Host Range of *Phytophthora capsici* from Pumpkin and Pathogenicity of Isolates

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ABSTRACT

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This study was conducted to determine the host range of *Phytophthora capsici* isolates from pumpkin and virulence of the isolates on pumpkin cultivars. The pathogenicity of *P. capsici* isolates from pumpkin was evaluated on 45 species of herbaceous plants, including 36 species of crops grown in rotation sequences with pumpkin and nine species of weeds that commonly grow in pumpkin fields in Illinois. Plants were grown in the greenhouse, and 4-week-old seedlings were inoculated by adding 5 ml of a zoospore suspension (2×10^5 spores per ml of water) onto the soil surface around the stem of each plant in the pot. Twenty-two crop species and two weed species became infected with *P. capsici* and developed symptoms. *P. capsici* was reisolated from all of the symptomatic plants by culturing tissues onto a semiselective medium (PARP). Also, *P. capsici* was detected in 87.5% of symptomatic plants by a polymerase chain reaction (PCR) method using PCAP and IT5 primers. Cucurbits and pepper were the most susceptible hosts of *P. capsici*. Five crop species or varieties, beet (*Beta vulgaris*), Swiss-chard (*Beta vulgaris* var. *cicla*), lima beans (*Phaseolus lunatus*), turnip (*Brassica rapa*), and spinach (*Spinacia oleracea*), and one weed species, velvet-leaf (*Abutilon theophrasti*), were found to be hosts of *P. capsici* for the first time. Six isolates of *P. capsici* were inoculated onto six pumpkin cultivars (three processing and three jack-o-lantern pumpkins) in the greenhouse and resulted in significant interactions between pathogen isolates and pumpkin types. *P. capsici* isolates were more virulent on jack-o-lantern pumpkins than on processing pumpkins.

Additional keywords: *Cucurbita moschata, C. pepo,* Phytophthora blight

Phytophthora blight, caused by *Phytophthora capsici* Leonian, has become one of the most serious threats to production of cucurbits, eggplant, and pepper in the United States and worldwide (2,4,6,11,14,18,21). Recently, the incidence of damping-off, foliar blight, and fruit rot on pumpkins caused by *P. capsici* has dramatically increased in Illinois (1,2), causing yield losses of up to 100%.

Jack-o-lantern pumpkin (*Cucurbita pepo*) is an important crop in Illinois, and approximately 90% of the commercial processing pumpkin (*Cucurbita moschata*) produced in the United States are grown in Illinois (2). The economic importance of Phytophthora blight to cucurbit crops, particularly to processing pumpkin, lack of resistant or tolerant cultivars (1), and inadequate effect of chemicals on controlling the diseases prompted our investigation to utilize all effective practices to develop feasible strategies to manage the disease and minimize crop losses. Crop rotation to decrease initial inoculum of *P. capsici* in infested fields has been included as an important component of disease management strategies. Most pumpkin growers in Illinois follow at least a short-term crop rotation. However, most growers have experienced heavy losses when carrot, lima beans, pea, snap bean, and tomato were grown prior to pumpkin (M. Babadoost, *unpublished*). To establish effective crop rotation sequences for management of Phytophthora blight of cucurbits, determination of host range of *P. capsici* in the field is essential (4,11,17,21).

Forty-nine plant species have been reported infected by *P. capsici* (4). Among the major hosts of *P. capsici* are red and green peppers (*Capsicum annuum*), watermelon (*Citrullus lanatus*), cantaloupe (*Cucumis melo*), honeydew melon (*C. melo*), cucumber (*Cucumis sativus*), blue Hubbard squash (*Cucurbita maxima*), acorn squash (*Cucurbita moschata*), gourd (*C. moschata*), processing pumpkin (*C. moschata*), yellow squash (*Cucurbita pepo*), zucchini squash (*C. pepo*), tomato (*Lycopersicon esculentum*), black pepper (*Piper nigrum*), and eggplant (*Solanum melongena*).

