Susceptibility of Greenhouse Ornamentals to *Phytophthora capsici* and *P. tropicalis*

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Abstract

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The susceptibility of fabaceous (*Lupinus* and *Lathyrus* spp.) and solanaceous (*Calibrachoa*, *Browallia*, *Nicotiana*, *Nierembergia*, and *Petunia* spp.) ornamental plants compared with straightneck squash (*Cucurbita pepo*) inoculated with *Phytophthora capsici* and *P. tropicalis* was investigated in greenhouse studies. Four *P. capsici* isolates and one *P. tropicalis* isolate were evaluated. Flowering tobacco (*Nicotiana* × *sanderiae*), sweet pea (*Lathyrus latifolius*), lupine (*Lupinus polyphyllus*), squash, and million bells (*Calibrachoa* × *hybrida*) were susceptible to *P. capsici* and *P. tropicalis*. Bush violet (*Browallia speciosa*) and cup flower (*Nierembergia scoparia*) were not susceptible to either pathogen. *Petunia* (*Petunia* × *hybrida*) was susceptible to *P. capsici* but not *P. tropicalis*. Area under the plant growth curve (AUPGC) was also affected in some susceptible plants. AUPGC was significantly different in inoculated plants compared with

the untreated controls of *Nicotiana* and *Calibrachoa*. In addition, six *Calibrachoa* cultivars were evaluated for susceptibility to *P. capsici* and *P. tropicalis* in a separate experiment. Although all *Calibrachoa* cultivars were susceptible to *P. capsici* and *P. tropicalis*, 'Celebration Purple Star' displayed limited disease following inoculation with either pathogen. *Calibrachoa* 'Cabaret' and 'Can-Can' inoculated with *P. capsici* or *P. tropicalis* displayed significant differences in AUPGC compared with the uninoculated controls. 'Callie', 'Million Bells Cherry Pink', and 'Superbells' had significantly reduced AUPGC compared with the controls when inoculated with *P. tropicalis* but not *P. capsici*. These results expand the host range of *P. capsici* to include *Calibrachoa* spp., *L. polyphyllus*, and *Lathyrus latifolius*, and *P. tropicalis* to include *L. latifolius*, *Nicotiana* spp., and straightneck squash.

In 2013, floricultural sales in Michigan were approximately \$406 million, almost 10% of the United States total (\$4.4 billion) (USDA 2014). Michigan is ranked third in sales among the top five floricultural states in the United States for production of annuals, perennials, cut flowers, foliage plants, and propagative materials (USDA 2014). These ornamentals, grown entirely for aesthetic value, require diligent disease management (Baker and Linderman 1979). High humidity, warm temperatures, and moist conditions present in greenhouse and nursery environments are conducive to the growth, reproduction, and colonization of root rot pathogens. Greenhouse growers utilize a range of media, including packaged peat-based mixes and custom blends that incorporate a field soil component. Utilizing field soil for greenhouse-grown crops increases the potential for long-lived root rot pathogens such as *Phytophthora* spp. to enter the production system. Plants exhibiting aboveground root rot symptoms such as crown lesions, stunting, and wilting are not salable and result in financial losses to the grower (Baker and Linderman 1979).

Phytophthora tropicalis Aragaki & J. Y. Uchida causes disease on numerous herbaceous ornamentals, including annual vinca (*Catharanthus roseus*) (Hao et al. 2010), cyclamen (*Cyclamen persicum*) (Gerlach and Schubert 2001), pothos (*Epipremnum aureum*), gloxinia (*Sinningia speciosa*), and verbena (*Verbena* × *hybrida*) (Olson and Benson 2011). Greenhouse studies have identified additional *P. tropicalis*-susceptible floriculture crops, including begonia (*Begonia* sp.), gerbera daisy (*Gerbera jamesonii*), lupine (*Lupinus albus*), and dusty miller (*Senecio bicolor*) (Hong et al. 2008). Greenhouse evaluations of important solanaceous ornamentals such as *Petunia* spp., and *Calibrachoa* spp. to *P. tropicalis*, have been limited (Ampuero et al. 2008; Omer et al. 2011). *Calibrachoa* is a relatively new genus to the ornamental industry because the first hybrids were

introduced in the early 1990s with high economic importance (Schultz Nelson 2008). In 2007, *Calibrachoa* × *hybrida* Cerv. plants with crown and stem rot in a wholesale New York greenhouse were reported as being infected with *P. capsici* but the pathogen was later reidentified as *P. tropicalis* based on sequencing (Daughtrey and Tobiasz 2008; Quesada-Ocampo et al. 2011).

P. tropicalis was previously conspecific with *P. capsici* Leonian, and the two species share considerable morphological characteristics and host overlap (Alizadeh and Tsao 1985; Brasier and Griffin 1979; Lamour 2009; Uchida and Aragaki 1980). *P. tropicalis* was given a separate species taxon from *P. capsici* in 2001 based on the morphological characteristics, absence or minimal growth at 35°C, and having weak or no pathogenicity on pepper (*Capsicum annuum* L.) (Aragaki and Uchida 2001; Leonian 1922). *P. capsici* is a major production limitation for susceptible vegetables in Michigan (Hausbeck and Lamour 2004), the United States (Babadoost 2000; Isakeit 2007; Mathis et al. 1999; Ploetz and Haynes 2000; Ristaino and Johnston 1999), and globally (Hwang and Kim 1995; Silvar et al. 2006) but has not been considered a major pathogen of ornamentals.

