Irrigation Frequency and Volume has Little Influence on Phytophthora Root Rot in Container-grown Rhododendron[1]

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Abstract

We evaluated whether reducing irrigation frequency and volume alters the ability of *Phytophthora plurivora* and *P. cinnamomi* to cause root rot on rhododendron grown in a noninfested potting medium or media infested with 1 or 100 propagules per gram (ppg) of pathogen. Plants were irrigated to maintain a substrate moisture of >70% container capacity (1.0X), one-half volume of 1.0X (0.5X), or two times the volume of 1.0X at each irrigation event for one week, followed by no irrigation, until soil moisture reached <50% container capacity. Aboveground disease symptoms (chlorosis, stomatal conductance, wilting, and plant death) were evaluated weekly and root rot, pathogen presence, plant biomass, and nutrient uptake were measured at the end of each trial. Both pathogens generally caused mild disease at 1 ppg and severe disease at 100 ppg. Reducing irrigation did little to lessen disease caused by either pathogen once infection had occurred. Instead, severe root infection often led to increased soil moisture and root rot across all irrigation treatments as roots became progressively compromised in their ability to take up water. Results show that reducing irrigation after infection has occurred is unlikely to effectively control root rot.

Species used in this study: *Phytophthora* species (*Phytophthora cinnamomi* Rands; *Phytophthora plurivora* T. Jung and T.I. Burgess); rhododendron, *Rhododendron catawbiense* Michx. 'Album', 'Roseum Elegans', and 'Roseum Pink'.

Index words: Phytophthora root rot, *Phytophthora cinnamomi*, *Phytophthora plurivora*, rhododendron.

Significance to the Horticulture Industry

Plant pathogens in the genus *Phytophthora* cause root rot that decreases product quality and results in plant death and economic losses to the nursery industry. Nursery production of rhododendron is often severely compromised by root rot and there are few cultural practices to mitigate the disease. Recently, we found that *Phytophthora plurivora* is prevalent on rhododendron in nurseries in the Pacific Northwest, USA, but there is little information available to compare its pathogenicity in different environments to *P. cinnamomi*, a more well-studied Phytophthora root rot pathogen. While it is well known that *Phytophthora* infection is favored by abundant soil moisture, it is unclear whether irrigation management can be used to decrease root rot incidence or severity in container-grown rhododendron nursery plants. Our results indicate that: (1) low inoculum levels of either pathogen cause mild disease whereas higher levels cause severe disease; (2) *P. plurivora* causes similar losses in rhododendron plants as *P. cinnamomi*; (2) *Phytophthora* can be isolated from asymptomatic plants and may pose a risk to pathogen spread since even low inoculum levels can decrease plant health; (3) plants grown in media free of *Phytophthora* can adapt better to a broader range of irrigation regimes than plants grown in pathogen-infested media; and (4) reducing irrigation after infection has occurred is ineffective at reducing the amount of root rot caused by either *Phytophthora* species. This work provides novel insights into water management for control of *Phytophthora* infection in container nurseries.

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Introduction

Oregon recently ranked third in the United States for nursery stock production, with only 26% staying in-state and the remainder exported to other states (69%), or sold internationally (5%) (USDA National Agricultural Statistics Service 2020). Rhododendrons (*Rhododendron* species and cultivars) are an important component of the Pacific Northwest (PNW) nursery industry, with an annual value of over $11.6 M (USDA National Agricultural Statistics Service 2020). Nursery production of rhododendron is often severely compromised by Phytophthora root rot, with losses of up to 100% reported (Benson et al. 1982, Weiland et al. 2020).

Many *Phytophthora* species cause root rot, including *P. cactorum*, *P. cinnamomi*, *P. citricola* or *P. plurivora*, *P. pini*, *P. cryptogea*, and *P. pseudocryptogea* (Hoitink et al. 2014, Parke et al. 2014, Sacher et al. 2021, Weiland et al. 2018, Weiland et al. 2020). A recent survey of Oregon nurseries found that *P. cinnamomi* and *P. plurivora* were the most prevalent *Phytophthora* species isolated from rhododendrons with symptoms of root rot (Weiland et al 2020). Most research on Phytophthora root rot has focused on *P. cinnamomi*, and except for our recent research, little is known about the potential impact of *P. plurivora* to the industry (Sacher et al. 2021, Weiland et al. 2018, Weiland et al. 2020). *Phytophthora plurivora* was only formally

described ~12 years ago and was previously recognized as *P. citricola* (sensu lato), a highly aggressive pathogen of major native tree species both in North America and Europe (Jung and Burgess 2009).

Phytophthora species and isolates can differ in their sensitivity to both low and elevated substrate moisture (SM) (Browne and Mircetich 1988, Davis et al. 2021, Gisi et al. 1980). *Phytophthora* infection is favored by abundant SM because the zoospores produced by the pathogen need water to move to the roots and infect the host (Blaker and MacDonald 1981, Hoitink et al. 2014, Krebs 2013). Therefore, root rot is often more severe when SM is high (Blaker and MacDonald 1981, Krebs 2013, Ownley and Benson 1991, Mestas et al. 2022). In blueberry fields, irrigation practices that reduce water saturation are associated with less root rot by *P. cinnamomi* (Bryla and Linderman 2007, Vargas et al. 2015, Yeo et al. 2017). Similarly, root rot of rhododendron is much less severe on substrates that retain less water (Ownley and Benson 1991). Although reducing water availability can reduce infection, it may also increase plant water stress (Scagel et al. 2011, 2014) and susceptibility to the pathogen (Blaker and MacDonald 1981). Development of Phytophthora root rot in some plant species appears to be more marked in climates that alternate between wet and dry periods (Burgess et al. 2017). Wet-dry cycles maximize the frequency and the duration of periods in which soil is wet, but not saturated at field capacity. In addition, plants infected during wet periods may become more susceptible to colonization by *Phytophthora* due to the stress induced by prolonged periods of drought (Desprez-Loustau et al. 2006). Rhododendron growers commonly keep plants consistently moist or unintentionally follow a "boom/bust" regimen (similar to a wet-dry cycle), where growers do not water plants until there are signs of water stress (wilting) and then water abundantly until the plants have recovered.

Together, these observations suggest that cultural methods that reduce soil water availability while maintaining plant growth may be useful for managing Phytophthora root rot of rhododendron. We have recently reported differences in pathogenicity and fungicide sensitivity among isolates of *P. cinnamomi* and *P. plurivora*, and reported how the amount of inoculum influences disease progression (Sacher et al. 2021, Weiland et al. 2018, Weiland et al. 2021). Understanding how *P. cinnamomi* and *P. plurivora* react to different irrigation practices and to reduced soil moisture will help us incorporate what we have learned regarding pathogen biology and fungicide control into an integrated package for Phytophthora root rot management. Our objectives were to determine whether reducing irrigation frequency and volume would alter the incidence and severity of Phytophthora root rot in container-grown rhododendron plants inoculated with either *P. cinnamomi* or *P. plurivora* at low and high inoculum levels.

Materials and Methods

Isolate selection. One isolate each of *P. cinnamomi* (R001, GenBank accession number MG560190) and *P. plurivora* (R003, GenBank accession number MG560192) were selected based on species prevalence in the PNW rhododendron industry (Weiland et al. 2020) and on their ability to cause disease (Sacher et al. 2021, Weiland et al. 2018, Weiland et al. 2021).

