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Improving Containerized Nursery Crop Sustainability: Effects of Conservation-driven Adaptations in Soilless Substrate and Water Use on Plant Growth and Soil-borne Disease Development

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Abstract. **Containerized crop production faces increasing sustainability challenges with both soilless substrate and water use. To facilitate use of sustainable practices, we evaluated plant health impacts of two substrates, bark and wood fiber, which we contrasted with peat, a substrate that is slower to renew; this was overlaid with an analysis of the effects of water-saving–targeted irrigation reductions, compared with typical well-watered conditions. Health impacts were evaluated in two crops, considering both physiological and disease impacts for tomato with and without *Phytophthora capsici,* and chrysanthemum with and without *Phytopythium helicoides*. Substrate type was a strong determinant of plant health, wherein crops grown in a HydraFiber-peat mix ("fiber") performed worse than those in bark and peat, with up to a 50% and 45% reduction in shoot biomass in tomato and chrysanthemum, respectively ($P < 0.001$). Tomato decline incidence from *P. capsici* was 3–6 times higher in fiber than other substrates, and fiber was the only substrate where the effect of *P. capsici* enhanced decline and rot development compared with noninoculated plants ($P < 0.05$). In bark, reduced irrigation consistently inhibited tomato and chrysanthemum growth and shoot water content (typically $P < 0.001$). In peat, whereas tomato growth was inhibited under reduced irrigation ($P = 0.012$–0.013), chrysanthemum growth was often unaffected. Growth in fiber was uniformly poor regardless of irrigation regime for both crops, and an irrigation treatment effect was not typically apparent. Reduced irrigation enhanced pathogen effects in fiber and peat for tomato and fiber and bark for chrysanthemum ($P < 0.05$). This is perhaps the first study to evaluate HydraFiber interactions with disease and reduced irrigation and suggests that this product consistently incurs costs to crop productivity. However, the peat-replacing bark substrate has strong potential to optimize plant growth physiologically and via disease suppression and can be used under reduced irrigation without compromising economic productivity of the system.**

Nursery crop production faces significant sustainability challenges in many facets of production; two of the most notable challenges are substrate and water sustainability. As typically soilless systems, this industry is highly dependent on use of potting media, which are usually comprised of a mix of substrates. For example, a Florida survey found that participating nurseries used 16 different substrate components, resulting in 26 different mixtures (Yeager and Newton, 2001). Peat moss has been a component of transplant and potting media for containerized vegetable and ornamental crops for the last 90 years (Alexander et al., 2008). It became a major component when it replaced the heavy and difficult-to-source loams and production of containerized plants increased (Alexander et al., 2008). Peat has many advantages, including abundance and affordability, high water holding and ion exchange capacity, decomposition resistance, low weight, and the relative ability to adsorb and release nutrients added as fertilizers (Bachmann et al., 2018; Barrett et al., 2016; Kingston et al., 2017; Robbins and Evans, 2011). However, in many regions peat is harvested from wetland ecosystems at rates deemed unsustainable; furthermore, peat extraction releases stable, sequestered carbon into the active carbon cycle, exacerbating climate change (Barber, 1993; Barkham, 1993; Cleary et al., 2005; Dunn and Freeman, 2011; Huth et al., 2022). As a result, there has been increasing pressure on legislators, retailers, and growers to reduce the environmental impact of containerized nursery and greenhouse operations (Alexander et al., 2008), which has in turn led to exploration of alternative materials that can be produced more sustainably than peat (Evans and Stamps, 1996; Frenkel et al., 2017).

Many alternatives exist that are arguably more sustainable, including coconut fiber (coir) and milled tree bark. Pine bark has been used in Mexico and the United States for several decades (Madrid-Aispuro et al., 2020). It is valued for its high porosity and drainage (Stewart et al., 2019) as well as potential disease-suppression traits associated with phenol production, high pH, and other properties that may create hostile or favorable conditions for specific plant pathogens (Bonanomi et al., 2010; Friend, 1979; Nicholson and Hammerschmidt, 1992). Hardwood biochar is a derivation of bark that has also been examined as a peat replacement (Bachmann et al., 2018; Yan et al., 2020). Coir is a renewable peat-replacing substrate that is derived from the fibrous material from coconut husks; coir is considered a peat alternative due to similar physical traits, including high water holding capacity (Evans and Stamps, 1996; Kingston et al., 2017). There are conflicting reports on the plant health impacts of coir, and in many cases it seems that this product can be harmful to crop growth (Arenas et al., 2002; Meerow, 1994). In addition, coir can cause salt pollution as part of production (Eveleens et al., 2021). As an alternative to coir, there is a new wood- and bark-based fiber product, HydraFiber, that can be used as a partial substitute for peat or coir (Eveleens et al., 2021). This product is marketed as improving air content, and producers (C.L. Swett, personal communication) report that substrate traits appear to reduce risk of overirrigation. Studies on this substrate are only just emerging and thus far indicate no negative effect on rate of development and plant weight:length ratio (Eveleens et al., 2021).

Water is arguably the most important resource in any plant nursery operation; among its many uses, water is required for irrigation, pesticide applications, fertilization, and temperature control. Historically, water conservation has not been a priority in the containerized crop industry. Risk aversion and a desire to prevent plant water stress and associated yield impacts has translated to irrigation methods that optimize water delivery and do not calibrate based on minimum crop requirements, often resulting in overirrigation (Chappell et al., 2013; Lea-Cox et al., 2017). However, increasing pressures on water supplies due to reductions in rainfall and resulting surface water availability, runoff restrictions,

and associated increases in water prices are motivating growers to improve water use efficiency. Additionally, the general shift from mostly field production to containerized production (≈75% of U.S. nursery sales originate from container nurseries) (USDA NASS, 2020) is increasing water demands.

There are several strategies for adapting water use to these pressures (Chartzoulakis and Bertaki, 2015; Patle et al., 2019; Pereira et al., 2009; Steduto et al., 2012). This can include collecting irrigation runoff for reuse, altering plant spacing to improve water uptake, and improving the precision of irrigation systems. Within the latter, set-point irrigation offers an appealing high-precision tool for the nursery industry. With this method, controlled set-points irrigate only when soil moisture levels drop below a chosen threshold (Bayer et al., 2015). This can allow growers to fine-tune water inputs to avoid overwatering and can optimize water use reductions without decreasing quality or yields (Bayer et al., 2015; Belayneh et al., 2013; Chappell et al., 2013). However, many studies (Swett 2020) as well as grower observations (C.L. Swett, personal communication) indicate that reduced irrigation regimes that are not harmful physiologically may pose increased risk of disease-driven losses, creating an adoption barrier for non-users and a production risk to users.

With these increasing constraints, understanding plant health risks of sustainability-driven shifts in substrate and water use, both alone and as interacting factors, is paramount to the long-term future of containerized cropping systems. In the context of plant health, most if not all previous studies focus on physiological responses to media shifts and do not consider effects on other plant health drivers, such as soil-borne diseases. The overarching goal of this study was to assess how shifts in soilless substrate use influence plant health directly and under both water-use reduction and pathogen pressure scenarios. Within this, we were interested in testing the hypotheses that certain soilless substrates such as bark may be pathogen suppressive and that substrates may differentially influence plant performance under reduced irrigation.