There is considerable host overlap between *P. tropicalis* and *P. capsici*, which may be due, in part, to difficulties in distinguishing the two species (Lamour 2009). Both cause disease on tropical species, including macadamia (*Macadamia* spp.), cacao (*Theobroma cacao*), eggplant (*Solanum melongena* L.) (Erwin and Ribeiro 1996), flamingo flower (*Anthurium* spp.), carnation (*Dianthus* spp.), pothos (*Epipremnum* spp.) (Orlikowski et al. 2006; Wick and Dicklow 2002), and pincushion flower (*Leucospermum* spp.) (Aragaki and Uchida 2001; Donahoo and Lamour 2008; Oudemans and Coffey 1991). Although *P. capsici* and *P. tropicalis* share common morphological characteristics and hosts, the presence of two distinct species is supported by genetic and phylogenetic analyses (Donahoo and Lamour 2008; Quesada-Ocampo et al. 2011; Zhang et al. 2004).

Historically, *P. capsici* has not been a problem on most ornamentals. However, many *P. capsici*-susceptible vegetable and weed hosts are members of the Fabaceae and Solanaceae families (Davidson et al. 2002; Erwin and Ribeiro 1996; Gevens et al. 2008; Hausbeck and Lamour 2004), which include important ornamentals such as

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L. polyphyllus, *Lathyrus latifolius*, and *Petunia* spp. The ornamental plants *Lupinus polyphyllus* and *Calibrachoa* spp. are known fabaceous and solanaceous hosts, respectively, of *P. tropicalis* (Daughtrey and Tobiasz 2008; Hong et al. 2008; Quesada-Ocampo et al. 2011). However, the susceptibility of economically important and common floriculture crops within these families to *P. capsici* has not been well investigated.

P. tropicalis and *P. capsici* are closely related taxa (Donahoo and Lamour 2008) infecting similar families, and the host range of both pathogens has continued to expand. Determining the susceptibility and symptoms of ornamental fabaceous and solanaceous plants to these two pathogens may provide important insight into strategies for effective disease management in greenhouse and field production of ornamentals and vegetables. The objectives of this research were to (i) investigate the etiology of *P. capsici* and *P. tropicalis* on economically important ornamental plants within the fabaceous and solanaceous families and (ii) compare the susceptibility and growth of *Calibrachoa* cultivars infected with these pathogens.

Materials and Methods

Isolate selection, identification, and maintenance. Four *P. capsici* isolates from the collection of Dr. Mary K. Hausbeck (Michigan State University [MSU]) and one *P. tropicalis* isolate from the collection of Dr. Margery Daughtrey (Cornell) were used as inocula. Isolates differed in phenotype (mating compatibility type [CT] and sensitivity to the fungicide mefenoxam [MS]) and host origin and were characterized by CT and MS, as described by Lamour and Hausbeck (2000). *P. capsici* isolates OP97 (CT = A1, MS = sensitive, host = pickling cucumber), SP98 (A2, sensitive, pumpkin), and 12889 (A1, insensitive, pepper) have been shown to be highly virulent on various hosts (Enzenbacher and Hausbeck 2012; Foster and Hausbeck 2010; Quesada-Ocampo et al. 2009; Quesada-Ocampo and Hausbeck 2010). Isolates had been previously identified to species and characterized by sequencing (Quesada-Ocampo et al. 2011). *P. capsici* isolate 13351 (A1, sensitive, eggplant) was previously evaluated on eggplant and pepper (Foster et al. 2013). *P. tropicalis* isolate 13715 (A1, sensitive, *Calibrachoa* spp.) was previously reported as *P. capsici* (Daughtrey and Tobiasz 2008) but was reclassified as *P. tropicalis* following polymerase chain reaction (PCR) and sequencing of 10 genes (Quesada-Ocampo et al. 2011).

Isolates were obtained from long-term storage (microcentrifuge tubes containing 1 ml of sterile water and 1 sterile hemp seed at 20°C) and plated on unclarified V8 juice agar (UCV8; 16 g of agar, 3 g of calcium chloride [CaCO₃], 160 ml of V8 juice, and 840 ml of distilled water) amended with 0.50 g of benomyl, 2 ml of ampicillin, and 2 ml of rifampicin. Agar plugs (5 mm in diameter) from 5- to 7-day-old cultures were used to inoculate straightneck squash (*Cucurbita pepo*) fruit prior to use in experiments to confirm pathogenicity. Five days postinoculation (dpi), symptomatic fruit tissue was excised and plated on BARP-amended UCV8 agar (12 g of agar, 0.3 g of CaCO₃, 40 ml of V8 juice, 960 ml of distilled water, 0.50 g of benomyl, 2 ml of ampicillin, 2 ml of rifampicin, and 0.10 g of pentachloronitrobenzene). Cultures were observed 3 days after plating using a compound microscope at ×100 magnification to confirm *P. capsici* morphological characteristics according to Waterhouse (1963). *P. tropicalis* was confirmed according to Aragaki and Uchida (2001). Isolates were hyphal tipped and transferred to new UCV8 agar. Cultures were maintained at room temperature (21 to 23°C) under continuous fluorescent lighting and were transferred every 5 to 7 days to new UCV8 agar.

