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ORIGINAL PAPER

Photosynthesis, growth, and water use of *Hydrangea paniculata* 'Silver Dollar' using a physiological-based or a substrate physical properties-based irrigation schedule and a biochar substrate amendment

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Abstract

Developing management practices that make more efficient use of irrigation is important for improving the sustainability of nursery crop production. Integrating refined irrigation scheduling with a substrate amendment like biochar can improve irrigation efficiency. The objective of this research was to evaluate the impact of biochar and need-based irrigation scheduling on gas exchange, plant water relations, and biomass gain of container-grown *Hydrangea paniculata* 'Silver Dollar' with the goal of reducing water use and maintaining or shortening production cycles. Containers were filled with pine bark and amended with either 10% or 25% by volume of hardwood biochar. Plants were automatically irrigated by one of the three irrigation schedules. The irrigation schedules were conventional irrigation, delivering 1.8 cm of water in one event each day, and two on-demand, need-based irrigation schedules. The first was based on the moisture characteristic curve for each of the three substrates developed via the evaporative method. The second was a plant physiology-based irrigation scheduling regime built on the relationship between photosynthesis and substrate moisture content. Scheduling irrigation using a plant physiology or substrate physical properties basis, in combination with biochar, reduced the water requirement for 'Silver Dollar' hydrangea without any negative effect on plant dry weight by maintaining sufficient plant water status and gas exchange even just prior to irrigation. Automated irrigation systems coupled with a plant physiology or substrate-based actuation and a water retentive substrate amendment have the potential to reduce nursery crops water use.

Introduction

Inefficient use of irrigation can exacerbate water shortages not only in times of drought but also during non-drought periods (Caron et al. 2005). Appropriate irrigation scheduling applies the correct amount of water when needed to support plant growth and avoids over- or under-watering (Nemali and Van Iersel 2006). Integrating precise irrigation application systems with irrigation scheduling can increase water use efficiency in nursery production (Basiri Jahromi et al. 2018b; Regan 1999).

Scheduling irrigation based on estimated crop water use results in higher irrigation efficiency compared to relying on periodically adjusting irrigation volume and timing based on perceived water needs (van Iersel et al. 2013). Estimating crop water requirements by measurements derived from the physiological status of the plant (e.g., Cifre et al. 2005; Jones 2004) can be used as an irrigation-scheduling basis. Irrigation based on the relationship between photosynthesis rate and substrate moisture content has been successfully used to improve crop water use efficiency (Fulcher et al. 2012; Hagen et al. 2014; Nambuthiri et al. 2017). However, visual indicators of physiological response to water deficit such as wilting cannot generally be used to schedule irrigation because plant growth is negatively affected at the water deficit associated with wilting (Jones 2004; Slatyer 1967).

One of the limitations of plant physiology-based irrigation system development is the expertise needed to operate an infrared gas analyzer (LI-COR 6400) and the cost of this instrument. The high number of plant species produced and

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substrates used in nursery production are another potential challenge to this system being widely adopted. However, there is a growing body of literature that suggests that fairly limited model development experiments such as the ones reported here and other studies (Fulcher et al. 2012; Hagen et al. 2014) are sufficient to determine irrigation set points. Further, because plant available water is both substrate and species-dependent (O'Meara et al. 2014) the model development is a practical approach to determine plant available water and has been successfully used across substrates, crops, and growth stages (Nambuthiri et al. 2017).

Another irrigation scheduling technique, particularly suited for low water availability such as during water restrictions, is one in which irrigation actuation is based on substrate moisture availability derived from a moisture characteristic curve (Fields et al. 2016). Using substrate moisture sensors to implement water potential-based irrigation scheduling that maintains plant-available water in the range of − 1 to − 10 kPa can conserve water while also avoiding plant water stress (Arguedas-Rodriguez 2009). Recent research suggests further water savings are possible by exploiting the area beyond − 10 kPa tension (Fields et al. 2016). Scheduling irrigation based on substrate water status or a calculated crop evapotranspiration model reduced water use without affecting plant growth and quality in comparison with timer-based irrigation (Incrocci et al. 2014).

Using amendments such as biochar can modify the average substrate particle size, reducing the proportion of larger-sized components. Such substrate particle size manipulation can increase the amount of available water, which can improve plant growth and irrigation efficiency (Caron et al. 2005). Biochar is produced from thermochemical decomposition of organic materials at high temperatures in an oxygen-limited atmosphere (Lehmann and Joseph 2009). Biochar can improve nutrient use efficiency by increasing cation exchange capacity (CEC), surface area and water retention of the soil/substrate (Altland and Locke 2013; Glaser et al. 2002; Lehmann et al. 2006). Biochar can also increase nutrient concentration by increasing CEC and nutrient content and consequently improving nutrient availability (Headlee et al. 2014). These factors, either individually or in combination, can result in higher crop yield in soil systems (Major et al. 2010; Vaccari et al. 2011; Zhang et al. 2011).

Applications of 10% and 25% biochar amendment to pine bark substrate increased water-holding capacity and reduced water consumption of a high water use crop, *Hydrangea paniculata* (Pinky Winky® hardy hydrangea) (Basiri Jahromi et al. 2018a). However, the reduction of plant biomass in the 25% biochar treatment suggested that sufficient water might not be available to plants in this substrate. The lower irrigation frequency associated with 25% biochar amendment might have resulted in an insufficient plant available water in each cycle and eventually exceeding the water buffering capacity (Basiri Jahromi et al. 2018a). Further research was required to more fully understand the effect of biochar on plant water availability. This study was initiated to address this problem using physiological parameters to monitor plant water status under different irrigation schedules that were designed to maximize plant available water. The objective of this research was to evaluate the effect of biochar and two on-demand, need-based irrigation schedules on gas exchange, plant water relations, and biomass gain of container-grown *H. paniculata* 'Silver Dollar' with the goal of reducing water use by exploiting the water buffering capacity while maintaining or shortening production cycles.

