The Influence of Substrate Hydraulic Conductivity on Plant Water Status of an Ornamental Container Crop Grown in Suboptimal Substrate Water Potentials

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Abstract. Many soilless substrates are inefficient with regard to water (i.e., high porosity and low water holding capacity), which provides an excellent opportunity to increase water efficiency in containerized production. We suggest that increasing hydraulic conductivity in the dry range of substrate moisture content occurring during production can increase water availability, reduce irrigation volume, and produce high quality, marketable crops. Three substrates were engineered using screened pine bark (PB) and amending with either Sphagnum peatmoss or coir to have higher unsaturated hydraulic conductivity between water potentials of –100 and –300 hPa. There was no correlation between substrate unsaturated hydraulic conductivity and saturated hydraulic conductivity (r = 0.04, P = 0.8985). Established Hydrangea arborescens (L.) ‘Annabelle’ plants were grown in the three engineered and a conventional (control) PB substrates exposed to suboptimal irrigation levels (i.e., held at substrate water potentials between –100 and –300 hPa) for 32 days. The plants in the engineered substrates outperformed the control in every growth and morphological metric measured, as well as exhibiting fewer (or no) physiological drought stress indicators (i.e., vigor, growth, plant development, etc.) compared with the control. We observed increased vigor measures in plants grown in substrates with higher unsaturated hydraulic conductivity, as well as greater plant water uptake. The coir increased unsaturated hydraulic conductivity and provided an increased air space when incorporated into coarse bark vs. if peat was incorporated into bark at the same ratio by volume. Increasing PB hydraulic conductivity, through screening bark or amending bark with fibrous materials, in concert with low irrigations can produce marketable, vigorous crops while reducing water consumed and minimizing water wasted in ornamental container production.

Fresh water is a limited resource that is necessary for the production of all plants. Forty percent of freshwater withdrawn in the United States is used for irrigation of crops (Kenney et al., 2009). Furthermore, plants in intensively controlled container production systems must receive quality fresh water daily or multiple times per day, in the absence of precipitation, to prevent actual or perceived plant water stress. Because of this, growers often apply excess water to container crops to alleviate concerns of underwatering that could render the plant unmarketable or delay time to sale (Mathers et al., 2005). This has led to container nurseries applying upward of 180 m3 of irrigation per hectare per day during the warm season (Fulcher and Fernandez, 2013). With potential future water restrictions, growers will have to adopt more sustainable cultural practices to thrive.

Most container nurseries use overhead irrigation on all or a portion of their operation and may not have the infrastructure to switch to more sustainable irrigation systems (Beeson et al., 2004). Therefore, growers must expand their efforts beyond irrigation technology to increase water sustainability (Fulcher et al., 2016). One area where growers can make modifications that provide potential water savings, without additional infrastructure, is selecting more sustainable soilless substrates (Barrett et al., 2016). Substrates with increased sustainability would include those that increase water storage capacity or more effectively deliver stored water to the plant. Conventional soilless substrates were initially developed to provide growers with increased control over the container system. Substrates are highly porous so that they drain rapidly, prevent salt stress, and are initially pathogen-free (Raviv and Lieth, 2008). Furthermore, these substrates were developed to allow containers to receive excess water from precipitation without concerns of flood stress as observed in some mineral soils. As a result, the current best management practices (BMPs) for container nursery production recommend maximum water holding capacity or container capacities (CCs) >45% and air spaces (ASs) <30% of the container volume (45% to 65% vol. and 10% to 30% by vol., respectively; Bilderback et al., 2013). These increased AS values, compared with a field soil, allude to the primary focus of substrate design being able to release water as opposed to water retention or storage. Furthermore, conventional wisdom based on past research infers that the degree of water availability has strict cutoffs of easily available water [between –10 and –50 hPa substrate water potential (Ψs)] and water buffering capacity (Ψ between –50 and –100 hPa), with all water held at Ψ < –100 hPa not readily accessible to plants (de Boodt and Verdonck, 1972; Pustjarvi and Robertson, 1975). We believe substrates should provide a better balance of sufficient drainage and water retention. Such substrates should retain water during and after irrigation events to reduce the volume of water required to grow containerized crops.

As substrate science develops, understanding more about using dynamic hydraulic properties as measures of substrate productivity as it relates to resource (i.e., water and mineral nutrient) sustainability is becoming imperative (Caron et al., 2014). For example, moisture characteristic curves (MCC) provide information on dynamic hydraulic properties that depict the relationship between volumetric water contents (VWCs) and Ψ (Bunt, 1961). Better defining the relationship between hydraulic conductivity (K) and MCC provides information on substrate environmental sustainability (through increased resource retention; Naasz et al., 2005) and water availability (O’Meara et al., 2014).

While the relationships between substrate K and Ψ or VWC are not commonly measured, saturated hydraulic conductivity (KS) is increasingly used. Concurrent work by the
Materials and Methods

Substrate preparation. On 10 Mar. 2016, we acquired ~1.2 m$^3$ of aged (~6 months) lobolly PB (Pinus taeda L.) passed through a 12.6-mm screen at a commercial bark processing plant (Pacific Organics, Henderson, NC). The bark was then separated into two particle size fractions by shaking it through a 4-mm screen (W.S. Tyler, Mentor, OH) rotating at about eight oscillations per second in a custom fabricated shaker (Steve’s Welding, Williamson, SC) at the Substrates Processing and Research Center at North Carolina State University, Raleigh, NC. The process entailed shoveling ~0.1 m$^3$ of PB (66.4% ± 1.1% se moisture content) into the shaking tray to a depth of ~7 cm and shaking for 5 min. The bark was then separated into two separate 0.19 m$^3$ drums; we stored the bark that passed through the 4-mm screen, termed as fine bark (FB), and bark that did not pass through the 4-mm screen. The screening process separated the bark by ~50% by volume (i.e., the volume of the bark that passed through the screen was equal to that did not pass through). An additional 0.19 m$^3$ drum was filled with <12.6 mm PB termed unprocessed bark (UB). All the drums were sealed to prevent moisture loss and transported to the Virginia Tech Hampton Roads Agricultural Research and Extension Center in Virginia Beach, VA for blending, analysis, and experimentation. Using particles that did not pass through the 4.0-mm screen, we blended two additional substrates with 35% (by vol.) compressed Sphagnum peatmoss [bark-peat (BP); Fafard, Agawam, MA] or 35% (by vol.) coir [bark-coir (BC); FibreDust, LLC, Glastonbury, CT] that were previously hydrated in sealed plastic tubs for 24 h to equilibrate. These component amendment ratios were based on preliminary analyses to mimic static physical properties to that of the conventional bark, while keeping equal amendment ratios of the two fibrous additions (data not shown), even though ~50% of the volume of the unaltered bark was removed. These two substrates were then placed into 0.19 m$^3$ drums and sealed.

