Growth Response of Three Containerized Woody Plant Taxa to Varying Low Phosphorus Fertilizer Concentrations

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Abstract. Phosphorus (P) uptake efficiency (PUE; percent of applied P absorbed by roots) for containerized crops is ≈27% to 62%. Reducing P fertilization may increase PUE without decreasing growth and may reduce P leaching from containers, thus mitigating the environmental impact of containerized production while potentially reducing fertilizer input costs for growers. The objective of this study was to determine the minimum P application concentration and the resulting substrate pore-water (i.e., solution residing within and between substrate particles) P concentration that maintains maximal growth of three containerized woody plant taxa grown in pine bark substrate. *Hydrangea paniculata* Sieb. ‘Limelight’ (hydrangea), *Ilex crenata* Thunb. ‘Helleri’ (holly), and *Rhododendron* L. ‘Karen’ (azalea) were potted in pine bark substrate amended with dolomite and micronutrients and grown for 81 d in an open-wall greenhouse. Plants received either one of five constant liquid-feed treatments with varying P concentrations [80 mg·L⁻¹ nitrogen (N), 50 mg·L⁻¹ potassium (K), and 0.5, 1.0, 2.0, 4.0, or 6.0 mg·L⁻¹ P] or a single application of controlled-release fertilizer (CRF; control) at experiment initiation. Calculated lowest P fertilizer concentration that sustained maximal shoot dry weight (SDW) in hydrangea and azalea was 4.7 and 2.9 mg·L⁻¹, respectively, and holly SDW was the same across all liquid fertilizer treatments. In all three taxa, CRF-fertilized plants achieved <50% of maximal SDW observed in liquid-fertilized plants. Hydrangea root dry weight (RDW) nearly doubled as fertilizer P increased from 0.5 to 2.0 mg·L⁻¹ P, but higher P concentrations did not further increase RDW. Holly RDW was unaffected by liquid P treatment. Pore-water P concentrations of treatments that sustained maximal SDW of hydrangea and azalea were as low as 0.6 and 2.2 mg·L⁻¹ P, respectively. Our findings suggest that when using constant liquid feed, applied P levels more accurately predict plant growth responses than pore-water P levels.

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Rising fertilizer prices and environmental implications of fertilizer runoff substantiates the need to select fertilization rates that optimize crop growth and nutrient use efficiency, yet minimize the effect on the surrounding ecosystem. From 2007 to 2008, the U.S. farm price of phosphate (PO₄³⁻) fertilizer nearly doubled, reaching an all-time high of ≈\$909 per tonne (\$825 per short ton; USDA ERS, 2013). By 2013, U.S. PO₄³⁻ fertilizer prices were 56% higher than those in 2007 (USDA ERS, 2013), and this trend of increasing P fertilizer prices is expected to continue as quality rock phosphate reserves are depleted (Smil, 2000) and global crop demand continues to rise with the world’s growing population. Agriculture, including container nurseries, is a “primary” contributor of P pollution in U.S. surface waters (USEPA, 2017). Phosphorus is often the greatest contributing factor for eutrophic

conditions in freshwater ecosystems (USEPA, 2002) and is, therefore, a focus of federal and state monitoring and regulation within impaired watersheds (e.g., the Chesapeake Bay Watershed and the Everglades Watershed). Thus, to preserve water quality or facilitate remediation of surface waters, agricultural nutrient management programs are being implemented throughout the United States.

Fertilizing containerized nursery crops via CRF in complete or partial substitution for soluble granular or aqueous forms is a best management practice (BMP; Bilderback et al., 2013) and has been widely adopted by containerized crop growers (Dennis et al., 2010). When using CRF to fertilize containerized nursery crops grown in a pine bark-based substrate, PUE (percent of applied P absorbed by roots) has been reported to be ≈27% to 62% (Owen et al., 2008; Tyler et al., 1996; Warren et al., 1995, 2001). The observed low PUE is, in part, because containerized crop producers use soilless substrates (e.g., pine bark) that have low anion exchange capacity, high total porosity, and relatively low specific surface area for P adsorption compared with soils used in conventional agricultural production. Continuous fertilization with controlled-release, soluble granular, or liquid fertilizer coupled with daily irrigation, commonplace in container nurseries, give rise to P losses via leaching and subsequent runoff from the growing area.

To reduce nutrient leaching, BMPs recommend applying the minimum amount of fertilizer that achieves the desired growth and quality (Bilderback et al., 2013). Phosphorus uptake efficiency of containerized crops improves with a marginal decrease in P fertilization amount (Ku and Hershey, 1997; Lea-Cox and Ristvey, 2003; Owen et al., 2008; Ristvey et al., 2004, 2007). Ristvey et al. (2007), when growing liquid-fed *Rhododendron* L. ‘Karen’ in a substrate comprising one composted pine bark: one *Sphagnum* peat: one rice hulls (by volume), increased PUE from ≈15% to 49% without decreasing SDW by reducing P fertilizer from 25 to 5 mg per week. Owen et al. (2008) increased PUE from 21% to 34% in *Cotoneaster dammeri* Schnied. ‘Skogholm’ grown in pine bark amended with 11% builder’s sand (by volume) with no reduction in total dry weight when P in CRF was reduced by half. Reduced PUE in response to superfluous P fertilization of container-grown plants can be explained by the relatively large proportion of applied P that is inaccessible to roots for absorption. Much of the fertilizer P is inaccessible because of the slow rate of P diffusion from bulk solution to roots (i.e., 10⁻⁸–10⁻¹¹ cm²·s⁻¹; Heinrich and Patrick, 1985; Jungk and Claassen, 1997) coupled with the spatial separation between the roots and much of the P supply (i.e., that which is not within 0.4 cm of the roots; Jungk and Claassen, 1997; Temple-Smith and Menary, 1977). Thus, as P fertilization increases, the ratio of available P to nonavailable P decreases, concurrently reducing PUE. These studies imply that

fertilizing with minimally sufficient P levels for maximal plant growth may optimize PUE when all other factors (e.g., leaching fraction, amendments, substrate physical properties, etc.) are kept constant.

Fertilizer recommendations for container-grown crops are often based on nutrient levels found in solution extracted via the pour-through method (Wright, 1986). Currently, BMPs suggest 5–15 mg·L⁻¹ P be maintained in pour-through-extracted substrate pore-water (Bilderback et al., 2013). This recommendation is, in part, based on studies by Yeager and Wright (1982) and Wright and Niemiera (1985) who grew *Ilex crenata* Thunb. ‘Helleri’ in 100% pine bark and 100% quartz sand, respectively. In both studies, shoot growth increased as applied P was increased from 0 to 5 mg·L⁻¹, but ≥5 mg·L⁻¹ P did not increase shoot growth. Despite BMP recommendations, there is evidence that <5 mg·L⁻¹ P in substrate pore-water is sufficient for growing salable woody plants in soilless substrates. In a substrate consisting of 2 perlite : 1 peat (by volume), Havis and Baker (1985) observed maximal growth of *Rhododendron* L. ‘Victor’ when liquid fertilizing with 2.5 mg·L⁻¹ P. Million et al. (2007) observed no change in plant size index [i.e., (plant height + plant width)/2] of CRF-fertilized *Viburnum odoratissimum* Ker Gawl. grown in 2 aged pine bark : 1 sphagnum peatmoss : 1 coarse sand (by volume) when doubling the irrigation rate reduced pour-through-extracted P concentration ranges from 5 to 11 mg·L⁻¹ down to 1–4 mg·L⁻¹. When growing CRF-fertilized *C. dammeri* Schnied. ‘Skogholm’ in 8 pine bark : 1 sand (by volume), Groves et al. (1998) observed no apparent plant growth reduction even though pour-through-extracted P levels were consistently lower than 5 mg·L⁻¹.

Based on the preponderance of previous research, maximal growth of containerized woody plants should be achievable with applied P concentrations between 0 and 5 mg·L⁻¹. Therefore, our objective was to determine the minimum fertilizer P concentration and the resulting substrate pore-water P concentration that maintains maximal growth of three containerized woody plant taxa grown in pine bark substrate.