Plant selection. Hybrids of *R. catawbiense* (RHS 58) were selected based on their susceptibility to *P. cinnamomi* and *P. plurivora* in previous experiments (Sacher et al. 2021, Weiland et al. 2021). Plants were obtained as 15 cm (6 in) rooted cuttings grown in polystyrene liner trays [4.5 × 4.5 × 40 cm (1.8 × 1.8 × 15.7 in); 310 cm^3 (19 in^3) root volume cells). Each trial used a different *R. catawbiense* hybrid: *R.* 'Album' (trial 1, 2015), *R.* 'Roseum Elegans' (trial 2, 2016), and *R.* 'Roseum Pink' (trial 3, 2017) because of changes in cultivar availability at the source nursery. Biomass (oven dry weight, DW) of 10 random plants was measured at the beginning of trials 2 and 3 to estimate plant size. At the beginning of trial 2 and 3, respectively, total plant biomass was 6 ± 2 g and 3 ± 1 g and the root to shoot ratio was 0.44 ± 0.10 and 2.1 ± 0.80. Plant size was not determined at the start of trial 1.

Inoculum preparation and inoculation method. Pathogen isolates were grown in fungal spawn bags (Fungi Perfecti, Olympia, WA) as previously described (Weiland et al. 2018, Weiland et al. 2021). Noninfested vermiculite incubated under the same conditions was used for noninoculated control plants. Inoculum was removed from the bags, air-dried for up to 3 days, and stored in resealable polyethylene bags at 20 C (68 F) until used to infest a soilless potting medium. For each isolate, inoculum was diluted to infest the potting medium (60 sphagnum peat moss: 30 bark: 10 coarse perlite; SunGro Metro-Mix 840PC, SunGro Horticulture, Agawam, MA) at 1 and 100 propagules per gram (ppg) of mix using established procedures (Weiland et al. 2018). Infested and noninfested soilless media were then distributed into 2.84 L (0.75 gal) polypropylene pots (Elite 300 nursery pot, The HC Companies, Twinsburg, OH) and planted with a single rhododendron plant. Ten replicate plants per each inoculation treatment × irrigation regime were transplanted into pots of infested and noninfested media.

Growing conditions and fertilization. All trials were conducted outside (Corvallis, OR; lat. 45°59′04″ N, long. 123°27′22″ W) on raised benches. Environmental sensors measured air temperature (T_{air}), relative humidity (RH) (Vaisala HMP60, Vaisala Co., Helsinki, Finland) and photosynthetically active radiation (PAR) (Licor Quantum, LI-COR Inc., Lincoln, NE) and data were logged hourly (LI 1400, LI- COR Inc., Lincoln, NE). During inoculation, T_{air} was much warmer in trial 1 [average 21 C (70 F), maximum 32 C (90 F)] than in trials 2 and 3 [average 18 C (64 F), maximum 26 C (79 F)]. In general, trial 3 was warmer and drier during the study than trials 1 and 2 (Fig. 1). Maximum substrate temperatures were generally greater than maximum air temperatures and during trial 3, temperatures exceeded 35 C (95 F) for 1-6 hours (ten times) and exceeded 40 C (104 F) for 2-4 hours twice (Fig. 2, Trial 1 and 2 not shown). Trial 1 plants were fertilized 8 weeks after inoculation (WAI) with 200 ml (6.8 oz) per pot

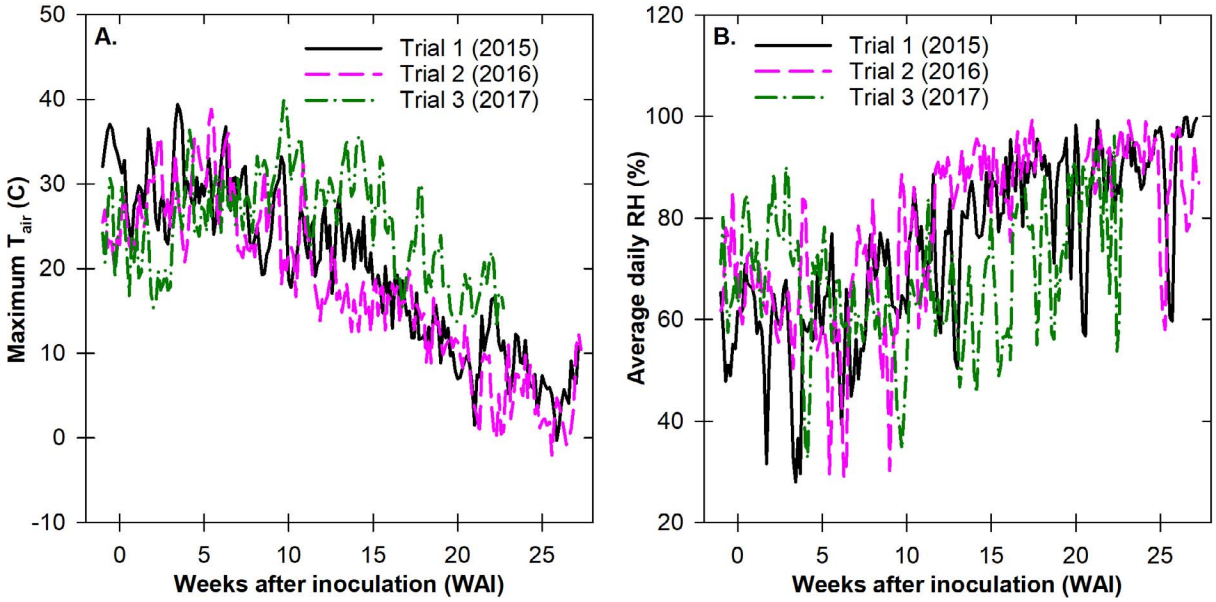

Fig. 1. Maximum daily air temperature (T_{air}) and average daily relative humidity (RH) during each trial. For trials 1 to 3, respectively, plants inoculated on 06 July 2015, 12 July 2016, or 05 May 2017; flooded 2, 2, or 3 weeks after inoculation (WAI); and harvested 27, 26, or 23 WAI. (1 C = 33.8 F).

of 0.5X strength liquid fertilizer [Miracle-Gro Azalea, Camellia, Rhododendron Plant Food (30-10-10), Miracle-Gro, Inc., Marysville, OH]. In trials 2 and 3, soilless media was amended with 3.6 $g \cdot L^{-1}$ (0.48 $oz \cdot gal^{-1}$) slow-release Harrell's 21-5-6 fertilizer (Harrell's, LLC, Lakeland, FL) while the media was mixing with the vermiculite inoculum in the cement mixer. In addition, plants in trials 2 and 3 were fertilized with 200 ml (6.8 fl oz) of the same liquid fertilizer used in trial 1 at 7 WAI (trial 2) and 4 WAI (trial 3). Liquid fertilizer applications were scheduled based on whether leaf greenness (estimated using a Dualex Scientific meter, Force-A, Orsay Cedex, France) was consistently <25 relative chlorophyll units in the noninoculated control plants. When liquid fertilizer was used, irrigation systems were turned off for 12 h prior to, and resumed 8 h after, fertilization.

Experimental design. The experimental design was a full factorial, complete randomized block design with ten replicate blocks (one plant of each treatment per block) containing five inoculation treatments (noninoculated control, and *P. cinnamomi* and *P. plurivora* at 1 ppg and 100 ppg), and 3 irrigation regimes (1X, 0.5X, and BB). Inoculations were performed on 06 July 2015 (trial 1), 12 July 2016 (trial 2), and 25 May 2017 (trial 3). Irrigation treatments were implemented starting two days after inoculation (DAI) (except during flooding, described below). Trials ran for 27 (trial 1), 26 (trial 2), and 23 (trial 3) WAI.