Materials and methods

Plant species and substrate formulations

Six-inch tall rooted stem cuttings were obtained from a commercial nursery (Griffith Propagation Nursery Inc. Watkinsville, GA). 'Silver Dollar' hydrangea cuttings were transplanted into 7.6 L containers, filled with 1-year-old pine bark and amended with 0%, 10% or 25% biochar by volume. The biochar amendment rate was chosen based on the results of our previous studies (Basiri Jahromi et al. 2018a, b). The biochar (Proton Power Inc. Lenoir City, TN) was a mixed hardwood comprised of oak (*Quercus* spp.), hickory (*Carya* spp.) and yellow poplar (*Liriodendron tulipifera*) subjected to fast pyrolysis (a few seconds) at ≈ 1000 °C (Basiri Jahromi et al. 2019; Sohi et al. 2009) with chemical and physical properties shown in Table 1.

One week after transplanting, all of the plants were top-dressed with 40 g per container of 18N–2.6P–9.9K controlled-release fertilizer (Osmocote Classic, Everris,

Table 1 Chemical and physical properties of a hardwood biochar used as a substrate amendment for container nursery production

Parameter	Units	Value
Chemical properties		
pH[a]		10.5
EC	dS m^{-1}	4.6
Carbon	%	88.6
Nitrate	mg kg^{-1}	0.8
Ammonia	mg kg^{-1}	14.5
Phosphorus	%	0.1
Potassium	%	0.5
Physical properties		
Bulk density	g cm^{-1}	0.1
Surface area	m^2 g^{-1}	366

[a] The results that are shown in this table were obtained from Control Laboratories, Watsonville, CA

Marysville, OH), which included 10% NH_4–N, 8% NO_3–N, 6% P_2O_5 and 12% K_2O. Substrates were also drenched twice with a surfactant (Aquagro L, Aquatrols, Paulsboro, NJ) at a rate of 600 ppm to prevent the substrate from becoming hydrophobic.

Substrate physical properties were determined for each substrate using a 15-cm tall porometer (694 cm^3 volume), according to Fonteno and Harden (2010) with three replications (Table 2). In addition, particle size distribution was determined with three replications of each substrate by passing the substrate through seven sieves (6.30, 2.00, 0.71, 0.50, 0.25, 0.11 mm openings) and a lower catch pan, which was shaken for 5 min with a Ro-Tap shaker (Rx-29; W.S. Tyler, Mentor, OH).

The treatment design was a 3 × 3 factorial with three substrates (100% pine bark with biochar at 0%, 10%, or 25% by volume) and three irrigation schedules (conventional irrigation, substrate physical properties-based and plant physiology-based). The experiment was arranged in a randomized complete block design with 8 replications.

Model development

Three substrate-specific moisture release curves were developed with the evaporative method to establish the substrate physical properties-based irrigation schedule setpoints. Moisture characteristic curves were developed using the Hyprop System (UMS, Munich, Germany). Samples and devices were prepared according to Fields et al. (2016). Each sample and device was placed on a scale and connected to a computer with Tensionview software (UMS, Munich, Germany). Water potential from the two tensiometers and total weight were recorded every 10 min. Data were fitted using HypropFit software (UMS, Munich, Germany) to generate moisture characteristic curves describing the relationship between water potential and VWC.

Setpoints for the plant physiology-based irrigation schedule were established by determining the relationship between photosynthetic rate and substrate moisture content of the plants grown in the greenhouse. Six-inch tall rooted stem cuttings were transplanted into 7.6 L containers filled with each substrate (0%, 10%, or 25% biochar by volume) and hand-watered until the roots reached the container sidewall. The experiment was started when the roots reached the pots sidewall (4 weeks after transplanting) when plants were still in the vegetative stage. Just prior to initiating the experiment, plants were hand watered and soaked in water to evenly saturate the substrate, and drained to container capacity. Further irrigation was withheld. Photosynthesis was measured as the substrate dried for 14 days following the method of Fulcher et al. (2012) using an infrared gas analyzer (LI-6400, LI-COR, Lincoln, NE, USA). Photosynthesis measurements were taken at 390 mg L^{-1} carbon dioxide (CO_2) and light intensity at 1500 µmol m^{-2} s^{-1} on the most fully expanded, recently matured top leaf of each of the five replicate plants. Substrate VWC was estimated using capacitance sensors (ECHO-5, Decagon Devices Inc., Pullman, WA) connected to a data logger (CR1000, Campbell Scientific Inc., Logan, UT) and substrate weight was recorded concurrent to photosynthetic measurements. Each probe was calibrated for each of the three substrates. The relationship between photosynthetic rate and VWC of ‘Silver Dollar’ hydrangea plants was characterized by a 3 parameter sigmoidal curve (SigmaPlot v 14, San Jose, CA). The experiment was in a complete randomized block design with five replications.

Model evaluation

Following model development, model evaluation experiments were initiated. Eight-week experiments were initiated on 20 July 2016 and 20 March 2017 at the University of Tennessee North Greenhouse Complex, Knoxville, Tennessee. Supplemental lighting was used in the greenhouse when outside light conditions were below 400 µmol m^{-2} s^{-1}, and the photoperiod was set to 16 h (light from 7 a.m. to 11 p.m.). The daytime and nighttime thermostat setpoints were 26 and 18 °C, respectively.

Plants were hand-watered until the roots reached the container sidewall and just prior to initiating the experiment,

Table 2 Physical properties of pine bark substrate amended with 0%, 10%, or 25% by volume of hardwood biochar ($n = 3$)

Biochar amendment	Container capacity	Air space	Total porosity	Bulk density	Particle size distribution (%)			
	%			g cm^{-3}	X-Large (> 6.3 mm)	Large (2–6.3 mm)	Medium (0.71–2 mm)	Fines (< 0.71 mm)
0%	57.1c^z	30.0a	87.1a	0.24a	9.3a	42.7a	29.4c	18.5b
10%	62.3b	26.0b	88.2a	0.23ab	7.5a	34.8b	34.4a	23.3b
25%	65.7a	20.4c	86.2b	0.22b	7.2a	24.7c	31.7b	36.3a
P value	0.0005	0.0004	0.0167	0.0324	0.7495	0.0022	0.0051	0.0151

Substrate physical properties were determined using a 15-cm tall porometer, according to the methods described by Fonteno and Harden (2010)

^{z}Means within a column followed by the same letter are not significantly different ($\alpha = 0.05$)

plants were hand watered and soaked in water to evenly saturate the substrate and drained to container capacity. Then the substrate moisture level was monitored and plants were irrigated by one of the three automatic irrigation schedules. Substrate VWC was estimated using capacitance sensors (ECHO-5, Decagon Devices Inc.) connected to a data logger (CR1000, Campbell Scientific Inc.) with multiplexer (AM16/32, Campbell Scientific Inc.).

