Host Specificity and Variations in Aggressiveness of North Carolina Isolates of *Phytophthora cryptogea* and *P. drechsleri* in Greenhouse Ornamental Plants

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Abstract

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Three isolates of *Phytophthora cryptogea* and three isolates of *P. drechsleri* were evaluated for host specificity and variations in aggressiveness on eight floriculture crops commonly grown in North Carolina. Plants were monitored for the development of foliar symptoms stemming from root rot caused by *Phytophthora*. No isolates of *P. cryptogea* or *P. drechsleri* had the same host range, though all *P. cryptogea* isolates caused foliar symptoms on gerbera daisy and annual stock, and all *P. drechsleri* isolates incited disease on osteospermum. No African marigold plants developed foliar symptoms of *Phytophthora* root rot. All *P. cryptogea* isolates caused foliar symptoms on at least three tested plant species. Isolates of *P. drechsleri* varied from

highly specific and only causing disease on a single host species to relatively nonspecific and causing foliar symptoms on the majority of host plants. This is the first report of host specificity of ornamental isolates of *P. drechsleri*, and several of the tested plants are not reported hosts of *P. drechsleri*. Differences in isolate aggressiveness were found and depended on plant species; overall, isolates of *P. drechsleri* were more aggressive than *P. cryptogea* isolates. Isolations from non-symptomatic inoculated plants suggest that these *Phytophthora* spp. could be moved between growers or from growers to consumers on non-symptomatic infected ornamentals.

Phytophthora cryptogea and *P. drechsleri* cause root and crown rot on numerous plants, including multiple greenhouse-produced ornamentals. Both species, along with *P. nicotianae* and *P. tropicalis*, were recovered during a 2007 to 2008 survey of floriculture crops in North Carolina greenhouses (25). *P. cryptogea* was isolated from blue daze (*Evolvulus glomeratus*), gerbera daisy (*Gerbera jamesonii*), dusty miller (*Senecio cineraria*), and verbena (*Verbena × hybrida*), while *P. drechsleri* was collected from gerbera daisy and fuchsia (*Fuchsia × hybrida*). In a 2001 to 2002 survey of North Carolina greenhouses, gerbera daisy and dusty miller were found to be hosts of *P. drechsleri* (12,25). Worldwide, *P. cryptogea* has over 140 reported hosts in approximately 50 plant families (6). Of the reported hosts, approximately 40 are floriculture crops. Similarly, *P. drechsleri* has over 110 reported hosts in 40 plant families (7). Approximately 25 of the reported hosts are floriculture crops.

Host specificity has been reported in both species; however, little research has focused specifically on floriculture crops, and host specificity within floriculture crops has only been reported for *P. cryptogea*. In early experimental host range studies, Tompkins and Tucker (34) and Middleton et al. (24) identified isolates of *P. cryptogea* collected from ornamental hosts exhibiting host specificity. More recently, Kröber (19) proposed the name *P. cryptogea* f. sp. *begoniae* for isolates collected from Elatior begonia (*Begonia × hiemalis*) that were morphologically similar to the description of *P. cryptogea* but had larger oospores, and because gerbera daisy isolates from Kröber's collection were not pathogenic to Elatior begonia.

Understanding the host ranges of isolates obtained from greenhouses could help growers manage *Phytophthora* root rot in orna-

mentals. For example, highly susceptible plant species could be targeted for closer monitoring, allowing more timely fungicide applications. In addition, plant species particularly susceptible to isolates of *P. cryptogea* or *P. drechsleri* could be maintained on separate flood or ebb-and-flow irrigation systems to slow the potential spread from crop to crop. In order to evaluate the host ranges of North Carolina isolates of *P. cryptogea* and *P. drechsleri* obtained from greenhouse-produced ornamentals, select isolates were tested for host specificity and variations in aggressiveness on eight floriculture crop species commonly produced in North Carolina greenhouses.