Irrigation treatments and watering. Plants were hand watered during the first 2 DAI. Irrigation treatments started 3 DAI using an automated drip system set to deliver water in one of 3 regimes. All irrigation treatments were delivered two times per day (at 0600 and 2000) using drip irrigation [3.8 L (1 gal)$\cdot h^{-1}$ drip emitter in each pot: model DPC02-MA-AL-Blue; Toro Company, El Cajon, CA, U.S.A.]. Irrigation volume was adjusted throughout each trial based on substrate volumetric water content (VWC or Θ) in the 1.0X regime of control plants. The 1.0X treatment was irrigated with a target of an average daily substrate moisture at a VWC of >0.34 $m^3 \cdot m^{-3}$ (>70% container capacity, CC); the 0.5X treatments was irrigated with half the volume of the 1.0X at each irrigation event; and plants in the "boom-bust" treatments (BB) were irrigated with two times the volume of the 1.0X at each irrigation event for one week, followed by no irrigation, until volumetric water content reached ∼0.15 $m^3 \cdot m^{-3}$ (∼50% CC). Irrigation treatment were altered in trial 1 based on daily measurements and in trials 2 and 3 based on average daily measurements. All plants were flooded 2 WAI (trial 1 and 2) or 3 WAI (trial 3) to encourage zoospore release and infection according to previous methods (Mestas et al. 2022, Sacher et al. 2021, Weiland et al. 2018). Maximum air temperatures (T_{max}) during flooding were cooler during trial 3 [average 13 C (55 F), maximum 18 C (64 F)] than in trials 1 and 2 [average 20 C (68 F), maximum 28 C (82 F)] (Fig. 1, average temperature not shown). Maximum recorded mid-day substrate temperature was greater than 38 C (90 F) after flooding in trial 3, 29 C (84 F) in trial 1, and 31 C (88 F) in trial 2 (Fig. 2, trial 1 and trial 2 not shown).

Substrate environmental variables [VWC, substrate temperature (T_{sub}), and electrical conductivity (EC)] were monitored differently among trials (T_{sub} and EC data not presented). In trial 1, substrate measurements were taken five times per week at mid-day using a hand-held probe (GS3 probe with ProCheck meter, Decagon Devices, Inc., Pullman WA) from each irrigation treatment in control plants from 2 WAI to 12 WAI and plants inoculated with *P. cinnamomi* at 100 ppg from 6 WAI to 12 WAI (n=10). In trials 2 and 3, substrate measurements were collected continuously using EM50 data loggers (Meter Group, WA)

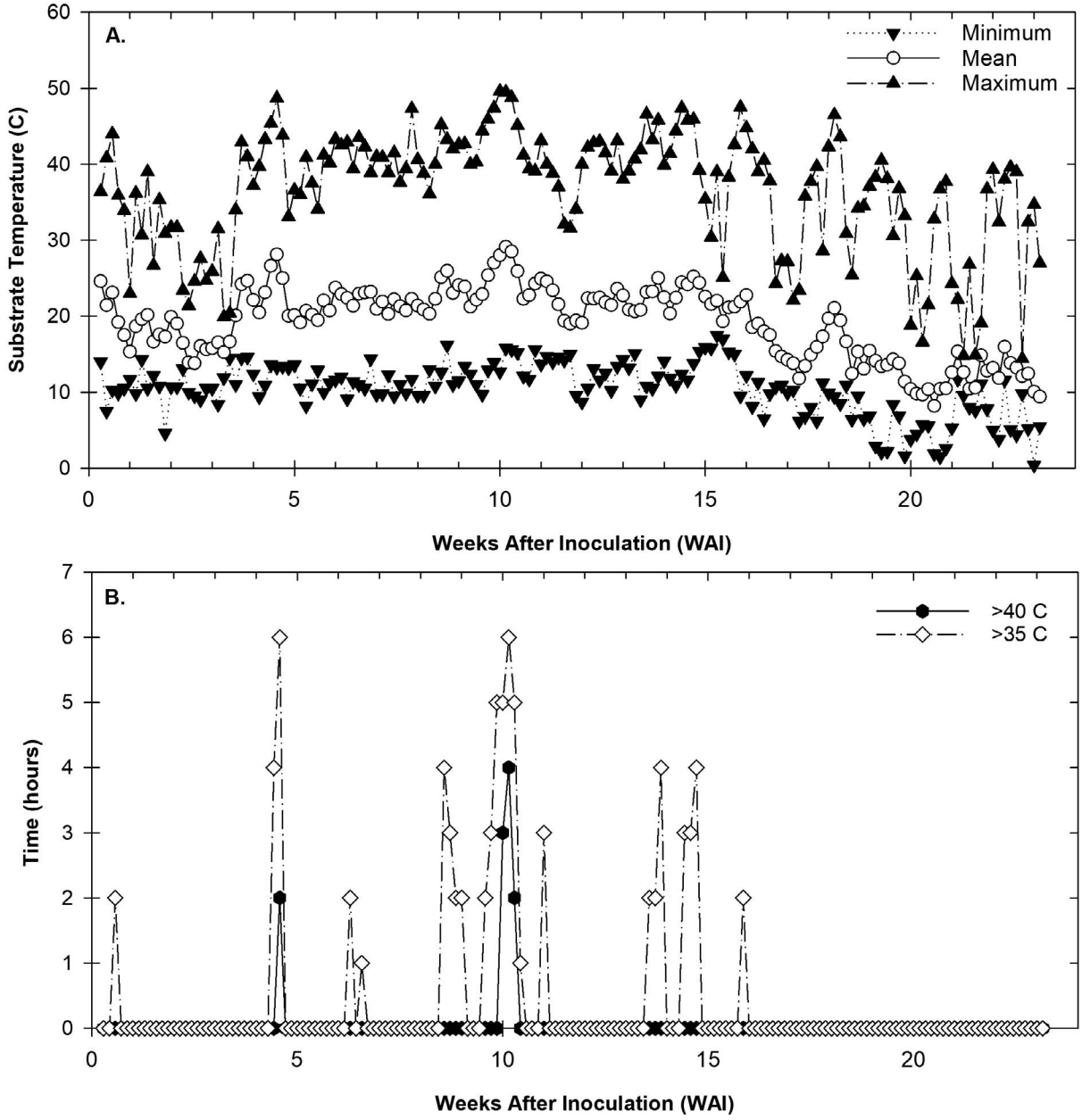

Fig. 2. Maximum daily substrate temperature (T_{sub}) and number of hours per day with temperatures >40 C and 35 C during Trial 3. Plants inoculated on 05 May 2017, flooded 3 weeks after inoculation (WAI); and harvested 23 WAI. (1 C = 33.8 F).

connected to ECH20 5TE probes (Meter Group, WA) (n=5). In trial 2, substrate measurements were taken in each irrigation treatment from 2 WAI to 14 WAI in control plants, from 2 WAI to 6 WAI in plants inoculated with pathogens at 100 ppg. In trial 3, substrate measurements were taken in each irrigation treatment from 0 WAI to 24 WAI in control plants and those inoculated with pathogens at 100 ppg. Probe VWC output was calibrated to substrate container capacity (CC) at the beginning of each trial using the same substrate and containers used in the trial. Irrigation treatments were stopped at the end of September in each year, ~12 WAI (trial 1), 13 (trial 2), and 19 (trial 3) WAI.