Materials and Methods

This study was performed at the Hampton Roads Agriculture Research and Extension Center in Virginia Beach, Virginia (lat. 36°53′31″N; long. 76°10′44″W; USDA Plant Hardiness Zone 8a). The three plant taxa used were *Rhododendron* L. ‘Karen’ (azalea), *I. crenata* Thunb. ‘Helleri’ (holly), and *H. paniculata* Sieb. ‘Limelight’ (hydrangea). On 10 Apr. 2014, liners were acquired in 36-cell flats with either two-rooted stem cuttings (hydrangea; Bennett’s Creek Nursery, Suffolk, VA) or three-rooted stem cuttings (holly and azalea; Saunders Brothers Nursery, Piney River, VA) per cell. Rooted stem cuttings within each cell were separated and roots rinsed with a high-pressure water

stream to remove existing substrate and fertilizer. Single-plant bare-root liners were then potted individually into 3.8-L black plastic containers (#1 gal; Nursery Supplies, Inc., Chambersburg, PA). Hydrangea and holly were potted in an aged pine bark substrate (pH 4.3 ± 0.06 SE; 1.6 cm screen; Carolina Bark Products, Seaboard, NC) amended with 0.89 kg·m⁻³ granular micro-nutrient fertilizer (Micromax; Everris, Dublin, OH), 2.37 kg·m⁻³ ground dolomite [97% calcium carbonate equivalent (CCE), Rockdale Quarries Corporation, Roanoke, VA], and 2.37 kg·m⁻³ pulverized dolomite (94% CCE; Old Castle Lawn and Garden, Thomasville, PA). Azalea was potted in the same pine bark substrate but amended with 1.19 kg·m⁻³ ground dolomite and no pulverized dolomite to maintain crop-specific low pH. Dolomite was selected as a lime source to ensure calcium (Ca) and magnesium (Mg) were not growth limiting. Container capacity and air space of the substrate were 33% and 36% (by volume), respectively, and bulk density was 0.24 g·cm⁻³ (NCSU porometer method; Fonteno et al., 1995). All amendments were incorporated using a 11.5 m³ ribbon mixer for a duration of 5 min. Before treatment initiation, plants were fertilized with a single 350-mL aliquot of P-free nutrient solution [80 mg·L⁻¹ nitrogen (N) from ammonium nitrate (NH₄NO₃), and 50 mg·L⁻¹ potassium (K) from potassium sulfate (K₂SO₄)] every 7 d for 35 d.

Experiment initiation. On 16 May 2014, all plants were moved into an 8 m × 29 m greenhouse running northwest to southeast and roofed with a polyolefin reflective shade cover [FLS 50 W/B; Svensson, Kinna, Sweden (49% direct photosynthetically active radiation transmission)]. Greenhouse walls remained rolled up ≈1 m above the ground to facilitate passive cooling throughout the study. The experiment was arranged in a randomized complete block design in a 3 (plant taxa) × 6 (fertilizer treatments) factorial treatment arrangement with three replications and three plants per replication. This experiment was blocked to account for potential differences in shading from the greenhouse structure. Plants were placed in 18 rows running perpendicular to the greenhouse length, each row containing three plants per taxon, totaling 54 plants per taxon. Every six rows of plants from northwest to southeast were one complete block.

Injectors (D25F1; Dosatron Intl., Clearwater, FL), which had a 1:100 fixed injection rate, were used to formulate target fertilizer concentrations by diluting each of the five concentrated nutrient solutions with potable water. Postinjector nutrient solutions were delivered to plants via pressure-compensating spray stakes [01PSDS-PL1-B; Netafim, Fresno, CA (202 mL·min⁻¹)] every 3 d or as needed in two consecutive 2-min intervals with ≈34 min between intervals. To ensure full pore-water exchange with fertilizer solution and prevent salt accumulation, leaching fractions (i.e., mL leached divided by mL applied) for hydrangea, azalea, and holly were maintained at 0.84 ± 0.01 SE, 0.88 ±

0.01 SE, and 0.88 ± 0.01 SE, respectively. Target fertilizer nutrient concentrations were 80 mg·L⁻¹ N (NH₄NO₃), 50 mg·L⁻¹ K [K₂SO₄ and monopotassium phosphate (KH₂PO₄)], and one of five P concentrations (i.e., treatments): 0.5, 1.0, 2.0, 4.0, or 6.0 mg·L⁻¹ P (KH₂PO₄).

Irrigation source water was sent to the Brookside Laboratories (New Bremen, OH) for complete water analysis. Source water contained <0.20 mg·L⁻¹ P, 4.49 mg·L⁻¹ K, 3.69 mg·L⁻¹ N, <0.20 mg·L⁻¹ aluminum (Al), <0.10 mg·L⁻¹ iron (Fe), 15.92 mg·L⁻¹ Ca, and 24.19 mg·L⁻¹ alkalinity. In addition, spray stake-emitted nutrient solution was periodically analyzed for N, P, and K concentration to confirm that target nutrient concentrations were being applied. Observed applied N and K concentrations were 64.5 ± 3.44 SE and 42.3 ± 2.23 SE mg·L⁻¹, respectively, and observed applied P concentrations were 0.4 ± 0.11 SE, 1.3 ± 0.11 SE, 2.0 ± 0.24 SE, 4.2 ± 0.63 SE, and 6.3 ± 0.41 SE mg·L⁻¹ P, in order of lowest to highest P treatment.

Injector mixing chambers and suction tubes were wrapped in aluminum foil to reduce biofilm accumulation. Every 2–3 weeks, suction tubes and strainers were rinsed with deionized water and concentrated fertilizer solutions were made. Injection rate was checked 1, 42, and 84 d(s) after experiment initiation (DAI) to ensure a 1:100 dilution factor remained constant.

On 17 May 2014 (day 0), plants within the control treatment were top-dressed with 17.0 g of 18N–2.6P–10.0K polymer-coated, 8–9 month CRF (Harrell’s LLC, Lakeland, FL), a standard fertilization practice in the southeastern U.S. nursery industry. In the CRF treatment, 93% of N was derived from polymer-coated NH₄NO₃ and 7% from polymer-coated monoammonium phosphate (NH₄H₂PO₄). Immediately after top-dressing, CRF was incorporated into the top 2–3 cm of the substrate surface to ensure consistent fertilizer release via full contact of granules with substrate and to prevent loss from other factors (e.g., spillage). Irrigation regime was similar to those liquid-fertilized, except CRF-fertilized plants received only one 2-min irrigation event to reduce leaching and mimic irrigation practices used in conventional nursery production. Leaching fractions for the CRF treatment were the same across taxa, averaging 0.55 ± 0.02 SE.

Hydrangea flowers were removed to ensure continued vegetative growth and were inspected weekly for flower bud swelling. Stems with swollen flower buds were pruned just above the first node below the basal-most flower bud. Removed plant tissue was dried at 58 °C and added to the final SDW. In this experiment, SDW indicates the aboveground portion of the plant.

Data collection and analysis. Pore-water extracts were collected via the pour-through method (Wright, 1986) from one randomly selected plant per replication 0, 20, 41, 62, and 81 DAI. Pour-through extractions were performed ≈1 h after a normal fertigation event by hand pouring 120 mL deionized water over the surface of the substrate and

collecting ≥ 50 mL of subsequent leachate. Using a benchtop meter (Orion 4-Star Plus pH/Conductivity Meter, Thermo Fisher Scientific Inc., Beverly, MA), substrate pH and electrical conductivity (EC) were measured on all five sampling dates within 12 h of pour-through extraction.