Materials and Methods

Host plants. Eight ornamental plant species commonly grown in North Carolina greenhouses were tested as hosts of isolates of *P. cryptogea* and *P. drechsleri*. Seed of dusty miller 'Maritima Silverdust', snapdragon (*Antirrhinum majus*) 'Snapshot Pink', annual stock (*Matthiola incana*) 'Hot Cakes Rose', and African marigold (*Tagetes erecta*) 'Marvel Gold', and rooted cuttings of osteospermum (*Osteospermum* sp.) 'Serenity Lemonade' were obtained from Ball Horticultural Company. Rooted cuttings of gerbera daisy 'Revolution Yellow' were provided by Van Wingerden International Inc.. Stock plants of verbena 'Lanai White' and rooted cuttings of fuchsia 'Winston Churchill' were produced by North Carolina Farms, Indian Trail. To produce rooted plugs of dusty miller, snapdragon, annual stock, and African marigold, seed were sown into 162-cell plug trays containing Fafard 2 peat-based potting mix (Conrad Fafard Inc.). Trays were maintained on a greenhouse bench with intermittent mist irrigation that cycled on for 1 min six times daily until a significant root system was established. To produce rooted plugs of verbena, terminal cuttings containing four to six leaves were taken from stock plants with sterile hand clippers. Cuttings were placed in 162-cell plug trays containing Fafard 2 peat-based potting mix and maintained under mist irrigation as described above for 10 to 14 days. Rooted plugs were transplanted into 460-cm³ plastic pots containing Fafard 4P peat-based potting mix (Conrad Fafard Inc.). Once transplanted, plants were watered by drip irrigation for 1 min twice daily. Plants were fertilized with Peters 20-20-20 (N-P-K at 200 ppm; Scotts) weekly.

***Phytophthora* isolates and inoculum preparation.** Three isolates of *P. cryptogea* (Pc597, Pc1105, and Pc1146) and three iso-

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lates of *P. drechsleri* (Pd103, Pd957, and Pdfdm5) were chosen from a collection of isolates obtained during two surveys of North Carolina greenhouse ornamentals (Table 1) (12,25). The isolates were chosen based on host of origin. Inoculum was prepared by transferring five 4-mm-diameter agar disks from an actively growing culture into 125-ml flasks of twice-autoclaved rice grains (25 g of rice and 17 ml of water) (11). Cultures were incubated 7 days at 20 to 25°C. Flasks were shaken briefly each day to ensure uniform colonization of rice grains.

Host specificity and isolate aggressiveness. Greenhouse trials were conducted to test the host specificity and aggressiveness of the isolates of *P. cryptogea* and *P. drechsleri*. Plant species were divided into two groups arbitrarily, depending on the availability of planting material. Group 1 included annual stock, dusty miller, osteospermum, and snapdragon, and group 2 was composed of African marigold, fuchsia, gerbera daisy, and verbena. Plants were inoculated by placing one rice grain colonized by mycelia in each of three holes 1 cm deep in the potting mix of each pot. Noninoculated plants were included as controls. A factorial treatment design was utilized, and plants were arranged in a randomized complete block design with eight replications of each host-isolate treatment combination. The experiment was repeated twice for each group of plants. Plants were monitored for the development of foliar symptoms of Phytophthora root rot, including wilting, chlorosis, and necrosis. The plants were maintained in the greenhouse until no new plants in a test developed foliar symptoms for 10 days. Greenhouse average maximum and minimum temperatures for the tests were recorded (group 1 trial 1: 33 ± 8°C day and 18 ± 2°C night, group 1 trial 2: 34 ± 5°C day and 20 ± 3°C night, group 2 trial 1: 35 ± 7°C day and 19 ± 4°C night, and group 2 trial 2: 38 ± 7°C day and 23 ± 3°C night).

Host specificity was evaluated by rating each plant as symptomatic (= 1) or nonsymptomatic (= 0) for plants developing foliar symptoms of root rot. Logistic regression was used to identify the factors (trial, block, host, isolate, and the host-isolate interaction) significantly associated with foliar symptom development. The model for each group of plants was fit with PROC LOGISTIC (SAS 9.2; SAS Institute), and Firth's bias correction was utilized to account for quasi-separation of the data (8). For both host groups, data were pooled for the two trials because trial was not a significant factor in the model ($P = 0.05$). The host-isolate interaction was significant (group 1: $P < 0.0001$ and group 2: $P = 0.0155$); therefore, the probability of an isolate causing foliar symptom development on each host plant compared with the noninoculated control was determined by the analysis of maximum likelihood estimates (1).

