Phytophthora Root and Crown Rot of Lavender: New Host-Pathogen Relationships Involving Six Species of *Phytophthora* and Three Species of *Lavandula*

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Abstract

Phytophthora root and crown rot has become a major threat to the lavender industry worldwide. Isolations from symptomatic plants between 2015 and 2019 revealed a number of potential causal agents in the United States. In this study, we tested nine species of *Phytophthora* and four species of *Lavandula* and used Koch's Postulates to prove pathogenicity for six new host-pathogen relationships and confirm two pathogenic relationships for the first time in the United States. A total of 10 experiments were conducted with each consisting of two independent trials. Only host-pathogen combinations that occurred in the field were evaluated. All isolates used in these experiments were recovered from diseased lavender plants or, for one isolate, soil associated with a diseased plant sent to our lab or the Clemson University Plant and Pest Diagnostic Clinic for diagnosis. Experiments were conducted over 3 years, 2017 to 2019, in a research greenhouse under relatively uniform environmental conditions following a standard protocol. Plants were evaluated weekly for foliage symptom severity, and, at the end of each trial, plants were scored for final foliage symptom severity and root rot severity, area under the disease progress curve was calculated, fresh plant mass was weighed, and isolation of pathogens from roots was attempted. These studies successfully demonstrated for the first time pathogenicity of *Phytophthora nicotianae*, *P. palmivora*, and *P. cinnamomi* to hybrid lavender (*Lavandula* × *intermedia*), *P. nicotianae* to sweet lavender (*L. heterophylla*), and *P. cryptogea* and *P. drechsleri* to English lavender (*L. angustifolia*). In addition, a soil isolate of *P. tropicalis* was shown to be potentially pathogenic to *L.* × *intermedia*. Our results also documented for the first time in the United States pathogenicity of *P. palmivora* and *P. citrophthora* to *L. angustifolia*. We were not able to confirm pathogenicity for three host-pathogen relationships: *P. megasperma* on English lavender, *P. cactorum* on hybrid lavender, and *P. nicotianae* on Spanish lavender (*L. stoechas*). Results from this study expand the list of *Phytophthora* species causing root rot on lavender (*Lavandula* species) in the United States and elsewhere.

Keywords: Koch's postulates, *Lavandula* species, lavender, pathogenicity, Phytophthora root and crown rot, *Phytophthora* species

Lavender (*Lavandula* spp.) is a commercially important genus in the Lamiaceae/Labiatae family (USDA NRCS 2023; Zomlefler 1994). As with many other members of the family, species of *Lavandula* are popular for ornamental, culinary, and medical uses (Devecchi 2006; Naghibi et al. 2005). Reports of lavender occurred as early as 370 B.C. (Upson 2002), and, in its extensive written history, lavender has reported uses ranging from embalming to the taming of tigers (McCoy and Davis 2021). There are no published data on the acreage planted to lavender in the United States because it is a relatively new crop in the agriculture sector. However, results from surveys conducted by the National Agricultural Statistics Service (https://www.nass.usda.gov) show sales of lavender plants have increased consistently with each new survey, and the most recent survey showed an increase of over 22% between 2021 and 2022 (Pilon 2023).

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Currently, there are 32 known species of lavender plus hybrids (Upson 2002), with several of them being commercially important. *Lavandula angustifolia* Mill. (previously classified as *L. delphinensis* Jord. ex Billot, *L. officinalis* Chaix, *L. spica* L., and *L. vera* D.C. [Simon et al. 1984; Singh et al. 2007]) is commonly referred to as English lavender and is one of the most common and widely planted lavender species (McCoy and Davis 2021; Singh et al. 2007). The native range for this species is southern Europe, including Italy and Spain (Upson 2002). *L. stoechas*, Spanish lavender, is found throughout the Mediterranean region (Upson 2002), and spike lavender, *L. latifolia*, is a lower altitude species native to Spain, France, and the Mediterranean region (Guenther 1954; Simon et al. 1984). A cross between *L. angustifolia* and *L. latifolia* resulted in the hybrid lavender *L.* × *intermedia* (synonym *L.* × *hybrida*), commonly known as lavandin (Amidon 2013; Simon et al. 1984). Lavandin cultivars have been steadily growing in popularity due to their hardiness, heat tolerance, longevity, and high yields of essential oils, which are used for medical and aromatherapy purposes (Guenther 1954; Lis-Balchin 2002).

The first report of a disease on lavender caused by species of *Phytophthora* was root rot caused by *Phytophthora nicotianae* on *L. angustifolia* in a Maryland nursery (Putnam 1991). Symptoms included grey colored foliage, blackened roots, and vascular discoloration in roots and stems (Putnam 1991). In preliminary studies in our lab, symptoms of decay in the root crown led to this disease being renamed Phytophthora root and crown rot (PRCR) of lavender (Jeffers et al. 2016). In Europe, *P. nicotianae* became the leading cause of PRCR, and it is considered the most problematic disease of lavender in Italy and the greatest threat to lavender production (Davino et al. 2002; Faedda et al. 2013). *P. nicotianae* has also been reported to cause PRCR on *L. angustifolia* in Spain (Álvarez et al. 2007) and Bulgaria (Nakova 2011). This species was found associated with *L. angustifolia*, *L. stoechas*, *L.* × *hybrida*, and *Lavandula* sp. in nurseries and horticultural plantings in several European countries (Jung et al. 2016), and it was associated with diseased lavender plants in Canada (Anonymous 2022) and Australia (Mammella et al. 2013).

Other species of *Phytophthora* also cause or are associated with PRCR on lavender. *P. palmivora* was first reported as a pathogen of *L. angustifolia* in Sicily, Italy (Davino et al. 2002), and later in Turkey (Dervis et al. 2011); this pathogen was also reported on *L. spica* in South Korea (Cho and Shin 2004) and associated with lavender plants in Croatia and Italy (Jung et al. 2016). *P. cinnamomi* was found to be pathogenic on *L. angustifolia* in Lithuania (Orlikowski and Valjuskaite 2007) and associated with *L. angustifolia* in three European countries (Jung et al. 2016). *P. citrophthora* was isolated from and pathogenic to *L. angustifolia* 'Hidcote' in Hungary (Józsa et al. 2011). It also was isolated from *L. angustifolia* in South Carolina (Robayo Camacho 2009) and Pennsylvania (Molnar et al. 2020) and was reported to be associated with several lavender species in Croatia, Italy, and the United Kingdom (Jung et al. 2016).