At 41 and 81 DAI, an 8-mL aliquot of each pore-water extract and each spray stake-emitted fertilizer solution was filtered (0.2 μm , 30-mm syringe filter; Thermo Fisher Scientific) and stored at -18°C for later ion analysis. The samples were thawed and analyzed at $\approx 25^\circ\text{C}$ for ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), PO_4^{3-} , and K^+ concentration using an ion chromatography (IC) system (ICS-2100; Thermo Fisher Scientific). Anion- and cation-exchange columns as well as the autosampler used by the IC system were similar to those described in Hoskins et al. (2014a), except that both columns were 4 mm $\times$ 250 mm (i.d. $\times$ length) and a different anion-exchange column (AS19; Thermo Fisher Scientific) was used.

Growth index [GI; (widest width + perpendicular width + height)/3] was determined for holly and azalea at 0, 19, 40, 61, and 80 DAI. Hydrangea GI was not recorded because flower pruning often altered width and height. While measuring GI, symptoms of potential nutrient deficiency and pest damage were recorded. Pests (e.g., spider mites, beetles) were controlled via hand removal, pesticide sprays, or both. Bifenazate [Floramite; Mainland, PA (0.65 mL $\cdot$ L $^{-1}$)] was applied 45 DAI to all hydrangea and holly using a handheld, carbon dioxide-pressurized sprayer (276 kpa) with a boom nozzle.

Eighty-two DAI, foliar tissue samples were collected from each plant for nutrient concentration analysis. Four 5.1-cm ($\approx 11 \pm 0.8$ se leaves) and nine 6.1-cm ($\approx 11 \pm 0.3$ se leaves) apical stem cuttings were taken from young stems of each azalea and holly, respectively. For hydrangea, 30 leaf blade samples were taken from most recently matured leaves across three plants per replication. Tissue sample collection per species was carried out according to Bryson et al. (2014). All tissue samples were rinsed with deionized water, oven-dried (58°C), weighed, and analyzed for N, P, and K concentrations (Brookside Laboratories). Bryson et al. (2014), who provides foliar nutrient sufficiency ranges for a multitude of taxa based on survey data reported in the literature and by analytical laboratories, was used to determine if foliar nutrient levels were sufficient or growth limiting. Foliar sample dry weight and shoot weight were combined to provide final SDW.

After foliar sampling was complete, plants were severed at substrate level. Shoots were oven-dried (58°C) for a minimum of 72 h and weighed. Hydrangea and holly roots were first washed with a high-pressure stream of tap water over a screen to remove all substrate particles while minimally losing root mass. Roots were then oven-dried (58°C) for a minimum of 72 h and weighed for root dry weight (RDW). Roots of azalea were not

harvested because of difficulty in separating substrate from fine roots without losing root mass.

Statistical analysis. Data were subjected to analysis of variance (ANOVA) and *post hoc* comparison of means was accomplished

Fig. 1. Growth index [(widest width + perpendicular width + height)/3] over time (days after initiation) for holly (A) and azalea (B) fertilized with controlled-release fertilizer (CRF; control) or one of five liquid phosphorus (P) fertilizer treatments: 0.5, 1.0, 2.0, 4.0, or 6.0 mg $\cdot$ L $^{-1}$ P. Vertical bars indicate se.

Table 1. Substrate pore-water nitrogen (N) and potassium (K) concentrations (mg $\cdot$ L $^{-1}$) in pour-through leachate at 41 and 81 d after initiation (DAI) for hydrangea, holly, and azalea potted in pine bark amended with 0.89 kg $\cdot$ m $^{-3}$ micronutrients and either 4.75 kg $\cdot$ m $^{-3}$ (hydrangea and holly) or 1.19 kg $\cdot$ m $^{-3}$ (azalea) of dolomitic limestone and fertilized with controlled-release fertilizer (CRF; control; $n = 3$) or liquid fertilizer (LF; $n = 14$).

Treatment	Nutrient concns in pour-through leachate (mg $\cdot$ L $^{-1}$)					
	N			K		
	41 DAI	81 DAI	<i>P</i> value	41 DAI	81 DAI	<i>P</i> value
Hydrangea						
CRF	5.1	15.0	0.0215	18.0	17.2	0.7397
LF ²	35.6	44.5	0.0770	50.8	43.0	0.0770
<i>P</i> value	0.0010	0.0009		<0.0001	0.0040	
Holly						
CRF	6.3	32.4	0.0146	22.2	30.0	0.0125
LF	31.3	44.9	0.0197	50.2	47.6	0.6010
<i>P</i> value	0.0015	0.2562		0.0031	0.0351	
Azalea						
CRF	7.7	44.7	0.0145	29.3	30.2	0.8889
LF	54.2	66.7	0.0133	56.4	54.4	0.7095
<i>P</i> value	0.0003	0.0082		0.0062	0.0277	

²Pour-through leachate concentrations of N and K were not different between liquid fertilizer treatments, 0.5, 1.0, 2.0, 4.0, and 6.0 mg $\cdot$ L $^{-1}$ at the $\alpha = 0.05$ level. Thus, values indicate mean of liquid fertilizer treatments.

using the Tukey–Kramer honestly significant difference test or a *t* test. Dunnett’s test was used to compare the response of liquid-fertilized crops to those fertilized with CRF (control). The block effect was insignificant in all ANOVA and was removed from analysis to simplify the model. Correlations were determined using the Pearson correlation coefficient (*r*).

To determine the appropriate nonlinear model to regress SDWs and foliar P concentrations over P treatment, Akaike information criterion values were compared across exponential and logistic growth curves. Nonlinear models were used to calculate optimal P fertilizer concentrations for each taxon (i.e., the lowest pore-water P concentration that sustains maximal SDW). This was accomplished via the method proposed by Mischan et al. (2011) for calculating the asymptotic deceleration point in which data were fitted to a three-parameter logistic growth curve:

$$y = \frac{c}{\{1 + \exp[-a(x - b)]\}},$$

where *y* = SDW; *x* = fertilizer P concentration; *a* = growth rate; *b* = inflection point; and *c* = asymptote. Computer-generated estimates for parameters *a*, *b*, and *c* were obtained via JMP Pro (SAS Institute), then the fourth derivative equation was solved for *x*'''' by equating *y*'''' to zero to obtain the asymptotic deceleration point. Optimal foliar P concentrations were calculated by solving the logistic growth equation for foliar P over applied P concentration, with “*x*” equal to the calculated optimal applied P concentration for SDW. JMP Pro (Version 11.0; SAS Institute Cary, NC) was used to process all data.

Results and Discussion

Growth index. Highest GI values of holly at harvest were achieved with 1.0–6.0 mg·L⁻¹ P (*P* = 0.0413; *F* = 3.92; data not shown), whereas azalea attained highest GI values when fertilized with 4.0–6.0 mg·L⁻¹ P (*P* = 0.0005; *F* = 15.11; data not shown). Growth index of holly and azalea fertilized with 2.0–6.0 mg·L⁻¹ P increased linearly over time after 20 d (Fig. 1). Growth index of holly fertilized with 0.5–1.0 mg·L⁻¹ P and azalea fertilized with 1.0 mg·L⁻¹ P increased until 61 DAI, then plateaued, whereas GI of azalea fertilized with 0.5 mg·L⁻¹ P plateaued 40 DAI (Fig. 1). The finding that GI values were the same across all liquid fertilizer treatments for at least the first half of the experiment suggests that the P supply of the low-P treatments was adequate for the relatively low GI values of both taxa. As GI values increased for the higher P treatments (but not the lower treatments), a higher P supply was required. A possible implication for this finding is that growers using liquid fertilization can use relatively low P concentrations when plants are small and then increase concentrations commensurate with plant size. In support of this contention, Ingstad and Lund (1986) proposed that to achieve steady state

plant nutrition, nutrient solution concentrations be increased over time to correspond with the increasing plant growth rate and concomitant increase in nutrient requirement.

Growth index was the same until 61 DAI for holly and azalea fertilized with CRF and then increased 246% and 206%, respectively (Fig. 1). The belated growth response in CRF-fertilized plants is likely a result of delayed N release from CRF as indicated by lower substrate pore-water N concentrations for the CRF treatment at 41

relative to 81 DAI in all three taxa (Table 1). In addition, from 61 to 81 DAI, EC increased 63% and 41% in holly and azalea (Fig. 2), respectively, supporting the notion that CRF-N was withheld for the first 61 d. A lag in N release or availability from CRF has also been reported by Merhaut et al. (2006) and Newman et al. (2006).