Disease and plant health evaluation. Plants were visually evaluated weekly for disease symptoms (chlorosis, wilting, or plant mortality) on an absent (0) or present (1) basis until November in each year. Leaf color was evaluated near-weekly on the three most recently expanded leaves of each plant using a Dualex Scientific Force-A meter to estimate chlorophyll, anthocyanin and flavonol content (Orsay Cedex, France) or a SPAD-502 meter (Spectrum Technologies, Inc., Plainfield, IL) to estimate leaf chlorophyll content. The Dualex meter needed to be repaired during one field season and only chlorophyll data was taken consistently. Leaf color measurements were stopped at the end of September in each trial. Leaf stomatal conductance (g_s) was used to periodically assess plant water stress by measuring leaf water loss with a steady state porometer (LI-1600; LI-COR, Lincoln, Nebraska) (Scagel et al., 2012). Leaf g_s was evaluated on two fully-expanded current season leaves per plant at mid-day

(between 1030 and 1430) on 5 plants in selected treatments. Measurements of g_s were made on 5 dates between July and September in trial 1, 10 dates between July and September in trial 2, and 10 between June and September in trial 3. Where possible, the same plants used to measure substrate moisture were used for g_s measurements.

At the end of each trial, shoots were clipped from roots at soil line and potting mix was removed from roots by washing. Root samples (four 1-cm-long roots collected at random from around the root ball) and stem samples (2-cm segment from the base of each stem) were collected from each plant and plated onto PARP medium to confirm infection by the appropriate *Phytophthora* spp. or lack of infection in control plants. The remaining root system was then rated for root rot in one of the following categories: healthy = dense, white or tan root system with <10% root rot; moderate root rot = patchy or partially rotted root system with 10 to 75% of the roots appearing dark brown; and severe root rot = sparse, mostly or completely rotted root system with >75% of the roots appearing dark brown and having little structural integrity (Weiland et al. 2018).

All remaining plant tissue was oven dried at 60 C (140 F) for at least 4 d and weighed to obtain shoot and root dry weight (DW). Dried samples from control and 1 ppg pathogen treatments from trials 1 and 2 were ground to pass through a 40-mesh [425 μm (0.02 in)] screen then analyzed for C and N using a combustion analyzer (TruSpec CN, Leco Corp., St. Joseph MI), P, K, Ca, Mg, S, Fe, B, Cu, Mn, Zn, and Na using ICP-OES (Optima 3000DV, Perkin Elmer, Wellesley MA) following microwave digestion in 70% (v/v) nitric acid (Gavlak et al. 2005, Jones et al. 1990). Reference standard apple (*Malus domestica* Borkh.) leaves (no. 151, National Institute of Standards and Technology, Gaithersburg MD) were included in each set of samples to ensure accuracy of instrument and digestion procedures. Elemental content of each plant part was calculated by multiplying the DW of a given part by the concentration of each element therein and total plant content was calculated by adding the content of a specific element from each plant part (Chapin and Van Cleve 1989). Total plant concentrations of each element were calculated by dividing plant content by plant DW.

Data analyses. All data were analyzed using Statisica (version 14; TIBCO Software Inc. Palo Alto, CA) or JMP (version 15.1; SAS Institute Inc, Cary, NC). Binomial data (incidence of visual symptoms, pathogen isolation, and root rating category) were analyzed using X^2 with Yates' correction and generalized linear models with a logit link function. Data is presented as the percentage of plants or number of plants in each category and differences in frequency among treatments were assessed at $P < 0.05$. Disease progression was evaluated by calculating the area under a disease progress curve (AUDPC) (Madden et al. 2007, Simko and Piephon 2012) based on plant mortality and time of symptom occurrence (WAI). ANOVA assumptions for normality and homogeneity of variance of AUDPC, stomatal conductance (g_s), leaf color, biomass (DW), and nutrient content data were assessed by examining P-P plots, using the Shapiro-Wilk test for normality (Shapiro et al. 1968) and using Brown-Forsythe test for homogeneity of variance (Brown and Forsythe 1974). Data for AUDPC occurrence did not meet ANOVA assumptions for normality and homogeneity of variance and were analyzed using Kruskal-Wallis ANOVA by Ranks and differences assessed at $P < 0.05$.

Biomass data and nutrient uptake data were analyzed by ANOVA with trial, pathogen treatment, and irrigation treatment as main effects in a fully factorial model. To account for differences in plant size influencing nutrient content, plant nutrient uptake data were analyzed separately for each trial with DW as a covariate (Scagel et al. 2012). Leaf color and g_s data were analyzed separately for each trial by repeated measures ANOVA with date, pathogen treatment, and irrigation treatment as main effects in a fully factorial model. Differences in biomass were assessed at $P < 0.05$ using Tukey's honestly significant difference. Block effects were not observed in any analyses ($P > 0.05$) and are not described in the results.

Results and Discussion

Noninoculated control plants. Irrigation treatments had little influence on health of noninoculated controls even though substrate moisture and plant water stress differed among irrigation treatments. No control plants died (0%), few had symptoms of wilt or chlorosis (<10%), almost all had healthy root systems (99%), and no *Phytophthora* pathogens were isolated from plants at the end of the trials (Table 1, pathogen isolation data not shown). Differences in control substrate moisture and plant water stress among irrigation treatments only occurred on specific measurement dates in each trial. On average, control plants in the 1.0X irrigation treatment had the greatest VWC and the BB treatment had the lowest VWC (Fig. 3) and control plants in the 1.0X treatment had less water stress than in the other two irrigation treatments. For example, in trial 1, the average g_s in 1.0X plants was 347 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared to 295 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 274 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively, in the 0.5X and BB plants. During trial 1, g_s in 1.0X plants was 5% to 55% greater than in other irrigation treatments depending on the measurement date. In trials 2 and 3, when plants were larger, differences in g_s between 1.0X plants and other treatments were less than 15%.

Leaf chlorophyll and anthocyanin values in noninoculated control plants differed among irrigation treatments and measurement dates (data not shown). Lower available substrate moisture generally decreased anthocyanin values in control plants (e.g. BB and 0.5X had similar or lower anthocyanin values than 1.0X) and increased leaf chlorophyll values suggesting that the 1.0X treatment may have had lower nutrient availability because nutrients were leached from containers. Lower available substrate moisture generally increased nutrient uptake (total plant nutrient content, data not shown). In trial 1, plants in the 0.5X and BB treatments had the greatest uptake of most nutrients, including N, P, K, S, Ca, Mn, B, and Zn. In trial 2, plants in the 0.5X treatment had the greatest uptake of most nutrients. The effect of irrigation treatments on plant biomass differed among trials and irrigation treatments.

Table 1. Number of plants with aboveground disease symptoms, belowground disease symptoms (root rot), and area under the disease progress curve (AUDPC) for *Rhododendron catawbiense* 'Boursault' (Trial 1), 'Roseum Elegans' (Trial 2), and *R.* 'Roseum Pink' (Trial 3) grown in a noninfested potting medium (Control) or in media infested with *Phytophthora plurivora* or *P. cinnamomi* at 1 ppg or 100 ppg.[z]

