**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 \(\approx 27\%\) 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] on 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 \(\approx 50\%\) 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\(^{-1}\), 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\(^{-1}\), 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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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 *Hex crenata* Thumb. ‘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 coarse sand (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 *Rhododendron* L. ‘Victor’ when fertilizing with 2.5 mg L⁻¹ P did not increase plant size. et al. (2007) observed no change in plant size index [i.e., (plant height + plant width)/2] of *Rhododendron* L. ‘Victor’ when fertilizing with 2.5 mg L⁻¹ P did not increase plant size. 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 coarse sand (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 *Rhododendron* L. ‘Victor’ when fertilizing with 2.5 mg L⁻¹ P did not increase plant size. et al. (2007) observed no change in plant size index [i.e., (plant height + plant width)/2] of *Rhododendron* L. ‘Victor’ when fertilizing with 2.5 mg L⁻¹ P did not increase plant size.

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* Thumb. ‘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 micronutrient fertilizer (Micromax; Everris, Dublin, OH), 2.37 kg m⁻³ ground dolomite [97% calcium carbonate equivalent (CCE)], Rockystones Quarries Corporation, Roanoke, VA], and 2.27 kg m⁻³ pulverized dolomite [94% CCE; Old Castle Lawn and Garden, Thompson, OH]. 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 porimeter 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. Experimental initiation. On 16 May 2014, all plants were moved into an 8 m × 29 m greenhouse running northwest to southeast and roofed with a polylefín 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 (DS25F1; Dosatron Intl., Clearwater, FL), which had a 1:100 fixed injection ratio 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 Ca, Mg, K, and P concentrations to confirm that target nutrient concentrations were being applied. Observed applied N and K concentrations were 64.5 ± 3.44 SE and 423.± 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.

Injectors 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 (after experiment initiation (DAL) 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 DAL. 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 ≥25 °C for ammonium (NH₄⁺), nitrate (NO₃⁻), nitrite (NO₂⁻), PO₄³⁻, 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× 250 mm (i.d. × 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 [Fioramite; Mainland, PA (0.65 mL 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 (≥11 ± 0.8 SE leaves) and nine 6.1-cm (≥11 ± 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), and a different anion-exchange column (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.

Table 1. Substrate pore-water nitrogen (N) and potassium (K) concentrations (mg 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 m⁻³ micronutrients and either 4.75 kg m⁻³ (hydrangea and holly) or 1.19 kg m⁻³ (azalea) of dolomitic limestone and 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 L⁻¹. P. Vertical bars indicate SE.

| Nutrient concn in pour-through leachate (mg L⁻¹) | Treatment | N | K |
|-----------------------------------------------|----------|---|---|
| Hydrangea                                    | 41 DAI   | 81 DAI | P value | 41 DAI | 81 DAI | P value |
| CRF                                          | 5.1      | 15.0   | 0.0215  | 18.0   | 17.2   | 0.7397  |
| LF²                                          | 35.6     | 44.5   | 0.0770  | 50.8   | 43.0   | 0.0770  |
| P 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  |
| P 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  |
| P value                                      | 0.0003   | 0.0082 |         | 0.0062 | 0.0277 |         |

*Pour-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 L⁻¹ at the α = 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 \( y = \text{SDW} \); \( x = \text{fertilizer P concentration} \); \( a = \text{growth rate} \); \( b = \text{inflection point} \); and \( c = \text{asymptote} \). Computer-generated estimates for parameters \( a \), \( b \), and \( c \) were obtained via JMP Pro (SAS Institute), then the fourth derivative equation was solved for \( x^{IV} \) by equating \( y^{IV} \) 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, Ingestad 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...
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) | Hydrangea | Holly | Azalea |
|----------------------|-----------|-------|--------|
| CRF                  | 11.53     | 5.71  | 4.72   |
| 0.5                  | 4.95 a*** | 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** | 14.06 | 12.99 c** |
| 6.0                  | 27.52 c** | 10.56 | 12.30 bc** |
| P value              | <0.0001   | 0.0654| <0.0001 |

x Letters 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).