Physical properties. Measurement included minimum AS, CC, total porosity (TP), and bulk density (Db) via porometry analysis (Fonteno and Harden, 2010) for three replicates of each substrate using a 347 cm$^3$ aluminum core. Particle size distributions of three replicates were measured for each substrate by shaking 100 g of oven dried substrate for 5 min with a Ro-Tap shaker (Rx-29; W.S. Tyler, Mentor, OH) equipped with 6.30, 2.00, 0.71, 0.50, 0.25, and 0.11 mm sieve and a pan. Particles remaining on each sieve or in the pan after shaking were weighed and used to determine particle size distribution by weight. Water and air contents were measured to determine dry bulk density and porosity. Moisture contents were measured by drying each of the three replicates in the constant head measurement mode before being removed from the device.

Substrate water potentials < −1.0 MPa were measured via a dewpoint potentiometer (WP4C; Decagon Devices) following procedures described by Fields (2013). Each substrate was used to fill stainless steel sampling dishes (Decagon Devices) to completely cover the bottom surface of the dish (≤0.5 cm depth) and dripped to different degrees (to ensure varying MC in each dish before measurement). Each dish was sealed in the dewpoint potentiometer drawer, and substrate water potential (Ψ) was measured on “Precise Mode.” Dishes were immediately weighed after each measurement and then dripped in a forced air drying oven at 105 °C for 48 h. This process was repeated until five measurements between −1.0 and −4.0 MPa were attained for each substrate, and corresponding VWCs were calculated using measured Db.

MCCs and unsaturated K curves were developed for each substrate via the evaporative method using a Hyprop (UMS, Munich, Germany) following the procedures described by Fields et al. (2016). Each substrate was packed using a column assembly as with previous analyses. Data for each substrate, including TP, Ks, and values obtained via dewpoint potentiometry, were then compiled with the HypropFit software (UMS). Moisture characteristic data were modeled using the Brooks and Corey (1964) model to generate predictive curves of MCCs. The measured K(Ψ) data were plotted, and the MCC data based on effective saturation measured via the evaporative method were used along with the K(Ψ) measurements to fit a K(Ψ) model in HypropFit. This model predicted K across the measured tension range and weighted the actual K(Ψ) measurements to produce the strongest fit. The fit was computed (in HypropFit) with a nonlinear regression algorithm that minimized the sum of weighted squared residuals between model prediction (based on MCC measures) and measured K(Ψ) data.

Lower crop production. On 5 June 2016, the previously sealed drums containing the four substrates were agitated to ensure homogenization and uniform moisture distribution for each of the four substrates. A volume of 0.13 m$^3$ of each substrate was amended, each with 5.63 kg-m$^{-3}$ controlled-release fertilizer.
Techniques, Temecula, CA) with 29.2 cm² lysimeters [load cells (LSP-10; Transducer Techniques, Temecula, CA) with 29.2 cm² lysimeters (Carlton Plants, Dayton, OR) were planted in 21 containers of each substrate. Each plant was placed in the center of the container and again dropped once from a height of 5 cm to complete planting. The remaining 11 containers of each substrate remained unplanted (fallow), and five of these fallow containers were immediately oven-dried to determine substrate dry weight and Db. The 84 planted containers (four substrates × 21 containers) and 24 fallow containers (four substrates × six containers) were moved into a shaded mist house, hand watered, and left in the mist house for 7 d to allow for root establishment.

On 13 June 2016, all planted containers were moved onto an open air nursery gravel pad and placed under daily overhead irrigation (20 min d⁻¹) for 21 d for continued establishment. On 12 July 2016, the plants were pruned to an uniform size and placed on benches in a climate-controlled greenhouse. The benches had 12 separate irrigation zones. Each zone consisted of a solenoide valve controlling 10 individual pressure compensating spray stakes (Plum color; 12.1 L h⁻¹; Netafim USA, Fresno, CA) used to water nine containers and a water collection vessel, which measured application volume and frequency. Each irrigation zone was used for a single substrate (treatment) with three separate replicate zones (replicate) assigned to each treatment. We placed one plant and one fallow container on two randomly located lysimeters [load cells (LSP-10; Transducer Techniques, Temecula, CA) with 29.2 cm² plates mounted on each side] in each replication connected to a data logger (CR3000 Micrologger; Campbell Scientific, Logan, UT) via a multiplexer (AM16/32B Relay Multiplexer; Campbell Scientific) that recorded the weight of the container system every 5 min. Air temperature (T) and relative humidity (RH) at canopy height were measured every 5 min with a HMP60 probe (Vaisala, Vantaa, Finland) via the data logger. The total irrigation events for each replicate were logged and used to calculate irrigations per day, and total applied water volume was used to calculate time average application rate (mL H₂O per h).

One representative plant from each replicate was used for an initial baseline harvest on 14 July 2016. Data measured included leaf number, leaf length (LL; from leaf tip to leaf base) of the four most apical mature leaves, leaf area (LA; LI-3100C; LI-COR Biosciences, Lincoln, NE), leaf number, and root index [RI; (rooting depth + widest root width + perpendicular root width)/3]. Roots and shoots were separated, washed clean of debris, dried at 105 °C for 7 d, and weighed. In addition, we measured growth index [GI; (height + widest width + perpendicular width)/3] of each plant, extracted pore water (LeBude and Bilderbacher, 2009) on three randomly selected plants in each replicate to determine initial electrical conductivity and pH. One hundred fifty milliliters of liquid fertilizer solution (12 g L⁻¹ of soluble 20N–8.6P–16.6K fertilizer solution; JPR Peters, Inc., Allentown, PA) was then applied to each container by hand to provide additional nutrition levels through the remainder of the study.

