Evaluation of Winter Squash and Pumpkin Cultivars for Age-related Resistance to *Phytophthora capsici* Fruit Rot

Charles S. Krasnow and Mary K. Hausbeck[1]

Department of Plant, Soil, and Microbial Sciences, Michigan State University, East Lansing, MI 48824

Additional index words. ontogenetic, pepo, oomycete, Cucurbita

Abstract. *Phytophthora capsici* annually threatens production of cucurbit and solanaceous crops. Long-lived oospores produced by the pathogen incite primary infection of susceptible plants when conditions are wet. Limiting the rot of winter squash and pumpkin (*Cucurbita* sp.) fruits is difficult due to the long maturation period when fruits are often in direct contact with infested soil. Genetic resistance to fruit rot is not widely available within *Cucurbita* sp.; however, age-related resistance (ARR) to *P. capsici* fruit rot develops in specific cultivars during maturation. The objective of this study was to evaluate the fruits of 12 cultivars of *Cucurbita pepo*, *Cucurbita moschata*, and *Cucurbita maxima* for ARR to *P. capsici* using a mycelial-plug inoculation method. All *Cucurbita pepo* and *Cucurbita moschata* cultivars displayed ARR; 7 days postpollination (dpp) fruits were susceptible, limited lesion development occurred on fruits 22 dpp, and lesions did not develop at 56 dpp. Disease developed on both *Cucurbita maxima* cultivars tested at 7, 14, 22, and 56 dpp. Firmness of fruit exocarp was measured with a manual penetrometer. Exocarp firmness of all cultivars increased during maturation; however, there was no correlation between firmness and disease incidence among cultivars at 22 dpp ($R^2 = -0.01$, $P = 0.85$). When fruits of cultivars expressing ARR at 22 dpp were wounded before inoculation, fruit rot developed.

Phytophthora capsici is a destructive pathogen of cucurbit and solanaceous vegetables. All cultivars of squash are considered susceptible to phytophthora root, crown, and fruit rot (Babadoost and Islam, 2003; Cafe et al., 1995); losses in winter squash and pumpkin (*Cucurbita* sp.) production have exceeded 50% (Babadoost, 2000; Isakeit, 2007; Meyer and Hausbeck, 2013a). The pathogen overwinters in the soil and plant residue as long-lived oospores that serve as primary inoculum. The polycyclic production of sporangia and zoospores occurs on infected plant tissue. Movement of *P. capsici* in surface water used for irrigation has contributed to the dispersal of the pathogen in Michigan (Gevens et al., 2007). Managing phytophthora root and crown rot requires an integrated approach that includes raised plant beds in conjunction with fungicides applied via drip irrigation or soil-directed sprays (Foster and Hausbeck, 2010; Jones and McGovern, 1994; Meyer and

Hausbeck, 2013b). Tolerance to root rot has been identified in cultivars of summer (*Cucurbita pepo*) and winter squash (*Cucurbita moschata*) and cucumber (*Cucumis sativus*) (Hausbeck and Lamour, 2004; Meyer and Hausbeck, 2012; Ppoyil, 2011). Raised bed culture with plastic mulch-covered plant beds can limit soil splash onto fruit (Kousik et al., 2011); however, vines of winter squash and pumpkin typically grow off of the plastic mulch coming into direct contact with the soil between the plants beds. Foliar fungicides to

protect against fruit rot are limited by a dense foliar canopy and an inability to cover the fruit surface in contact with the soil (Newhall and Wilkinson, 1949). Additionally, raised plant beds covered with plastic mulch with trickle irrigation are not economical for growers of winter squash for processing where profit margins are narrow. Over 40,000 acres of winter squash and pumpkin grown in the Midwest (Anonymous, 2015) highlight the importance of developing effective strategies to limit fruit rot.