P. cactorum has been reported to be associated with lavender on three continents. A large planting of symptomatic *L. angustifolia* was found to be infected with this species in Jiangsu Province, China (Chen et al. 2017). *P. cactorum* has also been isolated from dead and dying lavender plants in Ontario, Canada (Anonymous 2022), and associated with *Lavandula* sp. in the United Kingdom (Jung et al. 2016). A hybrid between *P. nicotianae* and *P. cactorum*, *P.* × *pelgrandis*, was found on *L. stoechas* in Italy and was described as common on lavender and spreading worldwide through plant trade (Faedda et al. 2013). This hybrid pathogen was also found on *L. angustifolia* 'Hidcote' in Hungary (Szigethy et al. 2013) and was reported on lavender in the Netherlands before it was recognized as a hybrid species (Bonants et al. 2000).

Several species of *Phytophthora* have only been reported as associated with various species of *Lavandula* during nursery surveys and summaries of diagnostic efforts. Molnar et al. (2020) reported that *P. tropicalis* (three isolates) and *P. parvispora* (one isolate) were isolated from diseased lavender plant specimens submitted to the Pennsylvania Department of Agriculture for diagnosis. Jung et al. (2016) reported limited incidences of *P. cryptogea, P. hibernalis*, *P. kernoviae*, *P. megasperma*, *P. plurivora*, and unidentified species of *Phytophthora* associated with several species of lavender in Europe. Cho and Shin (2004) reported *P. capsici* and *P. drechsleri* on *L. spica* in South Korea. Farr and Rossman (2022) list two instances of unidentified species of *Phytophthora* associated with *Lavandula* species in Greece and California. Consequently, numerous species of *Phytophthora* have been found to be associated with various species of *Lavandula* worldwide, but proof of pathogenicity is lacking in most of these studies.

Since 2015, our lab at Clemson University and the Clemson University Plant and Pest Diagnostic Clinic (PPDC) have collaborated with the United States Lavender Association (USLGA) to receive and diagnose samples of lavender plants with PRCR symptoms from growers across the United States. Isolations from these plants and recovery from associated soil and container mix have resulted in a large collection of isolates of *Phytophthora* species. For this study, isolates collected from 2015 to 2019 were identified, and host-pathogen associations were determined. The objective of the study was to identify new lavender hosts of species of *Phytophthora* and to use Koch's postulates to determine pathogenicity and document new host-pathogen occurrences in the United States and worldwide. Preliminary reports have been published (Dlugos and Jeffers 2018, 2019, 2021).

Materials and Methods

The greenhouse and plants for inoculation

In total, 10 pathogenicity experiments were conducted, and six of these produced meaningful results. For each experiment, two independent trials were conducted between 2017 and 2019 in a research greenhouse at Clemson University in Clemson, SC (Table 1). Experiments were designed to test pathogenicity of nine species of *Phytophthora* to four species of *Lavandula*. Successful pathogenicity experiments involved eight species of *Phytophthora* and three species of *Lavandula* (Table 2). Trial durations varied from 9 to 18 weeks among experiments, but trial durations within an experiment were kept nearly identical for analysis purposes (Table 1). Experiments were run as long as necessary to allow for adequate symptom development because pathogen aggressiveness varied in the different host-pathogen relationships. During the trials, environmental conditions in the greenhouse were controlled and measured by a central computerized system (Argus Controls, Conviron, Winnipeg, Manitoba, Canada) to maintain uniformity between trials and among experiments (Table 1). Across all experiments, mean temperatures ranged from 21 to 24°C, and mean relative humidity measurements ranged from 50 to 78%. A 16-h photoperiod was maintained throughout all experiments with artificial lighting (provided by 1,000-W metal halide bulbs; color temperature 4,000 K cool white), which came on when outside light energy was below 350 W/m^2.

Lavender plants for the experiments were obtained from several commercial producers based on needs for the experiment and plant availability. All plants for each experiment were purchased at one time, so plants in Trial 2 were usually older than those in Trial 1. Species and, if possible, cultivars were selected to match the species and cultivar of symptomatic plants from which isolates originally were recovered (Table 2): *L.* × *intermedia* cultivars Grosso and Phenomenal were used in Experiment 1 (Ball Horticultural Co., West Chicago, IL), *L. angustifolia* 'Hidcote' was used in Experiments 2 and 4 (Ball Horticultural Co.), *L. heterophylla* was used in Experiment 3 (Mountain Valley Growers, Squaw Valley, CA); *L.* × *intermedia* 'Phenomenal' was used for Experiment 5 (Creek Hill

Table 1. Dates, durations, and environmental conditions for six experiments, each with two independent trials, conducted in a greenhouse to evaluate the pathogenicity of eight species of *Phytophthora* to three species of lavender over a 3-year period, 2017 to 2019

		Trial dates[x]		Trial duration	Temperature (°C)[z]				Relative humidity (%)[z]			
Experiment	Trial	Start	End	(weeks)[y]	Mean	SD	Min	Max	Mean	SD	Min	Max
1	1	09/15/2017	11/30/2017	11	22.3	2.7	15.7	28.8	58.2	14.7	18.4	80.3
	2	09/28/2017	12/14/2017	11	21.4	2.4	15.7	28.7	54.3	14.7	18.4	80.3
2	1	09/15/2017	11/16/2017	9	22.7	2.8	15.7	28.8	61.4	13.4	21.7	80.3
	2	09/28/2017	11/30/2017	9	21.7	2.5	15.7	28.7	55.8	14.7	18.4	80.3
3	1	09/21/2017	01/25/2018	18	21.2	2.4	15.7	28.8	51.9	16.3	12.6	80.3
	2	10/05/2017	02/08/2018	18	20.6	2.0	15.7	28.4	49.6	16.1	12.6	80.3
4	1	02/08/2018	05/10/2018	13	20.5	1.5	17.6	25.9	51.0	15.7	10.6	79.9
	2	02/22/2018	05/24/2018	13	21.0	2.0	17.6	27.5	53.1	16.7	10.6	83.5
5	1	07/23/2018	10/10/2018	11	24.2	2.1	18.5	32.1	78.4	7.5	38.6	91.4
	2	08/08/2018	10/24/2018	11	23.7	2.3	18.4	32.1	74.6	12.1	18.4	91.4
6	1	05/02/2019	07/09/2019	10	23.6	2.3	14.9	30.0	71.2	11.5	35.1	91.3
	2	05/14/2019	07/15/2019	9	23.9	2.3	14.9	30.0	72.8	11.1	35.1	91.3

[x] Start dates are when plants were inoculated; end dates are when plants were harvested for data collection.
[y] Numbers of weeks were counted to the nearest whole week.
[z] Temperature and relative humidity during each trial were summarized as the mean, standard deviation (SD), minimum (Min), and maximum (Max) values based on data collected every 15 min.