Carbon allocation. Final SDW of hydrangea and azalea was highest when liquid fertilized with 4.0–6.0 mg·L⁻¹ P, whereas

Fig. 2. Substrate pore-water electrical conductivity [EC (μS·cm⁻¹)] of hydrangea (A), holly (B), and azalea (C) amended with 0.89 kg·m⁻³ micronutrients and either 4.75 kg·m⁻³ (hydrangea and holly) or 1.19 kg·m⁻³ (azalea) of dolomitic limestone fertilized with either controlled-release fertilizer (CRF; —) or liquid fertilizer (LF; - - -) pooled across liquid fertilizer treatments, 0.5, 1.0, 2.0, 4.0, and 6.0 mg·L⁻¹ P over the duration of study. Vertical bars indicate SE.

Table 2. Effect of applied phosphorus (P) concentration versus controlled-release fertilizer (CRF; control) on shoot dry weight (SDW) of hydrangea, holly, and azalea grown for 82 d in pine bark amended with 0.89 kg·m⁻³ micronutrients and either 4.75 kg·m⁻³ (hydrangea and holly) or 1.19 kg·m⁻³ (azalea) of dolomitic limestone.

Treatment (mg·L ⁻¹ P) ^y	SDW ^z (g)		
	Hydrangea	Holly	Azalea
CRF	11.53	5.71	4.72
0.5	4.95 a ^{x**}	8.08	4.43 a
1.0	6.71 a*	10.11**	5.60 a
2.0	12.16 b	8.69*	9.77 b**
4.0	24.09 c**	11.06**	12.99 c**
6.0	27.52 c**	10.56**	12.30 bc**
P value	<0.0001	0.0654	<0.0001

^zSDW includes all portions of plant above substrate line.

^yn = 3 (three-plant mean for each of three blocks) for control and treatments 0.5, 2.0, 4.0, and 6.0; n = 2 for treatment 1.0 (three-plant mean for each of two blocks).

^xLetters within columns separate means by Tukey's honestly significant difference at P ≤ 0.05 (control not included).

*or ** indicates significant difference from control at P ≤ 0.05 and 0.01, respectively (Dunnett's test).

Fig. 3. Nonlinear logistic models describing the effect of applied phosphorus (P) concentration on shoot dry weight (SDW) of hydrangea (A), holly (B), and azalea (C), and foliar P concentration of hydrangea (D), holly (E), and azalea (F) at harvest. Model equations are listed in Table 3.

Table 3. Nonlinear logistic prediction models to describe shoot dry weight (SDW) and foliar phosphorus (P) response to P fertilizer concentrations for hydrangea (Fig. 3A and D, respectively) and azalea (Fig. 3C and F, respectively). Optimal P fertilizer concentration was determined by calculating the asymptotic deceleration point for each SDW curve; foliar P and SDW at optimal P fertilizer concentration was determined by solving respective prediction equations when x = optimal fertilizer P.

Taxa	SDW Prediction model ^z	Foliar P prediction model	Optimal fertilizer P (mg·L ⁻¹)	Foliar P ^y (%)	SDW ^x (g)
Hydrangea	$28.6 / (1 + e^{[-0.929 \times (x - 2.27)]})$	$0.237 / (1 + e^{[-0.997 \times (x - 1.48)]})$	4.74	0.23	25.9
Azalea	$12.8 / (1 + e^{[-1.28 \times (x - 1.08)]})$	$0.250 / (1 + e^{[-1.05 \times (x - 0.759)]})$	2.88	0.23	11.6

^zx = fertilizer P concentration (mg·L⁻¹).

^yPredicted foliar P concentration when fertilizer P is optimal for SDW.

^xPredicted SDW when fertilizer P is optimal for SDW.

holly SDW was unaffected by fertilizer P concentration (Table 2). Yeager and Wright (1982) and Wright and Niemiera (1985)

observed maximal shoot growth of 'Helleri' holly when fertilized with 5–15 mg·L⁻¹ P; however, P fertilizer concentrations between

0 and 5 mg·L⁻¹ P were not investigated. Havis and Baker (1985) found maximal shoot growth in *Rhododendron* 'Victor' and

Cotoneaster adpressus var. *praecox* Bois and Berthault when fertilized with 2.5 and 10 mg·L⁻¹ P, respectively. Shoot dry weights of CRF-fertilized hydrangea, holly, and azalea were lower than in those liquid fertilized with 4.0–6.0 mg·L⁻¹ (Table 2), indicating that liquid fertilizing with nonlimiting nutrient levels may generate more shoot growth than CRF in the first 80 d of production. Higher SDW of liquid-fertilized plants compared with those given CRF can be attributed to a relatively constant, nonlimiting nutrient supply in a liquid fertilization regime (Huett, 1997). By contrast to liquid fertilization, pore-water nutrient levels for CRF-fertilized plants depend on the rate and degree of nutrient diffusion out of CRF granules; CRF nutrient release may also be delayed due to low temperatures (Huett and Gogel, 2000; Husby et al., 2003).

Hydrangea and azalea SDW increased with increasing applied liquid P concentration in a nonlinear, logistic (sigmoidal) manner (Fig. 3). A sigmoid growth response to increasing P levels in field soils has also been observed in *Zea mays* L. and *Phaseolus vulgaris* L. (Postma and Lynch, 2011). Applied P concentrations in the 1.0–4.0 mg·L⁻¹ P range resulted in the greatest increase in SDW (i.e., grams SDW per mg·L⁻¹ P applied) in hydrangea and azalea when compared with low (i.e., 0.5–1.0 mg·L⁻¹ P) or high applied P concentrations (i.e., 4.0–6.0 mg·L⁻¹ P; Fig. 3). Nonlinear regression was used to describe the pattern of SDW increase over applied P treatments (Fig. 3) and estimate the optimal pore-water P concentration for each taxon (Table 3). Calculated optimal applied P concentrations (i.e., asymptotic deceleration point) for hydrangea and azalea SDW were 4.7 and 2.9 mg·L⁻¹ P, respectively. However, because there was an increasing trend in SDW from 4.0 to 6.0 mg·L⁻¹ P for hydrangea, SDW may have continued to increase if fertilized with P concentrations >6.0 mg·L⁻¹. Regression was not performed for holly because SDW was unaffected by P concentration (Table 2).

Increasing P fertilizer level from 0.5 to 2.0 mg·L⁻¹ P increased RDW 92% in hydrangea, but >2.0 mg·L⁻¹ P did not further increase RDW (Table 4). Similar to SDW, RDW of CRF-fertilized hydrangea was lower than in those that received the 4.0–6.0 mg·L⁻¹ P treatments. By contrast, holly RDW was the same across all fertilizer treatments. Havis and Baker (1985) observed increased root growth of *Cotoneaster adpressus* var. *praecox* when P fertilizer concentration was increased from 0 to 10 mg·L⁻¹ P. In one of the three experiments performed by Yeager and Wright (1982), RDW of *I. crenata* ‘Helleri’ was unaffected when applied P concentration was increased from 0 to 20 mg·L⁻¹ in 5 mg·L⁻¹ increments.

In hydrangea and holly, root: shoot values decreased by 43% and 46%, respectively, as applied P concentration increased from 0.5 to 4.0 mg·L⁻¹ P (Table 4), reflecting relatively high increases in SDW compared with RDW. Similarly, Kim and Li (2016) observed

decreasing root: shoot values in *Lantana camara* L. ‘New Gold’ when P fertilization was increased from 1 to 30 mg·L⁻¹. Yeager and Wright (1981) found that root: shoot values of *I. crenata* ‘Helleri’ were the same when fertilized with 17, 42, or 85 mg·L⁻¹ P; however, the absence of response was attributed to all P treatments being sufficient for maximal growth. These studies agree with our findings that fertilizing crops with P levels higher than those necessary for maximal shoot growth does not further increase root growth.