The ability of plants to acquire resistance to pathogens as they mature has been studied in many host–pathogen systems (Gadoury et al., 2003; Gerlach et al., 1976; Kennelly et al., 2005; Kim et al., 1989), especially resistance of seedlings to oomycete pathogens (Koh et al., 1987; Lazarovits et al., 1981; McClure and Robbins, 1942; Mellano et al., 1970). Vegetable crops in the Cucurbitaceae and Solanaceae families develop ARR to *P. capsici* fruit rot (Ando et al., 2009; Biles et al., 1993; Gevens et al., 2006; Meyer and Hausbeck, 2013a) and modifications to disease management programs have been suggested (Ando et al., 2009; Hausbeck and Lamour, 2004; Krasnow et al., 2014; Meyer and Hausbeck, 2013a). The fruits of cucurbit crops including acorn squash, pumpkin, and cucumber are highly susceptible to *P. capsici* during early fruit formation, but become increasingly resistant as they mature (Ando et al., 2009; Gevens et al., 2006). Watermelon, muskmelon, and summer squash do not appear to have appreciable levels of resistance (Ando et al., 2009). Meyer and Hausbeck (2013a) found differences in the onset and magnitude of ARR to *P. capsici* fruit rot between 'Dickenson Field' (*Cucurbita moschata*) and 'Golden Delicious' (*Cucurbita maxima*) processing squashes. Although both cultivars were susceptible to the pathogen up to 14 dpp, 'Dickenson Field' developed ARR at 21 dpp (<15% fruit rot), whereas 'Golden Delicious' remained susceptible (≈80% fruit rot). Mechanical harvesting of processing squash with incipient

Table 1. Cultivars, market use, and days to maturity of winter squash and pumpkin evaluated for age-related resistance to *Phytophthora capsici* fruit rot.

Cucurbita species	Cultivar	Intended use	Days to maturity
C. pepo			
Acorn squash	Autumn Delight[z]	Fresh market	90
Acorn squash	Table Ace[z]	Fresh market	70
Acorn squash	Table Gold[z]	Fresh market	80
Pie pumpkin	Chucky[z]	Fresh market	85
Pumpkin	Diablo[z]	Ornamental	100
Mini-pumpkin	Gold Dust[z]	Ornamental	95
Spaghetti squash	Vegetable Spaghetti[z]	Fresh market	100
C. moschata			
Butternut squash	Avalon[y]	Fresh/processing market	90
Butternut squash	Early Butternut[z]	Fresh market	82
Butternut squash	Waltham Butternut[z]	Fresh market	110
C. maxima			
Hubbard squash	Hubba Hubba[x]	Fresh market	95
Pumpkin	Lumina[y]	Ornamental	100

[z]Siegers Seeds, MI.
[y]Seedway, PA.
[x]Johnny's Selected Seeds, ME.

P. capsici infections can result in spread of the pathogen to surrounding fruit postharvest and during transportation, resulting in potential loss of entire truckloads (Hausbeck and Lamour, 2004; Kousik et al., 2014). The large acreage and low profit margin of squash grown for the processing market necessitate novel methods of disease control.

The differences in the onset of ARR among cucurbits (Ando et al., 2009; Gevens et al., 2006; Krasnow and Hausbeck, 2015) and the lack of ARR in cultivars of watermelon (*Citrullus lanatus*) and winter squash (*Cucurbita maxima*) (Kousik et al., 2012; Krasnow and Hausbeck, 2015; Meyer and Hausbeck, 2013a) have made it difficult to incorporate this feature into disease management programs. Fungicides are applied to pickling cucumbers during the period of rapid fruit growth when the fruit are highly susceptible to *P. capsici* (Hausbeck and Lamour, 2004). Identifying winter squash and pumpkin cultivars that express ARR could help growers make cultivar selections and time fungicide applications to protect developing fruit. The objectives of this study

were to 1) evaluate winter squash and pumpkin cultivars (*Cucurbita* sp.) for ARR to *P. capsici* and 2) determine the effect of morphophysiological changes during winter squash and pumpkin fruit development on ARR. A brief report of this work has been published (Krasnow and Hausbeck, 2015).