On 15 July 2016 [0 d after initiation (DAI)], automated irrigation control was initiated. A solenoid was actuated, via relays (SDM-CD16AC AC/DC Relay Controller; Campbell Scientific) when the minimum weight of the plant-container system on a lysimeter was equal to a corresponding Ψ of ~300 hPA. Plants continued to receive irrigation until the substrate reached a calculated weight corresponding to a Ψ of ~100 hPA. The critical weights (when irrigation was initiated and ended) of each substrate was determined using each substrate dry weight from previously collected fallow containers and substrate MCCs. A leaching pan, with riser, was placed under a random plant in each replicate to measure the volume of water leached after each irrigation. A single emitter from each zone was placed in a bottle to collect and quantify water application. The growth index was calculated about every 10 d (0 DAI, 11 DAI, 21 DAI, and 32 DAI).

### Instantaneous water use measurements.

On 17 and 32 DAI, a portable photosynthesis system (LI-6400XT; LI-COR Biosciences) with a light-emitting diode equipped gas exchange chamber was used to measure leaf gas flux including net photosynthesis (Pn), stomatal conductance (gₛ), and transpiration. Data were measured between 1100 and 1215 h on both days with the atmospheric and environmental parameters for the measurements on 17 DAI as follows: T = 30.1 °C ± 1.2 SD; RH = 46.3% ± 3.0 SD; photosynthetic active radiation (PAR) = 980 μmol m⁻² s⁻¹ ± 494 SD and for 32 DAI as follows: T = 29.6 °C ± 0.7 SD; RH = 66.5% ± 2.3 SE; PAR = 1455 μmol m⁻² s⁻¹ ± 426 SD. One representative plant of each replicate was selected for measurement and clamped the leaf chamber sample to an apical mature leaf ensuring that the leaf was not contorted, and the entire area of the chamber (6 cm²) covered the leaf tissue. This process was done quickly (<90 s) to minimize any possible shadowing that may affect the system or the plant. The chamber mimicked the PAR, T, and RH of the greenhouse environment at the time of measurement. The CO₂ concentration within the chamber was set to 404.8 and 400.5 μmol mol⁻¹ ± 0.2 SE for 17 and 32 DAI, respectively.

In addition, a pressure chamber (Model 600; PMS Instrument Co., Albany, OR) was used to measure the water potential of a severed apical stem consisting of three nodes (~10 cm) at 32 DAI immediately following gas exchange measurements. Once severed, the stem was immediately fit into a rubber stopper with clay to create an airtight seal. The stem was then sealed in the pressure chamber with the severed surface exposed to the atmosphere. We incrementally increased pressure of the chamber using compressed nitrogen gas until liquid was first observed exiting the severed stem surface. The entire process was conducted in <120 s to prevent tissue desiccation.

### Harvest

On 32 DAI, four plants in each replicate were harvested, including the plant used for instantaneous water status measurements and the plant used for irrigation control. The growth index was measured on all four plants harvested. The plant on the lysimeter of each replication had all leaves removed, LA measured, and total leaf number counted. The leaf length, as an indicator or plant water status throughout the experiment as impacted by cell elongation (Pallardy, 2008), was measured on (base to tip, excluding petiole) the four most apical mature leaves of all harvested plants. Compactness was calculated as the ratio of shoot dry mass to shoot height (van Iersel and Nemali, 2004). Shoots (above substrate plant material) were severed at the surface of the substrate, and roots were washed free of substrate. All plant tissue was dried in a convection oven at 58 °C for 7 d.

### Plant water availability.

Beginning 32 DAI, irrigation was turned off, spray stakes removed, and two plants and a fallow container in each replication were hand watered to effective CC. One plant and one fallow container were placed on a lysimeter in each irrigation zone and water loss through evaporation and/or transpiration was recorded until all plants were completely wilted for >2 d. The VWC determined to be the transition between evapotranspiration (ET) and evaporation was then converted to water potential using the MCC data for each substrate. Daily reductions in substrate VWC were plotted against the VWC and verified by fitting volumetric water content data to a model which calculated the point where the transition from nonlinear (during ET) to linear (evaporation) occurred (data not shown). Using these data plots, the intersection where the data become asymptotic was used to determine when water loss switched from primarily transpiration to primarily evaporation.

### Data analysis.

Data presented in tables with associated statistics were analyzed in JMP Pro (12.0.1; SAS Institute, Inc., Cary, NC) using the Dunnett’s test (α = 0.05) to compare the engineered substrates to the UB (control). We separated the means of the three engineered substrates using the Tukey’s Honestly Significant Difference (HSD; α = 0.05). The MCC and K(Y) model were computed (in HypropFit) using Brooks and Corey (1964) with a nonlinear regression algorithm that minimized the sum of weighted squared residuals between model
prediction (based on MCC measures) and measured $K(\Psi)$ data for the best fit. Root mean square error was computed to determine how strong the $K(\Psi)$ model fit the measured $K(\Psi)$ data.

Data in tables without accompanying statistics were computed or modeled from raw data. Correlation data were calculated using Pearson product-moment correlation coefficient in JMP Pro (12.0.1). Nonlinear regression for determining transition between linear and nonlinear data in the water availability study was calculated using PROC NLIN in SAS (9.3; SAS Institute).

Results and Discussion

Physical properties. The physical properties of FB and UB were within ranges recommended by BMPs (Bilderback et al., 2013). Minimum AS in BC and BP was outside of the BMP range (Table 1). TP varied with FB and BP being an average of 6.6% (by vol.) greater than UB and 3.3% less than BC. The BC had the largest TP, indicating increased porosity when coarse bark is equally amended with coir vs. peat. Minimum air space between BP, BC, and UB ranged from 30.7% to 40.6% (by vol.; Table 1). The UB was near the upper limit of recommended AS. The screening process removed 50% of the volume from the coarse bark, which was replaced by only 35% of the fibrous materials, and therefore, the BP and BC had a larger percentage of coarse bark particles. PB screened to <4 mm (FB) had an ≈18% shift in AS (18.2% by vol.) and CC (64.1% by vol.) increasing substrate water storage ≈650 mL compared with the other substrates in the study, when scaled up to a 3.9-L container.