Each probe was calibrated for each of the three substrates with the following method to determine VWC. A prescribed amount of air-dried substrate was mixed with water to create the three estimated VWC levels. The mass of dried substrate was calculated using the bulk density from the porometer measurements and pot volume (bulk density × pot volume = mass of substrate). Mass of water was calculated using the VWC and pot volume (VWC × pot volume = volume of water). After moisture equilibrium was reached, containers were filled and covered to prevent evaporation. Sensors were tested individually in the same position they were placed in pots for experiments. The millivolt measured by each sensor in each predetermined VWC was recorded. To correct for the small amount of moisture remaining in air-dried substrate, wet weight was recorded. Substrates were dried at 40 °C and the oven-dry weight was used to calculate actual VWC using linear regression.

Probes were installed halfway between the sidewall and the center of the container, perpendicular to the substrate surface so that the bottom of each probe was 9 cm below the substrate surface. Measurements from five sensors were used per irrigation and biochar rate combination to actuate irrigation for the eight plants in that treatment. A 16-channel relay controller (SDM-CD16AC, Campbell Scientific Inc.) was used to operate solenoid valves. When the average VWC estimated by the five sensors dropped below the irrigation set point, the data logger was programmed to supply power to the valve controlling irrigation to those containers. Nine independent irrigation zones were constructed with one irrigation line per biochar rate and irrigation schedule combination. Each irrigation line irrigated eight plants with a 10 cm dribble ring (Dramm Corp, Manitowoc, WI) connected to a 3.8 L per hour emitter. Irrigation run time for each treatment was individually calculated based on the lower setpoints, upper irrigation set points and the flow rate of each line.

The treatments were arranged in a 3 × 3 factorial with three substrates (100% pine bark with biochar at 0%, 10%, or 25% by volume) and three irrigation schedules (conventional irrigation, substrate physical properties-based and plant physiology-based). The experiment was a randomized complete block design with eight replications. Data were analyzed using mixed model analysis of variance with REML variance component estimation (SAS v9.4, Cary, NC), where replication was random, and substrate, irrigation schedules and their interaction were fixed effects. Least squares means were separated using Fisher's protected LSD at the 5% significance level. Data were pooled across years, as there was no significant effect of experimental year on the measurements.

Data collection

Photosynthesis, stomatal conductance, transpiration, and vapor pressure deficit (VPD) were measured with an infrared gas analyzer (LI-6400, LI-COR) at 390 mg L^{-1} CO_2 and light intensity at 1500 µmol m^{-2} s^{-1} on the most fully expanded, recently matured top leaf of each of the five replicate plants within each irrigation zone that contained capacitance sensors. These measurements were taken between 1 and 2 h before and after-irrigation and when it was between 10 a.m. and 3 p.m. to ensure light conditions supported maximum photosynthetic rates. Petiole water potential (hereafter referred to as leaf water potential) of the second most recently matured fully expanded leaf was measured immediately following photosynthetic measurements on five randomly selected plants per irrigation zone using a pressurized chamber (Soil Moisture Equipment Corp., Santa Barbara, CA).

Leachate samples were collected at the beginning (20 July 2016 and 20 March 2017) and the end (15 September 2016 and 15 May 2017) of each experiment using the pour through extraction method (Wright 1986). Samples were stored in plastic vials, and were kept refrigerated for 48–72 h, then analyzed. At the time of analysis, samples were filtered with a 0.45-µm syringe filter. The filtrate was then poured into 5-mL vials, capped, and analyzed on an ICS 1100 (Ion Chromatography System; Dionex, Bannockburn, IL) for concentrations of nitrate (NO_3), ammonium (NH_4), phosphate (PO_4), and potassium (K). Electrical conductivity (EC) was measured with a portable EC meter (HI 9811-5, Hanna Instruments, Smithfield, RI, USA) and pH was measured with a pH meter (Denver Instrument, Bohemia, NY).

The total amount of water applied was calculated using the frequency of irrigation × volume of water at each irrigation event. Time average application rate was calculated by the total volume of applied water/time of production (mL H_2O per h) as described by Fields et al. (2017). Growth index was determined at initiation and termination of the experiment using the formula [(plant width 1 + plant width perpendicular to width 1 + plant height)/3] (Hagen et al. 2014). For dry weight measurements, the above-ground portions of plants were harvested and hand-washed of the substrate. Plant shoots and leaves were dried at 55 °C until weight no longer decreased to obtain dry weight at initiation (from 8 extra plants of each substrate) and termination of the experiment. Water use efficiency (WUE) per plant was measured as increase in dry weight (g) per total irrigation volume applied (L) over the 8 weeks. After drying, plant leaves and shoots were ground to pass a 1.0-mm screen using a Wiley Mill (Thomas Scientific, Swedesboro, NJ). Samples from each treatment were thoroughly mixed and tissue samples were withdrawn for analysis. Plant tissue nitrogen (N) was determined using combustion CHNS/O analyzer (CE Elantech, Lakewood, NJ). Tissue for analysis was prepared by acid digestion using concentrated nitric acid (Jones and Case 1990) and analyzed by ICP-OES for phosphorus (P), K, calcium (Ca), and magnesium (Mg) concentrations.

Results

Substrate physical properties

Container capacity increased and air space decreased as the amount of biochar increased. Pine bark alone had the highest air space with a lowest percentage of fine particles. Application of 25% biochar caused a reduction in total porosity and bulk density compared to 0% biochar rate (Table 2). However, total porosity is on the upper end of the recommended range (Yeager et al. 2007) in all treatments. Increasing biochar rate to 25% also caused a decrease in large particles and a 96% increase in fine particles (Table 2).

Model development

Setpoints were established to actuate and terminate irrigation based on the moisture characteristic curves. Upper and lower setpoints for the substrate physical properties-based irrigation schedule were predicated on the generally accepted range of plant available water occurring between – 1 and – 10 kPa tension (de Boodt and Verdonck 1972). Irrigation was actuated once the substrate dried to the lower setpoint of 0.37, 0.34, and 0.34 $cm^3\ cm^{-3}$ for 0%, 10% and 25% biochar amendment rate, respectively. Upper set points, which terminated irrigation, corresponded to – 1 kPa tension and were 0.46, 0.44, 0.49 $cm^3\ cm^{-3}$ for 0%, 10% and 25% biochar rate, respectively (Fig. 1). Irrigation was applied once the lower set point was reached and consistently returned the substrate to the upper set points (Fig. 3).