Nursery, Leola, PA), and *L. angustifolia* 'Hidcote' was used for Experiment 6 (Creek Hill Nursery). All plants except those of *L. heterophylla* were received as rooted cuttings (i.e., plugs) in 72-cell trays (83 ml/cell). Only a limited number of *L. heterophylla* plants were available, and these were received in 7.6-cm-diameter pots. To confirm absence of *Phytophthora* species prior to use, subsamples of the plugs and plants used in all experiments were assayed by several methods—including visual inspection for PRCR symptoms; isolation from roots; and baiting of root clippings, root-wash debris, and root-associated container mix. *Phytophthora* species were not detected on any of the plants used in these experiments. Individual plugs were transplanted into 1.3-liter pots (15 cm in diameter); each pot contained 1 liter of a soilless peat- and bark-based container mix (Fafard 3B; Sun Gro Horticulture, Agawam, MA). In Experiment 3, *L. heterophylla* plants were transplanted into 300 ml of container mix in 400-ml pots (9 cm in diameter). All plants were placed in the greenhouse, watered overhead by hand as needed, and fertilized weekly with a fertilizer solution delivering 100 ppm of nitrogen (PowerPak 20-20-20 [N-P-K] Soluble Fertilizer with Minor Elements; Southern Agricultural Insecticides, Inc., Hendersonville, NC).

Isolates and identification

The isolates used in this study originated in nine states (Table 2). Most isolates were obtained from plant samples exhibiting typical PRCR symptoms that were submitted for diagnosis to the Clemson PPDC or our lab between 2015 and 2018 (Table 2). Pathogens were isolated by plating root or root-crown tissue on PARPH-V8 selective medium (Jeffers 2016a). One isolate, 15-1194.D, was recovered from soil around the roots of a plant with PRCR symptoms using a standard baiting bioassay with camellia and rhododendron leaf disks as baits (Ferguson and Jeffers 1999). Two isolates (PIN1 and Purdue 15-927A) were recovered from diseased lavender plants at diagnostic labs in New York and Indiana, respectively. All the plants and isolates tested in these experiments were received and used under USDA-APHIS PPQ 526 permits and are maintained in a permanent culture collection at Clemson University.

Isolates used in pathogenicity experiments were identified using standard molecular methods (Abad et al. 2023; Grünwald et al. 2011). DNA was extracted from mycelium of each isolate, and the internal transcribed spacer (ITS) region and *cox*1 and/or *cox*2 loci were amplified by polymerase chain reaction using the primer pairs ITS 6/ITS4, OomCox1-levup/OomCox1-levlo, and Cox2-F/Cox2-RC4, respectively (Choi et al. 2015; Cooke et al. 2000). DNA was extracted using one of two methods. A boiling extraction method was used in which mycelium was placed in 400 µl of sterile TE buffer in a 1.5-ml microcentrifuge tube (F. N. Martin, personal communication). The mixture was boiled in a water bath for 10 min, cooled on ice, and centrifuged to spin down the pellet. A second method utilized a DNeasy Plant Mini Kit (QIAGEN Sciences, Germantown, MD). Purified amplicons were sequenced by Sanger sequencing, and sequences were paired, trimmed, and compared with accessions in several databases using Geneious Prime (Dotmatics, Boston, MA). Isolate identities were further validated by examining morphological characters—colony and mycelium morphologies, sporangia and sporangiophores, and oogonia and antheridia if present—and comparing these to published descriptions (Abad et al. 2023; Erwin and Ribeiro 1996).

Inoculum preparation and treatments

For each experiment, isolates used were ones originally isolated from the lavender species being inoculated. Inoculum for each trial was prepared independently by growing each isolate on sterile vermiculite moistened with 10% V8 juice broth (2:1, v:v) in glass bottles

Table 2. Sources of 13 isolates of eight species of *Phytophthora* used in six pathogenicity experiments and the rationale for using these species and conducting the experiments

	Isolate source[t]				Original host plant			
Experiment	Species	Isolate number	State[u]	Year[v]	Species	Cultivar	Substrate[w]	Rationale
1	*Phytophthora nicotianae*	15-0450	SC	2015	*Lavandula* × *intermedia*	Phenomenal	Root	First report: *P. nicotianae* on *L.* × *intermedia*
		15-1123.B	NJ	2015	*L.* × *intermedia*	Grosso	Root	
	P. palmivora	17-0099	TN	2017	*L.* × *intermedia*	Provence	Root	First report: *P. palmivora* on *L.* × *intermedia*
	P. tropicalis	15-1194.D	TN	2015	*L.* × *intermedia*	Phenomenal	Soil	Potential pathogenicity: *P. tropicalis* on *L.* × *intermedia*
2	*P. nicotianae*	16-0718	PA	2016	*L. angustifolia*	Hidcote	Root	Known pathogen for comparison
	P. palmivora	15-1125.R1	NJ	2015	*L. angustifolia*	Hidcote	Root	First report in the United States: *P. palmivora* on *L. angustifolia*
		16-1107	SC	2016	*L. angustifolia*	Super Blue	Root	
3	*P. nicotianae*	17-0435	TX	2017	*L. heterophylla*	Sweet	Root	First report: *P. nicotianae* on *L. heterophylla*
		15-0450	SC	2015	*L.* × *intermedia*	Phenomenal	Root	Additional isolate for comparison
4	*P. citrophthora*	PIN1[x]	NY	2007	*L. angustifolia*	–[y]	Plant	First report in the United States: *P. citrophthora* on *L. angustifolia*
5	*P. cinnamomi*	SC.4308	SC	2018	*L.* × *intermedia*	Phenomenal	Root	First report: *P. cinnamomi* on *L.* × *intermedia*
6	*P. cryptogea*	15-1178	CO	2015	*L. angustifolia*	Buena Vista	Root	First report: *P. cryptogea* on *L. angustifolia*
	P. drechsleri	Purdue 15-927A[z]	IN	2015	*L. angustifolia*	–[y]	Plant	First report: *P. drechsleri* on *L. angustifolia*
	P. megasperma	16-0236	OH	2016	*L. angustifolia*	–[y]	Root	First report: *P. megasperma* on *L. angustifolia*

[t] All isolates were recovered from diseased lavender plant samples: 11 isolates were recovered from samples sent to the Plant and Pest Diagnostic Clinic or the S. N. Jeffers lab at Clemson University; the isolates of *P. citrophthora* and *P. drechsleri* were provided by colleagues (see below).
[u] State from which diseased lavender plant originated.
[v] Year in which sample was received and isolate was recovered.
[w] Isolates were recovered from soil, plant roots, or a part of the plant that was not specified (plant).
[x] Isolate provided by Margery Daughtrey at the Cornell University Long Island Horticultural Research and Extension Center.
[y] The cultivar for this host plant was not recorded.
[z] Isolate provided by Tom Creswell at the Purdue University Plant and Pest Diagnostic Lab.