Bulk density of engineered substrates (FB, BP, and BC) differed from conventional UB, with peat or coir amended bark being 0.06 g·cm⁻³ less and FB being 0.05 g·cm⁻³ greater (Table 1). This result demonstrates the dominance of the overall amount of PB in the container as seen in part by examining the particle texture class. FB had about twice the amount of fine (<0.7 mm) particles compared with the other substrates. The particle textures of UB increased by fine < medium < coarse particles, unlike the fiber amended substrates which had the largest percentage of coarse particles and lowest percentage of medium particles (Table 1). The removal of bark fines and subsequent replacement with fibrous materials (with lower Db than bark) resulted in reduced overall Db similar to previous observations by Pokorny et al. (1986). The Db of FB was greater than all other substrates resulting from reduced AS incurred from removing coarse particles. Bulk density is an important factor in developing soilless substrates, as lighter substrates are less costly to transport (Knox and Chappell, 2014). As a result, we believe that good growth occurred with crop water dynamics in BP and BC may be more advantageous than in FB.

Hydraulic properties. The $K$ models, calculated from the MCC data and weighted with measured values, provided adequate fit for data against the measured $K$ data within the $\Psi$ range of 0 to –300 hPa (RMSE = 2.7, 0.3, 3.6, and 3.3 log₁₀ cm·d⁻¹ for UB, FB, BP, and BC, respectively). Additional comparisons were made using $K$ at $\Psi$ = –200 hPa ($K_{-200}$) and the median $K$ value. The $K$ models revealed that the $K_{-200}$ from the greatest to the least was FB, BC, BP, and UB. The resulting increased container capacity and fine particles from FB resulted in increased $K_{-200}$ facilitating water movement within the substrate at lower $\Psi$ (Table 1). We further plotted the models based on our substrate $K(\Psi)$ measurements over the crop production range in this research [$Kp(\Psi$ between –100 and –300 hPa); Fig. 1] because a primary objective of the substrate engineering process was to increase $K$ when compared with UB. Across $K(\Psi)$, the FB models had increased $Kp$ by about an order of magnitude.

We were unable to detect any differences in $Kc$ between UB and BP or FB. However, $Kc$ of BC was more than twice the value of any other substrate (Table 1). In addition, we successfully increased $Kp$ in all three engineered substrates (Fig. 1) compared with UB. We wanted to know if $Kc$ was correlated with $Kp$ and as a result calculated the value of $K_{c-200}$ from the models represented in Table 1. We found little correlation ($r_2$ = 0.04, $P_2$ = 0.8985) between $K_{-200}$ and $Kc$. This leads us to believe that while $Kc$ is easily measured, knowing $Kc$ may not inform practitioners about $Kp$ at least at lower $\Psi$. However, this hypothesis will need to be tested when using other production $\Psi$, as often crops are produced at a less negative $\Psi$, closer to saturation, than in this study.

The MCCs of substrates with fibrous additions (BP, BC) fit using the Brooks and Corey model (1964; Fig. 2C and D) exhibit pronounced bimodal curvature, which is not observed in FB (Fig. 2B). We observe slight bimodal curvature in the UB (Fig. 2A). This is a result of increased tensions that must be applied to vacate the water from the associated pores. Therefore, the MCC shape leads us to theorize that there is a noncontinuous pore size distribution likely because of the variation in particle size between the largest fibrous particles and the smallest plate-like (bark) particles. These shifts occur at $\Psi$ between –25 and –75 hPa in both fiber containing substrates at which point water is considered to be readily available to plants (Pustjari and Robertson, 1975). This indicates that these substrates would retain more water in these ranges as the pore distribution may prevent water from readily vacating pores.

The Brooks and Corey model parameters were further used to provide estimations of the largest pore diameter and pore uniformity. The models provided a strong fit to the data for all substrates (Table 2). The air entry pressure, often considered to be indicative of the largest pore diameter, can be transformed using the Kelvin equation (Hillel, 1998) to calculate the pore diameters of the largest free void space across substrates as follows: $FB = 0.08 \text{ cm} < UB = 0.14 \text{ cm} < BC = 0.29 \text{ cm} < BP = 0.51 \text{ cm}$. The substrate with the greatest $\alpha$ and corresponding smallest entry pore was PB because of the increased fine texture particles compared with UB. We observed that the replacement of FB particles in BP and BC with fibers allowed larger pores to form within the substrate, when compared with UB. We hypothesize this is as a result of the physical form of the fibers themselves as coir tends to have longer fibers when compared with peat (Abad et al., 2005). While measures of air entry pressure is informative for some metrics such as gas diffusivity (Caron et al., 2005), it was weakly correlated with $Kc$ ($r_2 = –0.35, P_2 = 0.6502$) and with $K_{-200}$ ($r_2 = –0.71$, $P_2 = 0.04$).
which directly influences $K_s$. We can also interpret pore size distribution index ($\lambda$), in which a greater value indicates greater pore size uniformity; however, $\lambda$ was weakly correlated with $K_{-200}$ ($r = 0.27, P = 0.7291$) as well as with $K_s$ ($r = 0.32, P = 0.6773$) across substrates. Pore size distribution index was shown previously to be correlated with $\Psi$ for $\Psi$ between −50 and −100 hPa (Fields, 2017).

We can also use the MCC models to predict the VWC of the substrates at various $\Psi$. For instance, $\Psi = 1.5$ MPa have been used by soil scientists and engineers to provide estimations of unavailable water (UW) for agricultural crops. Using the models, we predict the VWC at −1.5 MPa for BP (9.65%) > BC (7.06%) > UB (5.44%) > FB (3.73%). These predictions correspond with previous research that fibrous materials will retain larger volumes of water at low tensions than bark (Fields et al., 2017). Furthermore, the increased $K_p$ of the FB leads us to believe that because water moves more easily at lower tensions, less water will be retained at $\Psi$ near −1.5 MPa, which is confirmed with the correlation between $K_p$ and UW ($r = -0.60, P = 0.4646$).