Pathogenicity on fabaceous and solanaceous plants. Seven ornamental species from two plant families were evaluated for their susceptibility to *P. capsici* and *P. tropicalis* compared with the *P. capsici*-susceptible control, squash (Table 1). The experimental design was a split-plot arrangement of a randomized complete block design, and the experiment was performed three times for disease incidence and two times for plant growth and volume. Runs 1 and 2 were performed in March 2010 at the MSU Horticulture Teaching and Research Center in Holt, MI, and run 3 was conducted in October 2010 at the MSU Plant Science Research Greenhouses in East Lansing, MI. Pathogen isolate and plant type were considered the whole-plot

and subplot factors, respectively. Number of replicates differed among plant types and runs due to limited plant availability (Table 1).

Susceptibility to *Phytophthora* spp. among *Calibrachoa* cultivars. Six cultivars of *Calibrachoa* were evaluated for their susceptibility to *P. capsici* (isolate SP98) and *P. tropicalis* (isolate 13715) during February 2011. The experimental design was a split-plot arrangement of a randomized complete block design, and the experiment was performed twice. Runs were conducted in two separate greenhouse ranges at the MSU Plant Science Research Greenhouses (Table 1). Pathogen isolate and plant type were considered the whole-plot and subplot factors, respectively. There were 12 replicates of each cultivar for each isolate and the control.

Inoculation and evaluation. Rooted cuttings or seedlings were received from commercial producers (Table 1). Plant replicates were transplanted into individual 386.7-cm³ pots containing soilless potting media (Baccto Professional Planting Mix; Michigan Peat Company, Houston) 14 days prior to inoculation. ‘Cougar’ straightneck squash seed (Rispen Seeds, Inc., Beecher, IL) were sown in a 128-cell plug tray filled with potting media 14 days prior to inoculation. Squash seedlings were transplanted into individual 386.7-cm³ pots containing potting media 7 days prior to inoculation. Plants were watered as necessary and fertilized three times weekly at 200 ppm with Peter’s 20-20-20 soluble liquid fertilizer (The Scott’s Company, Marysville, OH). Plants were acid treated weekly with 10% phosphoric acid to maintain an appropriate pH in the growing media for the plants being tested. The *Calibrachoa* plugs grown for the cultivar susceptibility experiment were drenched with thiophanate-methyl (OHP 6672 4.5L; OHP, Inc., Mainland, PA) 2 days prior to transplanting

Table 1. Ornamental plants evaluated for susceptibility to root rot caused by *Phytophthora capsici* and *P. tropicalis*

Host		N ^q	Experiment
Family, species (common name)	Cultivar		
Cucurbitaceae			
<i>Cucurbita pepo</i> (straightneck squash) ^f	Cougar	12	1
Fabaceae			
<i>Lathyrus latifolius</i> (sweet pea) ^s	Latifolia Mixed ^t	12	1
<i>Lupinus polyphyllus</i> (lupine) ^s	Gallery Pink ^t	10 ^u	1
Solanaceae			
<i>Browallia speciosa</i> (bush violet) ^s	Bells Silver ^t	12	1
<i>Calibrachoa</i> × <i>hybrid</i> (million bells) ^v	Callie Gold with Red Eye ^{r,w}	8	1,2
	Starlette Sunset ^{w,x}	12	1
	Cabaret Yellow ^{w,x}	12	2
	Can-Can Apricot ^{w,x}	12	2
	Celebration Purple Star ^{x,y}	12	2
	Million Bells Cherry Pink ^{w,x}	12	2
	Superbells White ^{x,z}	12	2
	Perfume Deep Purple ^t	12	1
<i>Nicotiana</i> × <i>sanderae</i> (flowering tobacco) ^s			
<i>Nierembergia scoparia</i> (cup flower) ^s	Purple Robe ^t	12	1
<i>Petunia</i> × <i>hybrida</i> (petunia) ^s	Prism Sunshine ^t	12	1

^q Number of replicates.

^r Rispen Seeds, CA.

^s Received as rooted cuttings or seedlings from C. Raker & Sons, MI.

^t Used in experiment 1 only.

^u In all, 10 replicates were evaluated in runs 1 and 2 and 12 replicates were evaluated in run 3; for the second experiment 12 replicates were evaluated for runs 1 and 2.

^v Run 3 did not include million bells due to the inability to acquire the same cultivars from commercial producers that were used in runs 1 and 2.