For isolates that caused foliar symptoms of root rot on a particular host, differences in isolate aggressiveness were evaluated by analyzing the number of days between inoculation and development of foliar symptoms of root rot. Data were analyzed for each plant group with PROC GLIMMIX (SAS 9.2; SAS Institute) and a Poisson distribution. Plants that did not develop foliar symptoms were regarded as missing data points. Host, isolate, and the interaction were treated as fixed effects, and trial and block were treated as random effects. Trial was not significant ($P = 0.05$) in the model; therefore, the data were pooled for the two trials for both groups. The host-isolate interaction was significant (groups 1 and 2: $P < 0.0001$); therefore, the least-squares means were calculated for the interactions and the simple effects were analyzed by host to determine significant isolate differences.

Isolation from nonsymptomatic plants. To determine whether inoculated plants that did not develop foliar symptoms of root rot were colonized by the *Phytophthora* isolate, the roots from up to four replicate plants per host-isolate combination were collected randomly from each trial, washed under running water to remove potting mix, and plated onto cornmeal agar (BD Diagnostics) amended with pimarin, ampicillin, rifamycin, and pentachloronitrobenzene (16). In addition, the roots of one symptomatic plant per host-isolate combination were plated as a control for the isolation procedure. Plates were incubated at 20 to 25°C in the dark for up to 7 days and observed for growth of *Phytophthora* spp. Colonies were observed with a microscope to confirm that the morphology was consistent with *Phytophthora* and that the hyphal growth was emerging from the plant root.

Results

Host specificity. No isolate of *P. cryptogea* or *P. drechsleri* caused disease on all tested plant species, and no tested isolate of *P. cryptogea* or *P. drechsleri* caused disease on African marigold (Fig. 1). Overall, the *P. cryptogea* isolates exhibited more variability in host range than the *P. drechsleri* isolates (Fig. 1). *P. cryptogea* isolates Pc594 and Pc1105 had very similar host ranges (Table 2). Osteospermum, annual stock, fuchsia, and gerbera daisy plants inoculated with Pc594 and Pc1105 had a significantly greater probability (osteospermum: $P = 0.0008$; annual stock: $P = 0.0008$ and 0.0025 , respectively; fuchsia: $P = 0.037$; gerbera daisy: $P = 0.0235$ and 0.0044 , respectively) of developing foliar symptoms of Phytophthora root rot than the noninoculated control (Fig. 1). In addition to these hosts, Pc1105 caused significant ($P = 0.0008$) disease on snapdragon. Approximately 20% of snapdragon plants inoculated with Pc594 wilted; however, the plants did not have a greater probability ($P = 0.05$) of developing disease than the noninoculated plants. Similarly, 30% of dusty miller plants inoculated with Pc1105 wilted and developed crown rot but the probability was not significantly ($P = 0.05$) greater than the noninoculated control plants (Fig. 1). Pc1146 had a smaller host range than the other isolates of *P. cryptogea* (Table 2). Dusty miller, annual stock, and gerbera daisy plants inoculated with Pc1146 developed significant ($P = 0.0044$, 0.0008 , and 0.0370 , respectively) foliar symptoms of Phytophthora root rot (Fig. 1). In addition, approximately 25% of snapdragon plants and 10% of verbena plants inoculated with Pc1146 wilted but the plants did not have a significantly greater probability ($P = 0.05$) of developing disease.

P. drechsleri isolates Pd957 and Pdfdm5 had very similar host ranges (Table 2). Both isolates caused significant ($P = 0.0008$) wilting of dusty miller, osteospermum, snapdragon, annual stock, and gerbera daisy (Fig. 1). In addition, Pd957 had a significantly greater probability ($P = 0.0008$) of causing foliar symptoms of Phytophthora root rot than the noninoculated control on fuchsia ($P = 0.037$) and verbena ($P = 0.0008$). In contrast, only 25% of fuchsia plants and 10% of verbena plants inoculated with Pdfdm5 wilted, which was not significantly greater ($P = 0.05$) than the noninoculated fuchsia and verbena plants. In contrast with isolates Pd957 and Pdfdm5, *P. drechsleri* isolate Pd103 only caused disease on osteospermum plants (Table 2). Approximately 50% of osteospermum plants inoculated with Pd103 wilted and developed crown rot, which was a significantly greater probability ($P = 0.0252$) than the noninoculated control (Fig. 1).