**Initial baseline harvest.** We were unable to detect any differences among the treatments for GI ($P = 0.0806$), LA ($P = 0.2243$), compactness ($P = 0.6728$), rooting depth ($P = 0.3150$), shoot dry weight ($P = 0.2170$), and root dry weight ($P = 0.1609$) at the initiation of the experiment (i.e., start of low water irrigation after plant establishment). There were detectable differences among treatments in R:S ($P = 0.0351$) and LL ($P = 0.0228$). The Tukey’s HSD detected that BP had a higher R:S than UB (5.34 to 3.06, respectively) and that BC had greater LL than FB (99.2 to 74.2 mm, respectively). Aside from these two anomalies, which were likely a result of the improved rooting of liners in the fibrous materials, no other differences were detected between plants at the initiation of the study. No treatment differences were detected for EC ($P = 0.4947$); however, we did observe a difference in pH ($P = 0.0003$) with the BP having ≈1.2 lower pH than the rest of the treatments (5.5 as opposed to ≈6.7). The difference in pH was expected, as the peat reduces the substrate pH more than bark (Chong et al., 1994) or coir (Abad et al., 2002) because of the inherent lower pH in peat. This should not have impacted crop growth because $H. arborescens$ is known to be pH insensitive (Dirr, 2009) and all four values fall within or just above the suggested optimal pH range of 5.5–6.5 (Halcomb and Reed, 2012).

**Low water crop production.** Throughout the experiment, the difference in GI ($\Delta$GI = culmination GI – initiation GI) indicates plant growth in FB and BC accelerated after...
After 21 DAI, plants began to grow faster in BP than those produced in UB (Fig. 3). Substrate $K_{200}$ decreases from $\log_{10} -3.70 \text{ cm d}^{-1}$ (BC) to $\log_{10} -6.77 \text{ cm d}^{-1}$ (UB), in the same sequence as observed in final GI (data not shown). The $\Delta$GI was correlated with $K_{200}$ ($r = 0.69, P = 0.0119$) which further provides evidence that $K_p$ impacts growth for container crops particularly when grown at substrate $\Psi$ between $-100$ and $-300$ hPa. However, the correlation between $\Delta$GI and $K_p$ was weak ($r = 0.15, P = 0.6326$); therefore, we conclude that $K_p$ is more informative in container production as opposed to $K_s$ which may be informative on water application rate and efficiency because of localized pore saturation during initial irrigation. Crop $\Delta$GI in FB and BC was greater than that of UB ($P = 0.0287$; Table 3). With the substrate water potential below optimal conditions, the UB (which aligns with the SNA BMP’s for static physical properties) was unable to supply the plant with sufficient water to support equal growth as compared with the other treatments with increased $K_s$. This inability to access water in UB is not believed to be a result of direct root contact as there were no differences in final rooting depth ($P = 0.8225$) nor R:S ($P = 0.4048$; data not shown).

There were no differences between treatments in $\Delta$ rooting depth, as nearly all plants had roots which reached the bottom of the container (Table 3). We observed increased $\Delta$L in FB plants when compared with those in UB and increased difference in $\Delta$LA in BC plants compared with UB plants (Table 3). We also observed overall treatment effects in $\Delta$LA ($P = 0.0313$) and $\Delta$LL ($P = 0.0460$) which indicate differences in water stress exhibited by the plants due to the substrate. LA and reduced LL have both shown to have a direct relationship with moisture content and subsequent drought stress (van Iersel and Nemali, 2004) or as a metric of drought stress indicated by leaf expansion (McCree, 1986), respectively. The correlation of $\Delta$LL with $K_{200}$ ($r = 0.68, P = 0.0142$) illustrates that $K_p$ can be potentially used to estimate any potential effects of water stress perceived by plants. There were also treatment differences in $\Delta$R:S ($P = 0.0292$), and BP plants had more negative $\Delta$R:S than UB plants (Table 3); however, this may be an artifact of the initial rooting differences. The plants grown in BC had increased $\Delta$compactness than those in UB ($P = 0.0782$; Table 3). The increased compactness indicates more mass per canopy volume and has been linked to increased substrate moisture (Bayer et al., 2013) and reduced drought stress (van Iersel and Nemali, 2004). Moreover, we observed that plants in BC had larger $\Delta$compactness than plants in BP, which points to the differences in the fiber amendments. We were unable to find any final morphological metrics with strong correlations with $K_s$ ($r < [0.4502]$ in all cases). In fact, all final physiological metrics were more strongly correlated with $K_{200}$ than $K_s$.

Table 3. Differences in plant physiological and morphological measures from initiation to culmination of low substrate water potential production (i.e., value at 32 DAI – 0 DAI). Root vigor rating is a subjective measure only of the final rooting determined by an author at harvest (32 DAI). Substrates include a control (UB), bark particles < 4 mm (FB), bark > 4 mm with 35% by vol. Sphagnum peatmoss (BP), and bark > 4 mm with 35% by vol. coir (coir-BC).

| Substrate    | Leaf length (mm) | Leaf area (cm²) | Root depth (mm) | Root:Shoot | Compactness (g cm⁻¹) | Growth index (cm) | Root vigor rating |
|--------------|------------------|-----------------|----------------|------------|----------------------|------------------|------------------|
| Unprocessed (UB) | 15.0             | 865.1           | 20.00         | -2.701     | 0.1341               | 60.7             | 1.3              |
| Fines (FB)    | 48.6*            | 1983.2          | 26.67         | -3.458     | 0.2397 ab*           | 169.5            | 2.8*             |
| Bark-peat (BP)| 29.5             | 1454.4          | 14.17         | -5.042*    | 0.2016 b             | 101.4            | 2.2              |
| Bark-coir (BC)| 18.7             | 2860.3*         | 9.17          | -3.846     | 0.3744 a*            | 151.0*           | 2.5*             |
| Prefl         | 0.0460           | 0.0313          | 0.4965        | 0.0292     | 0.0782               | 0.0162           | 0.0225           |

*Distance between the leaf tip and base (excluding petiole).
*Total area of leaves measured with a Leaf Area Meter (LI-3300c; LI-COR Biosciences).
*Deepest depth in container explored by the root system.
*Dry mass of root system + dry mass of shoot system.
*Shoot dry mass + shoot height.
*Canopy volume, calculated as [(height + widest width + perpendicular width) ÷ 3].
*Asterisk denotes detected differences between treatment and UB (control).
*Letters denote detected differences among means of three engineered substrates (FB, BP, and BC) using the Tukey’s HSD ($\alpha = 0.05$).
*Measures of overall treatment effects using analysis of variance.

