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Growth and foliar nutrition of *Spiraea alba* Du Roi and *Spiraea tomentosa* L. in response to root zone pH ☆☆

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ABSTRACT

Spiraea alba and *Spiraea tomentosa* are native to the eastern and northern U.S. with potential for wider use in urban landscapes. Both grow in acidic soils in their native habitats. To determine their pH requirements in container media, three seed sources of *S. alba* and two of *S. tomentosa* were planted in media adjusted to pH 5, 6 and 7. Biomass and leaf greenness were reduced at pH 7 in all seed sources. Foliar P and Ca were higher and Mg and Al lower in plants grown in pH 6 and 7. Foliar Mn was not affected by media pH and Fe decreased with increasing pH only in *S. alba*. Shoot dry weight was correlated with high foliar N and low Zn and chlorosis was correlated with an increased Ca:Mg ratio. Growth of both species was best in media with a pH of 5 or 6, similar to their native habitats.

1. Introduction

There is increasing interest in the U.S. in gardening with native plants (West, 2001) and some consumers are willing to pay more for native plantings than lawns (Helfand et al., 2006). One impediment to using native plant materials, according to landscape architects, is insufficient quantities of native plant materials (Brzuszek et al., 2007). Furthermore, in a 2007 survey of master gardeners, over 50% of respondents stated that the reasons they did not use more native plants was (1) they could not find them in retail outlets and (2) there were not enough native plants available (Brzuszek et al., 2010). Providing native plant producers with accurate information on cultural requirements of new species may help to increase the production and availability of new native plants for the landscape.

The shrubs *Spiraea alba* Du Roi and *Spiraea tomentosa* L. have a native range covering much of eastern North America (USDA, 2012) and have potential as landscape plants because of their prolonged summer flowering and moderate size (Weeks and Weeks, 2012). *Spiraea alba* and *S. tomentosa* grow to be 1–1.5 m tall with long-lasting terminal panicles present throughout the summer. *Spiraea alba* produces white flowers while *S. tomentosa* has pale pink flowers. *Spiraea tomentosa* was used as a landscape species as early as 1736 (Symes, 1983). Today, however, both species are primarily used in habitat restoration.

Soil or media pH primarily affects the availability of nutrients (Tinus, 1980) and deficiencies of zinc, copper, manganese, and/or iron often occur at high soil pH levels, causing chlorosis and ultimately affecting growth (Thomas, 1955; Tinus, 1980). Most assumptions about the cultural requirements of *S. alba* and *S. tomentosa*, including soil and/or substrate pH requirements, are based on their native habitats, which usually indicate the optimum soil pH for a species, but some species are capable of growing in soils with a pH outside of their native range (Symonds et al., 2001). *Spiraea alba* and *S. tomentosa* are typically found in wet, acidic soils (Braun, 1936; Ebinger et al., 2011). *Spiraea tomentosa* has been found in soils with a pH as low as 4 or as high as 7, but is rare in soils above pH 6 (Gille, 1950). *Spiraea alba* is also found in soils below pH 6 (Girardin et al., 2001; White, 1965). Although these species are found in areas with low soil pH, they can tolerate higher soil pH, with the consequence of reduced growth (Mickelbart et al., 2012).

In order to determine appropriate media pH for production of these species, the growth and appearance of *S. alba* and *S. tomentosa* were assessed in the same soilless media adjusted to different pH levels. Three accessions of *S. alba* and two accessions of *S. tomentosa* were evaluated for intra-specific variation in root zone pH tolerance

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Table 1
Seed sources of *S. alba* and *S. tomentosa* used in this study. The ID given to each seed source indicates species (A = *S. alba*, T = *S. tomentosa*) and the postal code of the state of each seed source (AB = Alberta, MI = Michigan).