	Aboveground symptoms (number of plants)				Root rot (number of plants)			AUDPC			
Treatments	**Trial 1**	**Trial 2**	**Trial 3**	**Total**	**None**	**Some**	**Severe**	**Trial 1**	**Trial 2**	**Trial 3**	**Total**
Pathogen Treatments											
Control	2cA	0bA	1cA	3d	89aA	1cB	0cB	-	-	-	-
P. plurivora											
1 ppg	7bcA	5bA	9bA	21c	77bA	9abB	4cB	150bA*	0bB	0bB	50c*
100 ppg	22aA	19aA	25aA	66a	20cB	8bC	62aA	1745aA*	1385aB*	1688aA*	1599a*
P. cinnamomi											
1 ppg	10bA	6bA	3bcA	19c	67bA	17aB	6cC	130bA*	0bB	71bB	67c*
100 ppg	22aA	23aA	5bcA	50b	30cB	14abC	46bA	1518aA*	1397aA*	72bB	991b*
Pathogen x Irrigation Treatments											
P. plurivora											
1 ppg											
1.0 X	2	3	4	9d	26aA	2aB	2cB	0	0	0	0e
0.5 X	1	0	1	2e	28aA	2aB	0cB	0	0	0	0e
BB	4	2	4	10cd*	23aA	5aB	2cB	450	0	0	150d*
100 ppg											
1.0 X	6	7	7	20ab*	9bB*	2aB	19abA*	1940	1125	1385	1483b*
0.5 X	8	5	8	21ab*	7bB*	3aB	20aA*	1410	1525	1617	1516b*
BB	8	7	10	25a*	4bB*	3aB	23aA*	1820	1505	2065	1797a*
P. cinnamomi											
1 ppg											
1.0 X	2	2	0	4de	22aA	5aB	3cB	195	0	55	80d*
0.5 X	6	2	1	9d	23aA	6aB	1cB	197	0	60	82d*
BB	2	2	2	6de	22aA	6aB	2cB	0	0	55	23e
100 ppg											
1.0 X	5	8	0	13bc*	10bB*	2aC	18abA*	1950	890	216	1010c*
0.5 X	10	6	3	19ab*	11bAB*	6aB	13bA*	1125	1710	0	945c*
BB	7	9	2	18abc*	9bAB*	6aB	15bA*	1480	1575	0	1018c*

[z]Diseased: Number of chlorotic, wilted, or dead plants in each trial and across all trials (Total) (trial, n=30; Total, n=90), and in each pathogen × irrigation treatment (Total, n=30). AUDPC: Area under the disease progress curve based on plant mortality for each trial and across all trials (Total) (trial, n=3; Total, n=9), and in each pathogen × irrigation treatment (Total, n=3). Root Rot: plants in each root rot category across all trials. Root rot categories: no visible sign of root rot (None), patchy or partially rotted root system with 10 to 75% of the roots appearing dark brown (Some), and sparse, mostly or completely rotted root system with >75% of the roots appearing dark brown and having little structure (Severe) (Weiland et al. 2018). For trials 1 to 3, respectively, plants inoculated on 06 July 2015, 12 July 2016, or 05 May 2017; flooded 2, 2, or 3 weeks after inoculation (WAI); and harvested 27, 26, or 23 WAI. Values within column followed by different lower case letters and within a row and response variable followed by different upper case letters are significantly different $P \leq 0.05$. Values followed by an asterisks (*) denote significant difference from controls.

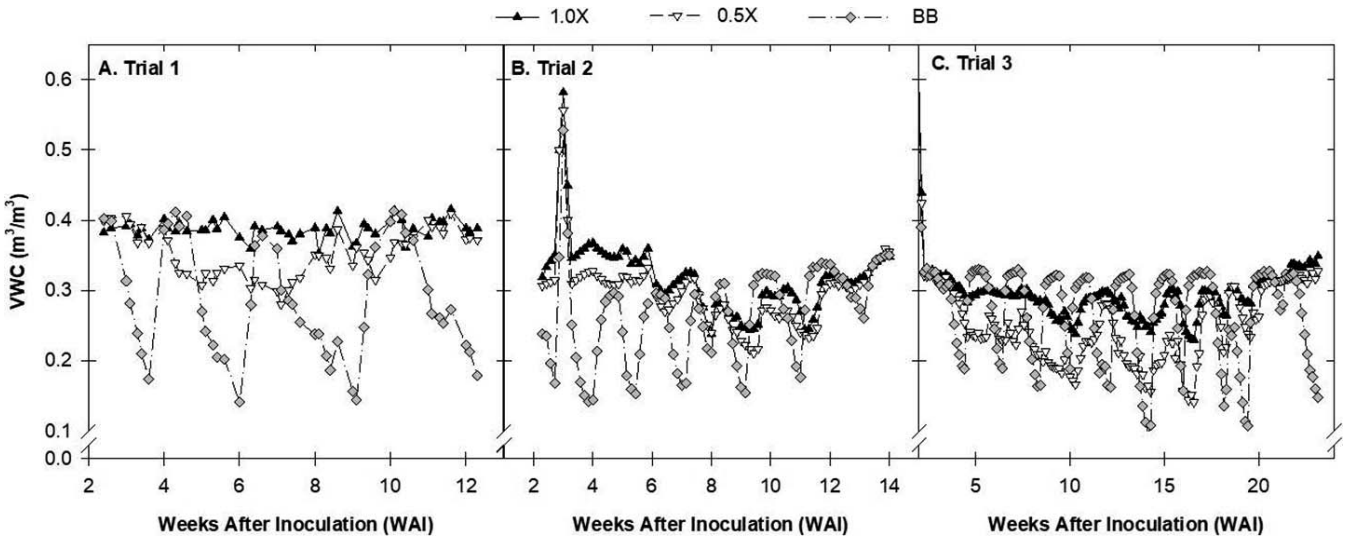

Fig. 3. Substrate volumetric water content (VWC) in *Rhododendron catawbiense* 'Boursault' (Trial 1), 'Roseum Elegans' (Trial 2), and 'Roseum Pink' (Trial 3) grown in a noninfested medium (Control) irrigated with one of three irrigation treatments (1X, 0.5X, and BB). Irrigation treatments: two times a day (1.0X), two times a day with half the volume in the 1.0X treatment (0.5X), and a "boom-bust" cycle (BB), with 1 week of 2 times the 1.0X volume two times a day, followed by no irrigation, until volumetric water content reached 0.15 m^3 m^{-3}. For trials 1 to 3, respectively, plants inoculated on 06 July 2015, 12 July 2016, or 05 May 2017, flooded 2, 2, or 3 weeks after inoculation (WAI) of plants in *Phytopthora* inoculated treatments; and harvested 27, 26, or 23 WAI. Average (A) mid-day (n=10) and (B, C) daily (n=5) VWC values with 95% LSD error bars (n=5).

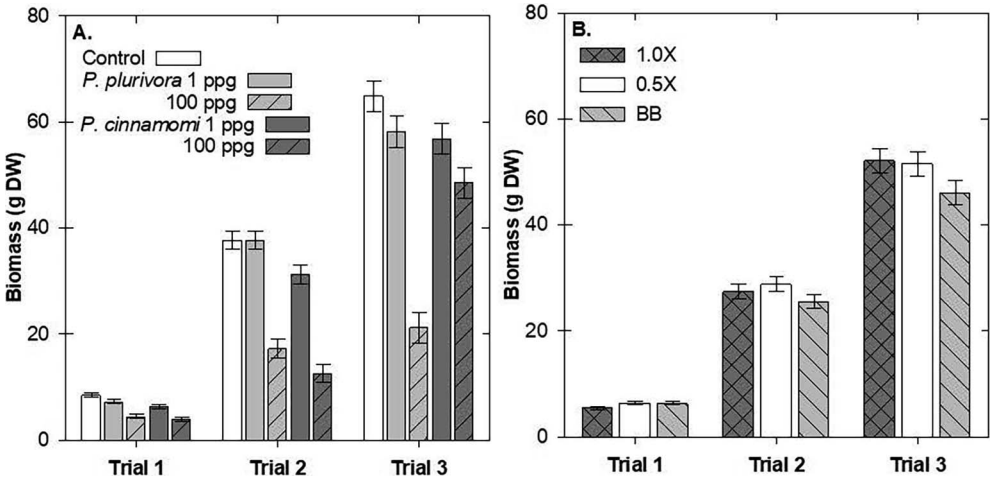

Fig. 4. Biomass in *Rhododendron catawbiense* 'Boursault' (2015), 'Roseum Elegans' (2016), and 'Roseum Pink' (2017) grown in noninfested media (Control) or media infested with *Phytophthora plurivora* or *P. cinnamomi* at 1 ppg or 100 ppg and irrigated with one of three irrigation treatments (1X, 0.5X, and BB). A -Data averaged over irrigation treatment. B- Data averaged over inoculation dose. Mean value for (A) each pathogen (n=30) and (B) irrigation (n=50) for each trial. Error bars are 95% LSDs within each trial. Irrigation treatments: 0.25L two times a day (1.0X), 0.13L two times a day (0.5X), and a "boom-bust" cycle, with 1 week of 0.5L two times a day, followed by no irrigation, until volumetric water content reached 0.15 m^3 m^{-3} (BB). For trials 1 to 3, respectively, plants inoculated on 06 July 2015, 12 July 2016, or 05 May 2017; flooded 2, 2, or 3 weeks after inoculation (WAI); and harvested 27, 26, or 23 WAI. (1 g = 0.035 oz).