DAI = day after initiation.
because of superior air exchange throughout establishment, acclimation, and experimentation. Plants grown in UB had the lowest final LA ($P = 0.0287$) and LL ($P < 0.0001$), as well as the lowest compactness ($P = 0.0396$) at the end of the study. As a result, the engineered substrates produced morphologically superior crops compared with the UB control (Fig. 4). Furthermore, the plants in BC had the greatest compactness, LA, and the plants in FB had the greatest LL. The plants produced in UB exhibited signs of drought stress in nearly every measured metric. We hypothesize that this is a result of increased $K_p$ in FB, BP, and BC allowing water to be attained when needed but not restricting the air space necessary for healthy growth. Also, the plants in BC established more rapidly after transplant (personal observation) which may have been due to the added airspace.

Plants in all treatments received little water throughout the production cycle (<6.7 L per plant; Table 4). Plants in FB and BC used ≈3 L more water than UB (2.8 L). This is a result of ET being influenced by treatment ($P = 0.0188$; Table 4). Irrigation systems driven by $\Psi$ have been shown to reduce water application (Scheiber and Beeson, 2006). In addition, we were able to detect differences between plants in UB and those in both FB and BC in ET and plant dry mass, as well as treatment effects for $\Delta$ plant dry mass ($P = 0.0017$; Table 4). Even with these effects, when we calculate WUE over the experiment (ET $\div \Delta$ plant dry mass), we are unable to detect any treatment effects ($P = 0.5749$; Table 4). Therefore, we did not effectively alter the WUE of plants by altering substrate hydrophysical properties. Conversely, plants in UB had the lowest shoot dry mass, indicating suboptimal irrigation ($P = 0.0077$; Klock-Moore and Broschat, 2001).

All treatments had leaching fractions (water leached $\div$ water applied) <0.09, which shows that between 91% and 99% of the water applied was used by the plants or evaporated from the container (Table 4). The irrigation system provided water on demand when $\Psi$ reached $\sim$300 hPa. We observed that plants in FB and BC were irrigated more frequently than plants in UB (Table 4). In addition, data were used to calculate time average application rate ($P = 0.0107$; Table 4) which confirmed that the rate of water application was greatest to crops produced in BC (8.6 mL·h$^{-1}$) and least in UB (3.9 mL·h$^{-1}$), indicating that the increased $K_p$ allowed these plants to readily draw water from the substrate at production $\Psi$ between −100 and −300 hPa ($\Psi_p$), thus increasing total irrigations over production. Consequently, there were no differences in irrigation frequency among the treatments (Table 4).

Net photosynthesis, measured 17 DAI, differed between crops grown in the FB and UB ($P = 0.0812$) using the Dunnett’s test (Table 5). There were no other differences among the three engineered treatments in $P_n$, $g_s$, and transpiration. Still correlations between $K_{200}$ and $P_n$, $g_s$, and transpiration existed ($r = 0.67, 0.61$, and $0.66$, respectively, $P = 0.0179, 0.0340$, and $0.0205$, respectively), further indicating the influence of $K_p$ on crop growth when $\Psi$ remained suboptimal. At 32 DAI, instantaneous gas exchange measurements of crops grown in UB and FB differed (Table 5). In addition, $g_s$ and transpiration were more strongly correlated with $K_{200}$ on 17 DAI ($r = 0.71$ and 0.74, respectively; $P = 0.0093$ and 0.0058, respectively), with $P_n$ correlation nearly identical ($r = 0.65, P = 0.0181$), alluding to the increasing importance of $K_p$ as the crop grows and requires more resources. The difference in gas exchange between 17 and 32 DAI is likely an artifact of increased plant vigor, as increased LA indicates increased transpiration (Vertessy et al., 1995). Stem water potential measures on 32 DAI were not influenced by treatment ($P = 0.6043$), nor was there a strong correlation with $K_{200}$ (Table 5). Conversely, stem water potential correlated with $P_n$, $g_s$, and transpiration on 32 DAI ($r$ between 0.64 and 0.67 for all three metrics). These instantaneous measures should be used as relative measures to compare treatments and not make assumptions of total crop performance as they are only indicative of the plants at a single point in time. Plants in the FB treatment had the largest measured $P_n$, $g_s$, and transpiration of all the treatments at 32 DAI. Instantaneous WUE ($P_n \div$ transpiration) values for UB (17 DAI 3.55, 32 DAI 2.69), FB (17 DAI 2.89, 32 DAI 2.67), BP (17 DAI 3.56, 32 DAI 3.05), and BC (17 DAI 3.76, 32 DAI 2.01) indicates that plants in all treatments were using water more efficiently on 17 DAI than 32 DAI, which is

![Fig. 4. A digital image of a representative plant from each of the four experimental substrate treatments collected 32 d after initiation of the low substrate water potential irrigation management. Substrates include a control (unprocessed bark, UB), bark particles < 4 mm (fine bark, FB), bark > 4 mm with 35% by vol. Sphagnum peatmoss (bark-peat, BP), and bark > 4 mm with 35% by vol. coir (bark-coir, BC).](image)

Table 4. Irrigation and water use efficiency (WUE) metrics for 32 d of containerized plant production for four substrates held at substrate water potentials between −100 and −300 hPa. Plants were irrigated with pressure compensating spray stakes based on lysimeter readings. Substrates include a control (UB), bark particles < 4 mm (FB), bark > 4 mm with 35% by vol. Sphagnum peatmoss (BP), and bark > 4 mm with 35% coir (BC).