These studies evaluated performance of both a containerized vegetable and a floricultural crop in two peat-replacing wood-based substrates, bark and Hydrafiber (wood fiber blended with peat), in comparison with peat. For the vegetable pathosystem we examined tomato (*Solanum lycopersicum* L.)–*Phytophthora capsici* (Phytophthora root rot) interactions; tomatoes are an important greenhouse vegetable crop worldwide, and this is a common model system for plant–pathogen–water stress interactions (Bostock et al., 2014; Del Castillo Múnera et al., 2019a). For the floriculture pathosystem, we examined chrysanthemum (*Chrysanthemum ×morifolium*)–*Phytopythium helicoides* (root rot) interactions. Chrysanthemums are an economically important crop; U.S. wholesale totals for potted and cut flowers amounted to $150 million in 2019 (USDA NASS, 2020). *Phytopythium helicoides* has been reported as a pathogen of several floriculture crops, including dahlia, miniature roses, begonia, and poinsettia (Afandi et al., 2018; Drechsler, 1930; Ishiguro et al., 2014; Miyake et al., 2014; Yang et al., 2013). Additionally, *P. helicoides* was recovered from a containment pond at a collaborating nursery; isolates were used to demonstrate pathogenicity on chrysanthemum in previous greenhouse trials (J. Beaulieu et al., unpublished data).

Materials and Methods

Experimental design

Three soilless substrates were chosen for this study: Sunshine/LC1 Peat mix ("Peat") (Sun Gro, Agawam, MA), pine bark ("Bark") (Fafard Metro Mix 852, Sun Gro, Agawam, MA), and a 40% HydraFiber (160)–60% peat (Hi-Point Industries, Newfoundland, Canada) mix created by a collaborating nursery ("Fiber"). HydraFiber is a product that refines wood and bark using a pressurized method, creating long, thin, fibrous strands with greater surface area. In all three substrates, 45% volumetric water content (VWC) was selected as the well-watered irrigation set point. Set points of 28% (fiber and peat) and 30% (bark) VWC were selected to represent the reduced irrigation/mild stress condition (determined using calibration curves, described below). Pathogen treatment consisted of either inoculated or noninoculated plants (described below).

The experiment was arranged in a randomized complete block split-plot design on four benches with irrigation treatment as the main plot and pathogen treatment as the subplot. There were two blocks comprised of two benches each. Tomatoes (southern side) and chrysanthemums (northern side) shared the four benches so that there were 48 3.8-L pots/host/bench. Of the 96 pots/host in each block, 48 were filled with bark, 32 were filled with peat, and 16 were filled with HydraFiber. The unbalanced numbers reflect adaptations in the experiment due to limitations in substrate availability. Each irrigation treatment was applied to half of the pots within each crop, and each pathogen treatment (inoculated or noninoculated) was randomly applied to half of the plants in each substrate × irrigation treatment. The experiment was conducted twice; Expt. 1 was conducted from June to July 2018, and Expt. 2 was conducted from July to Aug. 2018. Trials were run for 35 d, at which time all response variables were quantified. The daily mean air temperature ranged from 19.4 to 42.5 °C during the first experiment and from 19.1 to 37.8 °C during the second experiment, with a photoperiod of 12 h per day.

Plant preparation

Tomato cv. H8504 seeds were surface disinfested with 70% ethanol for 10 min and 50% sodium hypochlorite for 10 min and then rinsed with sterile water. Disinfested seeds were sown in 50 plug trays containing Sunshine/LC1 mix (Sun Gro, Agawam, MA) and covered with vermiculite. About 0.5 g of fertilizer (Osmocote N–P–K, SMG Brand, Marysville, OH) was added to the surface of each cell at seeding. Trays were placed on bottom heat on a raised plant bench at the University of Maryland Research Greenhouse Complex (College Park, MD). Seedlings were maintained at 20 to 25 °C, with a photoperiod of 12 h per day, and watered daily by mist. Chrysanthemum Chelsea cuttings propagated in a wood fiber substrate were provided by a collaborating nursery in Maryland.

Soilless substrate calibration and sensor network irrigation system setup

The VWC of each soilless substrate was calculated with EC5 substrate moisture sensors (METER Group, Inc., Pullman, WA) as described in Cobos and Chambers (2010). The procedure consisted of measuring the VWC of each substrate at its driest and increasing moisture to saturation (Cobos and Chambers, 2010). The resulting calibration curve coefficients (Fig. 1) were entered into the Sensorweb sensor-control software (Mayim, LLC, Pittsburgh, PA) used in the study to convert raw values from the EC5 capacitance sensors to corresponding VWC values. Based on these curves, two VWC levels were selected per substrate to represent well-watered and mild stress conditions. In all three substrates, 45% VWC was selected as the well-watered set point. To represent the mild stress condition, 28% (fiber and peat) and 30% (bark) VWC set points were selected.

A precision sensor network (Lea-Cox, 2012) was set up to control irrigation. Three irrigation laterals were laid out on each of four 5.8 m × 2.1 m (length × width) raised benches. Corresponding laterals on each bench were controlled by individual nR5-DC nodes (METER Group, Inc., Pullman, WA) that were attached to DC latching solenoids (Baccarra, Geva, Israel) on an irrigation manifold connected to a pressure-controlled main water line. Irrigation was delivered to individual plants using Netafim yellow spray stakes with 300 mL·min^{-1} output (Netafim USA, Fresno, CA) attached to the laterals using supply tubes.

To maintain the substrate VWC at their respective levels in the root zone of plants, the EC5 substrate moisture sensors were inserted halfway up the pots by cutting and folding back a rectangular strip on the side of the pot. The sensors were pushed into the substrate through the strip with prongs oriented horizontally. The substrate was packed around the sensors to ensure good contact, and the strip was then folded back into place and secured with waterproof tape. The EC5 substrate moisture

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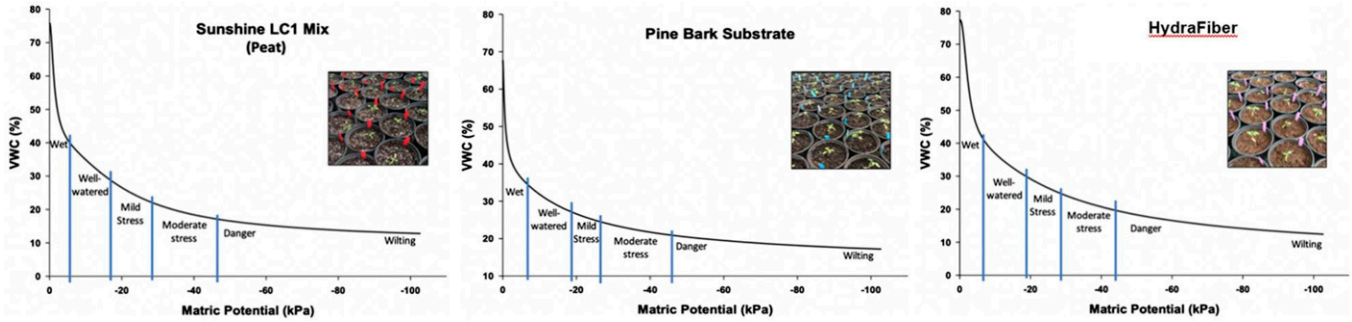

Fig. 1. Calibration curves for the peat, bark, and fiber substrates. The "well-watered irrigation" treatment corresponded to 45% volumetric water content (VWC) in all three substrates; "reduced irrigation" treatment corresponded to 28% VWC in the peat and fiber and 30% VWC in the bark.

data were recorded on a 15-min basis using a combination of em50R and nR5-DC radio data loggers (METER Group, Inc., Pullman, WA) and transmitted to the Sensorweb software.

Soilless substrate preparation

Other than moistening the substrates before potting, no alterations were made to the peat and bark substrates. The cooperating nursery provided 3.8-L pots filled with the HydraFiber substrate. Before potting, the peat was hydrated; then dolomite and gypsum were added to adjust the pH to 6.2. There were no starter charges added. Although wetting agents were used, the amount was negligible. All substrates were moistened until the point at which applied pressure would yield water. Trade 3.8-L pots were filled to the top with their respective substrates and then tamped down.