Pore-water P, N, and K concentrations. The 4.0 and 6.0 mg·L⁻¹ P fertilizer treatments, which achieved maximal SDW in hydrangea and azalea, had 0.6–2.0 mg·L⁻¹ P in substrate pore-water for hydrangea and 2.2–5.7 mg·L⁻¹ P in substrate pore-water for azalea (Table 5). These data suggest that the minimum recommended pour-through P concentration of 5 mg·L⁻¹ (Bilderback et al., 2013) is higher than that necessary to produce hydrangea and azalea without limiting growth. Measured pore-water P concentrations were consistently lower than applied P levels. Lower P concentrations in pour-through leachate compared with the fertilizer solution have also been observed in containerized *Tagetes erecta* L. ‘Inca Gold’ (Tolman et al., 1990) and *Euphorbia pulcherrima* ‘Freedom Red’ Willd. Ex Klotzsch. (Cavins et al., 2004). Phosphorus removal from substrate pore-water is likely because of uptake by roots before pour-through sampling. Although statistical analysis was not used to compare taxa, pore-water P concentrations within each treatment appeared to be lower in hydrangea than in holly or azalea, which may be attributed to genotypic variation in nutrient uptake characteristics across taxa (Marschner, 2012). Differences in growth (hydrangea > azalea > holly; according to SDW data) across taxa may also have contributed to apparent variation in pore-water P concentrations because growth is proportional to the rate of nutrient uptake (Ingestad and Lund, 1986). Although P chemical fate was not determined in this study, P adsorption to dolomite or precipitation with dolomite and micronutrient amendment dissolution products was not likely a major contributor to relatively low pore-water P concentrations because potential sorption sites were routinely flushed with fertilizer solution before the first pour-through extraction 41 DAI. Substrate pore-water P concentrations increased between 41 and 81 DAI for holly fertilized with 1.0 mg·L⁻¹ P or 4.0 mg·L⁻¹ P as well as azalea fertilized with 2.0 mg·L⁻¹ P (Table 5). For all other treatments within each taxon, pore-water P levels were the same over time. At 81 DAI, increasing the fertilizer treatment from 0.5 to 4.0 mg·L⁻¹ P in hydrangea or from 0.5 to 2.0 mg·L⁻¹ P in holly and azalea did not increase pore-water P levels (Table 5). Correlation values between pore-water P and SDW ($r = 0.71, 0.53$ and 0.73 for hydrangea, holly, and azalea, respectively; data not shown) were lower than those between

Table 4. Effect of applied phosphorus (P) concentration versus controlled-release fertilizer (CRF; control) on root:shoot ratio and root dry weight (RDW) of hydrangea, holly, and azalea grown for 82 d in pine bark amended with 0.89 kg·m⁻³ micronutrients and either 4.75 kg·m⁻³ (hydrangea and holly) or 1.19 kg·m⁻³ (azalea) of dolomitic limestone.

Treatment (mg·L ⁻¹ P)	RDW ^z (g)	Root:shoot ^y
Hydrangea		
CRF	3.11	0.28
0.5	2.12 a ^x	0.41 d**
1.0	2.25 a	0.34 cd
2.0	4.08 ab	0.30 bc
4.0	5.31 b*	0.22 ab
6.0	5.48 b*	0.21 a
P value	0.0026	0.0001
Holly		
CRF	2.90	0.52
0.5	3.35	0.44 c
1.0	4.11	0.40 c
2.0	3.03	0.36 bc*
4.0	2.78	0.25 ab**
6.0	2.56	0.24 a**
P value	0.1083	0.0007

^zRDW include all portions of plant below substrate level. For all treatments except 1.0, $n = 3$ (two-plant mean for each of three blocks). For treatment 1.0, $n = 2$ (two-plant mean for each of two blocks).

^yRoot:shoot = RDW (g)/shoot dry weight (g).

^xLetters within columns separate means by Tukey’s honestly significant difference at $P \leq 0.05$ (control not included).

*or ** indicates significant difference from control at $P \leq 0.05$ and 0.01 , respectively (Dunnnett’s test).

applied P concentrations and SDW ($r = 0.97, 0.57$, and 0.85 for hydrangea, holly, and azalea, respectively; data not shown). These correlations indicate that applied P concentrations more accurately predict growth responses than pore-water P concentrations.

Nitrogen (i.e., sum of $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and $\text{NO}_2^-\text{-N}$) and K^+ pore-water concentrations were unaffected by liquid P fertilizer treatment (data not shown). Thus, pore-water N and K^+ concentrations were pooled across liquid fertilizer treatments (Table 1) and collectively referred to as liquid fertilizer. At 41 DAI, pore-water N concentrations were 45%, 51%, and 16% lower than the measured applied N concentration (64.5 ± 3.44 SE mg·L⁻¹ N) in liquid-fertilized hydrangea, holly, and azalea, respectively. Relatively low N concentrations in pour-through leachate compared with applied levels have also been reported for containerized *Citrus* species (64% to 80% of applied; Maust and Williamson, 1994) and *Tagetes erecta* ‘Inca Gold’ (53% to 80% of applied; Tolman et al., 1990). Similar to pore-water P, relatively low pore-water N concentrations were attributed to plant uptake before pour-through sampling. Seemingly higher pore-water N concentrations (i.e., less N removal) for azalea relative to hydrangea and holly may be due to lower nutrient demand, which has been reported for *Rhododendron* sp. (Bilderback et al., 2013). In holly and azalea, pore-water N (primarily as NO_3^- ; data not shown)

Table 5. Observed pore-water phosphorus (P) concentrations in pour-through leachate of hydrangea, holly, and azalea fertilized with controlled-release fertilizer (CRF; control) or one of five liquid P treatments at 41 and 81 d after initiation (DAI). The substrate was amended with 0.89 kg·m⁻³ micronutrients and either 4.75 kg·m⁻³ (hydrangea and holly) or 1.19 kg·m⁻³ (azalea) of dolomitic limestone.

	Pore-water P (mg·L ⁻¹)		
Treatment ^z (mg·L ⁻¹ P applied)	41 DAI	81 DAI	
	Hydrangea		<i>P</i> value
CRF	0.16	0.24	0.4528
0.5	0.08 ^y a ^x	0.08 a	NA ^w
1.0	0.08 a	0.08 a	0.4226
2.0	0.59 ab	0.18 a	0.1501
4.0	1.43 bc**	0.55 ab	0.0963
6.0	2.02 c**	1.52 b*	0.4203
<i>P</i> value	0.0016	0.0088	
	Holly		<i>P</i> value
CRF	0.08	2.49	0.0140
0.5	0.08 a	0.08 a**	NA
1.0	0.08 a	0.18 a**	0.0002
2.0	0.27 a	0.85 a*	0.0898
4.0	1.11 a	2.64 b	0.0014
6.0	4.22 b*	5.03 c**	0.4494
<i>P</i> value	<0.0001	<0.0001	
	Azalea		<i>P</i> value
CRF	1.68	2.26	0.7419
0.5	0.08 a	0.08 a**	NA
1.0	0.08 a	0.14 a**	0.4226
2.0	0.15 a	0.71 a**	0.0227
4.0	2.39 a	2.18 b	0.7233
6.0	5.71 b*	4.58 c**	0.3486
<i>P</i> value	0.0002	<0.0001	

²For all treatments except 1.0, pore-water samples were collected from one randomly selected replication from each block on each sampling date ($n = 3$). For treatment 1.0, pore-water samples were collected from one randomly selected replication from two blocks on each sampling date ($n = 2$).

^yDetection limit was 0.08 mg·L⁻¹. For means comparisons, nondetectable values were assumed to be 0.08 to reduce type I error.

^xLetters within columns separate means by Tukey's honestly significant difference at $P \leq 0.05$ (control not included).

^wAll pore-water P concentrations were below detection limits at 41 and 81 DAI.