P. capsici can strike host plants at any stage of growth (4,8). The pathogen infects root, crown, stem, leaf, and fruit. Pre- and post-emergence damping-off on cucurbit crops and other host plants are common symptoms of *P. capsici* infection. Seedling death occurs in wet and warm (20 to 30°C) soil conditions (4,8). It has been reported that plants are more susceptible to *P. capsici* in seedling stages than as mature plants (9,20). Thus, screening seedlings for susceptibility to *P. capsici* is a more reliable approach for determining host range of *P. capsici* and plant resistance.

Determination of variation among isolates of *P. capsici* is essential for developing effective measures for controlling this pathogen in the fields. Distinct pathogenic strains of *P. capsici* from eggplant, pepper, pumpkin, squash, tomato, and watermelon have been reported (7,11,16,17,21). Tamietti and Valentino (21) grouped *P. capsici* isolates into 13 classes depending upon their ability to infect different plant species. They reported that all isolates tested were pathogenic on bell pepper, 95% on squash, 79% on tomato, 58% on nightshade, 38% on eggplant, 33% on pea, 20% on melon, and 8% on French bean. Ristaino (17) studied *P. capsici* isolates from cucurbits and pepper and reported significant interspecific interactions. Also, significant differences in virulence of *P. capsici* isolates from pumpkin and pepper have been reported (7,11).

Visual inspection of symptoms and isolation of the pathogen from infected tissue have been the methods employed for diagnosing the disease caused by *P. capsici* (2,4,15). However, this method is a time-consuming approach, and it is not a reliable method if opportunistic organisms grow on infected tissue. Therefore, a rapid and more reliable diagnostic method for detection of *P. capsici* in plant tissue is needed. The polymerase chain reaction (PCR) assay is one approach that allows rapid detection of *Phytophthora* species in plants (12,13,19,22,23).

The objectives of this research were: (i) to determine the susceptibility of crops grown in rotation with cucurbit crops, and of weeds that commonly grow in cucurbit fields, to *P. capsici*; (ii) to assess the virulence of *P. capsici* isolates from pumpkin on pumpkin cultivars; and (iii) to implement a molecular method for rapid detection of *P. capsici* isolates from pumpkin in plant tissue.

MATERIALS AND METHODS

Fungal isolates and preparation of inoculum. *P. capsici* was isolated from infected pumpkin tissues collected from Illinois by culturing diseased tissue onto a semiselective medium (PARP) (8,15). The isolates were maintained on lima bean agar (LBA; Difco Laboratories, Detroit, MI). Six isolates of *P. capsici*, three A1 and three A2 mating types from processing pumpkins, were used in this study (Table 1). Sporangial suspensions were prepared

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from 5-day-old culture plates of *P. capsici* grown on LBA at 24°C under continuous white fluorescent light. Ten milliliters of sterilized distilled water (SDW) was added to each plate, and the sporangia were dislodged using a soft brush. Sporangial suspensions from six isolates (equal numbers of plates of each isolate) were mixed. The suspension was then incubated at 20°C for 1 h to allow the sporangia to release their zoospores. Zoospores were separated from the empty sporangia by passing the suspension through a four-layered facial tissue. The concentration of zoospores was adjusted to 2×10^5 zoospores per ml of water using a hemacytometer (#3120, Hausser Scientific Co., Horsham, PA) and used in inoculation.

Table 1. Source and mating types of *Phytophthora capsici* isolates from processing pumpkin fields in Illinois used in inoculations

Isolate	Plant part	Field location[y]	Year isolated	Mating type	Growth pattern[z]
Pc-15	Petiole	Manito	2000	A2	Stellate
Pc-20	Seedling	S. Pekin	2000	A1	Stellate
Pc-24B	Fruit	Manito	2000	A1	Stellate
Pc-35#4	Petiole	Machinaw	2001	A2	Rosaceous
Pc-34#7	Petiole	Allentown	2001	A2	Stellate
Pc-38#15	Vine	Manito	2001	A1	Petaloid

[y] All locations are in central Illinois.
[z] Growth pattern on potato dextrose agar.