The plant physiology-based set points were developed using the sigmoidal relationship between substrate moisture content and crop photosynthetic rate. Irrigation was actuated at the VWC that was calculated to maintain photosynthesis at 90% of the predicted maximum photosynthetic rate as described by Fulcher et al. (2012). The lower setpoints were 0.25, 0.33 and 0.36 $cm^3\ cm^{-3}$ for 0%, 10% and 25% biochar rate, respectively (Fig. 2). The upper set point for each of the three substrates was the VWC at effective container capacity as determined following saturation and drainage as described in Hagen et al. (2015). Thus, upper set points terminated irrigation when the average probe measurement reached 0.46, 0.47 and 0.58 $cm^3\ cm^{-3}$ for 0%, 10% and 25% biochar rate, respectively (Fig. 3). The traditional industry approach to irrigation served as the control, delivering 1.8 cm of water in one daily event.

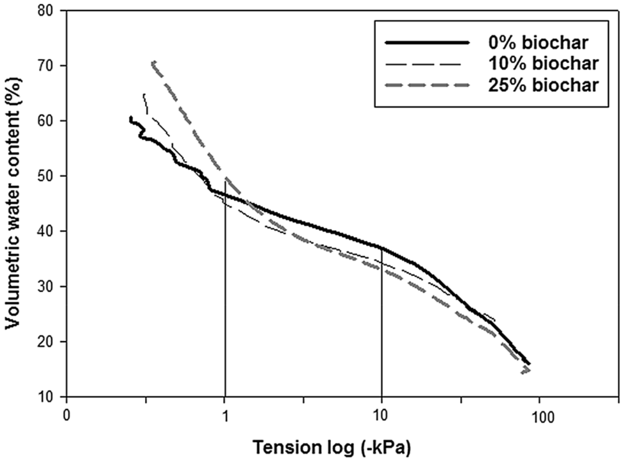

Fig. 1 Moisture characteristic curves for pine bark with 0% biochar, pine bark with 10% by volume of biochar and pine bark with 25% by volume of biochar measured with the evaporative method using the Hyprop. The lower set points were the VWC at – 10 kPa (0.37, 0.34 and 0.34 $cm^3\ cm^{-3}$ for 0%, 10% and 25% biochar amendment rate, respectively). The upper set points were the VWC at – 1 kPa (0.46, 0.44, 0.49 $cm^3\ cm^{-3}$ for 0, 10% and 25% biochar rate, respectively)

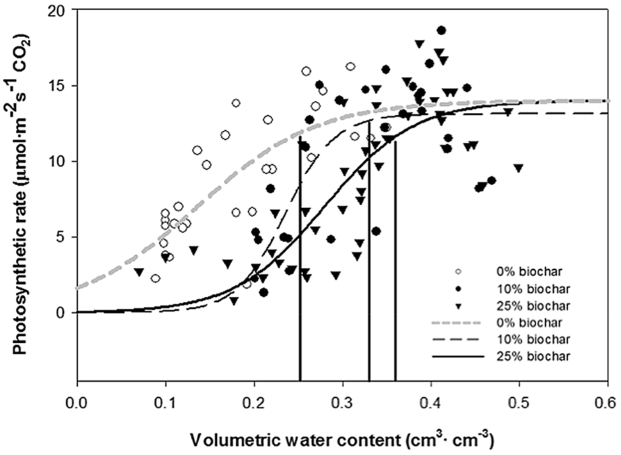

Fig. 2 The relationship between photosynthetic rate and volumetric water content (VWC) of '*H. paniculata* 'Silver Dollar' plants with 0% biochar, 10% by volume of biochar and 25% by volume of biochar was characterized by a 3 parameter sigmoidal curve. Photosynthetic rate = 13.9783/(1 + exp (– (VWC – 0.1357)/0.0672)), $r^2 = 0.59$ for 0% biochar. Photosynthetic rate = 13.1015/(1 + exp (– (VWC – 0.2354)/0.0278)), $r^2 = 0.55$ for 10% biochar. Photosynthetic rate = 14.0009/(1 + exp (– (VWC – 0.2796)/0.0507)), $r^2 = 0.64$ for 25% biochar. Irrigation set points corresponded to 90% of maximum predicted photosynthetic rate and were 0.25, 0.33 and 0.36 $cm^3\ cm^{-3}$ for 0%, 10% and 25% biochar amendment rate, respectively. Setpoints indicated by vertical bar ($n = 5$)