| Substrate     | Evapotranspiration ($L$) | Leaching fraction ($cm^3\cdot cm^{-3}$) | Increase in plant dry mass ($g$) | Irrigation frequency (irrigations/d) | Time avg application rate ($cm^3\cdot h^{-1}$) | WUE ($g\cdot cm^{-2}$) |
|---------------|-------------------------|----------------------------------------|---------------------------------|--------------------------------------|-----------------------------------------------|------------------------|
| Unprocessed   | 2.8                     | 0.05                                   | 15.3                            | 0.69                                 | 3.87                                          | 183.0                  |
| Fines (FB)    | 5.3**                   | 0.01                                   | 23.7 b*                         | 0.61                                 | 6.92*                                         | 223.6                  |
| Bark-peat (BP)| 4.5                     | 0.09                                   | 21.8 b                          | 0.71                                 | 6.37                                          | 206.4                  |
| Bark-coir (BC)| 6.3*                    | 0.06                                   | 32.5 a*                         | 0.71                                 | 8.59*                                         | 193.8                  |
| Pval¹         | x0.0188                 | 0.0992                                 | 0.0017                          | 0.2442                               | 0.0107                                        | 0.5749                 |

¹Water loss by substrate-plant system (excluding leaching) measured by lysimeter.
²Water leached $\div$ water applied.
³The difference in plant dry mass between initiation and culmination of the low substrate water potential production portion of this experimentation.
⁴Volume of water applied $\div$ time of production.
⁵Measured as evapotranspiration $\div$ carbon acquisition over low water potential production.
⁶Letters denote detected differences between treatment and UB control.
⁷Letters denote detected differences among means of three engineered substrates (FB, BP, and BC) using the Tukey’s HSD ($\alpha = 0.05$).
⁸Measures of overall treatment effects using analysis of variance.
Table 5. Instantaneous measures of plant water relations for four experimental bark substrates. Substrates include a control (UB), bark particles < 4 mm (FB), bark > 4 mm with 35% by vol. *Sphagnum* peatmoss (BP), and bark > 4 mm with 35% coir (BC). Data were measured on 17 and 32 d after initiation (DAI) of an experiment where substrate water potential was held between –100 and –300 hPa. Data were measured with a portable photosynthesis meter (LI-COR 6400xt).

| Substrate     | 17 DAI                  | 32 DAI                  |
|---------------|-------------------------|-------------------------|
|               | Net photosynthesis      | Stomatal conductance    | Transpiration | Net photosynthesis | Stomatal conductance | Transpiration | Stem water potential* |
|               | (mmol m⁻² s⁻¹ CO₂)      | (mol m⁻² s⁻¹ H₂O)      | (mmol m⁻² s⁻¹ H₂O) | (mmol m⁻² s⁻¹ CO₂) | (mol m⁻² s⁻¹ H₂O) | (mmol m⁻² s⁻¹ H₂O) | (MPa)          |
| Unprocessed (UB) | 3.62 0.0335 1.02      | 2.54 0.0472 1.12      | 1.03 1.41      |
| Fines (FB)     | 9.99* 0.1421 3.35      | 7.08* 0.1206 2.65*     | 1.03          |
| Bark-peat (BP) | 5.13 0.0493 1.44      | 4.21 0.0589 1.38      | 1.10          |
| Bark-coir (BC) | 8.13 0.0769 2.16      | 3.99 0.0859 1.99      | 1.15          |
| Pval†         | 0.1196 0.2625 0.1840   | 0.1403 0.0719 0.0964   | 0.6043        |
| r – K₂00w      | 0.6667 0.6131 0.6563   | 0.6656 0.7415 0.7123   | –0.3374       |

*Measured on apical stem consisting of three nodes immediately after severing, using a Model 600 pressure chamber (PMS Instruments).
†Asterisk denotes difference detected between representative treatment and the control (UB) according to the Dunnett’s test (α = 0.05).
‡Measured on apical stem consisting of three nodes immediately after severing, using a Model 600 pressure chamber (PMS Instruments).
§Values in parentheses represent a 95% confidence interval from the mean value.
∥Volumetric water content calculated at time of cessation of water withdrawal.
*Substrate water potential using substrate moisture characteristic data modeled to Brooks and Corey model for conversions.
yVolumetric water content calculated at time of cessation of water withdrawal.
zPearson’s correlation constant between substrate hydraulic conductivity at water potential = –200 hPa and the metric being analyzed.

Table 6. Plant water uptake cutoff points for four experimental bark substrates. Substrates include a control (UB), bark particles < 4 mm (FB), bark > 4 mm with 35% by vol. *Sphagnum* peatmoss (BP), and bark > 4 mm with 35% coir (BC). Planted substrate watered to maximum water holding capacity and allowed to dry down until plant stopped withdrawing water from substrate.

| Substrate       | 17 DAI                  | 32 DAI                  |
|-----------------|-------------------------|-------------------------|
|                 | Water content (m³ m⁻³)  | Water potential (MPa)  | Stem water potential* |
|                 | 0.126 (0.120, 0.133)†   | 0.101 (0.095, 0.107)   | –200 hPa          |
|                 | 0.09 (0.07, 0.10)       | 0.11 (0.09, 0.13)      | –100 hPa          |
|                 | 0.16 28.04              | 0.22 25.67            | 21.68            |
|                 | 0.102 (0.095, 0.109)   | 0.37 (0.29, 0.47)     | 21.68            |
|                 | 0.32 (0.25, 0.39)       | 0.37 (0.29, 0.47)     | 21.68            |

*Values in parentheses represent a 95% confidence interval from the mean value.
†Volumetric water content calculated at time of cessation of water withdrawal.
‡Substrate water potential using substrate moisture characteristic data modeled to Brooks and Corey model for conversions.
§Root mean square error (RMSE) of the data points to the nonlinear to linear regression model, based on container system mass.