(Jeffers 2016b; Roiger and Jeffers 1991). Bottles were placed in the dark at 25°C for 2 weeks to allow thorough colonization of the vermiculite in a bottle. After 10 to 12 days of incubation, a small aliquot (1 to 2 ml) of vermiculite from each bottle was spread on a plate of 10% clarified V8 juice agar (Jeffers 2016b) to ensure purity and uniform colonization of vermiculite particles before being used as inoculum.

For each trial of each experiment, inoculated and noninoculated plants were arranged in a completely randomized design on a greenhouse bench. Inoculum was applied by spreading approximately 5 to 12 ml of colonized vermiculite on the surface of each pot, and the inoculum was mixed by hand into the upper 1 cm of the container mix. A 1-cm layer of fresh container mix was added to each pot to cover the inoculum, and all pots were gently watered to incorporate the inoculum and prevent desiccation. Seven milliliters of inoculum were applied to plants in Experiment 1, but the amount was increased to 10 to 12 ml in all subsequent experiments, except Experiment 3, to increase infection and improve disease development. For the smaller pots used in Experiment 3, only 5 ml of inoculum was added to each pot. Plants in all noninoculated control treatments received no inoculum. After inoculation, plastic saucers (14 cm in diameter, 3.5 cm deep) were placed under all pots, and plants were watered from the bottom by adding water to the plastic saucers for the remainder of the experiment. This kept the container mix in each pot near field capacity throughout the trial, which promoted disease development and minimized splashing of infested container mix and pathogen propagules among pots. Replication of treatments varied among experiments based on availability of plants. Numbers of replicate plants per treatment within a trial were 12 for Experiment 1 (i.e., six of each of two cultivars); seven for Experiment 2; four for Experiments 3, 4, and 5; and six for Experiment 6. Replicate numbers were doubled when trials of an experiment were combined for analysis.

Data collection and analysis

Each trial was run for a period of 9 to 18 weeks postinoculation (Table 1), and five disease parameters were evaluated. Plants were evaluated weekly for foliage symptom severity, which was scored on a 0 to 5 scale based on the percentage of foliage showing symptoms of gray discoloration, wilting, or necrosis: 0 (0% of foliage symptomatic; no symptoms), 1 (1 to 10%), 2 (11 to 50%), 3 (51 to 90%), 4 (91 to 99%), and 5 (100% of foliage symptomatic; mortality). For all analyses, weekly and final foliage symptom severity scores were converted to the midpoint of each range—e.g., a score of 1 (1 to 10%) was converted to 5.5%. Area under the disease progress curve (AUDPC) was calculated based on weekly and final foliage evaluations using the method reported by Shaner and Finney (1977). At the end of each trial, plants were harvested independently, root systems were thoroughly washed under high pressure water until all container mix had been removed and blotted dry, roots were evaluated for root rot severity based on the percentage of roots with visible symptoms, and fresh plant masses were weighed. Noninoculated plants were always harvested before inoculated plants to prevent cross contamination. To document infection on inoculated plants and a lack of infection on noninoculated control plants—i.e., to fulfill Koch's postulates—root tissues were assayed for the presence of the pathogens. Five root bundles from each plant were embedded in PARPH-V8 medium to isolate the pathogen. Root bundles were composed of five to 10 segments, approximately 1 to 2 cm in length, of fibrous feeder roots. Isolation plates were held at 25°C in the dark for 7 days and examined regularly for characteristic hyphae of *Phytophthora* spp. Subcultures on PARPH-V8 produced colonies that were morphologically similar to the species used to inoculate the plants.

Data for all experiments were analyzed with JMP Pro, ver. 14, statistical software (Cary, NC). The data were initially examined using analysis of variance (ANOVA) along with Levene's and Shapiro-Wilk's tests for variance and normality assumptions. When necessary, data were transformed before analyses or subjected to nonparametric analyses. However, results from analyses using data transformations and nonparametric tests were consistent with those from standard analyses, so parametric analyses of nontransformed data were used for all experiments. Experiment 1 required a three-way ANOVA (with treatment, cultivar, and trial as factors), while the remainder of the experiments were analyzed with two-way ANOVAs (with treatment and trial as factors). The two trials of each experiment were analyzed together with blocking by trial as a factor. When a significant ($P < 0.05$) trial effect occurred, data for individual trials were not reported separately as this did not affect evaluation of inoculum treatments. When there was a significant treatment by trial interaction for any of the disease parameters in an experiment, a separate ANOVA was conducted for each trial, and means from each trial are reported. However, when treatment by trial interactions were not significant, data from the two trials were combined for analysis, and means for the combined trials are reported. When the effect of treatments was significant in an analysis, means were separated by individual pairwise comparisons ($P < 0.05$).

Results

This study examined the pathogenicity of nine species of *Phytophthora* to four commercially important *Lavandula* species. Multiple experiments were conducted over the course of a 3-year period as pathogens were isolated and identified and greenhouse space and lavender plants became available. Six experiments successfully demonstrated pathogenicity (Table 2). In experiments on two host-pathogen combinations, pathogenicity could not be demonstrated: *P. nicotianae* on *L. stoechas* (two experiments) and *P. cactorum* on *L.* × *intermedia* (two experiments); therefore, data are not presented for these four experiments. In all experiments, inoculated and noninoculated plants did not differ visually in root rot severity; instead, the overwhelming difference we observed between inoculation treatments was in the size of root systems with inoculated plants usually having much smaller root systems than noninoculated plants. Consequently, root rot severity scores are not reported, and root system size was reflected in measurements of plant mass. Of the four disease parameters analyzed for each experiment, the overwhelming majority lacked a treatment by trial interaction, signifying consistency among treatments in repeated trials. Occasionally, trial effects were significant, which may be because plants in the two trials were different ages. In some experiments, there was not a significant treatment effect for one of the disease parameters; however, there were significant treatment effects for other disease parameters, and consistent isolation of the pathogens from inoculated and symptomatic plants confirmed pathogenicity.