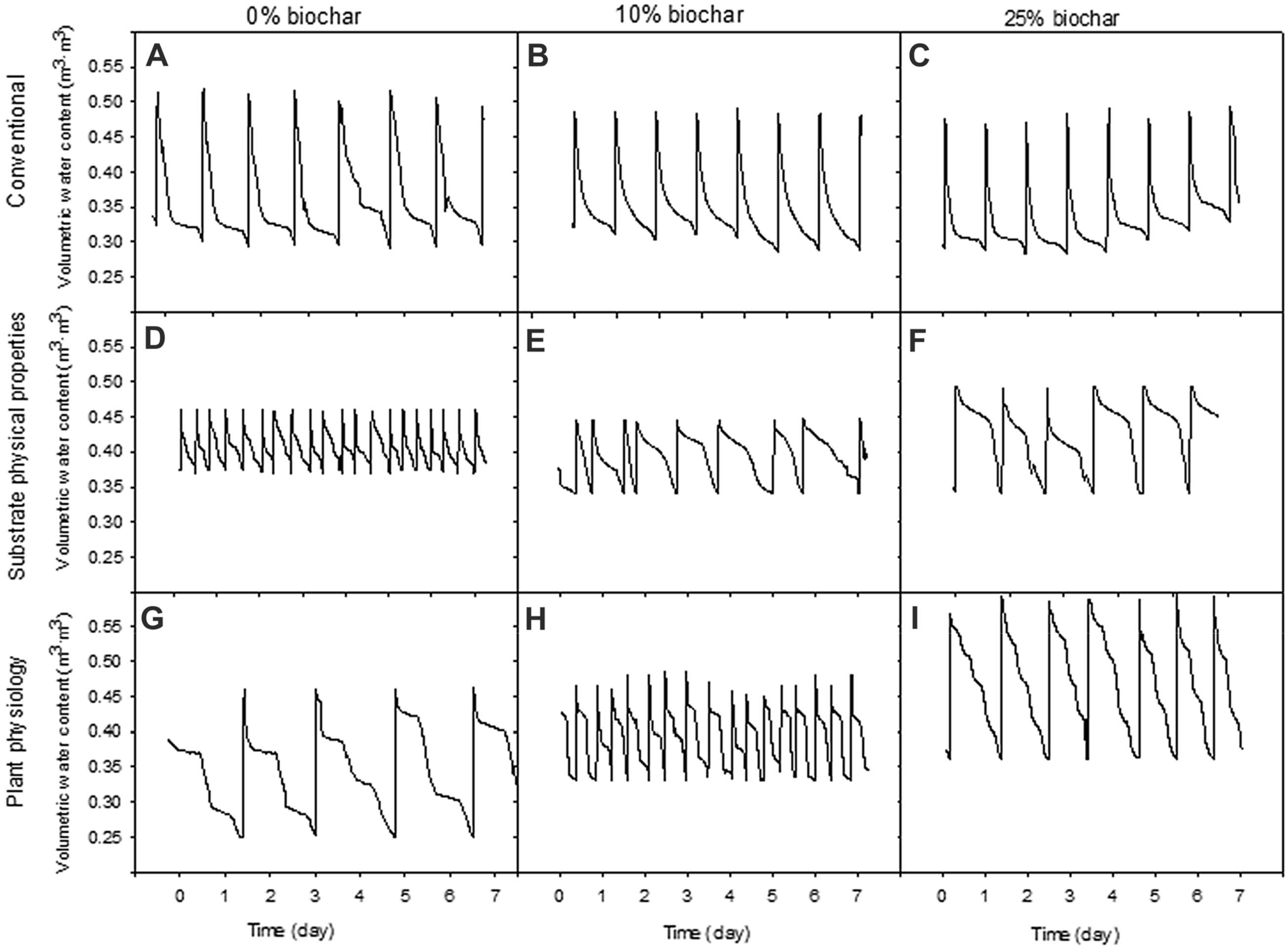

Fig. 3 Irrigation cycles of the six on-demand irrigation schedules and three conventional irrigation schedules in the third week. On-demand irrigation was triggered when the average probe reading reached the lower setpoint and remained on the time duration necessary to return the container to the upper set point. $A = 0\%$ biochar rate under conventional irrigation, $B = 10\%$ biochar rate under conventional irrigation, $C = 25\%$ biochar rate under conventional irrigation, $D = 0\%$ biochar rate under physical properties-based irrigation, $E = 10\%$ biochar rate under physical properties-based irrigation, $F = 25\%$ biochar rate under physical properties-based irrigation, $G = 0\%$ biochar rate under plant physiology-based irrigation, $H = 10\%$ biochar rate under plant physiology-based irrigation and $I = 25\%$ biochar rate under plant physiology-based irrigation

Model evaluation

Gas exchange and plant water potential

Results were similar in both model evaluation experiments in terms of how biochar rate affected plant physiological parameters under different irrigation systems so data were pooled across years. There was an interaction between biochar rate and irrigation system for photosynthetic rate ($P = 0.0486$), transpiration rate ($P = 0.0163$) and stomatal conductance ($P = 0.0006$). This was caused by increasing photosynthetic rate from 13.6 to 15.1 µmol CO_2 m^{-2} s^{-1}, transpiration rate from 3.7 to 4.5 mmol H_2O m^{-2} s^{-1} and stomatal conductance from 0.25 to 0.37 mmol H_2O m^{-2} s^{-1} under plant physiology-based irrigation regime as biochar rate went from 0 to 10%. However, photosynthetic rate, transpiration rate and stomatal conductance were similar in 0% and 10% biochar rate under the conventional and the physical properties-based irrigation regimes. The lowest photosynthetic rate (13.6 µmol CO_2 m^{-2} s^{-1}), transpiration rate (3.7 mmol H_2O m^{-2} s^{-1}), and stomatal conductance (0.25 mmol H_2O m^{-2} s^{-1}) were in 0% biochar treatment under plant physiology-based irrigation system (Table 3).

There was an interaction ($P = 0.0082$) between biochar rate and irrigation system with respect to VPD. This interaction was likely the result of increasing VPD from 1.4 to 1.6 kPa under physical properties-based irrigation system as biochar rate went from 0 to 10%, while there was no difference from biochar rate in conventional irrigation. There was no interaction between biochar rate and irrigation system

Table 3 Photosynthesis and gas exchange measurements before irrigation for *H. paniculata* 'Silver Dollar' grown in substrates amended with 0%, 10%, or 25% by volume of hardwood biochar under three irrigation schedules (conventional irrigation, substrate physical properties-based and plant physiology-based irrigation systems ($n=5$) over 8 weeks

Irrigation system	Biochar rate (%)	Photosynthetic rates (μmol CO_2 m^{-2} s^{-1})	Transpiration rates (mmol H_2O m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})	Vapor pressure deficit (kPa)	Leaf water potential (MPa)^z
Conventional	0	15.1ab^y	4.7ab	0.33ab	1.5bc	−0.33^{ns}
	10	15.0b	4.4ab	0.28bc	1.5bc	−0.32
	25	15.2ab	4.9a	0.35a	1.5bc	−0.39
Substrate physical properties	0	15.4ab	4.4b	0.33ab	1.4c	−0.33
	10	15.2ab	4.7ab	0.32ab	1.6ab	−0.33
	25	15.8a	4.8ab	0.32ab	1.6a	−0.34
Plant physiology	0	13.6c	3.7c	0.25c	1.6ab	−0.33
	10	15.1ab	4.5ab	0.37a	1.4c	−0.32
	25	15.0ab	4.7ab	0.36a	1.5bc	−0.35
P value						
Biochar		0.0474	0.0012	0.0939	0.7781	0.0393
Irrigation		0.0023	0.0269	0.9199	0.1568	0.6603
Biochar × irrigation		0.0486	0.0163	0.0006	0.0082	0.1939

^{z}Petiole water potential was measured but is reported as leaf water potential

^{y}Means within a column followed by the same letter were not significantly different ($\alpha=0.05$)

^{ns}Values in the same column followed by the ns letters are not significantly different ($\alpha=0.05$)

for leaf water potential ($P=0.1939$), although biochar main effect was significant ($P=0.0393$) and leaf water potential was highest in 25% biochar rate (Table 3).