ID	Species	Supplier	Seed collection site
A-AB	*S. alba*	NPGS	Alberta, Canada
A-MI1	*S. alba*	Wildtype Native Plant Nursery	Michigan, Jackson Co.
A-MI2	*S. alba*	NPGS	Michigan, Kent Co.
T-MI1	*S. tomentosa*	Wildtype Native Plant Nursery	Michigan, Jackson Co.
T-MI2	*S. tomentosa*	NPGS	Michigan, Wayne Co.

among accessions that are adapted to the wide range of local soil types.

2. Materials and methods

2.1. Plant materials and growth conditions

Seeds of all plants used in this experiment were germinated in the spring of 2008. The seeds supplied by the National Plant Germplasm System (Ames, Iowa) were planted on 4 April 2008, after 64 days of cold stratification (4 °C). The plugs supplied by a commercial native plant nursery (Wildtype Native Plant Nursery, Mason, Michigan) were grown at the nursery from seed germinated in the spring of 2008. Three *S. alba* ecotypes and two *S. tomentosa* accessions (Table 1) were planted in 1.7-L containers between 22 September and 3 October 2008.

Crushed limestone (Irving Materials Inc., Swayze, IN) was added at a rate of 0.3, 0.5, and 1.8 g L^{-1} to a 70:20:10 by volume mixture of sphagnum peat, coarse premium grade perlite, and coarse premium grade vermiculite (all media components Sun Gro Horticulture, Vancouver, BC, Canada), to achieve media pH values of 5, 6, and 7. The lime was sieved and ground into a powder with a mortar and pestle prior to incorporation into media. Fertilizer was supplied as 15N–2.2P_2O_5–12.5 K_2O water-soluble fertilizer (Excel Cal-Mag; Scotts, Marysville, OH) to provide the following (in mg L^{-1}): 200 N, 29 P, 167 K, 67 Ca, 27 Mg, 1.0 Fe, 0.5 Mn and Zn, 0.24 Cu and B, and 0.1 Mo. Irrigation water was supplemented with 93% (w/v) sulfuric acid (Ulrich Chemical, Indianapolis, IN, USA) at 0.08 mL L^{-1} to reduce water alkalinity to 100 mg L^{-1} and pH to a range of 5.7–6.3.

Plants were overwintered outside by covering them with pine bark mulch to a depth of 5 cm above media level, and were moved back into the greenhouse in early March, 2009. Two weeks after harvesting the initial above-ground biomass the plants were repotted in 4-L containers on 22–24 May 2009. The treatments and soil mixture remained the same, but a different peat was used (Premier, Rivière-du-Loup, QC, Canada).

2.2. Measurements

The pH of leachate obtained using the pour through method (Camberato et al., 2009) was measured with a Hanna HI9813 pH meter (Hanna Instruments, Woonsocket, RI, USA) in March (following overwintering), May (prior to pruning/biomass harvest), and August (prior to final biomass harvest).

Plants were pruned to 3 cm above the media surface level In May 2009 and again in August 2009. Leaves were separated from stems and washed in reverse-osmosis water. Both leaves and stems were dried to a constant weight at 70 °C to obtain leaf and stem dry weight.

Prior to both biomass harvests, height and leaf greenness were measured. Height was measured from the media surface to the tallest point of the plant. Leaf greenness was quantified prior to both harvests using a SPAD meter (Konica Minolta Sensing, Osaka, Japan). The average of three measurements on each of three recently matured, fully expanded leaves on three different stems was taken. The plants were also visually rated on a scale from 1 to 10 for the appearance of nutrient deficiency symptoms.

After the second pruning in August, leaves were ground to a fine powder using a coffee grinder. Nitrogen (N) was analyzed using the Dumas combustion procedure (Simonne et al., 1994). Leaf tissue was digested with 1 mL of HNO_3 (Mallinckrodt, AR Select grade) at 110 °C for 4 h and concentrations of all other elements were quantified by inductively coupled plasma spectrometry on a PerkinElmer Elan DRCe ICP-MS (PerkinElmer SCIEX. Shelton, CT, USA).