Experiment 1: Pathogenicity of *P. nicotianae*, *P. palmivora*, and *P. tropicalis* on hybrid lavender

This experiment tested the pathogenicity of two isolates of *P. nicotianae* and one isolate each of *P. palmivora* and *P. tropicalis* to two cultivars of hybrid lavender, *L.* × *intermedia*. All results from this trial are summarized in Table 3, and representative plants are shown in Supplementary Figure S1. For final foliage symptom severity, the three-way interaction was significant ($P = 0.0497$), but the two-way interactions were not significant. Therefore, trials were combined to evaluate this parameter. There were significant differences among treatments with foliage symptom severity greater on plants inoculated with each of the four isolates than on noninoculated plants; *P. palmivora* was significantly more virulent than either *P. nicotianae* or *P. tropicalis*.

For AUDPC, a significant treatment by trial interaction occurred in the three-way ANOVA, so results from individual trials were examined by two-way ANOVA. In each trial, there was a significant cultivar effect due to more rapid disease progress on 'Grosso' plants than on 'Phenomenal' plants (AUDPC values for trials combined = 389.8 and 266.3, respectively; data not shown); however, treatment by cultivar interactions were not significant, so cultivar did not differentially affect isolate performance. In Trial 1, disease progress was greater on plants inoculated with each of the four isolates compared with that on the noninoculated control plants, with *P. nicotianae* 15-0450 and *P. palmivora* being most virulent. In Trial 2, two isolates of *P. nicotianae* and the isolate of *P. palmivora* caused significant

disease, and disease was greatest on plants inoculated with *P. nicotianae* 15-1123.B and *P. palmivora*.

There also was a significant treatment by trial interaction in the three-way ANOVA for fresh plant mass, and, again, the treatment by cultivar interactions in two-way ANOVAs were not significant. All four isolates significantly reduced plant mass compared with control plants in Trial 1, with *P. nicotianae* 15-0450 and *P. palmivora* causing the greatest reductions. In Trial 2, only *P. palmivora* and *P. nicotianae* 15-1123.B caused significant reductions in plant mass. Pathogens were isolated from 100% of the inoculated plants and from 8.3% of noninoculated control plants. There was one instance of growth of a *Phytophthora* species on a root bundle from a non-inoculated control plant, suggesting splash contamination during the experiment or cross contamination during harvesting.

Experiment 2: Pathogenicity of *P. palmivora* and *P. nicotianae* on English lavender

In this experiment, we examined the pathogenicity of *P. palmivora* (two isolates) to English lavender, *L. angustifolia*, and confirmed pathogenicity of *P. nicotianae* (one isolate) to this host. The results from this experiment are summarized in Table 4, and symptoms on representative plants are shown in Supplementary Figure S2. The only disease parameter with a significant treatment by trial interaction was plant mass, so trials were analyzed separately for this disease parameter. For the other three disease parameters, trials were combined for analyses. For the four disease parameters assessed, all three isolates caused significant levels of disease compared with the noninoculated control plants. The three isolates were equally virulent except in Trial 1 for plant mass, where one isolate of *P. palmivora* was more virulent than the isolate of *P. nicotianae*. Pathogens were recovered from all inoculated plants, but a *Phytophthora* species was also isolated from one noninoculated control plant presumably from contamination during the experiment or at harvest.

Experiment 3: Pathogenicity of *P. nicotianae* on sweet lavender

In this experiment, the pathogenicity of two isolates of *P. nicotianae* to sweet lavender, *L. heterophylla*, was examined, and all results from the experiment are summarized in Table 5 with symptoms on representative plants shown in Supplementary Figure S3. Due to limited availability, only four replicate plants were available for each treatment. In Trial 2, two noninoculated control plants did not grow well and were determined to be outliers, so they were excluded from all statistical analyses. Both isolates were pathogenic and equally virulent based on final foliage symptom severity. There was a significant treatment by trial interaction for AUDPC, so trial means were examined individually. Based on AUDPC, the two isolates of *P. nicotianae* were each pathogenic—one in Trial 1 and one in Trial 2. Isolates had no significant effect on total plant mass, but the pathogens were isolated from all inoculated plants and were not isolated from any of the control plants.

Experiment 4: Pathogenicity of *P. citrophthora* on English lavender

The pathogenicity of *P. citrophthora* to English lavender was examined in this experiment; results are summarized in Table 6, and symptoms on representative plants are shown in Supplementary Figure S4. There was a significant treatment by trial interaction for final foliage symptom severity but not for the other three disease parameters. *P. citrophthora* caused significant foliage symptoms in Trial 1 but not in Trial 2. When disease was assessed by AUDPC and total plant mass, *P. citrophthora* was clearly pathogenic based on significant differences between parameter values on inoculated and noninoculated plants. This pathogen was isolated from all but one of the eight inoculated plants and from 34 out of 35 of the root bundles from the seven infected plants. *P. citrophthora* was not isolated from any of the noninoculated plants.

Experiment 5: Pathogenicity of *P. cinnamomi* on hybrid lavender

The pathogenicity of *P. cinnamomi* to hybrid lavender was tested in this experiment, and all results are summarized in Table 7 with symptoms on representative plants shown in Supplementary Figure S5. All four disease parameters confirmed *P. cinnamomi* as pathogenic, with inoculated plants having significantly more disease than

Table 3. Experiment 1: Pathogenicity of three species of *Phytophthora* to two cultivars of hybrid lavender, *Lavandula* × *intermedia* 'Phenomenal' and 'Grosso', in the greenhouse based on four disease parameters[u]

Treatment		Final foliage symptom severity (%)[v]	Foliage symptom AUDPC[w]			Total plant mass (g)[x]			Root isolation (%): plants, bundles[y]
Species	Isolate	Trial 1 + 2	Trial 1 + 2	Trial 1	Trial 2	Trial 1 + 2	Trial 1	Trial 2	Trial 1 + 2
Noninoculated control		27.6 a		99.1 a	174.1 a		136.6 a	96.4 ab	8.3, 0.8 a
Phytophthora tropicalis	15-1194.D	53.7 b		292.8 b	226.7 ab		79.2 b	100.1 a	100.0, 87.5 c
P. nicotianae	15-0450	65.5 bc		544.8 d	290.7 bc		37.3 cd	87.0 abc	100.0, 98.3 d
P. nicotianae	15-1123.B	73.0 c		387.9 bc	368.7 cd		57.3 bc	59.8 cd	100.0, 75.8 b
P. palmivora	17-0099	86.9 d		432.5 cd	463.5 d		23.6 d	41.3 d	100.0, 99.2 d
Three-way ANOVA[z]		*P* > *F*	*P* > *F*			*P* > *F*			*P* > *F*
Treatment		<0.0001	<0.0001			<0.0001			<0.0001
Trial		0.0027	0.0709			0.1202			0.8185
Cultivar		0.0551	<0.0001			0.1425			0.6465
Treatment × trial		0.0507	0.0011			0.0008			0.9947
Treatment × cultivar		0.0981	0.2565			0.6729			0.1487
Trial × cultivar		0.1161	0.1242			0.1632			0.1706
Treatment × trial × cultivar		0.0497	0.1701			0.1826			0.9456
Two-way ANOVA[z]				*P* > *F*	*P* > *F*		*P* > *F*	*P* > *F*	
Treatment				<0.0001	<0.0001		<0.0001	0.0005	
Cultivar				<0.0001	0.0204		0.9582	0.0501	
Treatment × cultivar				0.3763	0.1138		0.5596	0.2467	

