat nature area of Rothrock State Forest, (40° 25' longitude, 78° 00' latitude), in central PA, for inoculation. Nonmycorrhizal control plantlets were grown in the same soil which had been allowed to air dry, then autoclaved at 105 °C for 90 minutes. After 8 weeks, roots were cleared, stained and mycorrhizal infection level was determined using a modified grid-line intersect technique (Giovannetti and Mosse, 1980). Mycorrhizal (M) plantlets had 15–25% cortical cell infection, while nonmycorrhizal (NM) control plantlets remained uninfected.

Prior to transferring, the roots of M and NM plantlets were washed using dilute H<sub>2</sub>SO<sub>4</sub> solution (pH 4.5). At this time, plantlet fresh weight, canopy and root volume (cm<sup>3</sup>), canopy and root density (evaluated subjectively from 1 to 5, 1=sparse, 5=dense), and basal and lateral shoot number were recorded. Canopy size and root volume were estimated using the formula for a cylinder ( $\pi r^2 H$ ), where r=the average radius of canopy or root system, using two measurements per plantlet, H=canopy or root system height. A growth

index for canopy and root was developed by multiplying the canopy or root volume by canopy or root density.

Treatment factors were mycorrhizal status (M and NM plantlets), Al level in the nutrient solution (0 and 600  $\mu\text{M}$ ), and medium (sand and 1:1 soil:sand, by volume). Al levels were determined in a pre-experiment, which found that 600  $\mu\text{M}$  Al reduced growth of nonmycorrhizal blueberry plantlets after 4 weeks. The sand medium was a silica sand (20 mesh size) (R J Glass, Inc., Duncansville, PA 16635), which was acid washed with 0.5 N H<sub>2</sub>SO<sub>4</sub>. The medium was flushed with distilled water until medium pH reached 4.5. The soil medium was a mixture of half acid washed silica sand and half Hagerstown silt loam soil (Alfisol, top 15 cm soil. pH 6.8, organic matter 2.3%, P 0.03 mg g<sup>-1</sup>, K 0.10 mg g<sup>-1</sup>, Mg 0.16 mg g<sup>-1</sup>, Ca 1.55 mg g<sup>-1</sup>), obtained from the Horticulture Farm of the Russell E. Larson Agricultural Research Farm in Rock Springs, PA. Soil was passed through a 2 mm sieve, air dried, and autoclaved at 105 °C for 90 minutes. Soil was then acidified to pH 4.5 prior to mixing with the acid washed sand. The soil:sand medium will hereafter be referred to as the "soil" treatment.

Treatments were arranged in a randomized complete block (2×2×2 factorial design) with 8 replications. Plantlets were grouped into blocks by fresh weight so that plants in each block had the similar fresh weight. They were transplanted into 10 cm square pots with sand or soil medium. Following the transfer, plantlets were watered twice daily with 140 mL of a nutrient solution containing (in mM): 2.5 N (as NH<sub>4</sub>), 0.3 P, 1 K, 1 Mg, 0.5 Ca, 2.8 S, 1 Cl, and (in  $\mu\text{M}$ ) 89.5 Fe (as FeEDTA), 34.2 B, 10.0 Mn, 0.99 Zn, 0.01 Cu, and 0.02 Mo with or without 600  $\mu\text{M}$  Al addition (as Al<sub>2</sub>(SO<sub>4</sub>)<sub>3</sub>·18H<sub>2</sub>O). The pH of the nutrient solution was adjusted to 4.5 using 0.1 N NaOH. Free Al and P ion species and concentration in the solution (Table 1) were estimated using a computer program, SPECIES (Barak, 1990). 140 mL of nutrient solution were automatically delivered twice daily into each pot. Every 10 days, all the media were flushed with dilute H<sub>2</sub>SO<sub>4</sub> solution (pH 4.5) to remove residual ions. Plantlets were grown at an ambient temperature of 25 °C and a daylength of 16 hours with 300 micromoles m<sup>-2</sup> s<sup>-1</sup> photosynthetically active radiation provided by fluorescent and incandescent fixtures.