2.3. Experimental design and statistical analysis

The experiment was designed as a two-way factorial arrangement on a randomized complete block. Each of nine blocks contained 15 plants, including 1 plant of each of the 5 species-accessions assigned to each of the 3 treatments. The data were analyzed using the PROC GLIMMIX procedure in SAS 9.1 (SAS Institute Inc., Cary, NC, USA) with media pH and accession as fixed effects and block as a random effect. Transformations of measured variables were used as needed to correct for non-homogeneity of variance and deviation from normality. The transformations used are given in the tables in which the data are presented. All of the values presented are averages of the untransformed data.

3. Results and discussion

3.1. Media pH

Initial tests were conducted to determine the appropriate rates of limestone to achieve the treatment pH levels. Plugs of *S. alba* and *S. tomentosa* grown from different seed sources (Table 1) were planted in media amended with 0.3, 0.5, and 1.8 g L^{-1} crushed limestone to achieve target pH values of 5, 6, and 7. Finely ground limestone was used to increase the base pH level of a sphagnum peat–perlite–vermiculite mix from a pH of ca. 5 to 6 and 7 (Table 2). Finely ground limestone allows for a rapid increase in media pH

Table 2
Main effects *P*-values and means for pH of container-grown *Spiraea alba* (A-AB, A-MI1, and A-MI2) and *Spiraea tomentosa* (T-MI1 and T-MI2) with target media pH of 5, 6, or 7[a] in March (following overwintering), May (preceding the first pruning), and August (preceding final biomass collection).

	pH		
	March	May	August
pH (P)	***[b]	***	***
Genotype (G)	***	***	NS
P × G	NS	***	NS
S. alba vs *S. tomentosa*[c]	*	***	NS
pH			
5	4.38c[d]	5.85c	5.12c
6	6.02b	6.23b	5.96b
7	6.95a	7.05a	7.25a
Genotype			
A-AB	5.81a	6.50a	6.05
A-MI1	5.85a	6.40a	6.12
A-MI2	5.78a	6.37a	6.14
T-MI1	5.82a	6.37ab	6.08
T-MI2	5.66b	6.26b	6.16

[a] Values for pH main effects are the mean of 45 plants (5 genotypes and 9 blocks) and values for genotype main effects are the mean of 27 plants (3 pH levels and 9 blocks).
[b] NS, *, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
[c] Orthogonal contrasts were performed to determine overall species differences.
[d] Means within each column followed by the same letter are not different at $P \leq 0.05$ based on Tukey's honestly different significance test.

Table 3
Main effects *P*-values and means for above-ground biomass of container-grown *Spiraea alba* (A-AB, A-MI1, and A-MI2) and *Spiraea tomentosa* (T-MI1 and T-MI2) growing in media with a pH of 5, 6, or 7[a]. Plugs were planted in September, overwintered, and brought back into the greenhouse in March. Plants were pruned to 3 cm above media level to harvest above-ground biomass in May. Plants were then allowed to regrow, and biomass was harvested again in August. The total biomass is the sum of the biomass collected in May and August.

	Biomass (g)[b]		
	May	August	Total
pH (P)	***[c]	*	**
Genotype (G)	***	***	***
P × G	NS	NS	NS
S. alba vs *S. tomentosa*[d]	***	***	***
pH			
5	28.4a[e]	6.7a	37.3a
6	30.3a	6.8a	36.6a
7	22.0b	4.7b	26.6b
Genotype			
A-AB	30.3ab	4.7b	35.0ab
A-MI1	31.8ab	9.3a	41.2a
A-MI2	34.1a	7.7a	41.8a
T-MI1	11.5c	5.0b	20.8c
T-MI2	26.9b	3.5b	28.8bc

[a] Values for pH main effects are the mean of 45 plants (5 genotypes and 9 blocks) and values for genotype main effects are the mean of 27 plants (3 pH levels and 9 blocks).
[b] Square root values were analyzed to correct for non-normal distribution of the data.
[c] NS, *, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
[d] Orthogonal contrasts were performed to determine overall species differences.
[e] Means within each column followed by the same letter are not different at $P \leq 0.05$ based on Tukey's honestly different significance test.