[u] Two independent trials were conducted with 12 replicate plants (n = 12) per treatment in each trial; n = 24 when trials were combined. Differences between cultivars, when present, are not shown—see text.
[v] Final foliage symptom severity was assessed as the percentage of the foliage on each plant with disease symptoms at the end of a trial.
[w] Foliage symptoms were assessed weekly for 11 weeks, and the area under the disease progress curve (AUDPC) was then calculated.
[x] The fresh mass of each plant was measured at the end of a trial.
[y] At the end of each trial, isolation of the pathogen was attempted by placing five bundles of five to 10 root segments from each plant on selective medium. Data are mean percentages of plants and bundles that were positive for the pathogen; only data for bundles were analyzed statistically.
[z] Two- and three-way analyses of variance (ANOVA); $P > F$: The probability of a greater F statistic occurring. Based on appropriate ANOVAs, means within columns were separated by individual pairwise comparisons (P = 0.05); means with the same letter are not significantly different.

noninoculated control plants. There was a treatment by trial interaction in isolation of the pathogen from roots bundles but only due to a lower isolation percentage in Trial 2 compared with Trial 1. Across both trials, *P. cinnamomi* was isolated from all inoculated plants and was not isolated from any of the noninoculated control plants.

Experiment 6: Pathogenicity of *P. cryptogea*, *P. drechsleri*, and *P. megasperma* on English lavender

In this experiment, three species of *Phytophthora*—*P. cryptogea*, *P. drechsleri*, and *P. megasperma*—that were infrequently recovered from field samples were tested for pathogenicity on English lavender. All results are summarized in Table 8, and symptoms on representative plants are shown in Supplementary Figure S6. Significant treatment by trial interactions occurred for final foliage symptom severity and total plant mass, so data from individual trials were analyzed for these two disease parameters. When foliage symptoms were evaluated at the end of each trial, there was no difference in symptom severity among treatments in Trial 1, but a significant amount of foliage symptoms occurred on plants inoculated with both *P. cryptogea* and *P. drechsleri* in Trial 2. When the progress of foliage symptom development was recorded over time, both *P. cryptogea* and *P. drechsleri* had AUDPC values that were significantly greater than those for *P. megasperma* and the control treatment. However, total plant mass was not a useful parameter for determining pathogenicity in this experiment. There was no significant treatment effect in Trial 1, and in Trial 2, plants inoculated with *P. megasperma* had significantly greater mass than the plants in the other treatments. Only *P. cryptogea* significantly colonized roots on inoculated plants based on isolation from root bundles. However, all three species of *Phytophthora* were isolated from some of the 12 plants inoculated with each species: *P. cryptogea* from 11 plants, *P. drechsleri* from six plants, and *P. megasperma* from three plants. Pathogens were not isolated from control plants.

Table 4. Experiment 2: Pathogenicity of two species of *Phytophthora* to English lavender, *Lavandula angustifolia*, in the greenhouse based on four disease parameters[u]

Treatment		Final foliage symptom severity (%)[v]	Foliage symptom AUDPC[w]	Total plant mass (g)[x]			Root isolation (%): plants, bundles[y]
Species	Isolate	Trial 1 + 2	Trial 1 + 2	Trial 1 + 2	Trial 1	Trial 2	Trial 1 + 2
Noninoculated control		25.5 a	87.2 a		61.1 a	38.1 a	7.1, 7.1 a
Phytophthora nicotianae	16-0718	95.0 b	422.4 b		27.1 b	13.7 b	100.0, 97.1 b
P. palmivora	16-1107	97.9 b	425.8 b		25.7 bc	13.1 b	100.0, 90.7 b
P. palmivora	15-1125.R1	97.9 b	449.3 b		20.3 c	13.2 b	100.0, 95.7 b
Two-way ANOVA[z]		*P* > *F*	*P* > *F*	*P* > *F*			*P* > *F*
Treatment		<0.0001	<0.0001	<0.0001			<0.0001
Trial		0.5779	0.0867	<0.0001			0.9406
Treatment × trial		0.3497	0.171	0.0016			0.4181
One-way ANOVA[z]					*P* > *F*	*P* > *F*	
Treatment					<0.0001	<0.0001	

[u] Two independent trials were conducted with seven replicate plants ($n = 7$) per treatment in each trial; $n = 14$ when trials were combined.
[v] Final foliage symptom severity was assessed as the percentage of the foliage on each plant with disease symptoms at the end of a trial.
[w] Foliage symptoms were assessed weekly for 11 weeks, and the area under the disease progress curve (AUDPC) was then calculated.
[x] The fresh mass of each plant was measured at the end of a trial.
[y] At the end of each trial, isolation of the pathogen was attempted by placing five bundles of five to 10 root segments from each plant on selective medium. Data are mean percentages of plants and bundles that were positive for the pathogen; only data for bundles were analyzed statistically.
[z] One- and two-way analyses of variance (ANOVA); *P* > *F*: The probability of a greater *F* statistic occurring. Based on appropriate ANOVAs, means within columns were separated by individual pairwise comparisons ($P = 0.05$); means with the same letter are not significantly different.

Table 5. Experiment 3: Pathogenicity of *Phytophthora nicotianae* to sweet lavender, *Lavandula heterophylla*, in the greenhouse based on four disease parameters[u]

Treatment		Final foliage symptom severity (%)[v]	Foliage symptom AUDPC[w]			Total plant mass (g)[x]	Root isolation (%): plants, bundles[y]
Species	Isolate	Trial 1 + 2	Trial 1 + 2	Trial 1	Trial 2	Trial 1 + 2	Trial 1 + 2
Noninoculated control		13.8 a		103.0 a	109.5 a	24.3	0.0, 0.0 a
Phytophthora nicotianae	15-0450	54.2 b		449.8 b	403.6 ab	17.6	100.0, 92.5 b
P. nicotianae	17-0435	57.2 b		345.2 ab	916.5 b	14.6	100.0, 95.0 b
Two-way ANOVA[z]		*P* > *F*	*P* > *F*			*P* > *F*	*P* > *F*
Treatment		0.0247	0.0065			0.1291	<0.0001
Trial		0.7329	0.1171			0.3042	0.6806
Treatment × trial		0.1118	0.0447			0.1325	0.8269
One-way ANOVA[z]				*P* > *F*	*P* > *F*		
Treatment				0.0346	0.0456		