Fig. 5. The reduction in volumetric water content of four experimental pine bark-based substrates used to produce *Hydrangea arborescens* plants. Substrates included conventional pine bark (unprocessed bark, UB), bark particles that pass through a 4.0-mm screen (fine bark, FB), bark particles that do not pass through a 4.0-mm screen while at 65% moisture content amended with fibrous materials including 35% *Sphagnum* peat (bark-peat, BP) and 35% coir (bark-coir, BC) by volume. Substrates with fully rooted plants were watered to effective container capacity (maximum water holding capacity via spray stake irrigation) before allowing to dry past permanent wilt until the plant ceased withdrawing water from the substrate. Daily reduction in substrate volumetric water contents were plotted against volumetric water content for each substrate to illustrate at what volumetric water content evaportranspiration shifts to primarily evaporation due to plant water uptake diminishing.

hypothesized to be a result of increased growth and vigor (LA and GI), but could be an artifact of varying environmental conditions. Also, FB and BC grew faster and with increased vigor when compared with other plants, but the plants in BP were consuming the least water per carbon fixed at 32 DAI.

Instantaneous WUE was greatest in plants grown in PB at 32 DAI; however, this may have been a result of less developed plants grown in UB skewing measures (Fig. 4).

While all three engineered substrates (excluding UB) were capable of producing marketable crops at this *Ψ* (Fig. 4), the BC and FB produced marketable plants quicker than the BP, reducing time to market. Because the difference in water per plant was not extreme and the leaching fractions (water wasted) was minimal across all treatments, it would likely be worth the added water inputs to push plants to marketable levels sooner, which in itself would reduce water consumption. The UB, which was within the BMP recommendations for physical properties, was unable to maintain proper hydration throughout the experimental portion of the study. We hypothesize that this is likely a result of reduced *Kp*, which we believe will become more critical as *Ψ* is reduced in even drier production scenarios.

Plant available water. The plant used water in FB for 12.16 d, after being irrigated to effective CC and water withheld, at which point water loss was primarily due to evaporation (Table 6). This was the least time for a plant to reach this point; however, this is likely a result of increased plant size. The plants in BP, BC, and UB followed in sequence as a plant to reach this point; however, this is likely a result of increased plant size. The plant used water in FB for 12.16 d, after being irrigated to effective CC and water withheld, at which point water loss was primarily due to evaporation (Table 6). This was the least time for a plant to reach this point; however, this is likely a result of increased plant size. The plants in BP, BC, and UB followed in sequence as a plant to reach this point; however, this is likely a result of increased plant size. The plant used water in FB for 12.16 d, after being irrigated to effective CC and water withheld, at which point water loss was primarily due to evaporation (Table 6). This was the least time for a plant to reach this point; however, this is likely a result of increased plant size.
to reach the VWC that transpiration reduces and water loss was primarily driven by evaporation. However, since there was no difference in final GI between plants grown in FB and BC, we hypothesize that the increased $K$ allows for the plants to absorb water from the substrate at a higher rate, consuming available water more readily.

The reductions in VWC over each 24 h period (from 0000 to 0000 hr) were plotted against the total VWC for the substrate (Fig. 5). These data show a clear switch to an asymptotic relationship at the same calculated VWC water uptake cutoff point. We observed that the UB and BP were at similar VWC when water loss transitioned from ET to evaporation ($\approx$13.0 cm$^3$ cm$^{-3}$). Plants in FB and BC also ceased water uptake at similar VWC (10.1 cm$^3$ cm$^{-3}$; Table 6). The increased $K$ in the FB and BC may have allowed for more water to be removed; however, the slight difference between the four substrates may correspond with the lack of difference of final R.S., which has been known to indicate water availability (Harris, 1914). Further conversions of the VWC water uptake cutoff points, using MCC models, we see that the plants in the UB and FB ceased withdrawing water at $\Psi$ of $\sim$10 MPa, and the plants in BP and BC were at $\sim$0.35 MPa when plants stopped removing water from the substrate. These values were much higher than we had hypothesized based on previous research (Fields, 2013), as none of the crops approached $\Psi$ of $\sim$1.5 MPa. This is known to be a species-specific trait. Hydrangea sp. are known to flag, or readily wilt without continuous water during high temperatures (O’Meara et al., 2014). There was no correlation between $\Psi$ at which plants stopped absorbing water and $K_{200}$ or $K_s$. Conversely, the VWC point when water loss transitioned from ET to evaporation was correlated with $K_{200}$ ($r$ = $0.78$, $P$ = 0.2232). Both these values are based on models and therefore based on low total data points ($n$ = 4).

**Conclusions**

Measurement of substrate $K_p$ was correlated with measured parameters of crop morphology and physiology, suggesting it is a meaningful metric for evaluating and comparing substrates. Substrate $K_s$, while more commonly measured, is not correlated with $K_p$, nor strongly correlated with any physiologic or morphologic metric, and therefore, does not yield information that will help predict crop success as measured by growth and appearance. Furthermore, increased substrate $K_p$ will allow plants to access water not only to sustain vigor but also to produce marketable crops using less water. The increased $K_p$ likely allows for quicker time to market for ornamental containerized crops. Crops can be produced with minimal water loss from leaching when specialized, engineered substrates with increased $K$ are used and irrigation is managed to hold crops at $\Psi$ between $\sim$100 and $\sim$300. In addition, the low volumes of water the plant receives will provide growers with water savings during production. We also observed that lower production $\Psi$ did not enable plants to continue withdrawing water at low $\Psi$ unlike previous research and hypothesize that this is more of a species artifact. From previous research we understand that substrate $K$ is different over $\Psi$ ranges and therefore all substrates are not suitable for every $\Psi$ range. The crop fiber increases $K$ more than the peat fiber when at $\Psi < -100$ hPa and provides more AS which will benefit crop exchange if crops become over hydrated. The high percent- age of fine particles in FB, which was designed for this irrigation scenario, produced high quality plants in this research. However, if used in traditionally irrigated systems or in production that includes pre- cipitation, over hydration would likely occur, limiting gas exchange and deleteriously influencing crop vigor. Further research into the use of substrate $K$, VWC, and $\Psi$ relations- ships will lead to development of substrates that hold more sufficient when dry but continue to allow ample drainage readily when in higher moisture systems.

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