Biomass was similar among irrigation treatments in trials 1 and 2 but not in trial 3 (Fig. 4B). In trial 3, when plants were the largest and late season temperatures were the warmest (Fig. 1, Fig. 3), plants in the BB treatment had the lowest biomass, indicting the deficit irrigation in the BB treatment decreased plant growth.

Water stress during the growing season can alter the ability of container-grown rhododendron to assimilate carbon and lower substrate moisture can increase nutrient availability without altering plant biomass (Scagel et al. 2011, 2012). In the present study, transient differences in g_s among irrigation treatments occurred in all trials, indicating control plants were under different amounts of water stress among the irrigation treatments. However, none of the irrigation treatments in trials 1 and 2 were limiting to plant growth (biomass). In trial 3, plants were much larger than in the first two trials and the irrigation treatments with the lowest VWC (BB), had lower biomass, indicating this deficit irrigation treatment caused enough water stress to decrease growth. Nutrient stress can alter leaf color and increased anthocyanin and decreased chlorophyll are frequently associated with nutrient limiting conditions (Chalker-Scott 1999). Although differences in irrigation frequency and volume can alter nutrient availability and uptake in rhododendron (Scagel et al. 2012), the lower leaf anthocyanin values, greater leaf chlorophyll values, and greater nutrient uptake in the 0.5X and BB treatments in our study suggest that these irrigation treatments did not negatively affect plant nutrition in control plants.

Effects of Phytophthora on plant health. With the exception of *P. cinnamomi*-inoculated plants in trial 3, plants inoculated with either *Phytophthora* species were much more likely to develop disease than control plants. At 1 ppg, inoculated plants developed more aboveground and belowground symptoms of disease (Table 1), had lower leaf chlorophyll values (31-32 versus 35), and had less nutrient uptake and translocation than control plants (Table 2), even though biomass was similar between these three treatments (Fig. 4A). At 100 ppg, disease incidence and severity were higher, disease progress was more rapid, and AUDPC was greater in comparison to 1 ppg (Table 1, Fig. 5). Plants inoculated at 100 ppg also had lower g_s (288 versus 404 $\mu mol \cdot m^{-2} \cdot s^{-1}$), lower leaf chlorophyll values (28 versus 35), greater leaf anthocyanin values (0.33 versus 0.17), and lower biomass (Fig. 4) than either the 1 ppg treatment or control plants. Some measures of disease were slightly more severe in plants inoculated with *P. cinnamomi* than with *P. plurivora* in trials 1 and 2. For those two trials, plants inoculated with *P. cinnamomi* at 1 ppg had lower g_s (341 versus 374 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Table 2) and plants inoculated with *P. cinnamomi* at 100 ppg had lower leaf chlorophyll values (30 versus 33), greater anthocyanin values (0.28 versus 0.24), lower g_s (187 versus 260 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and lower biomass (Fig. 4) than plants inoculated with *P. plurivora*.

Little disease developed on plants inoculated with *P. cinnamomi* in trial 3, where we suspect inoculum viability may have been compromised during the air-drying step (see Materials and Methods) and/or by the soil temperature extremes experienced periodically throughout that trial. The air-drying step is designed to make the inoculum more friable and easier to incorporate into soilless potting media. However, our research has shown that if the moisture content of the inoculum drops below 78-80%, viability can be significantly reduced (Davis et al. 2021). Air drying can reduce inoculum moisture content to less than 80% within 24 hours. It is therefore possible that our *P. cinnamomi* inoculum in trial 3 may have dried out too much and reduced its viability. Alternatively, the periodic soil temperature extremes ranging from 35 to 40 C in trial 3 (Fig. 2) may have preferentially compromised the ability of *P. cinnamomi* to cause disease over that of *P. plurivora*. To our knowledge, there are no studies that directly compare

Table 2. Nutrient uptake and allocation in *Rhododendron catawbiense* 'Boursault' (Trial 1) and 'Roseum Elegans' (Trial 2), grown in a noninfested potting medium (Control) or media infested with *Phytophthora plurivora* or *P. cinnamomi* at 1 ppg[z].

Pathogen	N (mg)		P (mg)		K (mg)		S (mg)		Ca (mg)		B (µg)	
Treatment	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2	2015	2016
						Total						
Control	60c	383b	10b	51b	40a	180a	10a	52a	59a	214a	1.7a	8.3a
P. plurivora	50b*	379b	7a*	52b	34b	177a	9a	53a	49b	210a	1.5b	8.0b
P. cinnamomi	43a*	321a*	6a*	42a*	31b	142b*	7b*	43b*	44c	166b*	1.2c*	6.4c*
						Roots						
Control	33b	168a	5b	24b	15a	70a	6a	26a	25a	49a	0.7a	26a
P. plurivora	27a*	170a	3a	25b	11b	73a	5ab	27a	19b*	51a	0.6ab	26a
P. cinnamomi	24a*	150a	3a	20a*	11b	60b	4b	22b*	18b*	45b	0.5b	22b
						Shoots						
Control	27b	215bc	5b	27b	25a	109a	5a	26a	34a	165a	1.0a	5.7a
P. plurivora	23a*	209b	3a*	27b	22ab*	104a	4ab	26a	30b*	157a	0.9b	5.4a
P. cinnamomi	19a*	171a*	3a*	21a*	20b*	82b*	3b*	20b*	26c*	121b*	0.7c*	4.2b*

[z]For each trial (year) mean value across all irrigation treatment (n=30), averaged over inoculum dose. For Trial 1 and 3, respectively, plants inoculated on 06 July 2015 or 12 July 2016; flooded 2 or 3 weeks after inoculation (WAI); and harvested 27 or 26 WAI. Means within a column and structure followed by the same lower case letter are not significantly different ($P > 0.05$). Values followed by an asterisks (*) denote significantly lower concentrations and content than control plants. (100 mg = 0.003 oz)

the ability of these two pathogens to survive soil temperature extremes. However, there is overlap in the reported maximum temperatures for in vitro growth of *P. cinnamomi* and *P. plurivora* (30-36 and 32 C, respectively) depending on the isolates used (Jung and Burgess 2009, Zentmyer et al. 1976). Further research is needed to clarify how these two pathogens respond to temperature extremes that can occur during container production of rhododendron plants.