After 6 weeks, plantlets were harvested and canopy and root growth index determined followed the same protocol as described for initial data collection. Plantlets were then dried for 72 hours in a

<sup>1</sup> Soil type is a Leetonia extremely stony loamy sand which is a Spodosol. 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 Dr Yolande Dalpé at Center for Land and Biological Resource Research, Ottawa Ont., Canada.

Table 1. Aluminium and phosphorus ion species and concentration in the nutrient treatment solutions for highbush blueberry plantlets grown in sand and soil<sup>7</sup>

	Ion species and concentration ( $\mu M$ )						P concentration ( $\mu M$ )
	HPO <sub>4</sub>	H <sub>2</sub> PO <sub>4</sub>	AlHPO <sub>4</sub>	Al	Al(OH)	Al(OH) <sub>2</sub>	
0 $\mu M$ Al+300 $\mu M$ P	0.8	283	0	0	0	0	289
600 $\mu M$ Al+300 $\mu M$ P	0.005	0.2	300	120	22	3.6	97

<sup>7</sup> Ion species and concentration were determined by using SPECIES developed by Dr Philip Barak in the Department of Soil Science, University of Wisconsin. Solution P concentration was determined by the Murphy and Riley method (Murphy and Riley, 1962).

drying oven at 60 °C, and shoot and root dry weights recorded. Total plantlet dry weight and root to shoot ratio were calculated. Before drying, roots were examined for mycorrhizal infection. Within each treatment combination, plantlet leaves from replicate 1, 2 and 3, replicate 4, 5, and 6, and replicate 7 and 8 were pooled to 3 replications and ground to pass a 20-mesh screen using a mill. Foliar ion concentrations were analyzed by inductively coupled plasma emission (ICP) spectrophotometry (The Pennsylvania State University Agricultural Analytical Services Laboratory). Tissue ion content was estimated by multiplying foliar ion concentration by shoot dry weight. Root P and Al concentrations were determined respectively by the Murphy and Riley method (Murphy and Riley, 1962) and a modified aluminium method (Cabrera et al., 1981; Chenery, 1948).

Data for mycorrhizal infection level were square root transformed (Steel and Torrie, 1980). Covariance analysis was performed to account for variations due to the individual experimental unit. The covariates were initial plant weight, and canopy and root growth index. Although the effect of covariate for root growth index, shoot, root, and total dry weight as well as root to shoot ratio was not significant ( $p = 0.05$ ), the precision of the treatment effect was improved when it was included in the analysis. Since nonmycorrhizal treatment plants in soil became slightly infected and the mycorrhizal plant infection level was reduced in sand by the end of experiment (Table 2), the two mycorrhizal and two medium levels were examined as one factor consisting of four individual treatments (sand/mycorrhizal, sand/nonmycorrhizal, soil/mycorrhizal, and soil/nonmycorrhizal). Data then were analysed as a two factor factorial experiment with medium/mycorrhizal level and Al concentration as the 2 factors. All data analyses were performed using SAS procedures (SAS Institute, 1985).

## Results and discussion

### Plant growth

No interactions between medium/mycorrhizal and Al treatment were detected on plant growth responses. There were no differences in total plant dry weight, shoot dry weight, shoot number, or root growth index between M and NM plantlets in either sand or soil medium (Table 2). However, M plantlets had higher lateral shoot numbers in sand, and higher root dry weight in soil medium than NM plantlets. In soil, M plantlets also had a larger canopy growth index, and a higher root to shoot ratio compared to NM plantlets. Studies have suggested that mycorrhizal infection enhances the ability of roots to explore more soil and to acquire more nutrients through an extensive external hyphal network (Baylis, 1972, 1975). In the case of ericoid mycorrhizae, much more vegetative hyphae are found inside root cortical cells than outside (Read, 1985). The induction of chelating compounds in response to mineral nutrient stress has not been observed in blueberry plants (Korcak, 1988a). Therefore, the increased nutrient acquisition in mycorrhizal blueberry plantlets may come about, at least in part, by increased root growth which enables the roots to more fully explore the soil. The higher root to shoot ratio in M plantlets supports this hypothesis.