Materials and Methods

Plant culture and fruit inoculation. Twelve winter squash and pumpkin cultivars representing the three most economically important *Cucurbita* sp. were selected (Table 1). Seeds were planted into 72-cell flats containing soilless media (Suremix Michigan Grower Products Inc., Galesburg, MI) and grown for 3 weeks in a greenhouse with 27 °C day /25 °C night temperatures. Squash and pumpkin seedlings were transplanted into 15-cm raised plant beds covered with black polyethylene plastic at the Michigan State University Plant Pathology Farm in Lansing, MI. The soil type was a Capac loam that was previously cropped to pumpkin and had no history of *P. capsici* infestation. Watering was accomplished with trickle irrigation and plants were grown according to local commercial production standards for fertilizer and pest management (Bird et al., 2014). Once female flowers reached anthesis, male flowers were removed and used to pollinate female flowers of the same cultivar. Female flowers were tagged with the date of pollination and desired harvest age. Fruit were harvested 7, 14, 22, and 56 dpp, ages were selected based on developmental changes in fruit color, firmness, and size (Loy, 2004; Meyer and Hausbeck, 2013a). Following harvest, fruit were surface sterilized in 10% bleach for 5 min, rinsed with tap water, and air-dried on a laboratory bench. Fruit length from the apex to blossom end and the width at the fruit's widest point were measured. Two *P. capsici* isolates obtained from the culture collection of M. Hausbeck at Michigan State University, East Lansing, MI,

were used for fruit inoculation; OP97 (A1 mating type, sensitive to mefenoxam, isolated from pumpkin) and 12889 (A1 mating type, insensitive to mefenoxam, isolated from pepper). The isolates were grown on V8 juice agar (143 mL V8 juice, 3 g CaCO$_3$, 16 g agar/L). To ensure isolate virulence, the isolates were used to inoculate squash fruit and subsequently recovered from the diseased fruit before the initiation of the study (Quesada-Ocampo and Hausbeck, 2010). To inoculate fruit, a 7-mm agar plug from the margin of an actively growing colony was placed mycelial side down in the middle of each fruit on the unwounded fruit surface. The agar plug was covered with a sterile plastic screw cap (Axygen Inc., Union City, CA) using petroleum jelly as a fixative to prevent plug desiccation. Control fruit were inoculated with sterile V8-agar plugs. Isolate OP97 was not used to inoculate 56 dpp fruit as there was not an adequate supply of the large-fruited *Cucurbita* sp. The inoculated fruit were incubated in large clear plastic bins (Sterilite, Townsend, MA) lined with moist paper towel to maintain high relative humidity (RH). WatchDog Dataloggers (Spectrum Technologies, Inc., Aurora, IL) were used to monitor temperature and RH within the bins. The average temperature and RH were 24.0 °C and 99.7%, respectively, during the study.

Fruit were removed from the bins 4 d postinoculation and lesion diameter was measured on two axes. Pathogen growth and sporulation were rated on a 0 to 4 scale adapted from Meyer and Hausbeck (2013a) where 0 = no visible pathogen growth; 1 = water-soaking only; 2 = light visible mycelial growth; 3 = moderate mycelial growth; and 4 = dense mycelial growth. Fruit receiving a mean rating value ≤0.5 were considered resistant (R), and fruit with a mean rating value >0.5 but <1.5 were considered intermediately resistant (IR). After disease assessment, 1- to 2-mm tissue sections were removed from the margin of diseased tissue and plated onto BARP (50 ppm benomyl, 100 ppm ampicillin, 30 ppm rifampicin, and 100 ppm pentachloronitrobenzene)-amended V8 agar plates. Recovered isolates were identified as *P. capsici* by pathogen morphology on V8-agar (Waterhouse, 1963). Mefenoxam sensitivity (Lamour and Hausbeck, 2000) was determined to verify similarity to the isolate used for inoculation. Control fruit were observed for symptoms and tissue samples cultured to confirm the absence of *P. capsici* infection. There were four fruit per replication per isolate with one control. The experiment was conducted twice.