Host range. Forty-five species of plants were screened for their susceptibility to *P. capsici* (Table 2). Sixteen soybean cultivars (Bell, Harosoy 13, Harosoy 16, Harosoy 63, L75-3735, L76-1988, L83-570, L85-2352, L85-3059, L89-1581, L93-3258, Resink, Saloan, Williams, Williams 82, Union) were included in this test. Seeds of the plants were sown in 10-cm-diameter plastic pots (one seed per pot) containing steamed soil mix (soil:sand:

Table 2. Susceptibility of 45 plant species to *Phytophthora capsici* isolates[v] from pumpkin

Family	Common name	Scientific name	Cultivar	Diseased plants (%) 3 days	Diseased plants (%) 12 days	Reisolation	PCR detection
Amaranthaceae	Pigweed[w]	*Amaranthus etroflexus*		0	0	–[x]	Negative
	Water hemp[w]	*Amaranthus rudis*		0	0	–	Negative
Chenopodiaceae	Beet[y]	*Beta vulgaris*	Ruby Queen	21.7	55.6	+	Negative
	Lamb's-quarters[w]	*Chenopodium album*		0	0	–	Negative
	Spinach[y]	*Spinacia oleracea*	Old Dominion	41.7	83.9	+	Positive
	Swiss-chard[y]	*Beta vulgaris* var. *cicla*	Rhubarb	24.9	64.8	+	Negative
Compositae	Cocklebur[w]	*Xanthium strumarium*		0	0	–	Negative
Cruciferae	Radish	*Raphanus sativus*	French Breakfast	21.6	60.8	+	Positive
	Turnip[y]	*Brassica rapa*	Purple Top	27.7	53.9	+	Positive
	Broccoli	*Brassica oleracea*	Nomad	0	0	–	Negative
	Cabbage	*Brassica oleracea*	Jersey Wakefield	0	0	–	Negative
	Cauliflower	*Brassica oleracea*	Snow Ball X	0	0	–	Negative
	Kale	*Brassica oleracea*	White Russian	0	0	–	Negative
	Kohlrabi	*Brassica oleracea*	Early White Vienna	0	0	–	Negative
	Mustard	*Brassica nigra*	Tatsoi	0	0	–	Negative
Cucurbitaceae	Cantaloupe	*Cucumis melo*	Sweet Granite	80.5	100	+	Positive
	Cucumber	*Cucumis sativus*	Cayenne	75.9	100	+	Positive
	Gourd	*Cucurbita pepo*	Bird House	66.9	95.9	+	Positive
	Honeydew melon	*Cucurbita melo*	Honey Roch	80.7	100	+	Positive
	Melon	*Pisum melo*	Annanas	88.6	100	+	Positive
	Squash	*Cucurbita pepo*	Sebring F1	88.6	100	+	Positive
	Watermelon	*Citrullus lanatus*	SWT6703	80.7	100	+	Positive
	Zucchini	*Cucurbita pepo*	Dark Green	90.9	100	+	Positive
Gramineae	Corn	*Zea mays*	Wisconsin Black	0	0	–	Negative
	Wheat	*Triticum aestivum*	Clark	0	0	–	Negative
Labiatae	Basil	*Ocimum basilicum*	Thai	0	0	–	Negative
Leguminosae	Green bean	*Phaseolus vulgaris*	Bush Blue Lake	30.8	52.6	+	Positive
	Lima bean[y]	*Phaseolus lunatus*	Ford Hook 242	31.6	63.8	+	Positive
	Snow pea	*Pisum sativus*	Snow Flake	10.6	51.9	+	Negative
	Soybean[z]	*Glycine max*		0	0	–	Negative
Liliaceae	Chives	*Allium schoenoprasum*	Herb	0	0	–	Negative
	Onion	*Allium cepa*	Red Wether Field	20.6	41.9	+	Positive
Malvaceae	Velvet-leaf[w,y]	*Abutilon theophrasti*		34.9	78.3	+	Positive
Poaceae	Crabgrass[w]	*Digitaria sanguinalis*		0	0	–	Negative
	Sandbur[w]	*Cenchrus incertus*		0	0	–	Negative
Solanaceae	Eggplant	*Solanum melongena*	Classic	35.6	75.8	+	Positive
	Nightshade[w]	*Solanum nigrum*		45.7	92.9	+	Positive
	Pepper	*Capsicum annuum*	California wonder	51.4	100	+	Positive
	Tobacco	*Nicotiana tabacum*	Sacred	24.9	70.7	+	Positive
	Tomato	*Lycopersicon esculentum*	Popreco	45.8	85.7	+	Positive
Umbelliferae	Carrot	*Daucus carota*	Red Core Chantanay	30.6	85.9	+	Positive
	Celery	*Apium graveolens*	Giant Red	0	0	–	Negative
	Dill	*Anethum graveolens*	Long Island	0	0	–	Negative
	Parsley	*Petroselinum crispum*	Moss Curled	0	0	–	Negative
Zygophyllaceae	Puncture vine[w]	*Tribulus terrestris*		0	0	–	Negative