It was evident that both mycorrhizal and nonmycorrhizal plantlets grown in sand had higher shoot and total dry weight than did those grown in soil (Table 2). A larger root growth index was also observed in the plantlets grown in sand relative to those grown in soil. Studies have found that the growth of highbush blueberry is affected by soil physical properties (Blasing, 1985). Poor blueberry growth was found in soils with small total pore volume and high bulk density. Poor root growth could be induced by poor aeration and high penetration resistance in soil medium as compared to

Table 2. Effect of media and mycorrhizal status, and Al level on highbush blackberry plantlet growth

	Shoot dry weight (g)	Root dry weight (g)	Total dry weight (g)	Root to shoot ratio	Shoot number	Lateral shoot number	Root growth index (cm <sup>3</sup> )	Canopy growth index (cm <sup>3</sup> )	Mycorrhizal infection (%)
<i>Media and mycorrhizal treatments</i>									
Sand, mycorrhizal	4.20	0.76	4.95	0.180	2.69	9.13	213	11008	4.6
Sand, nonmycorrhizal	4.08	0.69	4.76	0.169	1.87	5.60	177	10007	0
Soil, mycorrhizal	3.11	0.65	3.86	0.201	3.0	4.67	78	10868	19.8
Soil, nonmycorrhizal	3.22	0.53	3.64	0.174	1.44	4.31	79	6957	5.0
lsd (0.05) <sup>z</sup>	0.51	0.08	0.56	0.020	1.60	3.22	59	3011	0.8
<i>Al level</i>									
0 $\mu$ M Al	4.00	0.70	4.70	0.172	2.28	5.91	145	10844	4.6
600 $\mu$ M Al	3.30	0.61	3.92	0.190	2.20	5.90	130	8404	5.1
p(F) <sup>y</sup>	<0.01	<0.05	<0.01	<0.01	0.890	0.967	0.436	<0.05	0.797

<sup>z</sup> lsd (0.05) = least significant difference for mean comparison within the factor ( $n=32$ ).

<sup>y</sup> p(F) values indicate significance level.

sand. Reductions in root growth associated with the soil medium would be expected to reduce shoot and total plantlet dry weight as compared to the plantlets grown in sand.

The growth of M and NM plantlets was affected to the same degree by the Al treatments, specifically, there were no interactions between medium/mycorrhizal treatment and Al concentration (Table 2). The high Al level decreased plantlet shoot, root, and total dry weight, as well as canopy growth index compared to non-Al treatment. There were no differences in plantlet shoot number, lateral number and root growth index between high Al and non-Al treatment. However, high Al treatment increased root to shoot ratio as compared to non-Al treatment. This increase was caused by a disproportional reduction in shoot growth relative to root growth. The reduction of shoot growth by high Al level may be a secondary effect which follows the primary action of Al on the root system (Rasmussen, 1968). The toxic effect of excessive Al ions on blueberry plants has been implied in several studies. The growth of rabbiteye blueberry plants was reduced by soil applied aluminum sulfate during soil acidification (Patten et al., 1988; Peterson et al., 1987). Poor root growth was also noticed in those studies. However, in the nutrient delivery system of this study, P availability was altered at 0 and 600  $\mu$ M Al levels (Table 1). The effect of Al on plant growth responses could also be caused by different P availability. Therefore,

the direct effect of high Al on the growth of plantlets was not clear due to Al and P interactions in the medium and the plantlet. These interactions obscured the mechanism of Al toxicity.