Fruit firmness testing and wound assay. Pericarp and exocarp firmness of healthy fruits were measured using a fruit penetrometer (model FT 327; QA Supplies LLC, Norfolk, VA) with a 5-mm-diameter press. The measurement was taken from squash or pumpkin tissue (≈25 cm^2) after rating pathogen growth. Exocarp firmness was measured by using the fruit penetrometer to directly penetrate the exocarp. Pericarp tissue

Table 2. Exocarp firmness during development of select winter squash and pumpkin cultivars.

| Cultivar | Exocarp firmness (kg)[z] | | | |
| | Days postpollination | | | |
	7	14	22	56
Autumn Delight	3.6	5.5	10.2	12.8
Chucky	3.3	6.3	10.0	12.3
Diablo	3.3	4.1	8.0	11.1
Gold Dust	3.1	8.2	12.7	13.0
Table Ace	3.2	7.9	11.9	13.0
Table Gold	3.8	7.2	11.1	12.5
Vegetable Spaghetti	2.7	5.2	10.0	12.7
Avalon	3.6	5.8	8.5	12.3
Early Butternut	3.1	5.9	9.0	11.6
Waltham Butternut	3.5	6.4	9.1	11.8
Hubba Hubba	3.4	5.0	7.2	10.1
Lumina	2.8	4.8	6.0	11.7

[z]Measurement made using a model FT 327 fruit penetrometer with 5-mm plunger. Value represents pressure (kg) required to puncture fruit surface.

Table 3. Growth rating and disease incidence 4 d after inoculation with *Phytophthora capsici* of winter squash and pumpkin cultivars 7, 14, and 22 d postpollination.

| Cultivar | *P. capsici* growth rating[z] | | | Infected fruit (%) | | |
| | Days postpollination | | | | | |
	7	14	22	7	14	22
Autumn	3.4[y]	1.5	0.2 d[x]	94	43	6
Chucky	3.1	2.7	2.3 a	76	75	75
Diablo	3.6	2.1	0.4 cd	94	63	19
Gold Dust	3.8	3.3	1.1 b	94	100	63
Table Ace	3.1	2.6	0.2 d	81	81	6
Table Gold	3.6	2.5	0.4 bcd	94	69	25
Vegetable Spaghetti	2.7	1.3	0.0 d	69	50	0
Avalon	3.6	1.4	0.2 d	94	75	19
Early Butternut	3.8	1.3	0.2 d	94	56	19
Waltham Butternut	3.6	1.7	0.4 bcd	100	88	44
Hubba Hubba	3.5	2.7	0.9 bc	88	75	31
Lumina	4.0	2.9	0.9 bc	100	94	56

[z]Rated 4 d postinoculation on a 0–4 scale, where 0 = no growth; 1 = watersoaking only; 2 = light pathogen growth; 3 = moderate pathogen growth; 4 = dense pathogen growth. Values represent the mean of two experiments with 8 fruit per age.
[y]Column means for *P. capsici* growth rating without a letter are not significantly different (*P* = 0.05).
[x]Column means with a common letter are not significantly different based on Fisher's least significant difference test (*P* = 0.05).

firmness was measured by removing the exocarp (0.5- to 1.0-mm depth) with a sterile scalpel before the measurement. For the wound assay, 22 dpp fruit from five cultivars representing each *Cucurbita* sp. were selected. Each fruit was wounded with a sterile needle to 1-cm depth before inoculation, and then incubated and assessed for disease as described previously. Isolate 12889 was used to inoculate fruit for the wound assay.

Data analysis. Data analysis was accomplished using SAS v9.3 (SAS Institute, Cary, NC). Differences among the variables including pathogen growth rating, lesion size, exo- and pericarp firmness, and fruit age were analyzed using analysis of variance in SAS Proc Mixed. Mean differences were separated using Fisher's least significant difference ($P = 0.05$). Correlations among morphological features and disease incidence and severity at the four selected ages were analyzed with Pearson's correlation coefficient ($P = 0.05$). Homogeneity of variance between isolates was assessed by residual analysis and data from each isolate were pooled as there were no significant differences in pathogen growth rating, lesion size, and disease incidence. Control fruit did not display symptoms after inoculation with sterile agar and were not included in the analyses.