^w Received as rooted cuttings from Sunbelt Greenhouse, GA.

^x Used in experiment 2 only.

^y Received as rooted cuttings from Mast Young Plants, MI.

^z Received as rooted cuttings from Four Star Greenhouse, MI.

and 12 days after transplanting at the rate of 124.9 ml/liter for prevention of black root rot (*Thielaviopsis basicola*). Greenhouse temperature and relative humidity were recorded hourly with a Watchdog data logger (450 series; Spectrum Technologies, Inc., East Plainfield, IL) and to calculate mean air temperature and relative humidity.

Inoculum was prepared according to the methods of Quesada-Ocampo et al. (2009). For runs 1 and 2, infested millet seed (approximately 1 g) were placed on the surface of potting media near plant stems for the experiment with fabaceous and solanaceous plants. At 14 dpi, approximately 0.5 g of infested millet seed were added to the potting media to ensure adequate disease development. For the *Calibrachoa* cultivar experiment and for run 3 of the experiment with fabaceous and solanaceous plants, millet seed were buried to a depth of 2 to 3 cm and about 1 cm away from the crown to prevent inoculum desiccation. Control plants were inoculated with sterile millet seed. Plants were watered after inoculation to prevent inoculum desiccation.

For both experiments, plants were assessed for disease symptoms at 2-day intervals from 0 to 42 dpi. Plant height and mean canopy width (calculated by averaging two width measurements [the second measurement perpendicular to the first]) of each replicate were measured (in centimeters) at 7-day intervals from 14 to 42 dpi in experiment 1 and from 0 to 42 dpi in experiment 2. Crown and root tissue of 50% of inoculated plants were excised upon death or experiment completion. Asymptomatic control plants were also sampled. Excess roots and foliage were removed, and plants were gently rinsed with water to remove remaining potting media. Plants were surface disinfested in a 5% bleach solution (0.31% sodium hypochlorite) for 3 min, submerged in distilled water for 1 min, and air dried. Squash plants were surface disinfested with 70% ethanol and air dried. Two sections of tissue were excised from the crown and roots and plated on BARP-amended UCV8 agar. Cultures were observed 3 days after plating using a compound microscope at $\times 100$ magnification and confirmed as *P. capsici* based on morphological characteristics according to Waterhouse (1963). *P. tropicalis* was confirmed according to Aragaki and Uchida (2001). Isolates were characterized for CT and MS as previously described (Lamour and Hausbeck 2000), and the phenotype of recovered isolates was compared with the original inoculum.

Statistical analyses. Plant height and mean canopy width were used to calculate plant volume (volume of a cylinder [$V = \pi r^2 h$]) to standardize height and canopy width measurements among plants. Mean plant volume (in cubic centimeters) of each plant type was determined by averaging the volume of the plant type–pathogen isolate pairing at every interval. Mean plant volume data were analyzed by analysis of variance (ANOVA) using the PROC MIXED procedure of SAS (version 9.2; SAS Institute Inc., Cary, NC). Repeated-measures

analyses were conducted by applying the REPEATED statement with autoregressive of order 1 with heterogeneous variance-covariance structure (with the lowest Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) values chosen) to make conclusions on mean plant volume. Variances were tested for heterogeneity using Levene's test and, when necessary, the GROUP option of the REPEATED statement (with the lowest AIC value = plant type $\times$ pathogen isolate) was used, with degrees of freedom calculated according to Kenward-Roger. Plant replicate volume calculations of each plant type–pathogen isolate pairing for each 7-day interval were placed into the area under the disease progress curve mathematical formula according to Shaner and Finney (1977) to assess stunting or death over time, and are referred to hereafter as area under the plant growth curve (AUPGC). Larger AUPGC values signify greater plant volume. AUPGC values were analyzed by ANOVA using the PROC MIXED procedure of SAS (version 9.2). If ANOVA was significant for mean plant volume or AUPGC value main effects or interaction terms, treatment means were compared using Fisher's protected least significant difference at $P = 0.05$. Estimates and + estimate standard errors were back transformed to report least square means and standard errors.

Results

Pathogenicity on fabaceous and solanaceous plants. Disease incidence varied among plant type–pathogen isolate pairings; some plants appeared healthy, while others became severely diseased (Table 2). Recovered *P. capsici* or *P. tropicalis* isolates from all plants were confirmed to have the same phenotype as the original inoculum (data not shown). Control seedlings did not exhibit disease symptoms, nor were the pathogens recovered (data not shown).