Variations in isolate aggressiveness. The days to initial visible symptom development ranged from approximately 7 days on snap-

Table 1. North Carolina isolates of *Phytophthora cryptogea* and *P. drechsleri* used in host specificity and aggressiveness testing

Isolate designation	Species	Year isolated	Host name
Pd103	<i>P. drechsleri</i>	2007	<i>Gerbera jamesonii</i> , Gerbera daisy
Pd957	<i>P. drechsleri</i>	2008	<i>Fuchsia</i> × <i>hybrida</i> , Fuchsia
Pdfdm5	<i>P. drechsleri</i>	2001	<i>Senecio cineraria</i> , Dusty miller
Pc597	<i>P. cryptogea</i>	2008	<i>G. jamesonii</i> , Gerbera daisy
Pc1105	<i>P. cryptogea</i>	2008	<i>Verbena</i> × <i>hybrida</i> , Verbena
Pc1146	<i>P. cryptogea</i>	2008	<i>Senecio cineraria</i> , Dusty miller

dragon and annual stock to over 30 days on fuchsia (Fig. 2). On verbena, there were no statistical differences ($P = 0.05$) between isolates with wilting developing in 20 to 30 days after inoculation for all isolates. Isolate aggressiveness depended on host but, overall, *P. drechsleri* isolates Pd957 and Pdfdm5 were more aggressive than the *P. cryptogea* isolates (Fig. 2).

For the *P. drechsleri* isolates, there was very little variability in isolate aggressiveness, and there were no significant differences ($P = 0.05$) in the days to foliar symptom development between Pd957 and Pdfdm5 on osteospermum, snapdragon, fuchsia, or gerbera

daisy (Fig. 2). On osteospermum, both isolates caused wilting and chlorosis to develop within 12 to 14 days, which was significantly faster than *P. drechsleri* isolate Pd103 ($P = 0.0001$). Annual stock plants inoculated with Pdfdm5 developed foliar symptoms significantly faster than plants inoculated with Pdfdm5 ($P = 0.0001$). In contrast, Pdfdm5 was significantly more aggressive than Pd957 on dusty miller ($P = 0.0065$).

The *P. cryptogea* isolates were more variable in aggressiveness than the isolates of *P. drechsleri* (Fig. 2). Isolate Pc1146 was more aggressive than Pc1105 on dusty miller ($P = 0.0002$) and Pc594

Fig. 1. Proportion of plants that developed foliar symptoms of *Phytophthora* root rot when inoculated with isolates of *Phytophthora drechsleri* (Pd103, Pd957, and Pdfdm5) and *P. cryptogea* (Pc594, Pc1105, and Pc1146). **A**, Dusty miller, osteospermum, snapdragon, and annual stock; **B**, fuchsia, gerbera daisy, African marigold, and verbena. Bars are means of data pooled across two trials with eight replications per trial. Bars marked with * indicate that plants inoculated with the corresponding isolate had a significantly greater probability ($P = 0.05$) of developing foliar symptoms of *Phytophthora* root rot than the noninoculated control (Noninoc) as determined by the analysis of maximum likelihood estimates from PROC LOGISTIC with Firth's bias correction (SAS 9.2; SAS Institute).

and Pc1105 on annual stock ($P = 0.0001$), with plants inoculated with Pc1146 developing foliar symptoms of root rot within 14 days (Fig. 2). On osteospermum, Pc1105 was significantly ($P = 0.0053$) more aggressive than Pc594. Isolates of *P. cryptogea* exhibited the greatest variability in aggressiveness on snapdragon (Fig. 2). Snapdragon plants inoculated with Pc1105 developed foliar symptoms within 10 days, which was significantly faster than Pc594 ($P = 0.0001$) and Pc1146 ($P = 0.0187$), and Pc1146 was significantly more aggressive than Pc594 ($P = 0.0001$), with symptoms developing in 14 and 20 days, respectively. Gerbera daisy plants inoculated with Pc1105 and Pc1146 developed foliar symptoms significantly faster than plants inoculated with Pc 594 ($P = 0.0010$ and 0.0218 , respectively). There was no significant ($P = 0.05$) difference between *P. cryptogea* isolates on fuchsia, with foliar symptoms developing 30 to 35 days after inoculation (Fig. 2).