*or ** indicates significant difference from control at $P \leq 0.05$ and 0.01, respectively (Dunnett's test).

concentrations of liquid-fertilized plants were higher at 81 DAI than at 41 DAI (Table 1). This finding is most likely because of the N supply exceeding plant demand, resulting in a slow buildup of NO₃⁻. Because N was the nutrient in highest concentration in the fertilizer solution and because NO₃⁻ is a leading contributor to the bulk EC relative to other fertilizer ions (e.g., SO₄²⁻, K⁺, PO₄³⁻, Mg²⁺, and Ca²⁺; Hoskins et al., 2014b), NO₃⁻ buildup is likely why EC increased over time (Fig. 2).

Pore-water N and K⁺ concentrations of CRF-fertilized plants were consistently lower than that of liquid-fertilized plants for all three taxa except for N in holly at 81 DAI in which the values were the same (Table 1). Pore-water K⁺ concentrations of CRF-fertilized plants were within or above the BMP-recommended range (10–20 mg·L⁻¹ K⁺; Bilderback et al., 2013) and, therefore, deemed sufficient for maximal vegetative growth for all three taxa and at both sampling dates. However, observed pore-water N concentrations for CRF-fertilized hydrangea (41 and 81 DAI) and holly (41 DAI) were less than the BMP recommendation (15–25 mg·L⁻¹ NO₃⁻-N; Bilderback et al., 2013). Therefore, consistently lower concentrations of pore-water N for CRF-fertilized plants compared with those liquid fertilized may partially explain why plants were smaller when given the CRF treatment. Pore-water

N concentrations at 81 DAI for CRF-fertilized hydrangea, holly, and azalea were 3-, 5-, and 5-fold higher, respectively, than at 41 DAI (Table 1), indicating a major release of N after the lag in N release from CRF granules as previously stated. Similar to the liquid fertilizer treatments, the observed increase in N, primarily in the form of NO₃⁻ (data not shown), suggests that NO₃⁻ is responsible for the increase in EC over time in the CRF treatment (Fig. 2).

Foliar P, N, and K concentrations. In all three taxa, foliar P concentrations increased with increasing P supply in a logistic fashion (Fig. 3). The calculated foliar P concentrations ($\pm 95\%$ confidence interval) for optimal SDW in hydrangea and azalea are 0.23 $\pm$ 0.03% and 0.23 $\pm$ 0.01%, respectively (Table 3).

Foliar P and SDW had a strong positive correlation in hydrangea ($r = 0.88$) and azalea ($r = 0.89$), whereas in holly, this correlation was relatively weak ($r = 0.52$) because SDW stayed the same despite increasing foliar P. The increase in foliar P concentration to levels higher than those required for maximal SDW in holly indicated luxury consumption. Superfluous foliar P accumulation has been reported for multiple containerized woody plant taxa, including *Rhododendron* 'Karen' (Ristvey et al., 2007), *Rhododendron* 'Victor' (Havis and Baker, 1985), *Rhododendron indicum* L. 'Formosa' (Dickey et al., 1967)

and *I. crenata* 'Helleri' (Yeager and Wright, 1982), and several herbaceous taxa, such as *Rudbeckia fulgida* var. *sullivantii* Ait. 'Goldsturm' (Kraus et al., 2011) and *L. camara* L. 'New Gold' (Kim and Li, 2016).

Foliar P sufficiency ranges (Bryson et al., 2014) for *H. paniculata* Siebold., *I. crenata* 'Helleri', and *Rhododendron* L. 'Herbert' are 0.23% to 0.59%, 0.08% to 0.11%, and 0.14% to 0.22%, respectively. Thus, foliar P concentrations were within the sufficiency range at harvest when fertilized with 6.0 mg·L⁻¹ P in hydrangea or 1.0–6.0 mg·L⁻¹ P in holly and azalea. These data also imply that optimal foliar P concentrations may vary between cultivars of the same interspecific hybrid because the calculated optimal foliar P level in 'Karen' azalea is higher than the upper threshold of the sufficiency range for another Gable hybrid azalea, *Rhododendron* 'Herbert', listed in Bryson et al. (2014). Cultivar-specific foliar nutrient sufficiency levels have been documented for *Vaccinium corymbosum* L. (Wilber and Williamson, 2008). In hydrangea, holly and azalea fertilized with CRF, foliar P concentrations were the same as in those that received the constant liquid feed treatments that resulted in maximal growth (Table 6) despite having lower than optimal SDW. Bi et al. (2007) demonstrated that following N fertilization of *Rhododendron* L. 'H-1 P.J.M.' or *Rhododendron* L. 'Cannon's Double', biomass increased

Table 6. Effect of applied phosphorus (P) concentration versus controlled-release fertilizer (CRF; control) on foliar nitrogen (N), P, and potassium (K) concentrations of hydrangea, holly, and azalea grown for 82 d in pine bark amended with 0.89 kg·m⁻³ micronutrients and either 4.75 kg·m⁻³ (hydrangea and holly) or 1.19 kg·m⁻³ (azalea) of dolomitic limestone.

Treatment ^c (mg·L ⁻¹ P applied)	Foliar nutrient concn (%)		
	N	P	K
		Hydrangea	
CRF	3.53	0.212	2.06
0.5	3.52	0.057 a***	0.88 a**
1.0	3.84	0.096 ab**	1.17 a**
2.0	3.46	0.155 bc	1.84 b
4.0	3.30	0.205 c	2.17 b
6.0	3.42	0.243 c	2.13 b
P value	0.2361	0.0004	<0.0001
		Holly	
CRF	2.35	0.202	1.29
0.5	1.44 a**	0.069 a**	0.98 a*
1.0	1.63 ab**	0.095 a**	1.06 a
2.0	1.88 bc**	0.156 b*	1.19 a
4.0	1.99 c**	0.207 c	1.46 b
6.0	2.09 c*	0.219 c	1.47 b
P value	<0.0001	<0.0001	<0.0001
		Azalea	
CRF	2.16	0.237	1.01
0.5	2.04 a*	0.103 a**	1.16 b*
1.0	2.03 a*	0.151 ab**	1.04 ab
2.0	2.12 ab	0.196 bc	0.91 a
4.0	2.15 ab	0.236 cd	0.89 a
6.0	2.23 b	0.255 d	0.90 a
P value	0.0029	<0.0001	0.0008

^a*n* = 3 (three-plant mean for each of three blocks) for control and treatments 0.5, 2.0, 4.0, and 6.0; *n* = 2 for treatment 1.0 (three-plant mean for each of two blocks).

^bSamples for foliar nutrient concentrations were obtained from 5.1- and 6.1-cm stem tip cuttings for azalea and holly, respectively; recently matured leaf blades were used for hydrangea.

^cLetters within columns separate means by Tukey's honestly significant difference at *P* ≤ 0.05 (control not included).

*or ** indicates significant difference from control at *P* ≤ 0.05 and 0.01, respectively (Dunnett's test).

2–4 weeks after tissue N accumulation. The delayed nutrient release from the CRF when growing hydrangea and holly may have allowed for adequate uptake and translocation of nutrients to leaves, but plants that were harvested before shoot growth could respond to increased nutrient availability.

Foliar N concentration had a strong, positive correlation with foliar P in holly and azalea (*r* = 0.93 and *r* = 0.81, respectively) but was poorly and negatively correlated with foliar P concentrations in hydrangea (*r* = -0.39). As applied P concentration increased from 0.5 to 6.0 mg·L⁻¹, foliar N concentrations of holly and azalea increased 45% and 9%, respectively. Although not measured, average leaf size appeared to decrease with decreasing P treatment in all taxa, and reduced leaf expansion is a common P deficiency symptom (Fredeen et al., 1989). In the case of holly and azalea, in which tissue samples were taken as terminal stem cuttings, increasing P fertilization may have resulted in a higher leaf to stem ratio in plants treated with higher P concentrations. Because nearly 66% of plant tissue N in *Rhododendron* 'Karen' has been shown to be partitioned in the leaves (Ristvey et al., 2007), the effect of P deficiency on leaf expansion may explain why foliar N in holly and azalea had a strong positive correlation with foliar P. Kraus et al. (2011) also observed an increase in foliar N concentration in *R. fulgida* Aiton var. *sullivantii* 'Goldsturm' and *Hibiscus moscheutos* L. in response to increasing P fertilizer

concentration. Foliar N concentrations in all three taxa and all six treatments were within the foliar N sufficiency range (Bryson et al., 2014). Similar to foliar P, foliar N concentrations in CRF-fertilized hydrangea, holly and azalea were the same as in those that received constant liquid feed treatments that resulted in optimal growth (Table 6).