Mean air temperature and relative humidity for the experiment with fabaceous and solanaceous plants were 21.1°C ($\pm 17.3^\circ\text{C}$) and 55.5% ($\pm 39.7\%$), respectively. Mean plant volume data were square root transformed prior to analyses to satisfy normality assumptions and variances were heterogeneous for plant type and pathogen isolate. Because the *Calibrachoa* cultivars were not included in run 3, statistical differences were detected among experimental runs. Statistical differences were not found among runs when *Calibrachoa* cultivars were removed from run 1 and 2 data sets. Plant type ($P < 0.0001$), pathogen isolate ($P < 0.0001$), dpi ($P < 0.0001$), and the interaction ($P < 0.0001$) were significant for mean plant volume. The interaction between plant type and pathogen isolate was significant, except for the squash plants inoculated with *P. capsici* isolates SP98 ($P = 0.4051$), 12889 ($P = 0.1435$), and 13351 ($P = 0.4121$). Plant type ($P < 0.0001$), pathogen isolate ($P < 0.0001$), and the interaction ($P < 0.0001$) were significant for plant AUPGC values. *Nicotiana* spp. ($P = 0.0395$), 'Callie Gold with Red Eye' ($P = 0.0013$) and 'Starlette Sunset' *Calibrachoa*

Table 2. Disease incidence of and pathogen recovery from ornamental plants evaluated for susceptibility to *Phytophthora capsici* isolates OP97, SP98, 12889, and 13351 and *P. tropicalis* isolate 13715

Plant	Disease incidence and pathogen recovery (%) ^y									
	<i>P. capsici</i> isolates								<i>P. tropicalis</i>	
	OP97		SP98		12889		13351		13715	
	DI	PR	DI	PR	DI	PR	DI	PR	DI	PR
<i>Browallia speciosa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nierembergia scoparia</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Nicotiana</i> $\times$ <i>sanderiae</i>	16.7	8.9	11.1	2.2	38.9	16.7	22.2	5.6	41.7	44.4
<i>Lupinus polyphyllus</i>	78.1	3.8	43.7	62.5	65.6	50.0	71.9	75.0	81.3	57.8
<i>Calibrachoa</i> $\times$ <i>hybrida</i> ^z										
'Callie Gold with Red Eye'	6.3	12.5	25.0	25.0	6.3	0.0	6.3	37.5	100.0	100.0
'Starlette Sunset'	25.0	0.0	12.5	25.0	20.8	0.0	16.7	33.3	100.0	100.0
<i>Petunia</i> $\times$ <i>hybrida</i>	0.0	5.6	0.0	5.6	0.0	5.6	0.0	11.1	0.0	0.0
<i>Cucurbita pepo</i>	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	86.0	75.0
<i>Lathyrus latifolius</i>	5.6	5.6	8.3	0.0	5.6	0.0	8.3	5.6	16.7	22.2

^y Disease incidence (DI) was calculated for plants inoculated with each isolate by dividing the number of plants that exhibited root rot symptoms by the total number of plants inoculated with each isolate and multiplying by 100. Pathogen recovery (PR) was calculated for plants inoculated with each isolate by the percentage of confirmed *P. capsici* or *P. tropicalis* isolates recovered from root or crown tissue of 50% of each plant type inoculated with each isolate and control plants. Control plants did not exhibit disease symptoms, nor were *P. capsici* or *P. tropicalis* recovered.

^z *Calibrachoa* cultivars were evaluated in runs 1 and 2 only.

($P < 0.0001$), squash ($P < 0.0001$), and all pathogen isolates ($P < 0.0001$) were significant for AUPGC when the interaction term was sliced by plant type and pathogen isolate.

Disease onset for *Nicotiana* spp. and *L. polyphyllus* inoculated with *P. capsici* or *P. tropicalis* occurred within 17 and 19 dpi, respectively. Symptoms included stunting, wilting, and chlorotic foliage that became necrotic, with occasional plant death (Fig. 1A to C). Roots of symptomatic *Nicotiana* spp. and *L. polyphyllus* ranged from slightly rotted to brown and decayed. Pathogen recovery from the host tissue ranged from 3.8 to 75.0% among isolates (Table 2). *Nicotiana* spp. inoculated with *P. capsici* isolates 12889 or 13351 or *P. tropicalis* were stunted compared with control plants 35 dpi (data not shown) but were similar in size 42 dpi (Fig. 2A). *Nicotiana* spp. inoculated with *P. capsici* isolates OP97 or 12889 or *P. tropicalis* had lower AUPGC values (414255, 358275, and 372571, respectively) than control plants (492544) (Fig. 2B). *L. polyphyllus* plants inoculated with *P. capsici* or *P. tropicalis* were similar in size 42 dpi and had AUPGC values similar to the control plants (Fig. 2).

Both cultivars of *Calibrachoa* included in this experiment became diseased when inoculated with *P. tropicalis*. Symptoms included necrotic crown lesions that progressed to the stems 12 dpi. Asymmetrical foliar wilting generally followed. Older foliage closest to the base wilted first (Fig. 1D), with all aboveground tissues eventually losing turgidity, resulting in plant death (Fig. 1E). Roots of diseased plants were brown and decayed. Disease incidence among *Calibrachoa* cultivar–*P. capsici* isolate pairings ranged from 6.3 to 25.0%,

with pathogen recovery varying among cultivars and isolates (Table 2). Symptomatic plants resembled those infected by *P. tropicalis*. Callie Gold with Red Eye and Starlette Sunset *Calibrachoa* inoculated with *P. tropicalis* were smaller than *P. capsici*-inoculated and control plants at 42 dpi (Fig. 2A). Callie Gold with Red Eye and Starlette Sunset *Calibrachoa* inoculated with *P. tropicalis* had lower AUPGC values (AUPGC values = 36,337 and 95,302, respectively) than *P. capsici*-inoculated and control plants (AUPGC values = 207,116 and 308,890, respectively) (Fig. 2B).