Root colonization of nonsymptomatic host plants. Upon visual inspection, root necrosis was evident in some inoculated plants that were not exhibiting foliar symptoms; however, in many inoculated plants, there was no root necrosis visible to the unaided eye. Overall, *Phytophthora* was isolated from 116 of 245 inoculated host plants not exhibiting foliar symptoms (Table 3). The only successful isolation from African marigold was a single plant inoculated with *P. drechsleri* isolate Pdfdm5. Isolate Pd103 was recovered from 50% of sampled osteospermum plants; however, there were no successful isolations of Pd103 from any other nonsymptomatic host plant species. Isolate Pd957 was recovered from all tested nonsymptomatic dusty miller and fuchsia plants (Table 3). Similarly, Pdfdm5 was isolated from 100% of sampled nonsymptomatic fuchsia plants and 63% of verbena plants. Isolate Pc594 of *P. cryptogea* was recovered from 38 to 100% of tested dusty miller, snapdragon, fuchsia, gerbera daisy, and verbena plants. Pc1105 was isolated from over 50% of dusty miller, annual stock, fuchsia, gerbera daisy, and verbena plants not exhibiting foliar symptoms. Likewise, over half of tested dusty miller, osteospermum, snapdragon, fuchsia, gerbera daisy, and verbena plants were colonized by Pc1146 yet plants were nonsymptomatic (Table 3).

Discussion

Inoculation studies in eight ornamental host plants with three isolates of *P. cryptogea* and three isolates of *P. drechsleri* originally isolated from ornamental plant species grown in North Carolina greenhouse facilities identified differences in host ranges. The host ranges varied between isolates within both species. No isolate of *P. cryptogea* or *P. drechsleri* caused foliar symptoms of *Phytophthora* root rot on all host species, and no plant species was susceptible to all isolates of both species. In addition, variations in aggressiveness as determined by the days to foliar symptom development between isolates on a host plants species were evident.

Of the three isolates of *P. cryptogea* evaluated, no isolate had the same host range. Other reports indicate that ornamental isolates of *P. cryptogea* frequently have differing host ranges. Tompkins and Tucker (34) tested isolates of *P. cryptogea* from China-aster, annual stock, and gerbera daisy. The China-aster isolate had the largest host range and caused disease on wallflower, annual stock, gerbera daisy, Michaelmas daisy, hybrid cineraria, and a variety of vegetable plants. In contrast, the annual stock isolate only infected China-aster and gerbera daisy, and only annual stock developed disease when inoculated with the gerbera daisy isolate (34). Similarly,

Middleton et al. (24) evaluated nine isolates of *P. cryptogea* on eight ornamental host species, and six of the nine isolates had unique host ranges. Rattink (30) tested isolates of *P. cryptogea* from begonia and gerbera daisy and demonstrated that the begonia isolate only caused disease on begonia and sinningia but the gerbera daisy isolate caused disease on begonia, gerbera daisy, and peperomia. Likewise, Kröber (19) determined that isolates from Elatior begonia could cause disease on Elatior begonia and gerbera daisy but that isolates from China-aster and gerbera daisy were not pathogenic to Elatior begonia.

In the present study, annual stock and gerbera daisy were the only host species on which all three isolates of *P. cryptogea* caused significant disease. These plant species are well-established hosts of *P. cryptogea* and frequently were infected in other ornamental host range investigations (9,13,15,18,26,34). Tompkins and Tucker (34) reported that an isolate of *P. cryptogea* from annual stock was pathogenic to gerbera daisy and that an isolate of *P. cryptogea* from gerbera daisy was pathogenic to annual stock. Similarly, Middleton et al. (24) found that all tested isolates of *P. cryptogea* caused root rot on annual stock and gerbera daisy regardless of the host of origin.