Foliar K concentration had a strong positive correlation with foliar P concentration in hydrangea (*r* = 0.92) and holly (*r* = 0.95) but a strong negative correlation with foliar P concentration in azalea (*r* = -0.82). Foliar K concentration increased 143% and 50% in hydrangea and holly, respectively, and decreased 22% in azalea as applied P concentration increased from 0.5 to 6.0 mg·L⁻¹ (Table 6). Similar to the trend observed in azalea, tissue P and K levels in *R. fulgida* var. *sullivantii* 'Goldsturm' linearly increased and decreased, respectively, in response to increasing P fertilizer concentrations (Kraus et al., 2011). In hydrangea, foliar K levels were below the sufficiency range (Bryson et al., 2014) in all treatments except 4.0 mg·L⁻¹ P, but were within or above the sufficiency range in holly and azalea. Thus, although foliar K levels varied with P treatment, pore-water K concentration was not likely growth limiting in holly and azalea. Similar to foliar P and N, foliar K concentrations in all three taxa fertilized with CRF were the same as in plants that received constant liquid feed treatments that resulted in optimal growth.

Pore-water pH. Substrate pH was the same across liquid fertilizer treatments within each taxon and sampling date (data not shown); therefore, data were pooled across liquid fertilizer treatments within each taxon and sampling date (Fig. 4). For CRF- and liquid-fertilized hydrangea and holly, substrate pore-water pH increased ≈0.3 units, from 6.9 ± 0.02 SE to 7.2 ± 0.02 SE, in the first 20 d. After 20 d, pH decreased until 81 DAI to 6.4 ± 0.05 SE (hydrangea) or 6.6 ± 0.07 SE (holly) when liquid fertilized and to 6.8 ± 0.04 SE (hydrangea) or 7.0 ± 0.02 SE (holly) when given the CRF treatment. In the CRF treatment, 93% of N was derived from NH₄NO₃ (610 kg·t⁻¹ CaCO₃ fertilizer potential acidity; Mortvedt and Sine, 1994) and the remainder from monoammonium phosphate (560 kg·t⁻¹ CaCO₃ fertilizer potential acidity; Mortvedt and Sine, 1994), and the liquid fertilizer N source was entirely from NH₄NO₃; thus, the potential acidity of the N sources was similar in both treatments. The 0.4 unit lower pH in the liquid fertilizer treatment relative to the CRF treatment at 81 DAI may be explained by the greater quantity of NH₄NO₃ applied to liquid-fertilized plants than CRF-fertilized plants over the course of the study. Substrate pore-water pH of liquid- and CRF-fertilized azalea (3.6 kg·m⁻³ less dolomite than for hydrangea and holly) generally decreased throughout the course of the study, ranging from 5.0 ± 0.03 SE to 4.7 ± 0.04 SE and 5.2 ± 0.04 SE to 4.7 ± 0.10 SE, respectively (Fig. 4).

Conclusions

Containerized hydrangea, holly, and azalea can be grown with less than 5 mg·L⁻¹ P in substrate pore-water, the current minimum pore-water P concentration recommended by BMPs, when fertigated with a complete liquid fertilizer containing ≈65 mg·L⁻¹ N and 42 mg·L⁻¹ K. However, minimum applied P requirements are taxa- and growth stage-specific. According to our calculations, hydrangea and azalea grown in 3.8-L containers maybe fertilized with 4.7 and 2.9 mg·L⁻¹ P, respectively, without affecting SDW, whereas in holly, 0.5 mg·L⁻¹ P was sufficient for growth.

Identifying optimal P concentrations by calculating the asymptotic deceleration point for logistic increase in SDW over P concentration is an informative method that should be evaluated and used to identify nutrient sufficiency in other ornamental plant taxa. When fertigating, applied P concentration is a better predictor of growth response than pour-through P levels. Although pour-through extraction is a simple method growers can use as a proxy for substrate pore-water fertility, nutrient concentrations in extracted solution may not accurately predict actual nutrient levels available for root uptake after fertigation. Our findings suggest that

pour-through P levels as low as 1.0 and 2.3 mg·L⁻¹ for hydrangea and azalea, respectively, are adequate for maximal shoot growth; these values are lower than the BMP recommendation of 5–15 mg·L⁻¹ P. Variables not considered in this study, including N:P:K ratio, container size, and frequency of fertilization and irrigation, can influence critical nutrient levels in plant tissue and may, therefore, also affect the optimal fertilizer level.

Literature Cited

- Bi, G., C.F. Scagel, L.H. Fuchigami, and R.P. Regan. 2007. Differences in growth, and nitrogen uptake and storage between two container-grown cultivars of rhododendron. *J. Environ. Hort.* 25:13–20.
- Bilderback, T., C. Boyer, M. Chappell, G. Fain, D. Fare, C. Gilliam, B.E. Jackson, J. Lea-Cox, A.V. LeBude, A. Niemiera, J. Owen, J. Ruter, K. Tilt, S. Warren, S. White, T. Whitwell, R. Wright, and T. Yeager. 2013. Best management practices: Guide for producing nursery crops. 3rd ed. Southern Nursery Association, Acworth, GA.
- Bryson, G.M., H.A. Mills, N.D. Sasseville, J.B. Jones, Jr., and A.B. Barker. 2014. Plant analysis handbook III: A guide to sampling, preparation, analysis, interpretation and use of results of agronomic and horticultural crop plant tissue. Macro-Micro Publishing, Inc., Athens, GA.
- Cavins, T.J., B.E. Whipker, and W.C. Fonteno. 2004. Establishment of calibration curves for comparing pour-through and saturated media extract nutrient values. *HortScience* 39:1635–1639.
- Dennis, J.H., R.G. Lopez, B.K. Behe, C.R. Hall, C. Yue, and B.L. Campbell. 2010. Sustainable production practices adopted by greenhouse and nursery plant growers. *HortScience* 45:1232–1237.
- Dickey, R.D., R.T. Poole, and J.N. Joiner. 1967. Effect of nitrogen, phosphorus and potassium levels on growth and chemical composition of *Rhododendron indicum* 'Formosa' and *Viburnum suspensum*. *Proc. Amer. Soc. Hort. Sci.* 91:762–770.
- Fonteno, W.C., C.T. Hardin, and J.P. Brewster. 1995. Procedures for determining physical properties of horticultural substrates using the NCSU Porometer. Horticultural Substrates Laboratory, NC State University, Raleigh, NC.
- Fredeen, A.L., I.M. Rao, and N. Terry. 1989. Influence of phosphorus nutrition on growth and carbon partitioning of *Glycine max*. *Plant Physiol.* 89:225–230.
- Groves, K.M., S.L. Warren, and T.E. Bilderback. 1998. Irrigation volume, application, and controlled-release fertilizer. II. Effect on substrate solution nutrient concentration and water efficiency in containerized plant production. *J. Environ. Hort.* 16:182–188.
- Havis, J.R. and J.H. Baker. 1985. Phosphorus requirement of *Rhododendron* 'Victor' and *Cotoneaster adpressa praecox* grown in a perlite-peat medium. *J. Environ. Hort.* 3:63–64.
- Heinrich, P.A. and J.W. Patrick. 1985. Phosphorus acquisition in the soil-root system of *Eucalyptus pilularis* Sm. seedlings. I characteristics of the soil system. *Austral. J. Soil Res.* 23:223–236.
- Hoskins, T.C., J.S. Owen, Jr., J.S. Fields, J.E. Altland, Z.M. Easton, and A.X. Niemiera. 2014a. Solute transport through a pine bark-based substrate under saturated and unsaturated conditions. *J. Amer. Soc. Hort. Sci.* 139:634–641.