[u] Two independent trials were conducted: In Trial 1, there were four replicate plants ($n = 4$) for each treatment; in Trial 2, $n = 4$ for the two inoculated treatments, and $n = 2$ for the control; when trials were combined, $n = 8$ for the two inoculated treatments, and $n = 6$ for the control.
[v] Final foliage symptom severity was assessed as the percentage of the foliage on each plant with disease symptoms at the end of a trial.
[w] Foliage symptoms were assessed weekly for 11 weeks, and the area under the disease progress curve (AUDPC) was then calculated.
[x] The fresh mass of each plant was measured at the end of a trial.
[y] At the end of each trial, isolation of the pathogen was attempted by placing five bundles of five to 10 root segments from each plant on selective medium. Data are mean percentages of plants and bundles that were positive for the pathogen; only data for bundles were analyzed statistically.
[z] One- and two-way analyses of variance (ANOVA); *P* > *F*: The probability of a greater *F* statistic occurring. Based on appropriate ANOVAs, means within columns were separated by individual pairwise comparisons ($P = 0.05$); means with the same letter are not significantly different.

Table 6. Experiment 4: Pathogenicity of *Phytophthora citrophthora* to English lavender, *Lavandula angustifolia*, in the greenhouse based on four disease parameters[u]

	Final foliage symptom severity (%)[v]			Foliage symptom AUDPC[w]	Total plant mass (g)[x]	Root isolation (%): plants, bundles[y]
Treatment	**Trial 1 + 2**	**Trial 1**	**Trial 2**	**Trial 1 + 2**	**Trial 1 + 2**	**Trial 1 + 2**
Noninoculated control		4.1 a	60.5	136.5 a	80.3 a	0.0, 0.0 a
Phytophthora citrophthora		91.4 b	72.6	507.8 b	34.3 b	87.5, 85.0 b
Two-way ANOVA[z]	*P* > *F*			*P* > *F*	*P* > *F*	*P* > *F*
Treatment	0.0021			0.0066	0.0096	<0.0001
Trial	0.1665			0.1962	0.8341	0.2315
Treatment × trial	0.0123			0.7685	0.7736	0.2315
One-way ANOVA[z]		*P* > *F*	*P* > *F*			
Treatment		<0.0001	0.6384			

[u] Two independent trials were conducted with four replicate plants ($n = 4$) per treatment in each trial; $n = 8$ when trials were combined.
[v] Final foliage symptom severity was assessed as the percentage of the foliage on each plant with disease symptoms at the end of a trial.
[w] Foliage symptoms were assessed weekly for 11 weeks, and the area under the disease progress curve (AUDPC) was then calculated.
[x] The fresh mass of each plant was measured at the end of a trial.
[y] At the end of each trial, isolation of the pathogen was attempted by placing five bundles of five to 10 root segments from each plant on selective medium. Data are mean percentages of plants and bundles that were positive for the pathogen; only data for bundles were analyzed statistically.
[z] One- and two-way analyses of variance (ANOVA); *P* > *F*: The probability of a greater *F* statistic occurring. Based on appropriate ANOVAs, means within columns were separated by individual pairwise comparisons ($P = 0.05$); means with the same letter are not significantly different.

Table 7. Experiment 5: Pathogenicity of *Phytophthora cinnamomi* to hybrid lavender, *Lavandula* × *intermedia*, in the greenhouse based on four disease parameters[u]

	Final foliage symptom severity (%)[v]	Foliage symptom AUDPC[w]	Total plant mass (g)[x]	Root isolation (%): plants, bundles[y]		
Treatment	**Trial 1 + 2**	**Trial 1 + 2**	**Trial 1 + 2**	**Trial 1 + 2**	**Trial 1**	**Trial 2**
Noninoculated control	0.0 a	0.0 a	176.2 a		0.0, 0.0 a	0.0, 0.0 a
Phytophthora cinnamomi	96.9 b	656.1 b	11.5 b		100.0, 90.0 b	100.0, 40.0 b
Two-way ANOVA[z]	*P* > *F*	*P* > *F*	*P* > *F*	*P* > *F*		
Treatment	<0.0001	<0.0001	<0.0001	<0.0001		
Trial	0.525	0.5577	0.2322	0.0003		
Treatment × trial	0.525	0.5577	0.2094	0.0003		
One-way ANOVA[z]					*P* > *F*	*P* > *F*
Treatment					<0.0001	0.0027

[u] Two independent trials were conducted with four replicate plants ($n = 4$) per treatment in each trial; $n = 8$ when trials were combined.
[v] Final foliage symptom severity was assessed as the percentage of the foliage on each plant with disease symptoms at the end of a trial.
[w] Foliage symptoms were assessed weekly for 11 weeks, and the area under the disease progress curve (AUDPC) was then calculated.
[x] The fresh mass of each plant was measured at the end of a trial.
[y] At the end of each trial, isolation of the pathogen was attempted by placing five bundles of five to 10 root segments from each plant on selective medium. Data are mean percentages of plants and bundles that were positive for the pathogen; only data for bundles were analyzed statistically.
[z] One- and two-way analyses of variance (ANOVA); *P* > *F*: The probability of a greater *F* statistic occurring. Based on appropriate ANOVAs, means within columns were separated by individual pairwise comparisons ($P = 0.05$); means with the same letter are not significantly different.

Table 8. Experiment 6: Pathogenicity of three species of *Phytophthora* to English lavender, *Lavandula angustifolia*, in the greenhouse based on four disease parameters[u]

	Final foliage symptom severity (%)[v]			Foliage symptom AUDPC[w]	Total plant mass (g)[x]			Root isolation (%): plants, bundles[y]
Treatment	**Trial 1 + 2**	**Trial 1**	**Trial 2**	**Trial 1 + 2**	**Trial 1 + 2**	**Trial 1**	**Trial 2**	**Trial 1 + 2**
Noninoculated control		22.2	18.0 a	88.5 a		12.7	17.0 b	0.0, 0.0 a
Phytophthora megasperma		24.7	9.7 a	82.0 a		10.2	30.8 a	25.0, 5.0 a
P. cryptogea		49.4	70.2 b	306.2 b		10.2	8.1 b	91.7, 56.7 b
P. drechsleri		46.3	92.6 b	321.4 b		8.0	5.3 b	50.0, 13.3 a
Two-way ANOVA[z]	*P* > *F*			*P* > *F*	*P* > *F*			*P* > *F*
Treatment	<0.0001			0.0003	0.0042			<0.0001
Trial	0.1447			0.7312	0.0726			0.435
Treatment × trial	0.0474			0.0566	0.0149			0.8792
One-way ANOVA[z]		*P* > *F*	*P* > *F*			*P* > *F*	*P* > *F*	
Treatment		0.3438	<0.0001			0.7232	0.0041	