During the 1970s, *P. cryptogea* was first identified as a serious pathogen of osteospermum in California, where it was causing a destructive root rot in outdoor ornamental plantings (10). Recently, *P. cryptogea* was reported causing stem rot on osteospermum in commercial nurseries in South Africa (23). In the present study, two isolates of *P. cryptogea* caused foliar symptoms of root rot on all inoculated osteospermum plants in approximately 14 to 18 days in the greenhouse. This indicates that *P. cryptogea* still has the potential to be a serious pathogen in this host, even though there are few published reports of *P. cryptogea* attacking osteospermum. It was expected that all isolates of *P. cryptogea* would cause foliar symptoms of root rot on osteospermum because it is in the same plant family (Asteraceae) as gerbera daisy, which was a host for all *P. cryptogea* isolates. Likewise, it was anticipated that all isolates of *P. drechsleri* would incite root rot on gerbera daisy because all isolates caused disease on osteospermum. However, in both instances, only two isolates of *P. cryptogea* and two isolates of *P. drechsleri* caused foliar symptoms of root rot on osteospermum and gerbera daisy, respectively. This suggests that host range may be more specific than the plant family level. Stirling and Irwin (31) reported that plant family was not a predictor of host range for isolates of *P. cryptogea*. An isolate from guar bean did not cause disease on cowpea, mung bean, common bean, or chickpea, which are in the Fabaceae family with guar bean, whereas sunflower and safflower, which are in the Asteraceae family, were highly susceptible to the guar bean isolate.

To our knowledge, this is the first work investigating the host range of ornamental isolates of *P. drechsleri* obtained from greenhouses. The isolates of *P. drechsleri* evaluated in this study varied greatly in their host ranges, with isolate Pd103 only causing symptoms on osteospermum whereas isolates Pd957 and Pdfdm5 were relatively nonspecific and caused disease on the majority of tested host species. Pratt et al. (29) compared the pathogenicity of 35 isolates of *P. drechsleri* obtained from native forests, safflower, and citrus orchard soil on safflower, sunflower, and watermelon. All inoculated safflower plants developed severe disease symptoms regardless of the isolate origin. However, no sunflower or water-

Table 2. Summary of host ranges for isolates of *Phytophthora drechsleri* and *P. cryptogea* determined from hosts that had a significantly greater probability of developing disease (+) than the noninoculated control

Isolate	Host							
	Dusty miller	Osteospermum	Snapdragon	Annual stock	Fuchsia	Gerbera daisy	African marigold	Verbena
Pd103	—	+	—	—	—	—	—	—
Pd957	+	+	+	+	—	+	—	+
Pdfdm5	+	+	+	+	—	+	—	—
Pc594	—	+	—	+	+	+	—	—
Pc1105	—	+	+	+	+	+	—	—
Pc1146	+	—	—	+	—	+	—	—

melon plants developed root rot. Most host range investigations with *P. drechsleri* have involved evaluating a single isolate of *P. drechsleri* on a range of host plants with no comparison of isolates from different hosts. However, by comparing across studies, it is evident that, similar to the host range variation observed in our ornamental isolates, *P. drechsleri* isolates collected from fruit and other crops plants appear to range from nonspecific to highly specific. Alavi (2) reported that an isolate of *P. drechsleri* obtained from cantaloupe was nonspecific and caused root rot on all tested plant species, including soybean, pigweed, lambsquarter, puslane,

and black nightshade. Likewise, an isolate from watermelon fruit evaluated by Katsura (17) was nonspecific and infected fruit of cucumber, eggplant, plum, carrot roots, and kidney bean pods. In contrast, an isolate of *P. drechsleri* from an unknown host origin was evaluated on 15 weed and 17 cultivated plant species (4). Of the 32 tested plant species, only alfalfa, safflower, and skeleton weed developed significant disease.

The reported host range of *P. drechsleri* in greenhouse-produced ornamentals is limited to approximately 25 species (7). Pathogenicity of isolate Pd957, originally collected from fuchsia (25),

Fig. 2. Days to development of foliar symptoms for plants inoculated with *Phytophthora drechsleri* isolates Pd103, Pd957, and Pd957m5 and *P. cryptogea* isolates Pc594, Pc1105, and Pc1146. **A**, Dusty miller, osteospermum, snapdragon, and annual stock; **B**, fuchsia, gerbera daisy, African marigold, and verbena. Isolates within each host shown with a different letter are significantly different (**A**, host-isolate $P < 0.0001$; **B**, host-isolate $P = 0.002$) according to an analysis of simple effect comparisons of the interaction least square means using pairwise t tests. Each bar is the mean of data pooled from two independent trials with eight replications per trial. Error bars represent the standard error.