Fig. 4. Substrate pore-water pH of hydrangea (A), holly (B), and azalea (C) amended with 0.89 kg·m⁻³ micronutrients and either 4.75 kg·m⁻³ (hydrangea and holly) or 1.19 kg·m⁻³ (azalea) of dolomitic limestone fertilized with either controlled-release fertilizer (CRF; —) or liquid fertilizer (LF; - -) pooled across five phosphorus (P) concentration treatments (0.5, 1.0, 2.0, 4.0 and 6.0 mg·L⁻¹ P) over the duration of study (80 d). Vertical bars indicate SE.

- Hoskins, T.C., J.S. Owen, Jr., and A.X. Niemiera. 2014b. Controlled-release fertilizer placement affects the leaching pattern of nutrients from nursery containers during irrigation. *HortScience* 49:1341–1345.
- Huett, D.O. 1997. Fertiliser use efficiency by containerized nursery plants 1. plant growth and nutrient uptake. *Austral. J. Agr. Res.* 48:251–258.
- Huett, D.O. and B.J. Gogel. 2000. Longevities and nitrogen, phosphorus, and potassium release patterns of polymer-coated controlled-release fertilizers at 30°C and 40°C. *Commun. Soil Sci. Plant Anal.* 31:959–973.
- Husby, C.E., A.X. Niemiera, J.R. Harris, and R.D. Wright. 2003. Influence of diurnal temperature on nutrient release patterns of three polymer-coated fertilizers. *HortScience* 38:387–389.
- Ingestad, T. and A. Lund. 1986. Theory and techniques for steady state mineral nutrition and growth of plants. *Scand. J. For. Res.* 1:439–453.
- Jungk, A. and N. Claassen. 1997. Ion diffusion in the soil-root system. *Adv. Agron.* 61:53–110.
- Kim, H. and X. Li. 2016. Effects of phosphorus on shoot and root growth, partitioning, and phosphorus utilization efficiency in lantana. *HortScience* 51:1001–1009.
- Kraus, H.T., S.L. Warren, G.J. Bjorkquist, A.W. Lowder, C.M. Tchir, and K.N. Walton. 2011. Nitrogen: Phosphorus:potassium ratios affect production of two herbaceous perennials. *HortScience* 46:776–783.
- Ku, C.S. and D.R. Hershey. 1997. Growth response, nutrient leaching, and mass balance for potted poinsettia. II. Phosphorus. *J. Amer. Soc. Hort. Sci.* 122:459–464.
- Lea-Cox, J.D. and A.G. Ristvey. 2003. Why are nutrient uptake efficiencies so low in ornamental plant production. *Proc. South Nurs. Assoc. Res. Conf.* 48:116–122.
- Marschner, H. 2012. Mineral nutrition of higher plants. 3rd ed. Academic Press, San Diego, CA.
- Maust, B.E. and J.G. Williamson. 1994. Nitrogen nutrition of containerized citrus nursery plants. *J. Amer. Soc. Hort. Sci.* 119:195–201.
- Merhaut, D.J., E.K. Blythe, J.P. Newman, and J.P. Albano. 2006. Nutrient release from controlled-release fertilizers in acid substrate in a greenhouse environment: I. Leachate electrical conductivity, pH, and nitrogen, phosphorus, and potassium concentrations. *HortScience* 41:780–787.
- Million, J., T. Yeager, and J. Albano. 2007. Consequences of excessive overhead irrigation on runoff during container production of sweet viburnum. *J. Environ. Hort.* 25:117–125.
- Mischan, M.M., S.Z.D. Pinho, and L.R.D. Carvalho. 2011. Determination of a point sufficiently close to the asymptote in nonlinear growth functions. *Sci. Agr.* 68(1):109–114.
- Mortvedt, J.J. and C. Sine (eds.). 1994. Fertilizer dictionary. In: Farm chemicals handbook. Meister Publishing, Willoughby, OH.
- Newman, J.P., J.P. Albano, D.J. Merhaut, and E.K. Blythe. 2006. Nutrient release from controlled-release fertilizers in a neutral-pH substrate in an outdoor environment: I. Leachate electrical conductivity, pH, and nitrogen, phosphorus, and potassium concentrations. *HortScience* 41:1674–1682.
- Owen, J.S., S.L. Warren, T.E. Bilderback, and J.P. Albano. 2008. Phosphorus rate, leaching fraction, and substrate influence on influent quantity, effluent nutrient content, and response of a containerized woody ornamental crop. *HortScience* 43:906–912.
- Postma, J.A. and J.P. Lynch. 2011. Theoretical evidence for the functional benefit of root cortical aerenchyma in soils with low phosphorus availability. *Ann. Bot.* 107:829–841.
- Ristvey, A.G., J.D. Lea-Cox, and D.S. Ross. 2004. Nutrient uptake, partitioning and leaching losses from container-nursery production systems. *Acta Hort.* 630:321–328.
- Ristvey, A.G., J.D. Lea-Cox, and D.S. Ross. 2007. Nitrogen and phosphorus uptake efficiency and partitioning of container-grown azalea during spring growth. *J. Amer. Soc. Hort. Sci.* 132:563–572.
- Smil, V. 2000. Phosphorus in the environment: Natural flows and human interferences. *Annu. Rev. Energy Environ.* 25:53–88.
- Temple-Smith, M.G. and R.C. Menary. 1977. Movement of ³²P to roots of cabbage and lettuce grown in two soil types. *Commun. Soil Sci. Plant Anal.* 8:67–79.
- Tolman, D.A., A.X. Niemiera, and R.D. Wright. 1990. Influence of plant age on nutrient absorption for marigold seedlings. *HortScience* 25:1612–1613.
- Tyler, H.H., S.L. Warren, and T.E. Bilderback. 1996. Reduced leaching fractions improve irrigation use efficiency and nutrient efficacy. *J. Environ. Hort.* 14:199–204.
- USDA ERS. 2013. Fertilizer use and price. Table 8. Fertilizer price indexes. 7 Apr. 2017. <<https://www.ers.usda.gov/data-products/fertilizer-use-and-price/>>.
- USEPA. 2002. Mid-Atlantic integrated assessment 1997–98. Summary report, EPA/620/R-02/003. U.S. Environmental Protection Agency, Atlantic Ecology Division, Narragansett, RI.
- USEPA. 2017. Nutrient pollution: Sources and solutions. 10 Nov. 2017. <<https://www.epa.gov/nutrientpollution/sources-and-solutions>>.
- Warren, S.L., T.E. Bilderback, and H.H. Kraus. 2001. Method of fertilizer application affects nutrient losses of controlled-release fertilizer. *Acta Hort.* 548:349–355.
- Warren, S.L., T.E. Bilderback, and H.H. Tyler. 1995. Efficacy of three nitrogen and phosphorus sources in container-grown azalea production. *J. Environ. Hort.* 13:147–151.
- Wilber, W.L. and J.G. Williamson. 2008. Effects of fertilizer rate on growth and fruiting of containerized southern highbush blueberry. *HortScience* 43:143–145.
- Wright, R.D. 1986. The pour-through nutrient extraction procedure. *HortScience* 21:227–229.
- Wright, R.D. and A.X. Niemiera. 1985. Influence of N, P and K fertilizer interactions on growth of *Ilex crenata* Thunb. ‘Helleri’. *J. Environ. Hort.* 3:8–10.
- Yeager, T.H. and R.D. Wright. 1981. Influence of nitrogen and phosphorus on shoot: Root ratio of *Ilex crenata* Thunb. ‘Helleri’. *HortScience* 16:564–565.
- Yeager, T.H. and R.D. Wright. 1982. Phosphorus requirement of *Ilex crenata* Thunb. cv. Helleri grown in a pine bark medium. *J. Amer. Soc. Hort. Sci.* 107:558–562.