(Huang et al., 2007), but the acidified water used in this study results in a subsequent decrease in pH (Elliott, 1996).

Target media pH values were achieved except for the pH 5 treatment in March, at which time the media of containers in this treatment group had an average pH of 4.38 (Table 2). Media pH was significantly different among target pH treatments at all sampling dates although they varied slightly over time, but in all accessions and all dates in which pH was measured, the pH treatments were different from each other (data not shown). The one exception to this was T-MI1, in which case the pH values measured in May were not different in the target pH 5 and 6 treatments. However, when pH was measured again in August, these treatments were different from each other.

For two of the three sampling dates, media pH was lower in the MI2 accession of *S. tomentosa* than that of the *S. alba* accessions (Table 2). Genotype-induced reductions in root zone pH have been demonstrated (Marschner and Römheld, 1983), but there were no differences in traits often correlated with genotype-induced root zone pH changes such as cation/anion balance (Hedley et al., 1982) or P uptake (Schjørring, 1986). Furthermore, though the differences were significant, they were less than 0.2 pH units, so at this time there is little evidence for plant-induced root zone pH changes in *S. tomentosa*.

3.2. Plant growth

At similar plant age, *S. tomentosa* is typically smaller than *S. alba* in the field (Mickelbart et al., 2012; Stanton et al., 2010a) and this was the case in container-grown plants as well (Table 3). As this study was being conducted, a concurrent study was under way to determine proper pruning techniques for these two species (Stanton et al., 2010b). Older recommendations for landscape maintenance of these species were to prune them to ground level in the spring (Catchpole, 1963), and we followed these recommendations. However, our subsequent pruning study demonstrated that severe pruning substantially reduced the ultimate size of the plants (Stanton et al., 2010b). Plants grew quickly following overwintering, so the decision was made to prune them and allow them to regrow. However, regrowth was minimal, and the majority of the biomass produced over the growing season was produced from March to May (Table 3).

When grown in media with a pH of 7, growth in all accessions of both species was reduced during each growth period—but this reduction was reflected overall in reduced biomass production (Table 3) and not plant height (data not shown). Prior to the May pruning, the height of most accessions was not affected by pH. There were two exceptions: A-AB height was lowest at pH 6 and the height of T-MI1 was lowest at pH 7. In August, height was not affected by pH except in T-MI1, which was shorter when grown in media with a pH of 7 (data not shown). The growth response results of both species to media pH were similar to the response of field-grown plants to soil pH: reductions in growth occur only when root zone pH is 7 or above (Mickelbart et al., 2012). Both leaf and stem dry weight decreased equally with increasing pH and therefore leaf:stem ratio was not different in plants grown at different pH levels (data not shown).

Several studies have demonstrated consistent genetic differences in the size of accessions of *S. alba* and *S. tomentosa* (Stanton et al., 2010a,b; Mickelbart et al., 2012) and this study confirms those findings (Table 3). However, there were no differences among genotypes in growth response to pH (i.e. no genotype × pH interaction). Similarly, different genotypes of these two species did not exhibit differences in growth response to soil pH in the field (Mickelbart et al., 2012), despite exhibiting clear genotypic differences for overall growth, flowering, and appearance (Mickelbart, unpublished). Genotypic differences in growth response to media pH have been demonstrated in other woody species such as *Acer rubrum* (Boyce and Sydnor, 1983) and *Dirca palustris* (Peterson and Graves, 2009). Although several accessions of each species were included in this experiment to account for genetic variability, this experiment was not designed to screen for genetic diversity—the number of accessions used was small, and their geographic distribution is limited.

3.3. Leaf greenness

Overall, both species had similar leaf greenness (Table 4). Within *S. alba*, the Alberta seed source tended to have darker green leaves (Table 4), which was also the case in earlier field experiments (Stanton et al., 2010a).