Results

The fruits of all winter squash and pumpkin cultivars tested increased in size and exo- and pericarp firmness as they matured from 7 to 56 dpp (Table 2). From 14 to 21 dpp, fruits increased in width for 'Diablo' (47%), 'Hubba Hubba' (25%), 'Lumina' (19%), and 'Vegetable Spaghetti' (14%); fruits from all other cultivars increased <5%. The length of fruits of all cultivars increased <15% from 14 to 21 dpp, with the exception of 'Diablo' (29%) (data not shown). At 22 dpp, 'Hubba Hubba' and 'Lumina' (*Cucurbita maxima*) had the least firm exocarp, whereas 'Gold Dust' and 'Table Ace' (*Cucurbita pepo*) had the firmest exocarp (Table 2). There was no correlation between exocarp firmness and disease incidence among cultivars at 22 dpp ($r = -0.01$; $P = 0.85$). Exo- and pericarp firmness was negatively correlated with disease incidence and pathogen growth when analyzed across all ages tested ($r = -0.53$; $P < 0.0001$). The exocarp of 'Table Ace' and 'Gold Dust' were the firmest among the cultivars tested at 14, 22, and 56 dpp (Table 2).

All cultivars were susceptible to *P. capsici* at 7 dpp with fruit rot incidence ranging from 69% to 100% (Table 3); pathogen growth was similar among cultivars ($P = 0.241$). 'Vegetable Spaghetti', 'Avalon', 'Early', and 'Waltham' were IR at 14 dpp with an average growth rating <1.5 (Table 3). 'Autumn Delight' and 'Vegetable Spaghetti' had the lowest disease incidence at this age (50%; Table 3). At 22 dpp, average disease ratings for all but two cultivars were <1 (Table 3) and disease incidence was >20% for six cultivars. Fruits from the two *Cucurbita maxima* cultivars Lumina and

Hubba Hubba were the only ones to become infected at 56 dpp, with 63% and 25% fruit rot, respectively (data not shown).

Wounding the fruits of five cultivars before inoculation significantly increased disease incidence and pathogen growth ($P \leq 0.0001$) compared with the unwounded inoculated fruits. 'Vegetable Spaghetti' had an average growth rating of <1 after wound inoculation due to a lack of pathogen sporulation and mycelial growth (Fig. 1); however, average lesion size was 4.1 cm, with 88% fruit rot incidence (Fig. 2). 'Table Ace', 'Gold Dust', 'Waltham', and 'Hubba Hubba' exhibited 100% fruit infection following

inoculation of the wounded fruits, with an average rating of 3.0, 2.5, 3.5, and 3.6, respectively (Fig. 2). Superficial wounding of 'Table Ace' fruit by removing a thin piece of the exocarp <1.0 mm thick with a scalpel before inoculation resulted in 100% infection (data not shown).