was confirmed because the isolate caused *Phytophthora* root rot on fuchsia during the greenhouse studies. Symptoms progressed from stunting and nutrient stress to defoliation starting with the lower leaves and eventual plant death. The present greenhouse inoculation studies also expand the potential ornamental host range of *P. drechsleri* considerably. *Osteospermum*, snapdragon, and annual stock have not been reported as hosts of *P. drechsleri*. In this study, *osteospermum* was the only host on which all three isolates of *P. drechsleri* caused disease, with foliar symptoms of *Phytophthora* root rot developing within 12 to 20 days. Similarly, isolates Pd957 and Pdfdm5 caused disease on all inoculated snapdragon and annual stock plants within 7 to 14 days. These results suggest that *P. drechsleri* has the potential to be a serious pathogen of *osteospermum*, snapdragon, and annual stock if introduced to a greenhouse producing these plants. Verbena also has not been reported as a host of *P. drechsleri*. However, only isolate Pd957 caused significant *Phytophthora* root rot on verbena; therefore, verbena may not be as susceptible of an ornamental species.

In several cases, isolates of both *Phytophthora* spp. caused disease on a small percentage of host plants but the probability of disease developing in a host species was not statistically significant. The host range of isolates potentially could fluctuate depending on the state of the host plant. Under conditions where the plant is stressed, the isolate could be pathogenic to the particular plant but, when the plant is not stressed, the isolate is not a serious pathogen. Thinggaard and Anderson (32) found that increasing the watering frequency in an ebb and flow system increased gerbera daisy mortality from *P. cryptogea* from 13.5 to 73.6%. In chrysanthemum, salinity stress within 24 h of inoculation and heat stress induced by exposing pots to direct sunlight increased susceptibility to *P. cryptogea* (21,22). In safflower screening studies, Zimmer and Urie (36) reported that increased irrigation frequency and intensity or moisture stress prior to irrigation increased safflower mortality in cultivars normally resistant to *P. drechsleri*.

Two isolates, Pd103 and Pc1105, did not cause disease on their hosts of origin, gerbera daisy and verbena, respectively. For these two isolates, the cultivar of each host used in this study was not the cultivar from which the isolate was collected originally; therefore, the lack of disease development could be a result of differences in cultivar susceptibility within plant species. While evaluating gerbera daisy cultivars for resistance to *Phytophthora* root rot caused by *P. cryptogea*, Yue et al. (35) demonstrated that pathogenicity of the six isolates used in the screening depended greatly on the cultivar being tested. Similarly, 15 cultivars of guar bean inoculated with an isolate of *P. cryptogea* exhibited a range of susceptibility from approximately 25 to 100% mortality (31). Orlikowski and Ptasek (27) reported significant differences in susceptibility to cultivars of houseleeks when inoculated with an isolate of *P. cryptogea*. Cultivar-isolate interactions have been reported in screening of safflower cultivars for resistance to *P. drechsleri*, leading several researchers to suggest the development of races within this species (33,36). Overcoming the possible effect of cultivar in future host range screenings of ornamental species for susceptibility to *Phytophthora* spp. likely will be difficult because of the large number of commercially available cultivars and the changing nature of the ornamental industry, where new

cultivars are introduced constantly and old cultivars become unavailable.