Squash inoculated with *P. tropicalis* exhibited disease symptoms 7 dpi. Plants developed water-soaked crown lesions that progressed to the stems but did not extend beyond cotyledons. Over time, lesions hardened and ceased to enlarge (Fig. 1F and G). First and second true leaves lost turgidity; however, seedlings did not collapse. Squash inoculated with *P. capsici* began to exhibit wilting and crown lesions at 5 dpi; seedlings then collapsed and died. Disease incidence and pathogen recovery among squash–*P. capsici* isolate pairings was 100%; disease incidence and pathogen recovery of *P. tropicalis*-inoculated squash was 86.0 and 75.0%, respectively (Table 2). Squash plants inoculated with *P. tropicalis* were similar in size to control plants at 42 dpi (Fig. 2A). The AUPGC values of *P. tropicalis*-inoculated and control squash plants were similar (Fig. 2B). Squash inoculated with *P. capsici* isolates had lower AUPGC values than *P. tropicalis*-inoculated and control plants (Fig. 2B).

Lathyrus latifolius became diseased when inoculated with either *P. capsici* or *P. tropicalis* (Table 2). Foliar chlorosis was observed

Fig. 1. Aboveground root rot symptoms caused by *Phytophthora capsici* or *P. tropicalis*. **A**, Stunting and **B**, death of *Nicotiana* × *sanderae*. **C**, Foliar and stem wilting of *Lupinus polyphyllus*. **D**, Asymmetrical foliar wilting and **E**, death of *Calibrachoa* × *hybrida*. **F** and **G**, Crown lesions on straightneck squash. **H**, Chlorotic and necrotic foliage of *Lathyrus latifolius*.

26 dpi (Fig. 1H); necrosis developed soon thereafter. Symptomatic plants were not vigorous, and roots ranged from healthy appearing to brown and decayed. Pathogen recovery varied among isolates (Table 2). Inoculated plants were similar in size and AUPGC values to control plants 42 dpi (Fig. 2).

Petunia plants inoculated with *P. capsici* remained asymptomatic but the pathogen was recovered (Table 2). *Petunia* plants inoculated with *P. tropicalis* displayed no symptoms, and the pathogen was not recovered. *Browallia speciosa* and *Nierembergia scoparia* inoculated with *P. capsici* or *P. tropicalis* also remained asymptomatic; neither pathogen was recovered (Table 2).

Susceptibility to *Phytophthora* spp. among *Calibrachoa* cultivars.

Disease incidence and pathogen recovery from *P. tropicalis*-inoculated cultivars was 100%. Disease incidence and pathogen recovery varied among *P. capsici*-inoculated cultivars and ranged from 75.0 to 92.0% and 16.7 to 100.0%, respectively (Table 3). AUPGC values of the *Calibrachoa* cultivar experiment were square root transformed prior to analyses to satisfy normality assumptions. Variances were heterogeneous for plant type and pathogen isolate. There were no significant differences among experiments and data were combined. For the *Calibrachoa* cultivar experiment, mean air temperature and relative humidity were 23.4°C ($\pm 12.5^\circ\text{C}$) and 30.5% ($\pm 26.6\%$), respectively.

Cultivar, pathogen isolate, dpi, and the interaction were significant ($P < 0.0001$) for mean plant volume. All interactions between pathogen isolate and dpi were significant, except for *P. capsici* at 21 ($P = 0.0489$) and 42 ($P = 0.3410$) dpi. All interactions between cultivar and pathogen isolate were significant ($P < 0.0001$). Interactions among plant

volume and date in 'Can-Can Apricot', 'Cabaret Yellow', Callie Gold with Red Eye, 'Million Bells Cherry Pink', and 'Superbells White' were significant. Cultivar, pathogen, and the interaction ($P = 0.0004$) were significant for AUPGC. All cultivar and pathogen isolate interactions were significant when sliced by cultivar and pathogen isolate, except for 'Celebration Purple Star' ($P = 0.7713$).

Can-Can Apricot *P. capsici*-inoculated and control plants were larger than *P. tropicalis*-inoculated plants 14 dpi (data not shown). At 42 dpi, Callie Gold with Red Eye and Million Bells Cherry Pink *P. capsici*-inoculated and control plants were larger than *P. tropicalis*-inoculated plants (Fig. 3A). When Cabaret Yellow and Can-Can Apricot were inoculated with *P. capsici*, they were smaller than control plants at 42 dpi (Fig. 3A). Superbells White *P. tropicalis*-inoculated plants were smaller than *P. capsici*-inoculated and control plants at 42 dpi (Fig. 3A). Celebration Purple Star *P. capsici*- or *P. tropicalis*-inoculated and control plants were similar in size throughout the experiment.