Foliar chlorosis is a common response to increased root zone pH in species adapted to low pH soils (Peterson and Graves, 2009). In both May and August, all accessions of both species grown in media with a pH of 7 exhibited a reduction in measured leaf greenness (Table 4) that was also evident in visual observations (data not shown). Interveinal chlorosis was apparent in the most recently-developed leaves, suggesting it was caused by a deficiency in an immobile nutrient.

3.4. Foliar nutrient concentrations

In general, *S. tomentosa* plants tend to have lower foliar nitrogen (N) and higher foliar zinc (Zn) and copper (Cu) concentrations than *S. alba* in both the field (Mickelbart et al., 2012) and in containers (Table 5). Within *S. alba*, the Alberta accession had higher foliar concentrations of phosphorus (P), potassium (K), and sulfur (S), and lower concentrations of calcium (Ca) than the Michigan accessions (Table 5).

There were differences in the response of accessions to media pH only in foliar manganese (Mn) and iron (Fe) (Fig. 1). Foliar Mn often decreases with increasing media pH (Peterson and Graves,

Table 4
Main effects *P*-values and means for leaf greenness (SPAD) of container-grown *Spiraea alba* (A-AB, A-MI1, and A-MI2) and *Spiraea tomentosa* (T-MI1 and T-MI2) growing in media with a pH of 5, 6, or 7[a]. Plugs were planted in September, overwintered, and brought back into the greenhouse in March. Leaf greenness was determined in May, plants were pruned and left to regrow, and greenness was measured again in August.

	Leaf greenness	
	May	August
pH (P)	**[b]	***
Genotype (G)	***	**
P × G	NS	NS
S. alba vs *S. tomentosa*[c]	NS	NS
pH		
5	33.7a[d]	34.1a
6	33.8a	33.3a
7	31.0b	29.5b
Genotype		
A-AB	39.2a	33.4a
A-MI1	31.6b	32.0ab
A-MI2	28.9c	30.0b
T-MI1	32.1b	34.0a
T-MI2	32.4b	32.0ab

[a] Values for pH main effects are the mean of 45 plants (5 genotypes and 9 blocks) and values for genotype main effects are the mean of 27 plants (3 pH levels and 9 blocks).
[b] NS, *, **, or *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
[c] Orthogonal contrasts were performed to determine overall species differences.
[d] Means within each column followed by the same letter are not different at $P \leq 0.05$ based on Tukey's honestly different significance test.