[v] Inoculum used was combined inocula of six isolates.
[w] Weed species.
[x] – = nonsymptomatic; + = symptomatic.
[y] First report as a host of *P. capsici*.
[z] Sixteen cultivars of soybean were tested.

vermiculite, 1:1:1) and were grown on a greenhouse bench at 18 to 26°C. Four-week-old seedlings were inoculated by adding the suspension of motile zoospores over the soil surface around the plant in each pot (5 ml per seedling per pot). Control seedlings received 5 ml of SDW. Seedlings were watered before inoculation to keep the soil wet. After inoculation, the pots were placed in plastic trays containing water that kept the soil moist for at least 12 h. The seedlings were then placed on the greenhouse bench and watered twice daily. Beginning the second day after inoculation, seedlings were evaluated for development of lesions on stems, defoliation, and damping-off symptoms every day for 3 weeks. The experiment was performed using a randomized complete block design with four replications each with 10 plants. The experiments were conducted twice. Beginning the second day after inoculation, plants were evaluated for disease development until 21 days after inoculation. Percentage of plants with symptoms 3 and 12 days after inoculation are presented (Table 2).

Virulence test. Three jack-o-lantern pumpkin cultivars (Gold Rush, Gold Medal, Pik-A-Pie) and three processing pumpkin cultivars (Dickinson, H-401, H-698) were used to determine virulence of *P. capsici* isolates to pumpkins. Seeds were planted in 10-cm-diameter pots containing steamed soil mix (soil:sand:vermiculite, 1:1:1) and grown in the greenhouse. Four-week-old seedlings were inoculated by adding 5 ml of the zoospore suspension to each pot as described above. Control plants received SDW. Beginning the second day after inoculation, plants were evaluated for disease incidence until 21 days after inoculation. Disease incidence was assessed as percentage of seedlings that died. Area under disease progress curve (AUDPC) was calculated using the formula: AUDPC = $n\Sigma i = 1(X_{i+1} + X_i)(t_{i+1} - t_i)/2$, where X_i = disease incidence at the ith observation, t_i = days at the ith observation, and n = total number of observations. The experiment was performed using a randomized complete block design with four replications, each with 10 plants. The experiment was conducted twice. Data were analyzed using analysis of variance procedures of SAS.

Reisolation and molecular detection of pathogen. Symptomatic and asymptomatic tissues of roots and stems of the seedlings were assayed for the presence of *P. capsici* by culturing tissue on PARP medium (8,15). Also, tissues of the symptomatic and asymptomatic roots and stems were assayed for the presence of *P. capsici* using the modified PCR procedures developed by Ristaino et al. (19). DNA was extracted from symptomatic and asymptomatic plants using the Bio-101 kit (Bio-101, Inc., Carlsbad, CA). Aliquots of 1 µl of the extract were used as the DNA template for PCR in 25-µl reaction mixture containing 0.1 µl of PCAP (5′-TCCTCCGCTTATTGATATGC) and 0.1 µl of IT5 (5′-GGAAGTAAAAGTCGTAACAAGG) primers. The thermal cycling was processed at 95°C for 2 min, followed by 35 cycles consisting of 94°C for 1 min, 60°C for 1 min, extension at 72°C for 1 min, and a final extension at 72°C for 10 min using PTC-200 (Peltier) Thermal Cycler (MJ Research, Inc., Waltham, MA). Amplified fragments were electrophoresed on a 2% agarose gel at 50 UV for 1.5 h.