Pathogen inoculum preparation

Inoculations were conducted with a single isolate per pathogen; *P. capsici* isolate SL897 was recovered from infected peppers in St. Mary's County, MD, and *Phytopythium helicoides* isolate SL1617 was recovered from an ornamental nursery retention pond in Frederick County, MD. Both isolates were confirmed to be pathogenic to their respective hosts in previous studies (J. Beaulieu et al., unpublished data; Del Castillo Múnera et al., 2019a). For each pathogen, infested millet inoculum was prepared by transferring 10 plugs (1 cm diameter) of actively growing mycelia on 1-week-old V8 petri dish cultures to flasks containing 40 g of millet seed mixed with asparagine (0.032 g) and water (30 mL) that had been autoclaved twice (Quesada-Ocampo et al., 2009). The inoculated millet was incubated at room temperature for 2 weeks.

Treatment application

Three-week-old seedlings were transplanted into pots, watered until saturation, and then placed under their target VWC set points. About 5 g fertilizer (Osmocote N–P–K; SMG Brand, Marysville, OH) was added to the top of the pots. Once the VWC set points were reached (≈1 week), plants were inoculated by pouring 1 g of infested millet seed into each of three 5-cm-deep wells spaced evenly around the plant, halfway from the base of the plant to the edge of the pot. The millet was then covered with the substrate. Negative pathogen controls were not inoculated. Irrigation was applied whenever the average VWC of four EC5 sensors per treatment dropped below the corresponding set-point. Irrigation duration was limited to 30 s per event.

Shoot growth, water content, and disease assessments

Plant height was measured at 0 d postinoculation (dpi) and at 35 dpi as the distance from the crown of the plant (substrate line) to the uppermost leaf. At the end of each experiment, any external crown rot in tomatoes was noted, and external stem lesions were measured. Plants were then cut at their bases and placed in brown paper bags. Shoot fresh weights were recorded separately for each plant. After 3 d in a drying oven, shoots were reweighed to record dry shoot weights. Shoot water content was calculated as the difference between fresh and dry weight. Shoot health was evaluated based on presence or absence of decline for each plant; plants were in decline if 50% or more of the shoot tissue was wilting or necrotic. Root balls were removed from pots and visually rated for both the coverage of root ball base (0% to 20% of the base with roots = rating of 5, 21% to 40% = 4, 41% to 60% = 3, 61% to 80% = 2, 81% to 100% = 1) (Fig. 2) and the percentage of roots that had lesions (0% to 20% of roots with lesions = rating of 1, 21% to 40% = 2, 41% to 60% = 3, 61% to 80% = 4, 81% to 100% = 5).

To confirm association of target pathogens with root rot, we conducted pathogen isolations from roots with rot symptoms from 12 tomato plants and 12 chrysanthemum plants (two plants from each substrate × irrigation treatment). Roots were rinsed in tap water and then dried with paper towels. Five 1cm pieces from the crown and roots were cut from each root system and placed on V8 medium amended with pimaricin (0.4 $mL \cdot L^{-1}$), ampicillin (0.25 $g \cdot L^{-1}$), rifampicin (0.01 $g \cdot L^{-1}$), and pentachloronitrobenzene (0.05 $g \cdot L^{-1}$). Cultures were incubated at room temperature under ambient light. Isolates were tentatively identified as *P. capsici* and *P. helicoides* based on morphological characteristics (growth rates, sporangia morphology) as described in Drenth and Sendall (2001) and Uzuhashi et al. (2010). To further confirm identities, mycelia of putative pathogens were transferred to V8 medium. Isolates were identified to species via polymerase chain reaction (PCR) using primers specific for oomycetes [internal transcribed spacer (ITS)4 and ITS6] (White et al., 1990). DNA was extracted from 7- to 10-d-old isolates growing on V8 medium using the Prep Man Ultra Kit (Life Technologies, Carlsbad, CA). PCRs were performed with the GoTaq green master mix (5 $U \cdot \mu L^{-1}$; Promega, Madison, WI) using a C1000 Touch thermal cycler (Bio Rad, Hercules, CA) according to manufacturer's instructions. The resulting PCR product was cleaned using ExoSAP-IT (Thermo Fisher Scientific, Waltham, MA), and the ITS region sequence was generated using the ITS4 forward primer (Macrogen, Rockville, MD). The resulting ITS sequence was used for species identification based on BLAST analysis in GenBank.

Statistical analysis

Analyses were all conducted in either SAS 9.4 (SAS Institute Inc., Cary, NC) or Rx64.4.1.0 with the Rcmdr plug-in. Experiment, block, and bench were considered random variables, and substrate moisture and pathogen treatments were considered fixed variables. Experiments were combined in the absence of significant experiment × treatment interactions but analyzed separately when the interaction was significant (based on ANOVA). Incidence analyses (decline incidence, crown rot

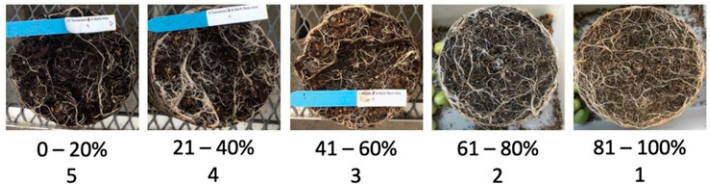

Fig. 2. Root ball base coverage rankings (shown for tomato; similar for chrysanthemums): 0% to 20% coverage of the root ball base = ranking of 5, 21% to 40% = 4, 41% to 60% = 3, 61% to 80% = 2, 81% to 100% = 1. Rankings differentiated based on both main lateral roots apparent in image and fine roots less apparent in image.

Table 1. Effects of substrate on tomato health in the absence and presence of the root and crown rot pathogen *Phytophthora capsici* in well-watered plants.[zy]

Pathogen	Substrate	Shoot fresh weight (g)	Shoot dry weight (g)	Shoot decline (%)-Expt. 1[x]	Crown rot (%)	Root ball coverage (rank)[w]	Root ball necrosis (rank)[v]
Noninoculated	Peat	82.6 ± 5.3 b	9.4 ± 0.7 b	0.0 ± 0.0 a	0.0 ± 0.0 a	4.4 ± 0.1 a	1.0 ± 0.0 a
	Bark	105.9 ± 4.6 c	10.1 ± 0.5 b	0.0 ± 0.0 a	0.0 ± 0.0 a	4.7 ± 0.1 a	1.0 ± 0.0 a
	Fiber	54.1 ± 3.7 a	5.6 ± 0.3 a	0.0 ± 0.0 a	0.0 ± 0.0 a	5.0 ± 0.0 a	1.1 ± 0.1 a
Inoculated	Peat	85.0 ± 4.8 b	9.5 ± 0.6 b	6.3 ± 6.3 ab	0.0 ± 0.0 a	4.7 ± 0.1 b	1.8 ± 0.1 b
	Bark	107.5 ± 5.2 c	10.6 ± 0.5 b	12.5 ± 4.2 ab	8.8 ± 3.4 a	4.9 ± 0.0 b	2.1 ± 0.2 b
	Fiber	46.6 ± 4.8 a	4.9 ± 0.5 a	37.5 ± 12.5 b	16.7 ± 16.7 a	5.0 ± 0.0 a	1.5 ± 0.2 b
P value							
Pathogen		0.995	0.739	0.002	0.054	0.006	<0.001
Substrate		<0.001	<0.001	0.123	0.355	<0.001	0.617
Pathogen × substrate		0.097	0.471	0.123	0.355	0.367	0.072

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using one-way and multiway ANOVA in Rx64.4.1.0 with the Rcmdr plug in. Experiments were combined unless otherwise indicated.