Discussion

The relatively long maturation time and growth habit of winter squash and pumpkin increases the risk of phytophthora fruit rot in growing regions with frequent rainfall and infested soil. Representative
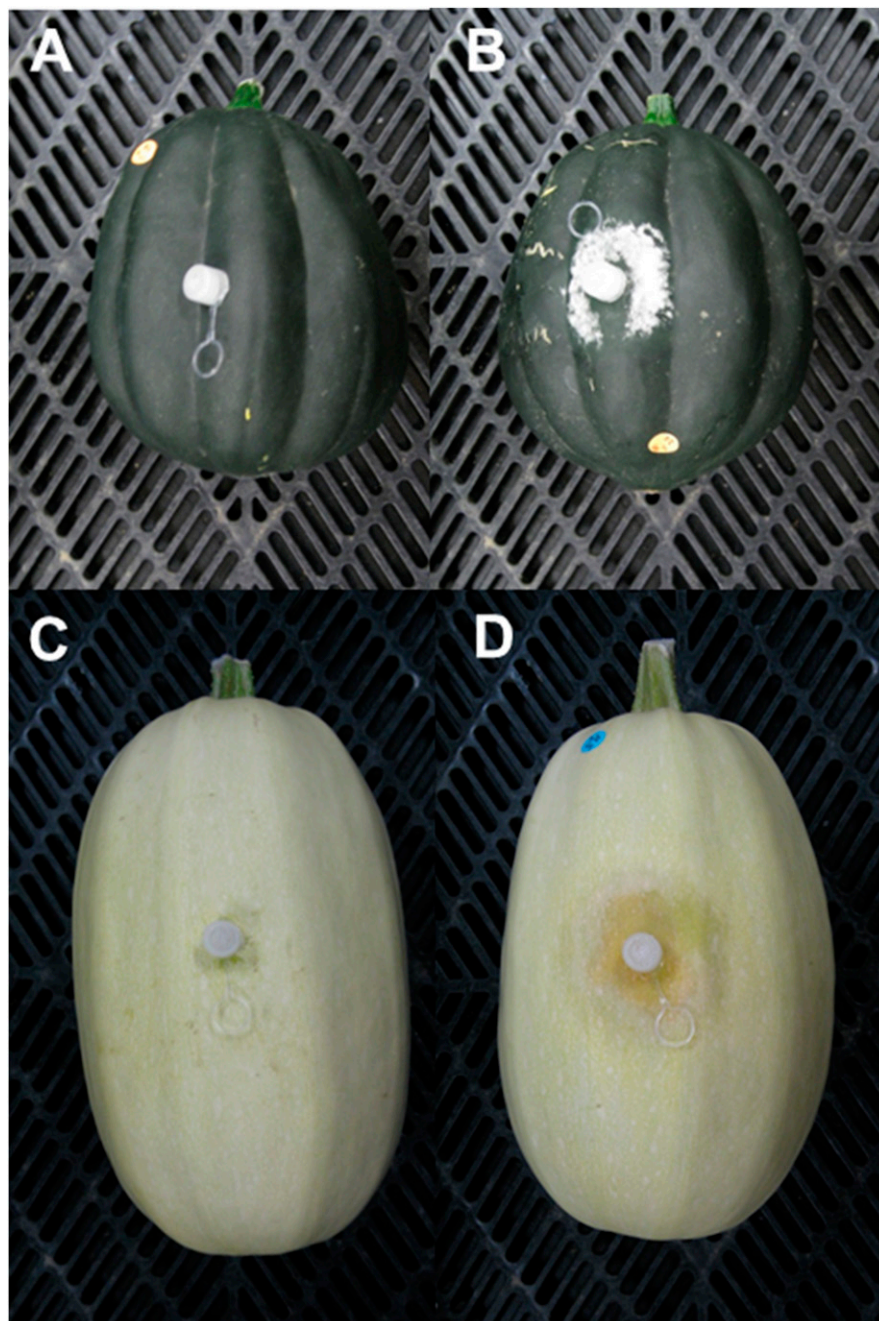