Mycorrhizal plantlets maintained much higher mycorrhizal infection levels in the soil than in the sand medium (Table 2). But NM plantlets became slightly infected after 6 weeks in soil while those grown in sand remained uninfected. However, in either medium, M plantlets had a higher infection level than did NM plants. Early studies reported that the intensity of mycorrhizal infection was affected by external factors and there was also seasonal variation (Rayner, 1927). It has been suggested more recently that the level of mycorrhizal infection is governed by the medium property, root and hyphal growth, and interactions between the degenerations of intracellular hyphal coils and cytoplasm of the host (Harley and Smith, 1983). Varied infection levels between the soil and the sand medium would be expected for M plantlets. Soil medium is clearly favorable for supporting mycorrhizal infection relative to sand. Rapid root elongation and growth in the sand versus the soil medium might make host carbohydrates less available or less necessary for support of the mycorrhizal fungi.

Table 3. Effect of media and mycorrhizal status, and Al level on highbush blueberry plantlet foliar ion concentration

	N	P	K	Mg	Mn	Fe	Cu	B	Al	Zn
	(%)				$(\mu\text{g g}^{-1})$					
<i>Media and mycorrhizal treatments</i>										
Sand, mycorrhizal	1.90	0.120	0.56	0.22	130	52	5.0	56	65	17.7
Sand, nonmycorrhizal	1.82	0.115	0.58	0.21	123	53	5.3	55	62	17.0
Soil, mycorrhizal	1.88	0.118	0.62	0.19	440	67	6.0	60	79	17.5
Soil, nonmycorrhizal	1.73	0.015	0.67	0.16	407	64	5.8	64	75	15.0
lsd (0.05) <sup>z</sup>	0.12	0.009	0.072	0.018	47	9	0.6	6	16	1.2
<i>Al level</i>										
0 $\mu\text{M}$ Al	1.87	0.116	0.59	0.20	280	58.6	5.7	58	55	16.9
600 $\mu\text{M}$ Al	1.80	0.113	0.63	0.19	270	58.8	5.4	60	86	16.7
<i>p</i> (F) <sup>y</sup>	0.120	0.414	0.153	0.107	0.533	0.954	0.224	0.505	0.001	0.521

<sup>z</sup> lsd (0.05) = least significant difference for mean comparison within the factor ( $n=32$ ).

<sup>y</sup> *p*(F) values indicate significance level.

Table 4. Effect of media and mycorrhizal status, and Al concentration on foliar Ca concentration of highbush blueberry plantlets

	Foliar Ca concentration (%)
<i>0 <math>\mu\text{M}</math> Al</i>	
Sand, mycorrhizal	0.367
Sand, nonmycorrhizal	0.350
Soil, mycorrhizal	0.483
Soil, nonmycorrhizal	0.383
<i>600 <math>\mu\text{M}</math> Al</i>	
Sand, mycorrhizal	0.347
Sand, nonmycorrhizal	0.360
Soil, mycorrhizal	0.383
Soil, nonmycorrhizal	0.360
lsd (0.05) <sup>z</sup>	0.023

<sup>z</sup> lsd (0.05) = least significant difference for mean comparison within the factor ( $n=6$ ).

### Tissue analysis

M plantlets had higher foliar N, P, Mg, and Zn concentrations than NM plantlets in the soil medium but not in the sand medium (Table 3). This was related with higher mycorrhizal infection rates for M plantlets in soil medium. The higher foliar N and P concentration in M plantlets was also in concurrence with the results from other studies (Read, 1983; Stribley and Read, 1974). The reason for increased foliar Mg concentration in