The after-irrigation photosynthetic rate and stomatal conductance were not different with respect to biochar rate or irrigation schedule (Table 4). All of the irrigation schedules had the same pattern of change over the weeks, thus there was no interaction between irrigation schedule and week in photosynthetic rate ($P=0.3090$) and stomatal conductance ($P=0.0817$). Photosynthetic rate, transpiration and stomatal conductance increased over the weeks and the values were higher at the termination of the experiment compared to the initiation regardless of substrate or irrigation schedules. The irrigation schedule began to affect the after-irrigation photosynthetic rate and stomatal conductance and increased beginning week four. There was an interaction between irrigation schedule and week in after-irrigation transpiration rate ($P=0.0004$) and VPD ($P=0.0021$) (Table 4). The

Table 4 Photosynthesis and gas exchange measurements after irrigation for *H. paniculata* 'Silver Dollar' grown in substrates amended with 0%, 10%, or 25% by volume of hardwood biochar under three irrigation schedules (conventional irrigation, substrate physical properties-based and plant physiology-based irrigation systems ($n=5$) over 8 weeks

Week	Photosynthetic rates (μmol CO_2 m^{-2} s^{-1})	Transpiration rates (mmol H_2O m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})	Vapor pressure deficit (kPa)
1	15.5bc^z	4.4c	0.30f	1.5bcd
2	15.6bc	5.1bc	0.33ef	1.6abc
3	14.8c	5.9a	0.34def	1.8a
4	16.9a	5.8a	0.40bcd	1.6ab
5	17.1a	5.3b	0.39cde	1.5bcd
6	16.6a	5.8a	0.44ab	1.4d
7	16.6ab	5.4ab	0.41abc	1.5cd
8	17.1a	5.2b	0.46a	1.3e
P value				
Biochar	0.7573	0.2431	0.4666	0.6121
Irrigation	0.7599	0.4811	0.0964	0.0324
Week	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Irrigation × week	0.3090	0.0004	0.0817	0.0021

The mean values pooled across all biochar and irrigation schedule treatments

^{z}Means within a column followed by the same letter were not significantly different ($\alpha=0.05$)

irrigation schedule began to affect after-irrigation transpiration from week two. An interaction was caused by increasing VPD from the first week to the third week and then decreasing over the time for the substrate physical-properties and conventional irrigation while the plant physiology-based irrigation was not different (data not shown).

Irrigation frequency, total water use, water use efficiency, final growth index and final dry weight

The irrigation frequency over 7 days was the same for all the biochar treatments under conventional irrigation schedules as all of the plants were irrigated once every day (Fig. 3). However, the irrigation frequency was different for the on-demand irrigation schedules due to the differences in the on-demand upper and lower irrigation set points for the plant physiology-based and physical properties-based irrigation treatments (Figs. 1, 2).

Total water use was the same in conventional irrigation (35 L), regardless of the biochar amendment rate, as all of the treatments were irrigated with 1.8 cm of water every day. During the 8-week period, total water use was lower in 0% biochar treatment irrigated by physical properties-based systems (28 L) and plant physiology-based (31.5 L) than the traditional industry irrigation practice. Total irrigation applied per container was reduced by 21% and 30% in 10% and 25% biochar rate, respectively, under physical properties-based irrigation and by 40% and 16% in 10% and 25% biochar rate, respectively, underplant physiology-based irrigation system. Time average application rate (data not presented) followed the same pattern as total irrigation applied. Increasing biochar application rate increased WUE under all of the irrigation systems ($P=0.0002$) (Table 5).

Growth index was not affected by biochar rate ($P=0.3248$). However, irrigation treatments had a significant effect ($P=0.0177$) on growth index, with conventional and physical properties-based treatments sharing the highest mean.

Plant dry weight was not affected by irrigation system ($P=0.0817$). However, biochar amendment had a significant effect ($P=0.0147$) on shoot final dry weight and the greatest shoot dry weight was in plants amended with 25% biochar rate (Table 5).

Substrate solution and foliar analysis

Substrate solution pH, EC and nutrient concentration were not affected by irrigation scheduling (Table 6). Biochar application rate affected substrate solution pH ($P<0.0001$). The 25% biochar-amended substrate resulted in the highest substrate solution pH with a 1.4 pH unit increase compared to 0% biochar rate. Substrate solution EC was not different in either biochar rate ($P=0.0942$) (Table 6). Additions of biochar resulted in higher NH_4 ($P=0.0151$) and K ($P<0.0001$) concentration. The 25% biochar rate had 83% higher NH_4 and 175% higher K concentration in leachate in comparison to 0% biochar amendment rate. However, NO_3, PO_4, Ca and Mg concentration were not affected by the biochar amendment rate or irrigation system (Table 6).

Foliar concentration of N, P and Ca was not affected by biochar rate ($P>0.05$) or irrigation system. Foliar K concentration increased with increasing biochar application rate

Table 5 Total irrigation applied per container, water use efficiency, final growth index and final dry weight for *H. paniculata* 'Silver Dollar' plants in substrates amended with 0%, 10%, or 25% by volume of hardwood biochar ($n=8$) over 8 weeks

Irrigation system	Biochar rate (%)	Total irrigation applied per container (L)	Water use efficiency (g L^{-1})	Final growth index (cm)	Final dry weight (g)
Conventional	0	35^{x}	2.1^{ns}	55.6^{ns}	87.3^{ns}
	10	35	2.6	58.3	86.2
	25	35	2.3	65.6	92.1
Substrate physical properties	0	28	1.7	54.9	74.2
	10	27.5	3.6	55.0	74.6
	25	24.5	2.1	56.2	86.5
Plant physiology	0	31.5	1.9	52.6	65.8
	10	21	2.9	54.3	77.6
	25	29.5	3.2	51.9	91.9
P value					
Biochar		–	0.0002	0.3248	0.0147
Irrigation		–	0.2676	0.0177	0.0817
Biochar × irrigation		–	0.0638	0.3375	0.5173