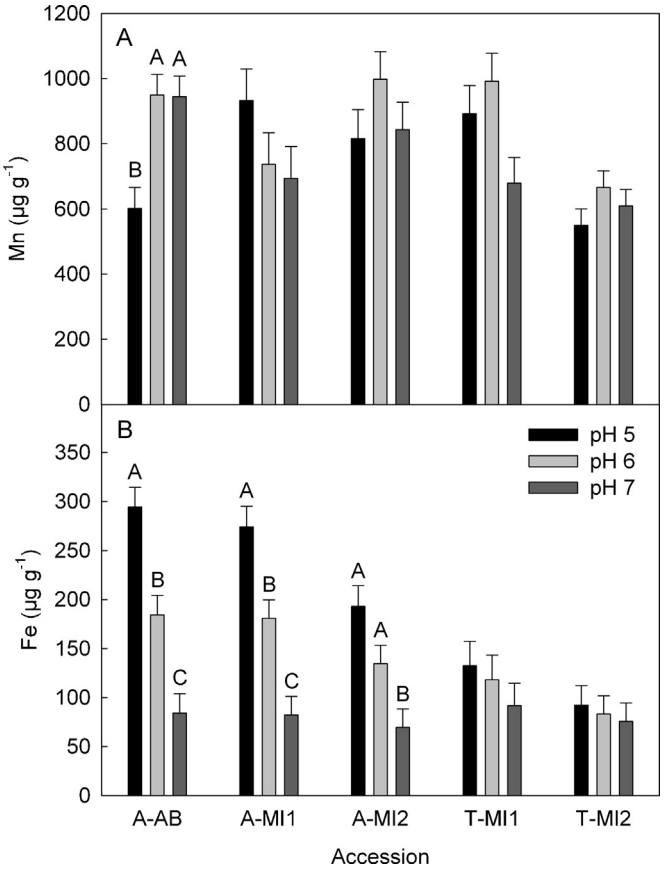

Fig. 1. Foliar concentrations of Mn (A) and Fe (B) in *S. alba* and *S. tomentosa* in response to media pH. Fe data were transformed ($Fe^{0.5}$) to correct for non-homogeneity of variance prior to analysis. Back-transformed data are presented. Letters above columns denote significant differences ($P < 0.05$) among pH levels within an accession.

2009; Silber et al., 2000). However, Mn did not differ in response to increased media pH except in A-AB, in which case, Mn actually increased with media pH (Fig. 1A). There was no change in foliar Fe with changes in media pH among the *S. tomentosa* accessions, but in all three *S. alba* accessions, foliar Fe decreased substantially with increased media pH (Fig. 1B), resulting in a significant reduction in foliar Fe:Mn in all *S. alba* accessions (data not shown).

The observed chlorosis patterns were typical of Fe and/or Mn deficiency, and the availability of these nutrients commonly decreases with increasing media pH (Whipker et al., 2000). Although Fe and/or Mn deficiencies are often related to high root zone pH, short-term studies such as this may not allow time for Mn deficiencies to develop. However, the fact that the plants grew in varying media pH levels from the time they were small plugs suggests that the absence of Mn deficiency is not due to Mn reserves stored in the plant. Instead, it appears as though Mn deficiency is not a result of growing in media pH above the normal pH of these

Table 5
Main effects *P*-values and means for foliar nutrient concentrations of container-grown *Spiraea alba* (A-AB, A-MI1, and A-MI2) and *Spiraea tomentosa* (T-MI1 and T-MI2) growing in media with a pH of 5, 6, and 7[a].

	N	P	K	Ca	Mg	S	Zn	Cu[b]	B	Al[b]
	%						µg g^{-1}			
pH (P)	NS[c]	**	NS	***	***	NS	NS	**	NS	**
Genotype (G)	***	***	***	***	***	***	***	***	**	**
P × G	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S. alba vs *S. tomentosa*[d]	***	*	NS	NS	***	NS	***	***	**	***
pH										
5	3.44	0.38b	1.54	1.04b	0.31a	0.29	107	17.1a	37.3	10.1a
6	3.52	0.46a	1.67	1.28a	0.28b	0.30	125	16.5a	35.3	7.2b
7	3.39	0.43a	1.67	1.27a	0.26b	0.29	124	13.9b	36.0	6.1b
Genotype										
A-AB	3.59a[e]	0.46a	1.84a	1.09b	0.32a	0.32a	97c	14.6bc	35.2ab	7.2ab
A-MI1	3.74a	0.38b	1.52b	1.25a	0.33a	0.29bc	87c	13.7c	38.3a	6.2ab
A-MI2	3.67a	0.39b	1.62b	1.31a	0.27b	0.28c	97c	14.0c	38.9a	7.0b
T-MI1	3.29b	0.50a	1.65ab	1.29a	0.27b	0.31ab	177a	19.3a	35.2ab	9.7a
T-MI2	2.97c	0.38b	1.52b	1.03b	0.22c	0.28bc	137b	17.7ab	33.3b	8.9a

[a] Values for pH main effects are the mean of 45 plants (5 genotypes and 9 blocks) and values for genotype main effects are the mean of 27 plants (3 pH levels and 9 blocks).
[b] log values were analyzed to correct for non-normal distribution of the data.
[c] NS, *, **, or *** indicates nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.
[d] Orthogonal contrasts were performed to determine overall species differences.
[e] Means within each column followed by the same letter are not different at $P \leq 0.05$ based on Tukey's honestly different significance test.