Root rot occurs after the pathogen infects fine roots and the disease progresses throughout the root system and into the shoot, killing tissues as it spreads. Eventually the root system is no longer able to transport water and nutrients to the canopy and shoots may wilt or become chlorotic or necrotic (Hoitink et al. 2014). Our results indicate that not only can both *Phytophthora* species cause plant mortality, but they can also decrease nutrient uptake and increase plant water stress even when a low *Phytophthora* population is present. This confirms our previous research showing the plant health consequences of low *Phytophthora* inoculum levels (Weiland et al. 2018) and the ability of both *Phytophthora* species to cause severe disease when soil inoculum levels are $\geq$ 50 ppg (Mestas et al. 2022, Sacher et al. 2021, Weiland et al. 2018). It also confirms that *P. cinnamomi* can be more aggressive than *P. plurivora* as a root rot pathogen on rhododendron (Mestas et al. 2022, Sacher et al. 2021, Weiland et al. 2018). Given the prevalence of *P. cinnamomi* and *P. plurivora* in the PNW rhododendron nursery industry and their potential for causing severe disease (Weiland et al. 2020), both species should continue to be included in Phytophthora root rot disease control studies.

Pathogen isolation. *Phytophthora cinnamomi* and *P. plurivora* were never isolated from control plants, but were frequently isolated from inoculated plants that had developed symptoms of root rot. Both pathogens were more frequently isolated from symptomatic plants that were inoculated at 100 ppg than at 1 ppg [*P. plurivora,* 63/90 (70%) at 100 ppg versus 11/90 (12%) at 1 ppg; *P. cinnamomi*, 51/90 (57%) at 100 ppg versus 17/90 (19%) at 1 ppg)]. Both pathogens were also isolated from inoculated, but otherwise healthy appearing plants that never developed aboveground symptoms of disease (chlorosis, wilting, or shoot death) nor belowground symptoms of root rot. *Phytophthora cinnamomi* was isolated approximately twice as often from inoculated, asymptomatic plants than *P. plurivora* [14/86 (16%) versus 9/88 (10%) at 1 ppg and 23/49 (49%) versus 7/26 (27%) at 100 ppg, respectively]. This is similar to observations from previous studies, where a number of inoculated plants would become infected, but never develop symptoms within the timeframe of the experiment (Mestas et al. 2022, Sacher et al. 2021, Weiland et al. 2018). It is unknown what effect these asymptomatic infections will have on long-term plant health (Weiland 2021). In nurseries, plants exhibiting aboveground visual symptoms of root rot are destroyed and represent a direct economic loss to the industry. However, symptomatic plants are often located next to apparently healthy plants in fields and container production blocks. It is likely that many of these healthy-appearing plants are also infected, but are not yet expressing disease symptoms, and that the soil underneath these plants is infested with pathogen inoculum (Weiland 2021). Together, infested soil and asymptomatic infections pose a threat to the industry because these plants may be shipped to other nurseries, states, and countries, and therefore result in the unintentional movement of new pathogen species or fungicide-resistant isolates to other locations and natural environments (Bienapfl and Balci 2014, Jung et al. 2016, Migliorini et al. 2015, Weiland et al. 2015, Weiland 2021). Therefore, there is a critical need for improved sampling strategies and diagnostic tools that can be used by growers and regulatory agencies to improve our ability to find pathogens of interest on imported and exported nursery stock.

Effects of disease on substrate moisture. The potting media in the containers with inoculated plants was often

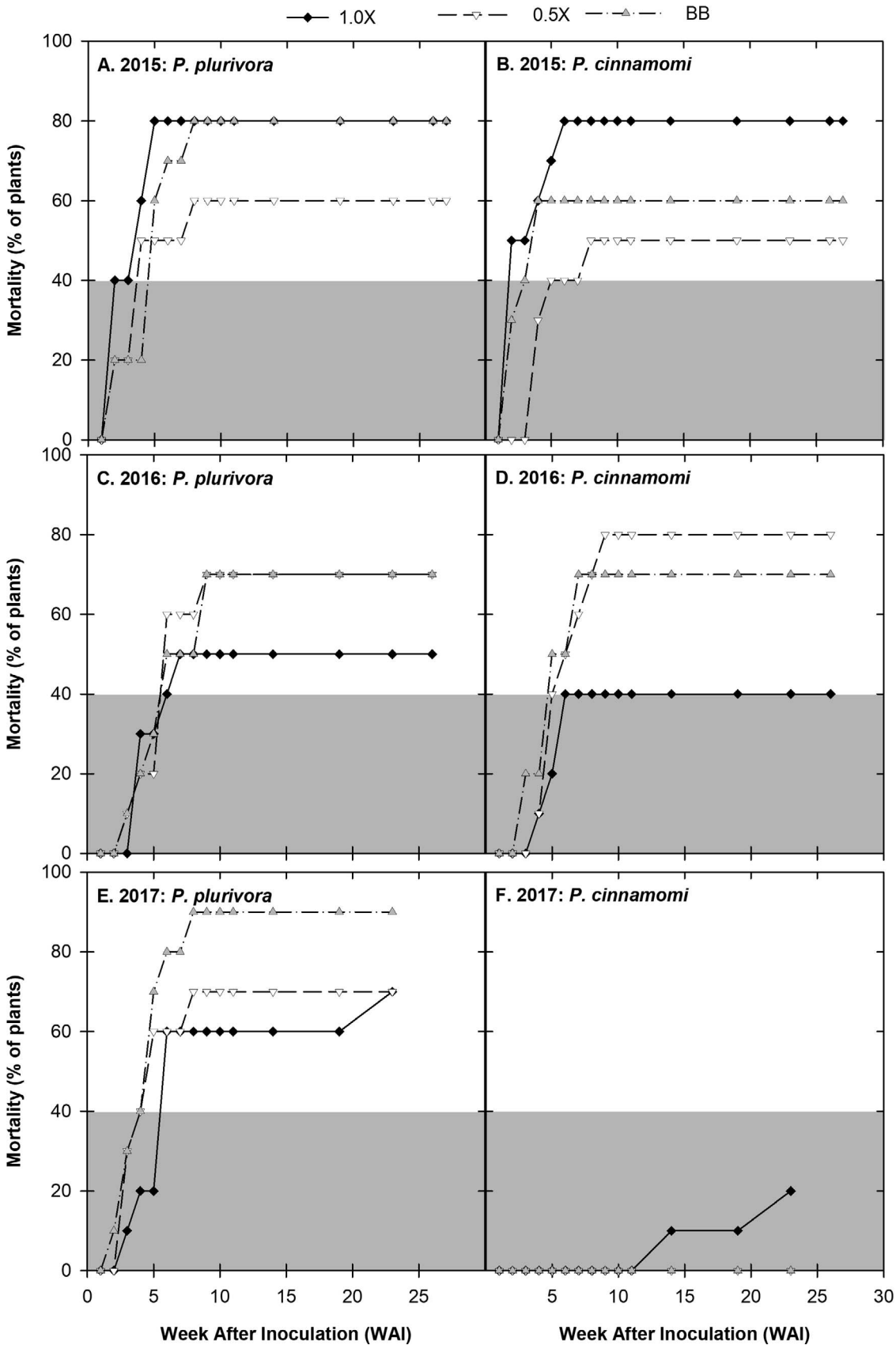

Fig. 5. **Mortality in *Rhododendron catawbiense* 'Boursault' (2015), 'Roseum Elegans' (2016), and 'Roseum Pink' (2017) grown in a noninfested medium (Control) or media infested with *Phytophthora plurivora* or *P. cinnamomi* at 100 ppg and irrigated with one of three irrigation treatments (1X, 0.5X, and BB). Percentage of plants in each 100 ppg pathogen treatment × irrigation treatment for each three trial (n=10). Irrigation treatments: two times a day (1.0X), two times a day with half the volume in the 1.0X treatment (0.5X), and a "boom-bust" cycle (BB), with 1 week of 2 times the 1.0X volume two times a day, followed by no irrigation, until volumetric water content reached 0.15 m^3 per m^3. For trials 1 to 3, respectively, plants inoculated on 06 July 2015, 12 July 2016, or 05 May 2017; flooded 2, 2, or 3 weeks after inoculation (WAI); and harvested 27, 26, or 23 WAI. Data points above grey bar are significantly ($P \leq 0.05$) greater than noninoculated controls.**