[y]Values after the ± symbol represent the standard error of the mean.

[x]Percentage of plants which exhibited symptoms of shoot decline, wherein 50% or more of the plant was wilting or leaves were turning necrotic; n = 2.

[w]Root ball coverage was ranked on a scale from 1 (80% to 100% coverage of root ball base) to 5 (0% to 20% coverage of root ball base) (Fig. 2). Nonparametric Kruskal–Wallis analysis was used to evaluate treatment effects; means comparisons reflect non–parametric-based comparisons of pathogen treatment within substrate (n = 15–50).

[v]Root ball necrosis ranking reflected the percentage of roots that had lesions (0% to 20% of roots with lesions = rating of 1, 21% to 40% = 2, 41% to 60% = 3, 61% to 80% = 4, 81% to 100% = 5). Data analyzed based on Kruskal–Wallis nonparametric test of significance (n = 15–50).

incidence) were conducted based on the percentage of data derived from each block, treating block as replicate, for a total of four replicates when experiments could be combined and two replicates when they could not. For non–proportion-based data (shoot weight, shoot height, water content, root ball evaluations, crown rot lesion length), plants were treated as replicates for a total of 24, 16, and 8 replicates per irrigation × pathogen combination for bark, peat, and fiber when experiments were combined and 12, 8, and 4 replicates for bark, peat, and fiber when experiments were not combined. The unbalanced replicate numbers for substrate reflect adaptations in the experiment due to a combination of changes in design and limitations in substrate availability as the first trial was starting; to be a true repeat, we retained these numbers for the second trial.

Data analysis for plant growth parameters (shoot weight, shoot height) as well as disease incidence measures (percentage of plants with severe symptoms and crown rot) and lesion length were conducted using ANOVA (lme4 package in SAS; one-way and multiway ANOVA in R). If ANOVA was significant for main effects or interaction terms, treatment means were compared using Tukey's pairwise means comparisons. Analysis for nonparametric data (rankings of root rot and coverage of the root ball base) were analyzed using the Kruskal–Wallis test; mean differences were evaluated based on separate pairwise analyses. Percent data were arcsine square root transformed before analysis. Differences in all analyses were considered significant based on a *P* value of 0.05 or lower.

Results

Tomato–*Phytophthora capsici*: Effect of soilless substrate type on plant health with and without a pathogen present (well-watered plants)

Shoot growth. Under standard irrigation conditions, shoot fresh weight was greatest in bark, intermediate in peat, and lowest in fiber (up to 56% reduction from bark) ($P < 0.001$; Table 1). Dry shoot weight was similar for both bark and peat and significantly lower in fiber (up to 53% reduction from bark) ($P < 0.001$; Table 1). Shoot weight (fresh and dry) did not differ between inoculated and noninoculated plants within any substrate ($P > 0.05$).

Shoot decline and crown rot. Decline was only evaluated for Expt. 1 because decline symptoms did not develop in Expt. 2. Although there was not a significant effect of substrate on shoot decline ($P = 0.123$), 3-fold to 6-fold more plants developed decline in fiber than peat or bark. In addition, fiber was the only substrate under which *P. capsici* increased mortality levels; 37.5% of *P. capsici* inoculated plants were in decline, whereas none declined in the noninoculated treatment (reflecting a significant pathogen effect) ($P = 0.002$; Table 1). Crown rot was similarly highest in fiber (17% of plants), was intermediate in bark (9% of plants), and did not develop in peat; however, these substrate differences were not significant ($P = 0.430$). Decline and crown rot did not develop in noninoculated plants in either experiment.

Root system health. There was a significant effect of both substrate ($P < 0.001$) and pathogen treatment ($P = 0.006$) on coverage of the root ball base (Table 1). Within the inoculated treatment ($P = 0.006$), root ball coverage was greatest in peat ($P = 0.011$) < bark ($P = 0.009$) < fiber ($P = 0.003$) as determined by pairwise comparison (not shown). Root ball necrosis was also significantly greater in the inoculated compared with noninoculated plants ($P < 0.001$). Based on molecular analysis, *P. capsici* was consistently recovered from root rot in the inoculated treatment.

Tomato: Effect of soilless substrate type on plant health under reduced irrigation regimes (noninoculated plants)

Shoot growth. Under the noninoculated treatment, plants in bark had consistently taller shoots than plants grown in the other substrates ($P < 0.001$, substrate effect), and plants grown under well-watered irrigation were typically taller than plants grown under reduced irrigation, although differences were only significant in Expt. 1 ($P < 0.001$, irrigation treatment effect; Table 2). In Expt. 1, substrate did not influence shoot height under well-watered irrigation; reducing irrigation inputs decreased shoot height by 27% in peat ($P < 0.001$), 17% in fiber ($P > 0.05$), and 15% in bark ($P < 0.001$) (Table 2). Unlike Expt. 1, in Expt. 2 peat significantly reduced shoot height under well-watered irrigation compared with bark, and there were no differences between substrates under reduced irrigation and within each substrate; the trend for shorter shoots under reduced irrigation was consistent for both bark (12% reduction) and fiber (5% reduction) (Table 2).

Across both experiments, shoot fresh weight was greater in bark compared with fiber and in some cases compared with peat under both well-watered and reduced irrigation, and there was typically a reduction in shoot weight under reduced irrigation. In peat, shoot weight was 7% lower under reduced irrigation compared with well-watered irrigation ($P < 0.05$); effects of irrigation treatment were not significant in bark or fiber, although biomass was lower under reduced irrigation for both substrates (Table 2). Under reduced irrigation, shoot weight in fiber was 28% and 46% lower than peat and bark, respectively (Table 2). In Expt. 2, shoot fresh weight remained the greatest in bark under both irrigation regimes ($P < 0.001$ for substrate effect). Under well-watered irrigation, plants grown in bark had greater biomass than those grown in both peat and fiber, and under reduced irrigation, biomass of plants grown in either bark or peat was greater than in plants grown in fiber ($P < 0.05$; Table 2). Within a substrate, well-watered or reduced irrigation did not influence shoot growth or mass.

Shoot water content. In both experiments, shoot water content was greatest in plants grown in bark. These values were similar to peat under standard irrigation in Expt. 1 and

Table 2. Effect of substrates on tomato growth and water content under well-watered and reduced irrigation regimes (noninoculated plants).[zy]

Irrigation	Substrate	Shoot ht (cm)		Shoot fresh wt (g)		Shoot water content (g)[x]	
		Expt. 1	Expt. 2	Expt. 1	Expt. 2	Expt. 1	Expt. 2
Well-watered (standard irrigation)	Peat	84.1 ± 2.3 cd	76.5 ± 4.0 a	133.4 ± 3.8 c	93.0 ± 10.6 ab	118.0 ± 3.2 cd	82.5 ± 9.1 ab
	Bark	91.1 ± 2.1 d	96.0 ± 2.9 b	147.2 ± 4.2 c	141.3 ± 5.2 d	133.3 ± 3.7 d	128.3 ± 4.6 d
	Fiber	81.0 ± 1.7 bd	83.9 ± 3.9 ab	75.9 ± 2.7 ab	67.1 ± 5.8 a	68.9 ± 2.4 ab	60.3 ± 5.0 a
Reduced (reversed irrigation)	Peat	61.0 ± 2.4 a	78.1 ± 2.8 a	99.0 ± 4.1 b	117.2 ± 4.1 bc	87.9 ± 3.7 b	103.3 ± 3.5 bc
	Bark	77.7 ± 3.8 bc	84.4 ± 3.6 ab	132.0 ± 6.1 c	135.1 ± 4.2 cd	117.5 ± 5.5 c	121.4 ± 3.8 cd
	Fiber	67.2 ± 3.2 ab	79.5 ± 3.2 ab	71.3 ± 4.1 a	72.5 ± 6.7 a	64.4 ± 3.9 a	65.6 ± 6.1 a
P value							
Irrigation treatment		<0.001	0.046	<0.001	0.317	>0.001	0.415
Substrate treatment		<0.001	<0.001	<0.001	<0.001	>0.001	>0.001
Irrigation × substrate treatment		0.198	0.137	0.041	0.0315	0.064	0.023

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using one-way and multiway ANOVA in Rx64.4.1.0 with the Rcmdr plug in. Data were analyzed for Expts. 1 and 2 separately due to a significant experiment × substrate treatment interaction for all response variables (n = 6–24 for all response variables).