Million Bells Cherry Pink control plants had the highest AUPGC value (AUPGC value = 2,242) compared with the control plants of all other cultivars and also had the highest AUPGC value (AUPGC value = 1,830) when inoculated with *P. capsici* (Fig. 3B). *P. capsici*-inoculated and control Callie Gold with Red Eye, Celebration Purple Star, Million Bells Cherry Pink, and Superbells White plants had similar AUPGC values (Fig. 3B). Cabaret Yellow had the lowest AUPGC value (AUPGC value = 1,178) following inoculation with *P. capsici* (Fig. 3B). Celebration Purple Star had the highest AUPGC value (AUPGC value = 1,266) of *P. tropicalis*-inoculated plants (Fig. 3B).

Fig. 2. A, Mean plant volume (in cubic centimeters) of fabaceous and solanaceous ornamental plants 42 days postinoculation evaluated for susceptibility to root rot caused by *Phytophthora capsici* isolates OP97, SP98, 12889, and 13351 and *P. tropicalis* isolate 13715. **B,** Area under the plant growth curve (AUPGC) values of ornamental plants evaluated for susceptibility to root rot caused by *Phytophthora capsici* isolates OP97, SP98, 12889, and 13351 and *P. tropicalis* isolate 13715. Plant height and canopy width measurements (in centimeters) taken at 7-day intervals from 14 to 42 days postinoculation were used to calculate a volume approximation (volume of a cylinder [$V = \pi r^2 h$]) to standardize height and canopy width measurements among plants. Volume measurements (in cubic centimeters) were placed into the area under the disease progress curve formula to assess stunting or death over time. Larger AUPGC values signify greater plant volume. **A and B,** Bars represent $\pm$ standard error. Symbols (*) represent significant differences among uninoculated and inoculated plants within each plant type (Fisher's protected least significant difference, $P = 0.05$). MB represents *Calibrachoa*.

AUPGC values of *P. capsici*- or *P. tropicalis*-inoculated and control Celebration Purple Star plants were similar (Fig. 3B).

Discussion

Phytophthora spp. incite root, crown, and stem rot of flowering annuals and perennials, in addition to vegetables and woody perennials (Aragaki and Uchida 2001; Daughtrey et al. 1995; Donahoe and Lamour 2008; Erwin and Ribeiro 1996; Gerlach and Schubert 2001; Hao et al. 2010; Hong et al. 2008; Olson and Benson 2011; Orlikowski et al. 2006; Oudemans and Coffey 1991; Quesada-Ocampo et al. 2009). In our study, *P. capsici* was able to cause disease on ornamentals as well as straightneck squash. *Lupinus polyphyllus*, *Calibrachoa* spp., and *Lathyrus latifolius* are newly identified hosts for *P. capsici*. In addition, squash and *L. latifolius* are newly described susceptible hosts for *P. tropicalis*. These results clearly show that *P. tropicalis* and *P. capsici* can cause disease on both ornamentals and vegetables. Molecular methods analyzing many genes may be necessary to differentiate *P. capsici* and *P. tropicalis* isolates, because morphology (Granke et al. 2011) and host pathogenicity cannot be relied upon for accurate differentiation.

Although *P. capsici* could be isolated from inoculated *Petunia* plants, disease symptoms were not observed. *Phytophthora*-infected plants may appear healthy and not show disease symptoms until stress occurs via suboptimal environmental conditions (Lamour et al. 2003). These latent or asymptomatic infections can facilitate the spread of infected propagules and materials. Future experiments are necessary to discern whether plant types which remained relatively asymptomatic, similar to petunia, may harbor *Phytophthora* spp. and be a source of inoculum in the greenhouse. Disease was not observed on nor was either pathogen recovered from *B. speciosa* or *N. scoparia* in this study, and they are not reported hosts of any *Phytophthora* spp. (Farr and Rossman 2011). Pathogen recovery varied greatly among the plant types but the crowns of several species were fibrous and woody, which may have contributed to low pathogen recovery. *Phytophthora* spp. recovery from woody host tissue is recognized to be difficult (Quesada-Ocampo et al. 2009).

In our study, all *Calibrachoa* cultivars were susceptible to both *P. capsici* and *P. tropicalis* but the degree of susceptibility differed. All cultivars died when inoculated with *P. tropicalis*, with the exception of Celebration Purple Star at 42 dpi. Though Celebration Purple Star survived, it was stunted compared with the uninoculated control. Differences in cultivar response to *P. capsici* were also observed, suggesting that host resistance to *P. capsici* and *P. tropicalis* is present in existing *Calibrachoa* cultivars. Additional experiments to

evaluate *Calibrachoa* cultivars with *P. capsici* and *P. tropicalis* may be of interest to propagators and breeders.

Squash plants and fruit are known to be very susceptible to *P. capsici* (Erwin and Ribeiro 1996; Hausbeck and Lamour 2004). In our study, squash fruit became diseased and seedlings also became minimally diseased when inoculated with *P. tropicalis*. Similarly, Hong et al. (2008) observed damping-off of cucumber seedlings following inoculation of *P. tropicalis*. Age-related resistance to *P. capsici* has been found in pumpkin (Lee et al. 2001), and further experiments could discern whether squash plants would exhibit disease if exposed to *P. tropicalis* inoculum at a later growth stage.