M plantlets may, as with N and P, be related to the increased root growth of the mycorrhizal plantlets. It is also possible that the increased foliar Mg concentration by M plantlets may be important for their tolerance to high Al levels. Rengel and Robinson (1990) found that increased Mg concentration in the nutrient solution alleviated the negative effects of Al on root and shoot dry weight. Foliar Al concentration was not affected by mycorrhizal infection level in either medium (Table 3). However, foliar Al concentration increased at the higher solution Al concentration, indicating Al was taken up and transported to both M and NM plantlet leaves. As a result, Al accumulated to the same degree in the leaves of M and NM plantlets irrespective of medium. It was documented that foliar Al concentrations of highbush and lowbush blueberry plants were in the range of 100 to 200  $\mu\text{g g}^{-1}$  (Korcak, 1988b; Sheppard, 1991); however, the foliar Al concentrations in our study were lower. Treatment interactions occurred between the medium/mycorrhizal treatments and Al concentration treatments for foliar Ca concentration (Table 4). Foliar Ca concentration of M and NM plantlets was decreased by high Al in the soil medium but not in sand. Foliar Ca concentration in M plantlets was higher than in NM plantlets in soil medium. However, foliar Ca concentration was not affected by high Al in either M or NM plantlets in sand (Table 4). It appears that foliar Ca concentration was reduced under Al stress in the soil medium. The effect of Al on Ca uptake may be via inhibiting Ca influx and blocking

Table 5. Effect of media and mycorrhizal status, and Al level on highbush blueberry plantlet issue ion uptake

	N	P	K	Ca	Mg	Mn	Fe	Cu	B	Al	Zn
	(mg/plant)					(μg/plant)					
<i>Media and mycorrhizal treatments</i>											
Sand, mycorrhizal	72.7	4.6	21.5	13.7	8.5	501	200	19	217	247	67
Sand, nonmycorrhizal	67.0	4.2	21.4	13.1	8.0	449	191	20	204	217	63
Soil, mycorrhizal	48.9	3.1	16.0	11.5	5.0	1158	174	15	155	201	45
Soil, nonmycorrhizal	54.1	3.3	20.4	11.6	5.2	1261	202	18	197	232	47
lsd(0.05 <sup>x</sup> )	15.6	0.90	5.0	3.1	1.5	285	60	5	57	89	16
<i>Al level</i>											
0 μM Al	70.9	4.4	22.5	14.9	7.8	1016	223	22	222	208	64
600 μM Al	50.3	3.2	17.1	10.0	5.5	668	161	15	164	240	47
<i>p(F)</i> <sup>y</sup>	<0.01	<0.01	<0.01	<0.001	<0.001	<0.01	<0.01	<0.01	<0.01	0.283	<0.01

<sup>x</sup> lsd (0.05) = least significant difference for mean comparison within the factor ( $n=32$ ).

<sup>y</sup> *p(F)* values indicate significance level.

Ca channels by competing for binding sites in roots (Ryan and Kochian, 1993).

Although the high Al treatment did not affect the foliar ion concentration except for foliar Al (Table 3), it dramatically decreased uptake of all ions of both M and NM plantlets grown in both media (Table 5). This was consistent with the decreased plant growth by high Al. General effects of excess Al on the root system include reduced cell division in the root tips, increased cell wall rigidity by cross-linked pectins, and decreased root respiration (Foy, 1983); all of which reduce the ability of roots to acquire nutrients and water. The disruption of root tip mucilage by high solution Al level may be also responsible for reduced nutrient uptake (Korcak, 1989b).

M and NM plantlets did not differ in ion uptake in either medium (Table 5). However, there was a general trend that the ion uptake in both M and NM plantlets was lower in the soil than in the sand medium. In particular, N, K, Mg, and Zn uptake was significantly lower in soil than in sand. The increased Mn uptake in plantlets grown in the soil as compared to the sand medium is probably a reflection of different availability levels. Because the uptake of most ions was decreased for the plantlets grown in soil versus sand medium, decreased plant growth in soil medium could have been due to limited nutrient uptake.

Root P concentration of M plantlets over that of NM plantlets in sand was not affected by Al levels (Table 6). However, in the soil medium, root P concentrations

were lower for both M and NM plantlets grown with high Al versus those with low Al, indicating excess Al is interfering with P nutrition. Previous studies have found the high Al can result in the precipitation of P as  $AlPO_4$  (Rasmussen, 1968; Rorison, 1965). It is also possible that Al binding with root cell pectins stops root elongation, further limiting the ability of roots to acquire soil labile P by limiting their foraging volume.