[y]Values after the ± symbol represent the standard error of the mean.

[x]Shoot water content calculated based on difference between fresh and dry weight.

under reduced irrigation in Expt. 2. Additionally, shoot water content was typically lower in fiber compared with bark and peat under both irrigation regimes ($P < 0.001$ for substrate effect) (Table 2). Under well-watered conditions, shoot water content was greatest in bark and in peat was 11% to 35% lower compared with bark and 48% to 53% lower in fiber ($P < 0.001$ in both experiments). Under reduced irrigation, all substrates differentiated; compared with bark, there was a 14% to 25% and 45% reduction in shoot water content in peat and fiber, respectively, across the two experiments. In Expt. 1, water contents of plants in the reduced-irrigation treatment were 25% and 11% less ($P < 0.001$) than plants grown in well-watered conditions in peat and bark, respectively. Water content was similar among reduced and well-watered conditions for tomatoes grown in fiber. There was no irrigation treatment effect in Expt. 2.

Tomato–*Phytophthora capsici*: Effect of soilless substrate type on tomato disease risk under reduced irrigation

Shoot fresh weight. Substrate dynamics under reduced irrigation were altered by pathogen presence, which enhanced the difference in shoot fresh weight in peat vs. fiber and significantly diminished fresh weight under fiber. The difference in shoot fresh weight in peat vs. bark was unaffected. In Expt. 1, within each substrate, weight was reduced from 16% to 79% in the *P. capsici* vs. the noninoculated treatment under reduced irrigation ($P < 0.001$ for pathogen treatment; Table 3). Shoot fresh weight of plants under reduced irrigation was lowest in fiber under inoculated conditions, with a 50% to 80% and a 59% to 87% reduction in weight when compared with peat and bark, respectively, across experiments, although significant substrate effects were only apparent in Expt. 1 ($P < 0.001$; Table 3).

Shoot decline, crown rot, and root rot. A greater percentage of reduced-irrigation plants exhibited shoot decline symptoms under inoculated vs. noninoculated conditions when grown in fiber (48% vs. 0% of plants) but not when grown in bark or peat ($P = 0.021$; Table 3). In Expt. 2, plants grown in the fiber substrate only developed disease under reduced irrigation (20% of plants), with all plants remaining healthy under well-watered conditions (Table 4). Similarly, in fiber there was a 2-fold increase in decline incidence in reduced vs. well-watered irrigation Expt. 1, but differences were not significant (Table 4). There was a similar trend for peat, with a 2-fold increase in disease under reduced vs. well-watered irrigation, but this effect was not significant; decline development in bark was uniform between reduced and well-watered irrigation (Table 4).

Although substrate did not influence crown rot incidence ($P = 0.139$), it was notable that crown rot was only observed in peat (21% of plants) and bark (12% of plants) but not in fiber (Table 3). In inoculated plants grown in peat, crown rot only developed under reduced irrigation (21% of plants), and crowns remained healthy under well-watered irrigation ($P = 0.038$ for irrigation treatment; Table 4). Conversely, plants grown in fiber only developed crown rot under well-watered irrigation (17% of plants), although the irrigation treatment effects were not significant ($P = 0.412$; Table 4). In bark there was no difference in crown rot development under the different irrigation regimes in inoculated plants ($P = 0.23$–1.0 across experiments) (Table 4). Crown rot severity did not vary across treatments, with average lesion lengths of 11.5 and 8.9 mm for

Table 3. Substrate–pathogen interactions under reduced irrigation in tomato.[zy]

Substrate	Pathogen	Shoot decline (%)[x]	Shoot fresh wt (g)[w]		Crown rot incidence (%)	Root ball necrosis (rank)[v]
			Expt. 1	Expt. 2		
Peat	Noninoculated	0.0 ± 0.0 a	99.0 ± 4.1 bc	117.2 ± 4.1 bc	0.0 ± 0.0 a	1.0 ± 0.0 a
	Inoculated	12.5 ± 12.5 ab	75.6 ± 11.5 b	113.7 ± 3.3 bc	21.3 ± 13.2 b	1.8 ± 0.1 b
Bark	Noninoculated	4.2 ± 2.3 a	132.0 ± 6.1 c	135.1 ± 4.2 bc	0.0 ± 0.0 ab	1.0 ± 0.0 a
	Inoculated	12.0 ± 7.3 ab	110.6 ± 11.7 bc	138.3 ± 6.4 c	11.8 ± 4.8 ab	2.1 ± 0.2 b
Fiber	Noninoculated	0.0 ± 0.0 a	71.3 ± 4.1 ab	72.5 ± 6.7 a	0.0 ± 0.0 ab	1.1 ± 0.1 a
	Inoculated	47.5 ± 18.8 b	14.8 ± 9.3 a	56.4 ± 11.9 a	0.0 ± 0.0 ab	1.5 ± 0.2 b
P value						
Substrate treatment		0.056	<0.001	0.742	0.139	0.837
Pathogen treatment		<0.001	<0.001	<0.001	0.003	<0.001
Substrate × pathogen treatment		0.021	0.281	0.458	0.097	NA

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using one-way and multiway ANOVA in Rx64.4.1.0 with the Rcmdr plug in.

[y]Values after the ± symbol represent the standard error of the mean.

[x]Percentage of plants that had poor shoot health based on severe chlorosis, death of older leaves and necrosis on younger leaves; only evaluated for Expt. 1 (n = 2).

[w]Experiments were kept separate for fresh weight due to a significant experiment × pathogen interaction (n = 30–98).

[v]Root necrosis ranking reflected the percentage of roots with lesions (0% to 20% of roots with lesions = rating of 1, 21% to 40% = 2, 41% to 60% = 3, 61% to 80% = 4, 81% to 100% = 5). Data analyzed based on Kruskal–Wallis nonparametric test of significance (n = 15–50).

Table 4. Effect of irrigation and pathogen treatment on disease development for each substrate in tomato.[zy]

		Shoot decline (%)[x]				Crown rot %			
				Fiber			Bark		
Pathogen	Irrigation	Peat	Bark	Expt. 1	Expt. 2	Peat	Expt. 1	Expt. 2	Fiber
Noninoculated	Well-watered	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a
	Reduced	0.0 ± 0.0 a	4.2 ± 2.3 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0 ± 0 a
Inoculated	Well-watered	6.3 ± 6.3 a	12.5 ± 4.2 a	38.0 ± 13.0 b	0.0 ± 0.0 a	0.0 ± 0.0 a	13.4 ± 3.3 b	4.2 ± 4.1 a	16.7 ± 16.7 a
	Reduced	12.5 ± 12.5 a	12.0 ± 7.3 a	75.0 ± 24.7 b	20.0 ± 0.0 b	21.3 ± 13.2 b	19.5 ± 2.8 b	4.2 ± 4.1 a	0.0 ± 0.0 a
P value									
Irrigation treatment		0.657	0.187	0.235	<0.001	0.038	0.237	1	0.412
Pathogen treatment		0.205	0.108	0.001	<0.001	0.038	<0.001	0.23	0.341
Irrigation × pathogen treatment		0.657	0.826	0.235	<0.001	0.038	0.237	1	0.377

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using one-way and multiway ANOVA in Rx64.4.1.0 with the Rcmdr plug in. Sample sizes were as follows: shoot decline n = 2, crown rot n = 2.