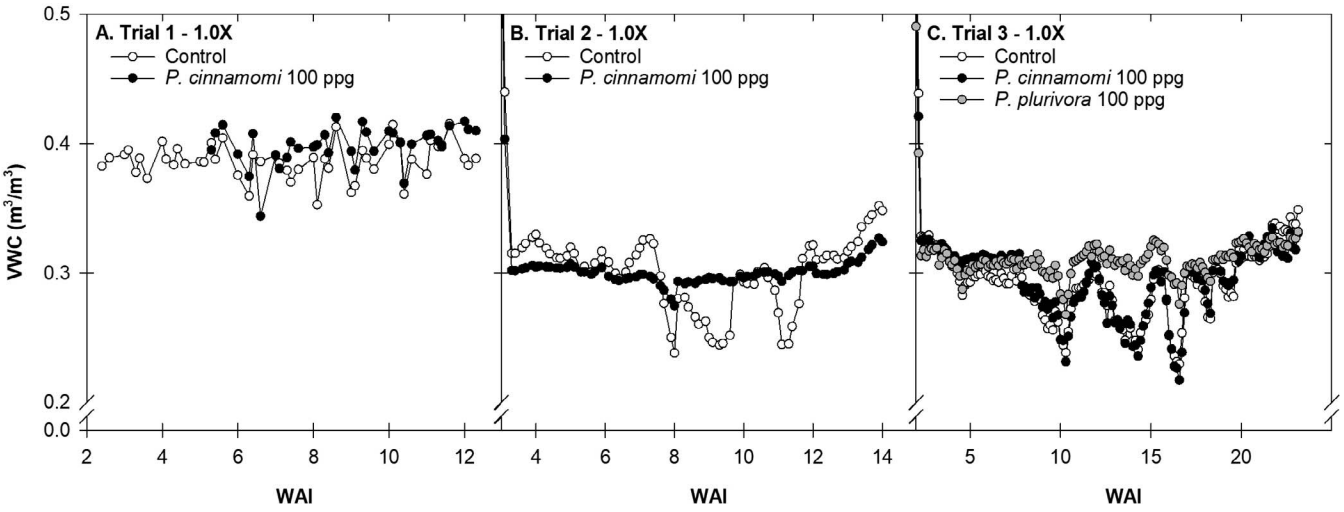

Fig. 6. Substrate volumetric water content (VWC) in *Rhododendron catawbiense* cultivars grown in a noninfested medium (Control) and media infested with *P. cinnamomi* or *P. plurivora* and irrigated two times a day (1.0X). (A) Average mid-day values (n=10) for *R. catawbiense* 'Boursault' (Trial 1). (B) Average daily (n=5) values in *Rhododendron catawbiense* 'Roseum Elegans' (Trial 2). *P. cinnamomi* data points to left of 6 WAI are for 100 ppg and those to the right for 1 ppg. (C) Average daily (n=5) values in *Rhododendron catawbiense* 'Roseum Pink' (Trial 3). For trials 1 to 3, respectively, plants inoculated on 06 July 2015, 12 July 2016, or 05 May 2017; flooded 2, 2, or 3 weeks after inoculation (WAI); and harvested 27, 26, or 23 WAI.

more wet than in the containers with noninoculated controls. For example, in trials 1 and 2, the mid-day VWC of the medium in the 100 ppg *P. cinnamomi* treatment was periodically greater than the controls for all three irrigation regimes (Fig. 6A and 6B, only 1.0X irrigation treatment shown). Similarly, the medium in the 100 ppg *P. plurivora* treatment periodically had greater VWC for all three irrigation regimes. For example, the 1.0X irrigation treatment for *P. plurivora* had, on average, 8% greater VWC than controls (Fig. 6C). In contrast, there was no difference in VWC between *P. cinnamomi*-inoculated plants or control plants in trial 3, where inoculum failure led to little disease (Fig. 6C, only 1.0X irrigation treatment shown). Most inoculated plants developed moderately to severely rotted root systems, which were compromised in their ability to pull water out of the potting media. As a consequence, less water was able to leave the pot via the transpiration stream and the VWC of the potting medium continued to increase. This apparently created a self-perpetuating cycle where increased SM favored increased pathogen activity and led to increasing amounts of root rot and further disruptions to water uptake by the roots. Over time, the root environment of infected plants became more conducive to disease.

Effects of irrigation on disease. Irrigation treatments had little influence on disease for either pathogen, although there was some indication that the BB treatment was more reliably conducive to disease caused by *P. plurivora* than the 0.5X and 1X treatments (AUDPC and disease progress in Table 1, Fig. 5). Generally, a similar number of plants developed disease in each of the irrigation treatments for each pathogen and inoculum level. AUDPC, disease progress, and biomass were also relatively similar regardless of irrigation treatment. Based on these results, we hypothesize that once the infection event had occurred (e.g., the flood event to encourage zoospores), there was little that irrigation management could do afterwards to slow or stop the development of root rot; the amount of water provided by each irrigation treatment, regardless of differences in volume, was still sufficient to allow disease to proceed. Once infected, the root system quickly became compromised in its ability to take up water, thus increasing soil VWC and creating an environment that was more favorable for additional root rot to occur. The amounts of disease that developed in the irrigation treatments with lower VWC (0.5X and BB) were similar to those that developed in the treatment with a higher VWC (1.0X) and also to those from previous studies where the moisture of the potting medium was kept relatively high (≥70% CC) to favor root rot (Mestas et al. 2022, Sacher et al. 2021, Weiland et al. 2018). Therefore, irrigation treatments that decrease substrate moisture further (to a VWC < 0.15 $m^3 \cdot m^{-3}$) or keep the soil drier for longer periods of time might be worth testing for their ability to control root rot after infection has occurred. Previous studies with *P. cinnamomi* have shown that treatments which reduce substrate moisture can reduce infection and root rot damage if they are in place before infection occurs (Bryla and Linderman 2007, Ownley and Benson 1991, Sterne et al. 1977a, Sterne et al. 1977b, Vargas et al. 2015, Yeo et al. 2017). These treatments would likely have proven somewhat less effective if the plants had already been infected by the pathogen. Drier conditions in the substrate may also negatively affect plant health. The biomass for the smaller plants in trials 1 and 2 were similar for all three irrigation treatments (<30 g DW), which suggests that there was sufficient moisture for plant growth even with the most restrictive irrigation treatment (BB). However, plant water stress was evident for the BB treatment in trial 3, where the plants were larger (>40 g DW) and the temperatures were periodically warmer. Further studies are needed to clarify the optimal moisture ranges for infection and disease development by *P. cinnamomi* and *P.*

plurivora, as well as for rhododendron growth and plant health in container production systems.

Overall, the results of this study indicate that decreasing irrigation frequency and volume has little effect on reducing root rot damage if infection has already occurred. Instead, emphasis should be placed on preventing infection in the first place by implementing practices that reduce or preclude substrate saturation from occurring. In container production systems, this can be achieved by not overwatering and by making sure that there is consistent, adequate drainage so that plants never sit in puddles of water (Mestas et al. 2022). This would be more difficult to achieve in field systems, however, where soils may periodically become saturated during extended periods of rain that are outside of the grower's control. In field situations, excess soil moisture can be managed by avoiding low-lying areas that collect water and by improving drainage through the use of drain tiles.

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