SDW includes all portions of plant above substrate line.

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).

**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 | Foliar P prediction model | Optimal fertilizer P (mg·L⁻¹) | Foliar P (%) | SDW (g) |
|----------|----------------------|---------------------------|--------------------------------|--------------|---------|
| Hydrangea| 28.6/(1 + e⁻¹·28)(x - 2.27) | 0.23/(1 + e⁻¹·05)(x - 1.08) | 4.74                           | 0.23         | 25.9    |
| Azalea   | 12.8/(1 + e⁻¹·28)(x - 1.08) | 0.25/(1 + e⁻¹·05)(x - 0.75) | 2.88                           | 0.23         | 11.6    |

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

y Predicted foliar P concentration when fertilizer P is optimal for SDW.

Azalea 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
concentrations (i.e., 4.0–6.0 mg·L⁻¹) in hydrangea and azalea when compared with other plants (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, 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 also has 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 P. 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 *Cotonaster 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 levels. Lower P concentrations in pour-through leachate compared with the fertilizer solution have also been observed in *Tagetes erecta* L. ‘Inca Gold’ (Tolman et al., 1990) and *Euphorbia pulcherrima* ‘Freedom Red’ Willd. Ex Klotzch. (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 to be 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 (g) Root:shoot | Hydrangea | Holly | Azalea |
|---------------------|--------------------|-----------|-------|--------|
| CRF                 |                    |           |       |        |
| 0.5                 | 2.12 a            | 0.41 d**  |        |        |
| 1.0                 | 2.25 a            | 0.34 cd   |        |        |
| 2.0                 | 4.06 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    |        |        |
| Hydrangea           |                    |           |       |        |
| 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    |        |        |

*RDW 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).

*Root shoot = RDW (g)/shoot dry weight (g).

*Letters 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 (Dunnnett’s test).

Nitrogen (i.e., sum of NH₄-N, NO₃-N, and NO₂-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 mg·L⁻¹ N) in liquid-fertilized hydrangea, holly, and azalea, respectively. Relatively low N concentrations in pour-through leachate 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 NO₃⁻; data not shown)
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 NO$_3^\text{-}$. Because N was the nutrient in highest concentration in the fertilizer solution and because NO$_3^\text{-}$ is a leading contributor to the bulk EC relative to other fertilizer ions (e.g., SO$_4^{2-}$, K$^+$, PO$_4^{3-}$, Mg$^{2+}$, and Ca$^{2+}$; Hoskins et al., 2014b), NO$_3^\text{-}$ 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 comparison with those liquid-fertilized may. This finding is most likely because of a 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 NO$_3^\text{-}$ (data not shown), suggests that NO$_3^\text{-}$ 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 were 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. Superficially, 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 (mg·L⁻¹ P applied) | Foliar nutrient concn (%) |   |   |
|-------------------------------|--------------------------|---|---|
|                               | N                      | P | K |
| CRF                           | 3.53                   | 0.212 | 2.06 |
| 0.5                           | 3.52                   | 0.197 | 0.88 a** |
| 1.0                           | 3.84                   | 0.189 | 1.17 a** |
| 2.0                           | 3.46                   | 0.155 b | 1.84 b |
| 4.0                           | 3.30                   | 0.205 c | 2.17 b |
| 6.0                           | 3.42                   | 0.224 c | 2.13 b |
| P value                       | <0.0001                | <0.0001 | <0.0001 |
| CRF                           | 2.16                   | 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 |
| 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                | 0.216 cd | 0.89 a |
| 6.0                           | 2.23 b                 | 0.255 d | 0.90 a |
| P value                       | <0.0009                | <0.0001 | 0.0008 |

<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).

*Samples 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.

*Letters 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 (Freeden 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 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 dolomitic limestone) was 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 may be 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 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.

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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.
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