RESULTS

Host range. Plants of 22 crop species and two weed species exhibited damping-off symptoms (Table 2). Plants of 14 crop species and seven weed species did not develop any symptoms. All plants from Cucurbitaceae and Solanaceae, and most of the plants from Chenopodiaceae, families became infected and developed symptoms. Cucurbits and pepper were the most susceptible to *P. capsici*, as more than 50 and 95% of their seedlings became infected and developed symptoms within 3 and 12 days after inoculation, respectively. Infection in beet, carrot, eggplant, green bean, lima bean, nightshade, radish, snow pea, spinach, Swiss-chard, tobacco, tomato, turnip, and velvet-leaf developed symptoms slowly. However, more than 50% of the seedlings of these crops developed symptoms within 12 days of inoculation (Table 2). Onion was less susceptible, and only 41.9% of its seedlings exhibited symptoms. No obvious changes in symptom development were observed after 12 days postinoculation. *P. capsici* was reisolated from all of the symptomatic plants on PARP culture medium. Using the PCR method, *P. capsici* was detected in all symptomatic plants with the exception of beet, snow pea, and Swiss-chard. We were unable to detect *P. capsici* in these species by the PCR method for reasons unknown. None of the control plants developed disease symptoms, and attempts to isolate *P. capsici* from their tissues were unsuccessful. Thus, the results of control plants were not presented. Control tissue was processed as diseased tissue was.

Basil, broccoli, cabbage, cauliflower, celery, chive, corn, dill, kale, kohlrabi, mustard, parsley, soybean, and wheat seedlings did not develop any symptoms. Likewise, the weed species of cocklebur, crab grass, lamb's-quarters, pigweed, puncture vine, sandbur, and water hemp did not develop symptoms. Attempts to reisolate *P. capsici* from asymptomatic plant tissues of inoculated plants, or detect the pathogen by the PCR method, did not provide any indication of presence of *P. capsici* in these plants.

Virulence test. The relative virulence of six isolates of *P. capsici* on six pumpkin cultivars was evaluated by comparing percentage of plant death. Percentage of plant death was significantly affected by pathogen isolate and pumpkin type × isolate interactions (Table 3). There was no significant effect of pumpkin cultivar on percentage of plant death. There was significant difference in percentage of seedling death between jack-o-lantern and processing pumpkins (Table 4, Fig. 1). The standard deviations in percentage of plant death for jack-o-lantern and processing pumpkin cultivars were 38.27 and 34.28, respectively.

DISCUSSION

The results of this study agree with the reports by other investigators (4,7,11,14, 17,24) that cucurbits and pepper are the most susceptible hosts of *P. capsici*. Lists of *P. capsici* hosts have been published by other investigators (3–5), with that of Erwin and Ribeiro (4) as the most comprehensive list worldwide. They state that 49 species of herbaceous and woody plants can be infected by *P. capsici*. Our investigations focused on plants used in rotation sequences with pumpkin in Illinois. Most of the plant species that have been previously reported as hosts of *P. capsici* (3–5)

Table 3. Analysis of variance for areas under disease progress curves (AUDPCs)[x] on pumpkins inoculated with six isolates of *Phytophthora capsici*

Source	df[y]	Mean square	*P* > *F*
Experiment	1	21,371.6	0.071
Reps (experiment)	3	6,828.6	0.531
Type × experiment	1	9,908.4	0.270
Cultivar × experiment	5	18,536.0	0.062
Type × cultivar × experiment	5	16,810.5	0.125
Isolate × experiment	5	10,435.9	0.271
Type[z]	1	206,668.7	<0.001
Type × isolate × experiment	5	3,313.7	0.746
Cultivar (type)	2	9,090.3	0.235
Isolate	5	39,537.8	<0.001
Type × isolate	5	36,113.9	<0.001
Isolate × cultivar (type)	10	25,372.0	<0.001
Isolate × cultivar × experiment	25	5,615.1	0.585

[x] AUDPC = $n\Sigma i = 1(X_{i+1} + X_i)(t_{i+1} - t_i)/2$, where X_i = disease incidence at the ith observation, t_i = days at the ith observation, and n = total number of observations.
[y] Degree of freedom.
[z] Jack-o-lantern and processing pumpkins.