[y]Values after the ± symbol represent the standard error of the mean.

[x]Percentage of plants that had poor shoot health based on severe chlorosis, death of older leaves, and necrosis on younger leaves.

plants grown under reduced and well-watered conditions, respectively. No noninoculated plants developed crown rot (Table 3 and Table 4). There were no effects of substrate on root rot development ($P = 0.837$), but there was a strong effect of pathogen ($P < 0.001$), reflecting more severe root rot in inoculated vs. noninoculated plants in every substrate (Table 3).

Chrysanthemum–*P. helicoides*: Effect of soilless substrate on chrysanthemum health with and without a pathogen present (well-watered)

Shoot growth. In Expt. 1, regardless of pathogen presence, plants grown in the bark and peat substrates were similar and resulted in taller plants than those grown in fiber; in Expt. 2, only the plants grown in peat were taller than those grown in fiber ($P < 0.001$ for substrate effect in both experiments; Table 5). Pathogen presence did not influence shoot growth in any of the substrates ($P = 0.558$ and 0.357 for Expts. 1 and 2, respectively; Table 5). Similarly, pathogen presence did not influence shoot fresh weight in any of the substrates ($P = 0.152$; Table 5). Shoot fresh weight was highest when plants were grown in bark, intermediate in peat and lowest in fiber under both noninoculated and inoculated conditions ($P < 0.001$; Table 5). Plants grown in fiber were 32% to 45% smaller than those grown in peat and bark, respectively (Table 5).

Root system health. Substrate had a significant effect on root ball coverage in Expt. 1 ($P < 0.001$) but not in Expt. 2, where root ball coverage was uniformly poor (ranking 4.9–5; $P = 0.289$ for substrate) (Table 5). In Expt. 1, plants grown in peat had healthier root balls than plants grown in bark and fiber, regardless of pathogen presence (Table 5). Pathogen treatment did not have any influence on root ball health in either experiment ($P = 1.000$ and 0.370, respectively). Pathogen presence (Y/N) influenced root ball necrosis rankings in both experiments, reflecting low to no root necrosis in noninoculated and consistently high root necrosis in *P. helicoides*–inoculated plants across substrates ($P < 0.001$) (Table 5). Substrate treatment did not influence root ball necrosis ($P > 0.05$). Based on molecular analysis, *P. helicoides* was consistently recovered from root rot in the inoculated treatment.

Chrysanthemum: Effect of soilless substrate type on chrysanthemum health under reduced irrigation (noninoculated)

Shoot growth. Under both well-watered and reduced irrigation, shoot growth in fiber was 21% to 34% lower than peat and bark across both experiments (differences were significantly different only between the peat and fiber treatments at $P < 0.001$; Table 6). Regardless of irrigation treatment, shoot fresh weight was greatest in bark, followed by peat and then fiber, with significant differences between all substrates in both experiments ($P < 0.001$; Table 6). Growth reductions under fiber ranged from 20% to 44% in comparison with peat and from 40% to 49% in comparison with bark across irrigation treatments and experiments (Table 6).

Shoot water content. Water content was consistently highest in plants grown in bark, with significant differences from fiber (42% to 49% reduction from bark) and in most

Table 5. Effects of substrate on chrysanthemum health in the absence and presence of the root rot pathogen *Phytopythium helicoides* in well-watered plants.[zy]

		Shoot ht (cm)[x]			Root ball coverage (rank)[w]		Root ball necrosis (rank)[v]	
Pathogen	Substrate	Expt. 1	Expt. 2	Shoot fresh wt (g)	Expt. 1	Expt. 2	Expt. 1	Expt. 2
Noninoculated	Peat	13.7 ± 0.9 b	11.1 ± 0.4 b	52.4 ± 1.3 b	4.6 ± 0.1 a	4.9 ± 0.1 a	1.1 ± 0.1 a	1.0 ± 0.0 b
	Bark	12.7 ± 0.4 ab	11.7 ± 0.3 b	66.2 ± 1.1 c	5.0 ± 0.0 b	5.0 ± 0.0 a	1.2 ± 0.2 a	1.0 ± 0.0 b
	Fiber	10.0 ± 0.5 a	8.2 ± 0.7 a	36.3 ± 1.9 a	5.0 ± 0.0 b	5.0 ± 0.0 a	1.3 ± 0.2 a	1.0 ± 0.0 b
Inoculated	Peat	13.1 ± 0.8 b	11.6 ± 0.5 b	52.2 ± 1.3 b	4.8 ± 0.1 a	5.0 ± 0.0 a	2.2 ± 0.3 ab	3.2 ± 0.2 a
	Bark	12.5 ± 0.3 ab	12.3 ± 0.4 b	63.9 ± 1.1 c	5.0 ± 0.0 b	5.0 ± 0.0 a	3.2 ± 0.3 b	2.9 ± 0.2 a
	Fiber	10.0 ± 0.2 a	8.0 ± 0.9 a	35.2 ± 1.8 a	5.0 ± 0.0 b	5.0 ± 0.0 a	2.1 ± 0.6 ab	3.6 ± 0.4 a
P value								
Pathogen treatment		0.558	0.357	0.152	1.000	0.370	<0.001	<0.001
Substrate treatment		<0.001	<0.001	<0.001	<0.001	0.289	0.098	0.277
Pathogen × substrate treatment treatment		0.882	0.769	0.694	NA	NA	NA	NA

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using a proc mixed procedure with SAS 9.4 (SAS Institute Inc., Cary, NC) (n = 8–24 for all response variables).

[y]Values after the ± symbol represent the standard error of the mean.

[x]Experiments analyzed separately due to significant experiment × treatment interaction ($P \leq 0.05$).

[w]Root ball coverage was ranked on a scale from 1 (80% to 100% coverage of root ball base) to 5 (0% to 20% coverage of root ball base) (Fig. 2); nonparametric Kruskal–Wallis analysis was used to evaluate treatment effects. Means comparisons reflect nonparametric based comparisons of pathogen treatment within substrate.

[v]Root necrosis ranking reflected the percentage of roots that had lesions (0% to 20% of roots with lesions = rating of 1, 21% to 40% = 2, 41% to 60% = 3, 61% to 80% = 4, 81% to 100% = 5). Data analyzed based on Kruskal–Wallis nonparametric test of significance.

Table 6. Effect of substrates on chrysanthemum growth and water content under well-watered and reduced irrigation regimes (noninoculated plants).[zy]

Irrigation	Substrate	Shoot ht (cm)		Shoot fresh wt (g)		Shoot water content (g)[x]	
		Expt. 1	Expt. 2	Expt. 1	Expt. 2	Expt. 1	Expt. 2
Well-watered	Peat	13.7 ± 0.9 c	11.1 ± 0.4 b	45.1 ± 1.1 c	59.8 ± 2.0 b	38.8 ± 1.1 b	54.3 ± 1.9 b
	Bark	12.7 ± 0.4 bc	11.7 ± 0.3 b	60.4 ± 1.6 d	72.0 ± 1.7 c	53.4 ± 1.4 c	65.4 ± 1.6 c
	Fiber	10.0 ± 0.5 ab	8.2 ± 0.7 a	35.7 ± 1.2 ab	37.0 ± 1.8 a	30.6 ± 1.1 a	33.4 ± 1.6 a
Reduced	Peat	14.1 ± 0.8 c	11.2 ± 0.4 b	40.1 ± 1.2 bc	64.0 ± 2.2 b	34.3 ± 0.9 ab	59.0 ± 2.2 bc
	Bark	12.1 ± 0.3 bc	10.5 ± 0.3 b	58.2 ± 2.1 d	65.5 ± 1.7 c	52.1 ± 1.9 c	59.2 ± 1.6 bc
	Fiber	9.3 ± 0.5 a	7.6 ± 0.4 a	30.3 ± 1.5 a	35.8 ± 1.8 a	26.3 ± 1.4 a	32.4 ± 1.7 a
P value							
Irrigation treatment		0.621	0.013	0.012	0.228	0.063	0.204
Substrate treatment		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Substrate × irrigation treatment		0.630	0.198	0.604	0.015	0.510	0.011

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using a proc mixed procedure with SAS 9.4 (SAS Institute Inc., Cary, NC) (n = 8–24 for all response variables). Experiments were separated based on significant experiment × treatment interaction.