Water use efficiency per plant was estimated as [increase in dry weight over the course of the experiment (g)/total irrigation water volume applied (L)]

^{x}ANOVA not conducted because there was only one solenoid valve for biochar × irrigation combination

^{ns}Values within a column followed by the ns letters are not significantly different ($\alpha=0.05$)

Table 6 *Hydrangea paniculata* 'Silver Dollar' substrate solution pH, electrical conductivity (EC), ammonium (NH_4), potassium (K), nitrate (NO_3), phosphorus (P), calcium (Ca) and magnesium (Mg) concentration in a pine bark substrate amended with either 0%, 10%, or 25% by volume of hardwood biochar ($n=5$) and a controlled release fertilizer (Osmocote, Everris, Marysville, OH. 18N–2.6P–9.9K at 40 g per container)

	Biochar rate (%)	PH	EC (dS m^{-1})	NH_4 (mg L^{-1})	K (mg L^{-1})	NO_3 (mg L^{-1})	PO_4 (mg L^{-1})	Ca (mg L^{-1})	Mg (mg L^{-1})
	0	5.0c^z	2.0 ^{ns}	18.5b	97.6b	320.1^{ns}	2.6^{ns}	5.1^{ns}	3.2^{ns}
	10	5.7b	2.3	30.3a	206.2a	396.8	3.0	5.4	3.2
	25	6.4a	1.9	33.8a	268.3a	344.2	2.8	5.4	3.5
P value	–	< 0.0001	0.0942	0.0151	< 0.0001	0.4957	0.4985	0.1265	0.3201

Samples were collected at the end (15 September 2016 and 15 May 2017) of the experiment with the pour through extraction method

^{z}Means within a column followed by the same letter are not significantly different ($\alpha=0.05$)

^{ns}Values within a column followed by ns are not significantly different ($\alpha=0.05$)

($P=0.0001$). The Mg concentration was higher in 0% and 10% biochar rate compared to 25% biochar application rate ($P=0.0001$) (Table 7).

Discussion

Application of biochar improved substrate physiochemical properties, water retention capacity, available water and WUE. Plant physiological-based and substrate physical properties-based on-demand irrigation schedules reduced water use compared to the conventional practice of applying 1.8 cm of water per day in a single event without a negative effect on plant dry weight and maintained high plant water status and gas exchange rates.

Biochar improved the physical properties of a pine bark based substrate. The fine particles of the biochar likely nested within the larger pores of the pine bark substrate, causing the increase in container capacity and decrease in air space (Table 2). The 25% biochar treatment increased substrate water holding capacity and plant available water (Fig. 1) by holding more water at lower tension (− 1 kPa), 0.49 cm^3 cm^{-3}, but held less water, 0.34 cm^3 cm^{-3}, at higher tension (− 10 kPa) compared to other treatments. Substrate physics results are provided in a previous study but in brief, application of biochar may improve plant water relations by increasing the water holding capacity and changing particle size distribution (Basiri Jahromi et al. 2018b). Changes in container capacity and air space are consistent with other published studies (Altland and Locke 2017; Bi and Evans 2009; Vaughn et al. 2013). Reducing substrate bulk density and increasing pore space removes significant limitations to root growth and increases water holding capacity. The biochar used in this study had lower bulk density (0.10 g cm^{-3}) compared to the pine bark substrate (0.24 g cm^{-3}). A composite material's bulk density can be predicted by the weighted average of the substrate components' bulk density (Altland and Locke 2013). Increasing percentages of lower-density materials cause a reduction in the bulk density of the composite material. Reduction in bulk density was reported in other studies following biochar application to soilless substrates (Altland and Locke 2012; Beck et al. 2011; Dumroese et al. 2011; Tian et al. 2012).

Both of the on-demand irrigation schedules were effective. Plant gas exchange parameters were relatively high when measured before irrigation events, which suggests each system maintained a sufficiently high plant water status between irrigation events regardless of irrigation scheduling treatment (Table 3; Fig. 2). High gas exchange parameters both before (Table 3) and after-irrigation (Table 4) and leaf

Table 7 Foliar nitrogen (N), phosphorus (P), calcium (Ca), potassium (K), and magnesium (Mg) concentration of *H. paniculata* 'Silver Dollar' grown in a pine bark substrate amended with either 0%, 10%, or 25% by volume of hardwood biochar ($n=5$) and a controlled release fertilizer (Osmocote 18N–2.6P–9.9K at 40 g per container)

	Biochar rate (%)	N (%)	P (mg kg^{-1})	Ca (mg kg^{-1})	K (mg kg^{-1})	Mg (mg kg^{-1})
	0	3.0 ^{ns}	128.7 ^{ns}	915.1^{ns}	462.3c^z	125.2a
	10	3.0	133.4	889.1	507.6b	125.5a
	25	2.9	129.9	882.6	564.5a	102.9b
P value	–	0.4273	0.6744	0.8035	0.0001	0.0001

^{z}Means within a column followed by the same letter are not significantly different ($\alpha=0.05$)

^{ns}Values within a column followed by the ns letters are not significantly different ($\alpha=0.05$)

water potential indicated that the plants were not stressed, demonstrating the suitability of the on-demand irrigation schedules. After-irrigation plant gas exchange parameters were not depressed by the irrigation schedule, but in fact, increased over time. In this study, plants experienced low VWC prior to irrigation but not for an extended period of time so as to cause a drought response. Severity and duration of water deficit affect crop's physiological responses to drought (Kim 2011). For example, stomatal conductance and photosynthesis acclimation under mild drought (0.20–0.30 $cm^3\ cm^{-3}$) were observed in petunia (*Petunia hybrida*) and loblolly pine (*Pinus taeda*). However, less or no acclimation was observed under severe drought (Kim 2011; Watkinson et al. 2003). Also van Iersel and Dove (2005) reported that whole-plant photosynthesis was stable in abelia (*Abelia grandiflora*) and hydrangea (*Hydrangea macrophylla*) as VWC reduced from 0.25 to 0.15 $cm^3\ cm^{-3}$ in a bark-based substrate. However, a pronounced reduction in photosynthesis was observed at lower VWC and photosynthesis did not recover to pre-drought levels following irrigation. In conclusion, allowing crops to experience low VWC (~ 0.25 $cm^3\ cm^{-3}$) by potting in 100% pine bark substrate and irrigating either on-demand schedule would not have negative effect on plant gas exchange parameters.