Table 4. Areas under disease progress curves (AUDPC) on six pumpkin cultivars in an evaluation of virulence of six *Phytophthora capsici* isolates from pumpkin

	AUDPC[y] on different cultivars					
	Jack-o-lantern pumpkins			Processing pumpkins		
Isolate	Gold Rush	Gold Medal	Pik-A-Pie	Dickinson	Hybrid-401	Hybrid-698
Pc-15	216.8 a[z]	216.8 a	208.3 bc	186.7 a	168.3 b	188.4 a
Pc-20	213.2 ab	206.7 abc	216.6 ab	156.8 b	175.8 ab	172.5 b
Pc-24B	226.7 a	208.3 ab	226.7 a	191.7 a	180.0 a	201.8 a
Pc-34#7	218.4 a	201.6 bcd	200.0 bc	158.4 b	172.5 ab	166.7 bc
Pc-35#4	191.7 c	190.0 d	196.7 c	143.3 c	155.0 c	155.8 c
Pc-38#15	200.0 bc	195.0 cd	201.8 bc	152.5 b	152.5 c	163.3 bc
LSD (P=0.05)	15.8	12.9	17.4	9.1	11.4	13.4

[y] AUDPC = $n\Sigma i = 1(X_{i+1} + X_i)(t_{i+1} - t_i)/2$, where X_i = disease incidence at the ith observation, t_i = days at the ith observation, and n = total number of observations.

[z] In each column, the values with a letter in common are not significantly different from each other according to Fisher's protected LSD (P = 0.05).