[y]Values after the ± symbol represent the standard error of the mean.

[x]Shoot water content was calculated by subtracting the dry weight of shoots from their fresh weight at the end of the experiment.

cases peat (3% to 34% reduction from bark) ($P < 0.001$ for substrate effect; Table 6). The shoot water content of plants grown in fiber was also lower than in peat in most cases (32% to 45% reduction). In peat, water content was lower in Expt. 1 but higher in Expt. 2 under reduced vs. well-watered irrigation; this differential effect of reduced irrigation in peat vs. fiber and bark in Expt. 2 was reflected by a significant substrate × irrigation treatment interaction ($P = 0.011$; Table 6).

Chrysanthemum–*Phytopythium helicoides*: Effect of soilless substrate type on disease risk of chrysanthemum under reduced irrigation

Shoot growth. Under reduced irrigation, pathogen treatment did not influence shoot height ($P = 0.973$) or shoot fresh weight in Expt. 2 ($P = 0.645$) (Table 7). However, shoot fresh weights were higher on average for noninoculated plants across substrates in Expt. 1 ($P = 0.018$), reflecting a reduction in fresh weight in inoculated vs. noninoculated plants (Table 7). Based on means comparisons, reducing irrigation did not shift plant health dynamics under pathogen pressure across the substrates (Table 7). However, compared with plants grown under well-watered irrigation without the pathogen, the combination of reduced irrigation and pathogen reduced shoot biomass in bark across both experiments (13% to 24% biomass reduction) and in fiber in Expt. 1 (23% reduction) (Table 8).

Root health. Under reduced irrigation, pathogen presence increased the incidence of root ball necrosis across all three substrates ($P < 0.001$; Table 7). Although differences were not significant ($P = 0.071$ for substrate effect), plants grown in peat developed less root necrosis than those grown in bark, which in turn had less necrosis that those grown in fiber (Table 7).

Discussion

Soilless substrate as a driver of plant health. Taken together, these studies indicate that HydraFiber as a more renewable peat-replacing substrate may pose risks to plant health under certain conditions. This effect was consistent between two very different crops—a greenhouse vegetable crop and an ornamental—indicating that these effects may apply generally. However, further investigation is merited across a wider crop range because some plants may be more suited to the fiber environment. Additionally, our studies indicate that bark, which is also arguably more renewable than peat, has a strong potential to optimize plant growth physiologically via disease suppression and has the potential to be used in combination with water-saving techniques such as reduced irrigation to optimize environmental and economic sustainability of the system.

Our studies suggest that HydraFiber differentially enhances disease impacts compared with other substrates. *Phytophthora capsici* increased tomato shoot decline only in plants grown in fiber. Tomato fresh and dry shoot weights were greatest in bark and peat and lowest in fiber, and these substrate differences became more pronounced when examined under *P. capsici* pressure. In chrysanthemum, shoot fresh weight was reduced with the combination of reduced irrigation and *P. helicoides* in both bark and fiber but not in peat, indicating that both sustainable substrates have some risk for compromising the health of this crop.

Our results are consistent with previous work on the relative disease suppressive and nonsuppressive traits of bark and peat, respectively. Peat is derived from the accumulation of plant and moss decomposing under waterlogged conditions; during decomposition, it generally loses the ability to suppress disease (Bonanomi et al., 2015). In contrast, several studies have found that composted tree bark is an effective peat substitute capable of controlling root rot, in some cases as well as

Table 7. Substrate × pathogen interactions under reduced irrigation in chrysanthemum.[zy]

Substrate	Pathogen	Shoot growth (cm)	Shoot fresh wt (g)		Shoot dry wt (g)		Root ball necrosis (rank)[x]
			Expt. 1	Expt. 2	Expt. 1	Expt. 2	
Peat	Noninoculated	12.6 ± 0.3 c	40.1 ± 1.2 b	64.0 ± 2.2 b	5.6 ± 0.4 b	5.1 ± 0.2 b	1.1 ± 0.1 a
	Inoculated	12.5 ± 0.3 bc	40.1 ± 1.0 b	61.5 ± 2.2 b	5.8 ± 0.3 b	5.4 ± 0.2 b	2.0 ± 0.2 b
Bark	Noninoculated	11.3 ± 0.3 b	58.2 ± 2.1 c	65.5 ± 1.7 b	6.1 ± 0.3 b	6.3 ± 0.2 c	1.3 ± 0.1 a
	Inoculated	11.3 ± 0.3 b	52.7 ± 1.2 c	65.6 ± 1.7 b	6.2 ± 0.2 b	5.7 ± 0.2 bc	2.2 ± 0.1 b
Fiber	Noninoculated	8.5 ± 0.5 a	30.3 ± 1.5 a	35.8 ± 1.8 a	4.3 ± 0.2 a	3.4 ± 0.2 a	1.1 ± 0.1 a
	Inoculated	8.4 ± 0.5 a	27.2 ± 1.5 a	39.0 ± 3.3 a	4.0 ± 0.4 a	3.3 ± 0.3 a	2.9 ± 0.4 b
P value							
Substrate treatment		<0.001	<0.001	<0.001	<0.001	<0.001	0.071
Pathogen treatment		0.973	0.018	0.645	0.881	0.456	<0.001
Substrate × pathogen treatment		0.990	0.200	0.520	0.910	0.078	NA

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P < 0.05$). Variables were analyzed using a proc mixed procedure with SAS 9.4 (SAS Institute Inc., Cary, NC). Sample sizes were n = 8–24 for all response variables.

[y]Values after the ± symbol represent the standard error of the mean.

[x]Root necrosis ranking reflected the percentage of roots that had lesions (0% to 20% of roots with lesions = rating of 1, 21% to 40% = 2, 41% to 60% = 3, 61% to 80% = 4, 81% to 100% = 5). Data analyzed based on Kruskal–Wallis nonparametric test of significance.

Table 8. Effect of irrigation and pathogen treatment on shoot fresh weight (g) for each substrate in chrysanthemum.[zy]

		Peat[x]		Bark[w]		Fiber[x]	
Pathogen	Irrigation	Expt. 1	Expt. 2	Expt. 1	Expt. 2	Expt. 1	Expt. 2
Noninoculated	Well-watered	45.1 ± 0.9 b	59.8 ± 2.0 a	60.4 ± 1.6 b	72.0 ± 1.5 a	35.7 ± 1.1 b	37.0 ± 1.8 a
	Reduced	40.1 ± 0.9 a	64.0 ± 2.2 a	58.2 ± 2.1 ab	65.5 ± 1.7 a	30.3 ± 0.9 a	35.8 ± 1.8 a
Inoculated	Well-watered	44.9 ± 1.2 b	59.5 ± 1.9 a	56.7 ± 1.4 ab	71.2 ± 1.8 a	28.9 ± 0.7 a	41.5 ± 4.3 a
	Reduced	40.1 ± 0.8 a	61.5 ± 2.2 a	52.7 ± 1.2 a	65.6 ± 1.7 a	27.2 ± 0.5 a	39.0 ± 3.3 a
P value							
Irrigation treatment		<0.001	0.156	0.052	0.001	0.017	0.460
Pathogen treatment		0.914	0.506	0.004	0.837	0.001	0.226
Irrigation × pathogen treatment		0.931	0.587	0.581	0.779	0.183	0.829

[z]Mean values in a column followed by the same letter are not significantly different according to Tukey's means comparison ($P > 0.05$). Variables were analyzed using a proc mixed procedure with SAS 9.4 (SAS Institute Inc., Cary, NC). Sample sizes were n = 8–24 for all response variables.