Integrated pest management (IPM) practices in greenhouse and nursery production are needed to mitigate the risk of pathogen infection and spread. *Phytophthora* spp. inocula may be introduced into greenhouse production areas via shipments of infected seed, cuttings, or plants (Daughtrey and Benson 2005; Lamour et al. 2003). If greenhouse growers incorporate field soil into the production system, the risk of introducing *P. capsici* also increases. *P. tropicalis* infections have been reported in multiple greenhouses and nurseries in the United States (Hao et al. 2010; Hong et al. 2006; Olson and Benson 2011) and Europe (Cacciola et al. 2006; Gerlach and Schubert 2001; Orlikowski et al. 2006). With the increased production of vegetable transplants for retail sale alongside ornamental plants, the prevalence of *Phytophthora* rot caused by *P. capsici* may rise in the greenhouse.

Once a pathogen is established in a facility, asexual propagules, mycelial fragments, or zoospores may be further disseminated (Lamour et al. 2003) via infested potting media that may be leached

Table 3. Disease incidence and pathogen recovery from ‘Million Bells’ (*Calibrachoa* × *hybrida*) cultivars evaluated for susceptibility to *Phytophthora capsici* and *P. tropicalis*

Cultivar	Disease incidence and pathogen recovery (%) ^z			
	<i>P. capsici</i>		<i>P. tropicalis</i>	
	DI	PR	DI	PR
Cabaret Yellow	75.0	91.7	100.0	100.0
Callie Gold with Red Eye	62.5	100.0	100.0	100.0
Can-Can Apricot	92.0	91.7	100.0	100.0
Celebration Purple Star	75.0	25.0	100.0	100.0
Million Bells Cherry Pink	79.2	91.7	100.0	100.0
Superbells White	79.2	16.7	100.0	100.0

^z Disease incidence (DI) was calculated for cultivars inoculated with each isolate by dividing the number of plants of each cultivar that exhibited root rot symptoms by the total number of plants of each cultivar inoculated with each isolate and multiplying by 100. Pathogen recovery (PR) was calculated for cultivars inoculated with each isolate by the percentage of confirmed *P. capsici* or *P. tropicalis* isolates recovered from root or crown tissue of 50% of plants of each cultivar inoculated with each isolate and control plants. Control plants did not exhibit disease symptoms, nor were *P. capsici* or *P. tropicalis* recovered.

Fig. 3. A, Mean plant volume (in cubic centimeters) of *Calibrachoa* × *hybrida* series 42 days postinoculation evaluated for susceptibility to root rot caused by *Phytophthora capsici* and *P. tropicalis*. B, Area under the plant growth curve (AUPGC) values of *Calibrachoa* series evaluated for susceptibility to root rot caused by *Phytophthora capsici* and *P. tropicalis*. Plant height and canopy width measurements (in centimeters) taken at 7-day intervals from 0 to 42 days postinoculation were used to calculate a volume approximation (volume of a cylinder [$V = \pi r^2 h$]) to standardize height and canopy width measurements among plants. Plant volume measurements were placed into the area under the disease progress curve formula to assess stunting or death over time. Larger AUPGC values signify greater plant volume. A and B, Bars represent + standard error. Bars with a letter in common are not significantly different within each series (Fisher's protected least significant difference, $P = 0.05$).

into irrigation water or nutrient solutions, which is reused and dispersed to other plants (Oh and Son 2008). In particular, *Phytophthora*-infested nutrient solutions administered through ebb-and-flow systems have been documented to cause root rot of gerbera daisy (Thinggaard and Andersen 1995; van der Gaag et al. 2001) and kalanchoe (*Kalanchoe blossfeldiana*) (Oh and Son 2008).

Surface water used for irrigation is frequently contaminated with *Phytophthora* spp. propagules, including *P. tropicalis* and *P. capsici* (Dreistadt 2001; Gevens et al. 2007; Granke and Hausbeck 2010; Hong and Moorman 2005). *P. tropicalis* was detected in irrigation water at a Virginia nursery during two consecutive growing seasons and was isolated from diseased garden center ornamentals (Hong et al. 2006). Contaminated water may pose a significant threat to susceptible greenhouse ornamentals and vegetables that are irrigated with surface water from nearby vegetable production fields.

In summary, the overlap of *P. capsici*- and *P. tropicalis*-susceptible hosts is increasing, and pathogen dispersal among and within production facilities is a considerable concern. The results of the study clearly demonstrate that some ornamentals may serve as symptomatic or asymptomatic hosts of *P. capsici* or *P. tropicalis*. With increased vegetable transplant production in ornamental greenhouses and asymptomatic infected ornamentals, further investigation into refining greenhouse production IPM programs to limit root rot caused by *P. capsici* and *P. tropicalis* should be conducted.

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