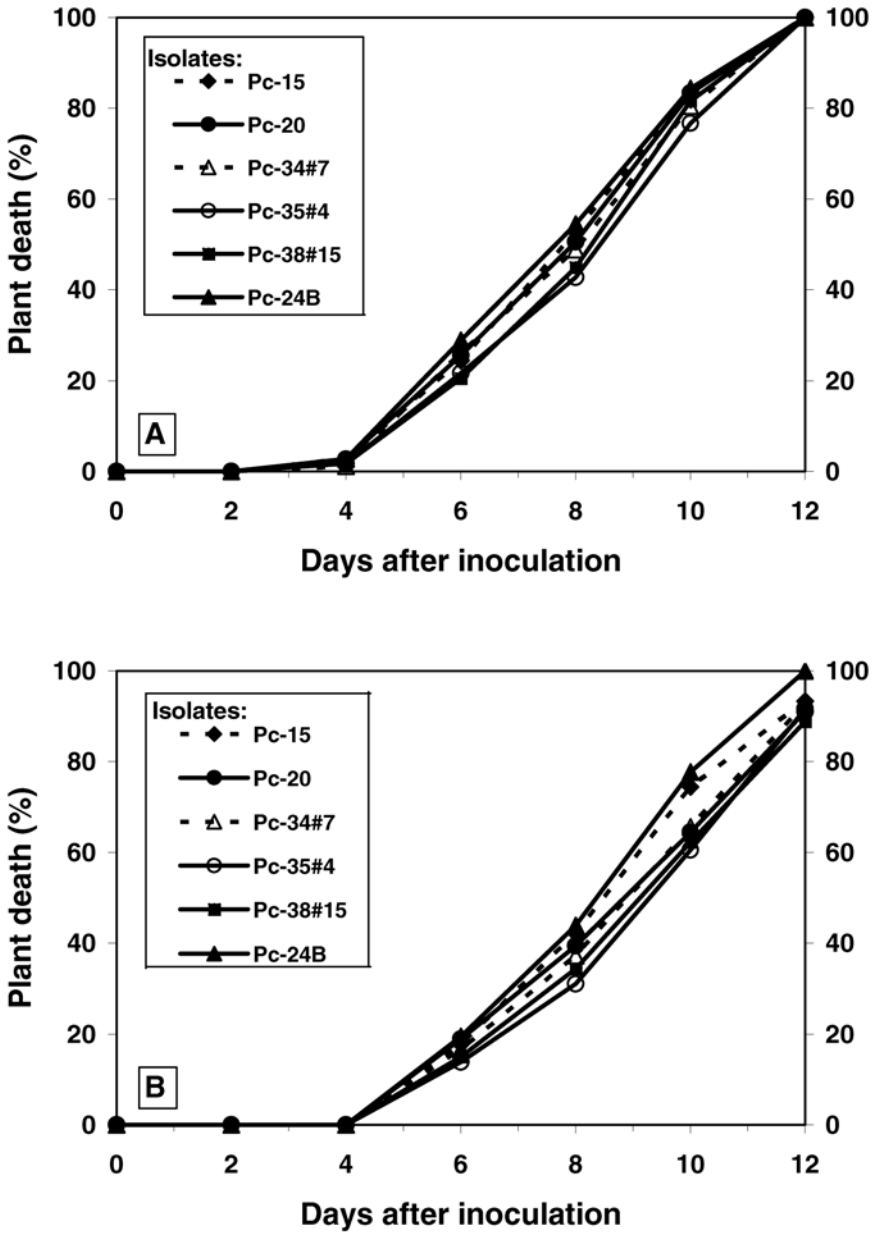

Fig. 1. Incidence of plant death in **A,** jack-o-lantern and **B,** processing pumpkins following inoculation of plants with six isolates of *Phytophthora capsici*. For each isolate, data represent mean disease incidence in 240 plants of three cultivars.

can be infected by isolates from Illinois pumpkin. However, cauliflower (*Brassica oleracea* var. *botrytis*), which has been listed as a host (4), was not infected in our test. This indicates that either cauliflower is not a host of *P. capsici*, it is resistant at early growth stages and may become susceptible as the plant matures, or *P. capsici* isolates from Illinois pumpkin do not cause disease on cauliflower while the isolates from other areas possibly do.

This is the first report of beet (*Beta vulgaris*), Swiss-chard (*Beta vulgaris* var. *cicla*), lima bean (*Phaseolus lunatus*), turnip (*Brassica rapa*), spinach (*Spinacia oleracea*), and velvet-leaf (*Abutilon theophrasti*) as hosts of *P. capsici*. Nightshade and velvet-leaf are weeds that commonly grow in commercial fields of pumpkins and other cucurbits. Soybean, corn, and wheat, the major crops grown in Illinois, were not infected with *P. capsici* in our study, and there is no report indicating that these crops could be infected with *P. capsici*. This report is expected to help in establishing effective rotations and weed management programs for sustainable pumpkin production.

Since inoculation tests were conducted under conditions highly conducive for disease development (tender greenhouse-grown seedlings and high inoculum dose), it is possible that some of the species susceptible to *P. capsici* in the greenhouse may not be as susceptible under field conditions. Field studies could provide additional information on the susceptibility of the species tested in the greenhouse in this study.

We found that isolates of *P. capsici* differ in virulence, which agrees with the reports by Hwang et al. (7), Lee et al. (11), and Ristaino (17). The isolates used in this study were less virulent on processing pumpkins than on jack-o-lantern pumpkins. Therefore, more effective measures are needed to manage *P. capsici* in jack-o-lantern pumpkin fields. None of the pumpkin cultivars used in this study was resistant to *P. capsici*. This may be another indication that there is no measurable resistance in pumpkin cultivars to *P. capsici,* as reported by Erwin and Ribeiro (4) and Latin and Rane (10). Consequently, the effectiveness of other methods (e.g., cultural practices, chemical treatments, induced resistance) should be investigated to develop effective integrated approaches for management of *P. capsici* in pumpkin fields.

The PCR method for detection of *P. capsici* in plant tissues developed by Ristaino et al. (19) and modified in this study detected *P. capsici* in infected plants of 21 of 24 (87.5%) species. Thus, this PCR method is a rapid and reliable tool for detection of *P. capsici* in plants, particularly at early infection stages. Since management of Phytophthora blight is based on prevention of disease spread, a rapid detection of *P. capsici* at early stages of disease

development in the field is very useful, as fungicide applications (e.g., dimethomorph spray) could suppress the growth and sporulation of the pathogen (M. Babadoost, *unpublished data*).

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