Plants had lower total water use under plant physiology-based and physical properties-based irrigation schedule compared to the conventional irrigation regardless of the substrate (Table 5). Therefore, irrigation should be based upon an estimate of crop or substrate water status rather than the conventional static irrigation schedule to reduce water use. The 10% biochar-amended substrate under physical properties-based irrigation system yielded the highest WUE and low water use, which makes it a promising irrigation scheduling and substrate combination. Similar to our results, Beeson et al. (2004) and van Iersel et al. (2013) reported that proper irrigation scheduling increased water use efficiency. And like previous research, irrigating on a physiological basis improved irrigation efficiency (Fulcher et al. 2012; Hagen et al. 2014; Nambuthiri et al. 2017).

Biochar may increase plant available water. The reduction of total irrigation applications seen in 10% and 25% biochar treatments, especially as the season progressed and as the crop size and atmospheric demand increased, did not negatively affect gas exchange metrics or leaf water potential, which suggests biochar not only increased substrate water holding capacity but also plant available water. The lowest photosynthetic rate, transpiration rate, and stomatal conductance were in 0% biochar treatment under plant physiology-based irrigation system (Table 3). This is likely due to its low irrigation set point, the lowest in this experiment (0.25 $cm^3\ cm^{-3}$), which would cause the VWC to be lower at the measurement time compared to other treatments and possibly exceed the water buffering capacity (< -10 kPa). The generally accepted lowest VWC with plant available water in soilless substrates is 0.20 $cm^3\ cm^{-3}$ (Drzal et al. 1999; Milks et al. 1989), although this value varies among different substrates and species. For example, *Gardenia jasminoides* 'Radicans' can extract water from a drier substrate (0.20 $cm^3\ cm^{-3}$) compared to *Hydrangea macrophylla* 'Fasan' (0.28 $cm^3\ cm^{-3}$) (O'Meara et al. 2014).

The substrate physical properties-based irrigation scheduling likely maintained matric potential in the range of plant-available water. Readily available water (− 1 to − 10 kPa) includes easily available water (− 1 to − 5 kPa) and water buffering capacity (− 5 to − 10 kPa) (de Boodt and Verdonck 1972). Plants can exploit the water buffering capacity but we hypothesize that treatments did not exceed it during irrigation cycles in the substrate physical properties-based irrigation, which provided an ideal opportunity to maintain crop growth while conserving water. The 0% biochar rate irrigated with the plant physiological-based schedule had the lowest irrigation set point (0.25 $cm^3\ cm^{-3}$) compared to other treatments. Substrate in this treatment dried below the water-buffering capacity (0.37 $cm^3\ cm^{-3}$), which would explain the low plant dry weight. Plant biomass metrics did not decrease correspondingly with decreases in photosynthetic rates except for the 0% biochar rate under plant physiological-based irrigation. In general, shoot dry weight was similar under different irrigation schedules and greater in 25% biochar rate. Results were the same as a previous study that reported a plant physiology-based irrigation schedule with set point of 0.33 $cm^3\ cm^{-3}$ reduced water use with no negative effect on oakleaf hydrangea (*Hydrangea quercifolia* 'Alice') and slender deutzia (*Deutzia gracilis*) photosynthetic rate or on biomass compared to daily water use irrigation system (Hagen et al. 2014; Nambuthiri et al. 2017). Plant growth is more dependent on changes in water relations than photosynthetic rate (Taiz and Zeiger 2006). By maintaining photosynthetic rate at 90% or greater of the maximum rate, growth was not reduced but substantial water savings could be achieved.

Addition of biochar affected substrate chemical properties. Biochar application increased substrate solution pH but did not affect EC. Substrate solution pH, EC or nutrient concentration were not affected by irrigation schedule (Table 6). Likewise, Incrocci et al. (2014) found that substrate water status and evapotranspiration-based irrigation scheduling did not affect leachate nutrient, EC and pH compared to timer-controlled irrigation. Leachate EC levels in all of the treatments were in the recommended range of 1.0–3.5 $dS\ m^{-1}$ for greenhouse crops as measured by the pour-through method (Cavins et al. 2000), but higher than the recommended range of 0.5–1.0 $dS\ m^{-1}$ for container substrate via pour through extraction method (Yeager et al. 2007). An increase in pH was also reported in other biochar amended soilless substrates (Conversa et al. 2015; Kaudal et al. 2016).

Biochar application affected substrate solution nutrient concentration. Biochar amended at 25% increased NH_4 and K in substrate solution compared to non-amended pine bark (Table 6) and foliar K increased with increasing biochar amendment in containers (Table 7) indicating biochar was a source of K for the crops. Similarly, Vaughn et al. (2013) reported that wood biochar had low levels of NO_3, acceptable levels of P (between 3 and 5 mg kg^{-1}) and Ca, and high levels of K. In another study, application of 10% gasified rice hull biochar increased K concentration in leachate compared to 0% or 1% biochar rate, and similar NO_3 concentrations were observed across all treatments (Altland and Locke 2013). A meta-analysis of 114 studies concluded that the addition of biochar to mineral soils caused an increase in plant tissue K concentration but did not affect plant tissue N or P concentration (Biederman and Harpole 2013). However, biochar may be a more important source of K in the soilless substrate (Altland and Locke 2013). In this study, the biochar application improved substrate physical properties, water retention capacity, available water, WUE, and increased substrate pH and K concentration and resulted in higher crop growth.

Conclusions

Different on-demand irrigation schedules that apply the appropriate amount of water when needed as determined by plant physiological status or substrate physical properties, reduced water use over the traditional practice of applying 1.8 cm of water per day in all of the treatments. These on-demand irrigation schedules reduced water use without a negative effect on plant dry weight by maintaining sufficient plant water status and gas exchange even just prior to irrigation, the driest point in the irrigation cycle. However, the very low set point in 0% biochar rate under plant physiology-based irrigation likely exceeded the water buffering capacity. The 10% biochar-amended substrate with a substrate-based irrigation schedule yielded the highest WUE and high water saving, making it a promising irrigation scheduling and substrate combination. Biochar provided a source of K by increasing K concentration in substrate solution and in plant foliage. Future work should focus on maximizing the plant biomass metrics by maintaining high plant water status and gas exchange without a negative effect on plant biomass metrics.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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