[u] Two independent trials were conducted with six replicate plants ($n = 6$) per treatment in each trial; $n = 12$ when trials were combined.
[v] Final foliage symptom severity was assessed as the percentage of the foliage on each plant with disease symptoms at the end of a trial.
[w] Foliage symptoms were assessed weekly for 11 weeks, and the area under the disease progress curve (AUDPC) was then calculated.
[x] The fresh mass of each plant was measured at the end of a trial.
[y] At the end of each trial, isolation of the pathogen was attempted by placing five bundles of five to 10 root segments from each plant on selective medium. Data are mean percentages of plants and bundles that were positive for the pathogen; only data for bundles were analyzed statistically.
[z] One- and two-way analyses of variance (ANOVA); *P* > *F*: The probability of a greater *F* statistic occurring. Based on appropriate ANOVAs, means within columns were separated by individual pairwise comparisons ($P = 0.05$); means with the same letter are not significantly different.

Discussion

The results of this study demonstrate that multiple species of *Phytophthora* are capable of causing PRCR on lavender plants. Six new pathogenic relationships were identified, and two pathogenic relationships were documented for the first time in the United States. Both *P. palmivora* and *P. citrophthora* were shown to be pathogenic to *L. angustifolia*; therefore, to the best of our knowledge, this represents the first documented report of these two host-pathogen relationships in the United States. Previously, *P. palmivora* was shown to be pathogenic to *L. angustifolia* in both Italy (Davino et al. 2002) and Turkey (Dervis et al. 2011). In our study, *P. palmivora* was as virulent as *P. nicotianae* on *L. angustifolia* 'Hidcote' plants, which demonstrated that this pathogen has the potential to become a major obstacle to commercial lavender production in the United States. *P. citrophthora* was first documented as pathogenic to *L. angustifolia* in Hungary (Józsa et al. 2011). This species was also found associated with *L. angustifolia* plants in the United States and several European countries (Jung et al. 2016; Molnar et al. 2020; Robayo Camacho 2009), but this is the first report documenting pathogenicity of *P. citrophthora* to English lavender in the United States.

This study successfully demonstrated for the first-time the pathogenicity of *P. nicotianae*, *P. palmivora*, and *P. cinnamomi* to hybrid lavender, *L.* × *intermedia*, and this is the first report of pathogenicity by any species of *Phytophthora* on hybrid lavender. Previous associations of *P. nicotianae* with hybrid lavender have been reported but without documenting pathogenicity (Jung et al. 2016). Pathogenicity of *P. tropicalis* to *L.* × *intermedia* cannot yet be confirmed as Koch's postulates were not fulfilled because the isolate we used was obtained from soil associated with the roots of diseased plants and not directly from root tissue. However, our results indicate a strong potential for pathogenicity of *P. tropicalis* to *L.* × *intermedia*.

Our results also documented first reports of other host-pathogen relationships. We proved that *P. nicotianae* can be pathogenic to sweet lavender, *L. heterophylla* (syn. *L.* × *heterophylla* [Upson 2002]). Previously, there were no reports or associations of *P. nicotianae* or any other species of *Phytophthora* with this species of lavender, so this expands the host range of *P. nicotianae* and identifies sweet lavender as susceptible to PRCR. However, our results also suggest that sweet lavender may be less susceptible than English and hybrid lavender. We also proved that *P. cryptogea* and *P. drechsleri* can be pathogens of English lavender, *L. angustifolia*. Both pathogens caused significant disease on inoculated plants as measured by several parameters, and they were readily isolated from roots of diseased plants upon completion of the trials. Previously, *P. cryptogea* and *P. drechsleri* have only been found associated with lavender plants (Cho and Shin 2004; Jung et al. 2016). Under the experimental conditions used in this study, pathogenicity of *P. megasperma* to *L. angustifolia* was not demonstrated even though it was isolated from a few of the inoculated plants. Previously, this pathogen was isolated from diseased lavender plants in Oregon and Washington (Pscheidt and Ocamb 2023) and was found associated with hybrid lavender in Croatia (Jung et al. 2016).

In addition to the above-mentioned host-pathogen relationships, there were two more experiments we attempted multiple times to document pathogenicity that did not yield success. *P. cactorum* was found associated with the roots of a hybrid lavender plant that was submitted from a grower in Kansas in 2016. It was baited from root washings but was not isolated from diseased roots. This pathogen had been documented as pathogenic to *L. angustifolia* in China (Chen et al. 2017) and has been reported to cause disease to field-grown lavender plants in Ontario, Canada (Anonymous 2022). *P. cactorum* is typically found in cool, temperate climates (Erwin and Ribeiro 1996), so the environmental conditions in the greenhouse used in this study may not have been conducive to disease development. Alternatively, this isolate might not be virulent to hybrid lavender because *P. cactorum* was present only in root washings and not in symptomatic root tissue.

The other host-pathogen relationship that could not be documented was *P. nicotianae* on Spanish lavender, *L. stoechas*, using an isolate originally recovered from a diseased plant in South Carolina in 2014. Previously, that host-pathogen association had only been reported in Italy (Jung et al. 2016). In our experiments with this host-pathogen relationship, we used *L. stoechas* 'Silver Anouk' plants from a South Carolina nursery. 'Silver Anouk' is a relatively new, patented, and compact cultivar that is reported to be resistant to foliage diseases (Darwin Perennials, https://www.darwinperennials.com/products/Plantinfo/?phid=037301435023707; Ball Seed Company, https://www.ballseed.com/PlantInfo/?phid=037301435023707). Consequently, this cultivar also may have some resistance to disease caused by species of *Phytophthora*.

In addition to the pathogenic relationships mentioned above, results from this study identified issues that merit further investigation. In Experiment 1, there were significant differences in disease progress on two cultivars of hybrid lavender, which suggests there may be differences in susceptibility between these cultivars. Identifying differences in susceptibility among cultivars of *L. angustifolia* and *L.* × *intermedia* would be very beneficial to the lavender industry. In experiments using multiple isolates, differences in virulence were sometimes noted. Therefore, it would be important to determine which species of *Phytophthora* are more virulent to the popular commercial species and cultivars of lavender and if isolates within a species vary in virulence—particularly if lavender species and cultivars are to be screened for resistance.

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