The majority of host range studies have evaluated only the development of disease (i.e., yes or no), with no considerations for differences in isolate aggressiveness on a particular host. Although isolates of *P. cryptogea* and *P. drechsleri* had overlapping host ranges, differences in isolate aggressiveness were evident when evaluated as a function of days to disease development. On the majority of host plants, the isolates of *P. drechsleri* were more aggressive than the isolates of *P. cryptogea*, the exception being on fuchsia. In contrast, on kiwifruit vines, Conn et al. (3) found that *P. cryptogea* isolates were consistently more aggressive than *P. drechsleri* isolates. Tompkins and Tucker (34) found that the average incubation period for isolates of *P. cryptogea* was 10 days for China aster, 24 days for annual stock, and 45 days for gerbera daisy. The days to disease development for most of our isolates of *P. cryptogea* on annual stock and gerbera daisy compared very closely to Tompkins and Tucker (34). Most annual stock plants wilted in approximately 18 to 24 days, whereas gerbera daisy plants developed disease more slowly, with symptoms appearing in 30 to 40 days. Within a species, no one isolate was consistently more aggressive and aggressiveness always depended on the host. Orlikowski and Ptasek (27) compared aggressiveness by lesion development on European columbine and houseleek inoculated with isolates of *P. cryptogea* from six ornamental species. After 5 days, variations in isolate aggressiveness were evident on both plants, and the isolate aggressiveness varied by plant. On European columbine, lesions were largest on plants inoculated with the isolates from gerbera daisy, European columbine, and White Mountain saxifrage. In contrast, *P. cryptogea* isolates from gerbera daisy, mossy saxifrage, and houseleek were the most aggressive on houseleek (27). Variations in aggressiveness of isolates of *P. cryptogea* have been reported in other crops. Larsson and Gerhardsson (20) tested an isolate of *P. cryptogea* obtained from spinach on spinach, sugarbeet, wheat, cucumber, oat, pea, and rape. The isolate caused disease on all tested hosts. However, the isolate was highly aggressive on spinach and sugarbeet; moderately aggressive on wheat, cucumber, and pea; and slightly aggressive on oat and rape. The growth rate of mycelium in tomato plants varied greatly between isolates of *P. cryptogea* from Edelweiss, gerbera daisy, melon, cucumber, aster, sugar beet, tomato, pepper, and strawberry (14). Isolates from tomato, pepper, and strawberry had the fastest growth on tomato, and isolates from Edelweiss, gerbera daisy, and melon had the slowest growth rate.

African marigold was the only host species that did not develop foliar symptoms of *Phytophthora* root rot. Although *P. cryptogea* has been reported as a causal agent of root rot in African marigold in the early literature (28), no isolate of *P. cryptogea* was found to infect the roots of African marigold based on the isolations from nonsymptomatic plants. African marigold has not been reported as a host of *P. drechsleri* and, like the *P. cryptogea* isolates, was not isolated readily from nonsymptomatic hosts. This suggests that African marigold may not be a common host of these *Phytophthora* spp. and should be investigated further for disease resistance. In contrast to African marigold, the roots of many nonsymptomatic test plants were found to be infected with *Phy-*

Table 3. Isolation of *Phytophthora drechsleri* and *P. cryptogea* from the roots of host plants not exhibiting foliar symptoms of *Phytophthora* root rot at the conclusion of the greenhouse studies

Isolate	Isolation from host plants not exhibiting foliar symptoms (success/total) ^a							
	Dusty miller	Osteospermum	Snapdragon	Annual stock	Fuchsia	Gerbera daisy	African marigold	Verbena
Pd103	0/8	4/8	0/8	0/8	0/8	0/8	0/8	0/8
Pd957	1/1	—	—	—	8/8	—	0/8	—
Pdfdm5	—	—	—	—	8/8	—	1/8	5/8
Pc594	6/8	—	8/8	—	7/8	8/8	0/8	3/8
Pc1105	6/8	—	—	3/3	6/8	2/4	0/8	5/8
Pc1146	4/5	8/8	7/8	—	4/8	5/8	0/8	7/8

^a Number of successful isolations/number of total isolations.

tophthora. In the floriculture industry, it is common for plant material to move around the United States and even from off-shore into the United States (5). Nonsymptomatic plant material infected with one of these *Phytophthora* spp. potentially could be shipped between growers or from production growers to retailers, thereby introducing *Phytophthora* spp. to new greenhouses or to landscapes. In the nursery industry, *Phytophthora* spp. are known to be moved between locations on nonsymptomatic plant material, the most notable recent example being *P. ramorum* (5). It seems likely that this also is occurring in the greenhouse industry, based on the number of nonsymptomatic plants infected with either *P. cryptogea* or *P. drechsleri*, and should be taken into consideration in the management of these pathogens.

Overall, these studies indicate that isolates of *P. cryptogea* and *P. drechsleri* have varying host ranges. *Osteospermum*, annual stock, and gerbera daisy were identified as being more likely to be attacked by these species than other plant species. This increased likelihood should be considered by growers when developing a disease management program for these plant species. Growers utilizing ebb-and-flow or flood-floor irrigation should consider separating these crops to minimize the potential for crop-to-crop spread. Scouting for root rot symptoms could target these plants to more quickly identify the onset of *Phytophthora* root rot epidemics. The large number of infected nonsymptomatic plants found is alarming and suggests that movement of such plants likely has a large role in the movement of these *Phytophthora* spp. throughout the industry and may result in these pathogens being introduced into the environment.

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