[y]Values after the ± symbol represent the standard error of the mean.

[x]Experiments were kept separate due to significant differences between them ($P < 0.001$).

[w]Experiments were kept separate due to a significant experiment by irrigation interaction ($P < 0.001$).

fungicides (Benson and Ownley, 1991; Hardy and Sivasithamparam, 1991; Hoitink and Han, 1997; Yu and Komada, 1999). In two studies comparing Phytophthora root rot of rhododendron (caused by *Phytophthora cinnamomi*), disease was positively correlated with less bulk density and smaller pore spaces, and plants growing in pine bark or pine bark mixtures were healthier than those growing in peat-based mixes (Benson and Ownley, 1991; Ownley et al., 1990). Beyond oomycete pathogens, a study comparing disease development of tomatoes growing on either rockwool or hinoki bark fiber slabs found that crown and root rot (caused by the fungus *Fusarium oxysporum* f. sp. *radicis-lycopersici*) and bacterial wilt (caused by *Pseudomonas solanacearum*) were greatly reduced in the bark fiber slabs (Yu and Komada, 1999). Disease suppression was credited to volatile oils and nonvolatile substances in the bark, with both neutral and acidic substances having high activity against the pathogen (Yu and Komada, 1999).

There has been very little work on the impacts of HydraFiber specifically. Although our finding that HydraFiber was more detrimental to growth runs contrary to one previous study, which indicated no negative impact of HydraFiber on begonia growth (Eveleens et al., 2021), our results are consistent with studies in coconut fiber (Arenas et al., 2002; Meerow, 1994) and wood fiber (Zawadzińska et al., 2021). Our study had an unbalanced design, with fewer replicates for HydraFiber, due to limited availability of this substrate from the collaborating producer. Future studies with a balanced design may provide more robust information on substrate performance. Previous work has shown that the addition of nitrogen fertilizer to wood fiber substrates can ameliorate negative impacts on growth (Gruda and Schnitzler, 1999; Zawadzińska et al., 2021). It is possible that the low fertilizer rates used in the study enhanced the differential effects of this substrate compared with bark and peat. Gruda and Schnitzler (1999) found that compaction of wood fiber in pots can lead to detrimental effects on tomato root growth. Future studies evaluating different fertilizers, compaction, and perhaps other conditions may be successful in identifying management methods that would eliminate the negative growth impacts of HydraFiber. The inclusion of pH and electroconductivity metrics in future studies could shed more light on the influences of the substrates on pathogens and plant health.

In addition to negative effects on growth, our work indicates that HydraFiber has potential disease-enhancing effects; rot enhancement was typically observed under well-watered conditions, which suggests poor drainage in this substrate. Some of these impacts may also be minimized through the improved management methods considered above. In addition, such impacts may be controlled through a more aggressive chemical management regime.

Interactions of soilless substrate with sustainable water use. Previous studies of reduced irrigation methods indicate that, although in many cases irrigation reductions can be achieved without physiological impacts on plant growth, certain reduced irrigation practices can also incur a growth cost to many crops, including greenhouse tomatoes (Chand et al., 2021; Del Castillo Múnera et al., 2019a; Pulupol et al., 1996) and chrysanthemums (Giordano et al., 2021). Further, studies with pathogens indicate that reduced irrigation regimes that are not harmful physiologically may still compromise production by enhancing disease impacts when a pathogen is present (Swett, 2020). Our work is consistent with previous studies of the tomato–*P. capsici* pathosystem, in which reducing irrigation inputs increased crown and root rot severity and enhanced incidence of vine decline (Del Castillo Múnera et al., 2019a). Although there are limited studies of chrysanthemum, in a study of the ornamental crop poinsettia, Pythium root rot (caused by Pythium *aphanidermatum*) was also enhanced under severe water reductions (Del Castillo Múnera et al., 2019b). This effect extends beyond oomycete pathogens to true fungi as well as fungal vectors of plant pathogens, such as viruses (Swett, 2020).

In our study, we furthered our understanding of the impacts of reduced irrigation inputs on plant health by contextualizing this practice in a substrate-use framework. Based on our analysis of two crops, substrate type has a significant effect on the impacts of irrigation reductions, wherein growth inhibition was most apparent in those substrates (bark, peat) where growth was otherwise optimal. In fiber, it is likely that the negative effects of reduced irrigation were not typically apparent because growth was uniformly poor. When a pathogen was present, reduced irrigation enhanced pathogen effects in fiber in both crops. Pathogen effects were also enhanced in peat for tomatoes and in bark for chrysanthemums. However, there was no negative effect of reduced irrigation on tomatoes grown in bark or chrysanthemums grown in peat—the two substrates that most optimized growth of these crops. This points to an interesting opportunity to use certain substrates to enhance grower capacity to optimize water reduction without affecting plant growth. Such an approach may have strongest appeal in water-scarce regions where the cost and availability of water are major determinants of production capacity and profit margins.

Relative informativeness of metrics for assessing plant health. To evaluate the effects of substrate, pathogen, and soil moisture on plant health, shoot height, shoot fresh weight, shoot dry weight, root ball health, and root ball necrosis were measured for all plants. Crown rot, a symptom of *P. capsici*, was also quantified in the tomato plants based on incidence and severity (lesion length). Although all metrics did not provide strong data for evaluating the influence of substrate, irrigation, and pathogen presence, several metrics were useful for each. For example, shoot weight was not a strong metric for pathogen effect but was helpful for evaluating substrate effects. Root ball necrosis rankings captured pathogen effects but were problematic; many of the roots were fully decayed at the time of root system evaluation, and root ball necrosis was only ranked for roots that were present. With a small percentage of roots present, this measure could not accurately reflect pathogen effects. Decline and crown rot incidence were compelling indicators of substrate effects on disease, although when experiments had to be separated, small replicate size often resulted in nonsignificant effects; lesion

length was also not a strong indicator of substrate–disease interactions.

Conclusion

As environmental sustainability challenges drive the containerized crop production industry to adapt, growers face increasing uncertainty about the economic sustainability of their production systems. Negative crop health impacts of "more sustainable" practices are poorly understood, and there is very little information on crop health mediators, such as pathogens. Further, very few studies have assessed the interactions between different sustainability-driven adaptions, such as adaptations in substrate and water use. These information gaps create strong barriers to adoption and, in cases of adoption, can allow for negative economic impacts of practices that are harmful to crop production. Our study points to the significant health risks of adopting fiber-based substrates, particularly Hydra-Fiber, based on both negative physiological effects and disease-enhancing impacts. On a more positive note, our study suggests that bark-based substrates (which have greater sustainability potential than peat) typically do not have growth costs and may further suppress root-infecting pathogens. Although reduced irrigation did have growth penalties, for both crops examined there was one substrate with which a growth cost was not incurred. This may indicate that substrate selection could be used as a tool for growers in water scare regions optimize water use.

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