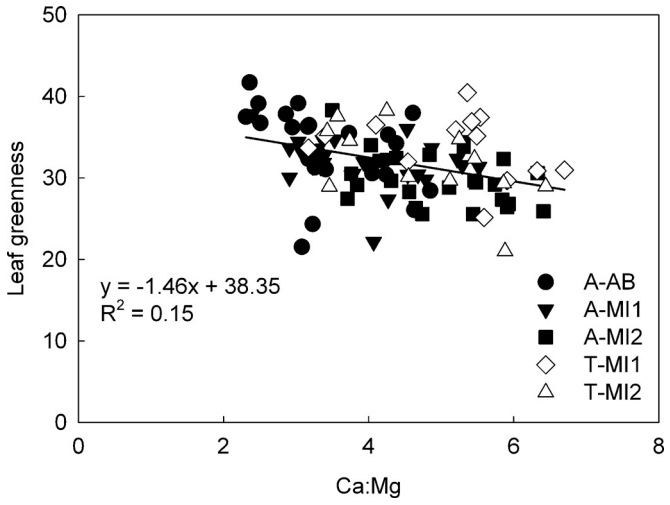

Fig. 2. Relationship between leaf greenness and the ratio of Ca:Mg in *S. alba* and *S. tomentosa* leaf tissue.

species in their native habitats. *Acer rubrum*, a species that is prone to chlorosis at high root zone pH (Altland, 2006), also did not exhibit lower foliar Mn concentrations at high pH in a soilless media experiment (Boyce and Sydnor, 1983). However, in both cases, this may be due to a constant supply of Mn in the fertilizer solution. Fe:Mn decreased with increasing pH in *S. alba* (data not shown) as has been demonstrated in other species (Smith et al., 2004a,b), but this was not correlated with leaf greenness, as observed in some annual species (Smith et al., 2004b).

Overall, plants grown in media with a pH of 5 had lower foliar concentrations of P and Ca, and higher concentrations of magnesium (Mg) and aluminum (Al) (Table 5). Substrate Ca and Mg increase with the incorporation of lime (Altland et al., 2008) and the reduced foliar concentration of Mg in plants grown in pH 6 and 7 is likely due to the increase in substrate Ca concentration, which led to a linear increase in leaf Ca:Mg with increasing media pH (data not shown). In turn, increases in foliar Ca:Mg resulted in a linear decrease in leaf greenness among accessions and treatments (Fig. 2). Although pH clearly affected leaf greenness (Table 4), the underlying factor may be the relative changes among accessions in foliar Ca:Mg with changes in media pH. Because limestone was used to alter pH, it is difficult to separate the effects of increased pH and Ca. The observed response could also be due to the increasing Ca content of the media with increases in pH. Leaf greenness was not correlated with any other nutrient concentrations or ratios (data not shown).

Foliar N concentrations did not differ among pH treatments (Table 5), and any observed chlorosis was in young leaves, which is inconsistent with N deficiency. Zinc (Zn) and copper (Cu) can become deficient at high soil pH (Tinus, 1980), but only Cu was low in the pH 7 treatment (Table 5). Phosphorus (P) and boron (B) can also become less available as media pH increases (Barker and Pilbeam, 2007). However, foliar P increased with increasing media pH, and B was not affected by pH.

4. Conclusions

Although optimal pH values for plant growth are typically lower in container media mixes (Landis, 1989), the results from this study reflect those of a field-based pH study conducted with these species (Mickelbart et al., 2012). The media pH required for optimum growth of *S. alba* and *S. tomentosa* is reflective of their natural habitat. Growth and the concentrations of some nutrients are reduced and chlorosis occurs in plants grown in media with a pH of 7. The chlorosis observed in young leaves of both species was not clearly related to deficiencies in micronutrients, but was related to an increasing Ca:Mg ratio. There were no differences in the growth or leaf greenness response to media pH among any of the accessions, although this may be due to the likely low genetic diversity of the accessions used. Both of these species should be grown in media with a pH maintained at 5 or 6. Because most woody ornamental species are produced in bark-based media with controlled-release fertilizer, further research may be required to confirm the responses observed under our experimental conditions.

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