In soil medium, M roots contained more Al than NM roots, however in sand, there was no difference in root Al concentration between M and NM plantlets (Table 7). The accumulation of Al in M roots suggests that Al ions could be sequestered in the hyphal coils of infected root cortical cell as with other metal ions in other studies (Bradley et al., 1982; Gildon and Tinker, 1983). This hypothesis is also consistent with the fact that the M roots in sand had much lower infection levels than those in the soil medium (Table 2). A possible mechanism of Al tolerance in ectomycorrhizal infected pines has been suggested by Cumming and Weinstein (1990). Al ions can be either sequestered inside the hyphae or form stable chelates in the rhizosphere due to ectomycorrhizal infection, thereby reducing movement of Al ions into the root cortex. In their studies, less Al was found in M plant leaves. However, foliar Al concentration did not differ in M and NM blueberry plantlets in this study, indicating Al ions were readily transported into leaves of both M and NM plantlets. Accumulation of Al ions in M roots may not effectively impede the movement of Al ion toward shoots

Table 6. Effect of media and mycorrhizal status and Al concentration on root P concentration of highbush blueberry plantlets

	Root P concentration (%)
<i>0 μM Al</i>	
Sand, mycorrhizal	3.61
Sand, nonmycorrhizal	3.44
Soil, mycorrhizal	4.44
Soil, nonmycorrhizal	4.50
<i>600 μM Al</i>	
Sand, mycorrhizal	4.74
Sand, nonmycorrhizal	4.28
Soil, mycorrhizal	3.24
Soil, nonmycorrhizal	3.47
Lsd (0.05) <sup>z</sup>	0.68

<sup>z</sup> Lsd (0.05) = least significant difference for mean comparison within the factor ( $n=32$ ).

Table 7. Effect of media and mycorrhizal status, and Al level on root Al concentration of highbush blueberry plantlets

	Root Al concentration (mg g <sup>-1</sup> )
<i>Media and mycorrhizal treatment</i>	
Sand, mycorrhizal	3.22
Sand, nonmycorrhizal	3.82
Soil, mycorrhizal	5.59
Soil, nonmycorrhizal	3.20
Lsd (0.05) <sup>z</sup>	1.77
<i>Al level</i>	
0 μM Al	3.67
600 μM Al	4.20
<i>p(F)</i> <sup>y</sup>	0.34

<sup>z</sup>Lsd (0.05) = least significant difference for mean comparison within the factor ( $n=32$ ).

<sup>y</sup>*p(F)* values indicate significance level.

when plantlets have been exposed to Al in solution for a long period of time. Therefore, it is unlikely that the mechanism Cumming and Weinstein (1990) describe to avoid Al toxicity in ectomycorrhizal pines occurs in mycorrhizal blueberry plantlets at the Al levels and delivery system of this study.

It is important to realize that Al concentrations in the soil solution of agricultural soils at pH 4.5 are normally below 150 μM (calculated after Magistad, 1925). It can be expected therefore, that soils in which blueberries typically grow, such as Berryland soils (Spodosols), have even less Al in their soil solution, because of their sandy, organic nature. The Al concentration (600 μM) used in our experiment was much higher than normally present in agricultural soils. Such a high level of Al could overwhelm the initial protection from Al toxicity by mycorrhizal infection. It is possible that Al sequestration in M roots could effectively alleviate the toxic effect of Al under realistic field situations.

## Conclusion

The growth of highbush blueberry and nutrient uptake in the soil medium was significantly decreased by high Al concentration. Al accumulated to higher levels in M roots, however Al was also readily transported into leaf tissues in both M and NM plantlets. Mycorrhizal blueberry plantlets had more root dry weight and developed

a larger canopy compared with NM plantlets in the soil medium. However, the presence of mycorrhizae did not reverse the effects of reduced dry weight which were induced by high Al.

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