Fig. 1. Effect of *Phytophthora capsici* inoculation on (**A**, **C**) unwounded and (**B**, **D**) puncture wounded fruits of (**A**, **B**) 'Table Ace' and (**C**, **D**) 'Vegetable Spaghetti' 4 d postinoculation. Note the lack of sporulation on diseased tissue in (**D**).
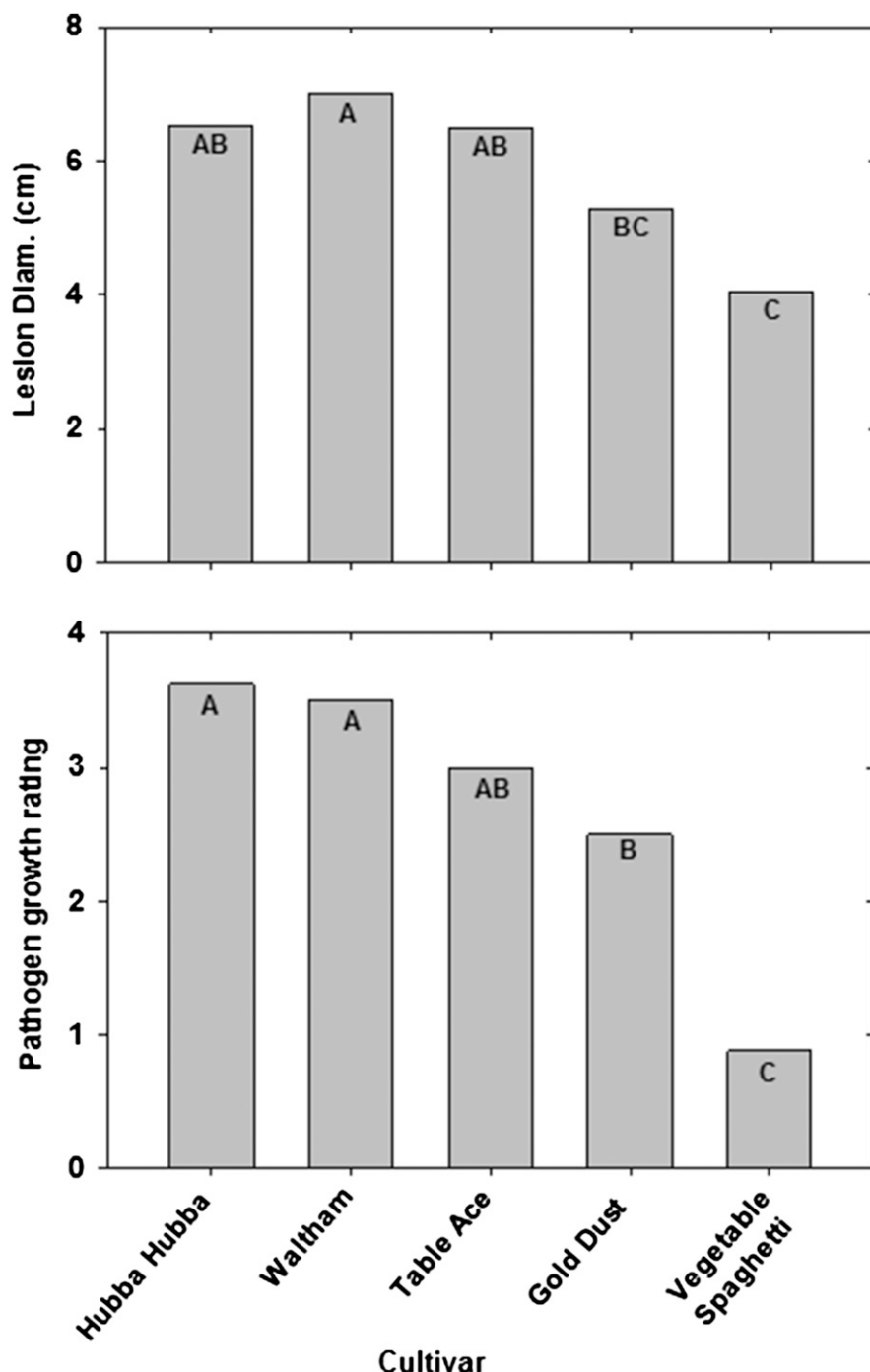
Fig. 2. Lesion diameter and pathogen growth rating 4 d postinoculation with *Phytophthora capsici* of 22 d postpollination puncture wounded winter squash and pumpkin fruits. Fruits were wounded with a sterile needle to 1-cm depth before inoculation. Each bar represents the mean of two trials with four replicate fruits per isolate per trial. Bars with a letter in common are not significantly different based on Fisher's least significant difference (*P* < 0.05).

cultivar types of *Cucurbita pepo*, *Cucurbita moschata*, and *Cucurbita maxima* include jack-o-lantern pumpkin, butternut squash, spaghetti squash, and processing squash and all are susceptible to *P. capsici* fruit rot (Babadoost, 2000; Isakeit, 2007; McGrath, 2000; Meyer and Hausbeck, 2013a). Cultural practices including trellising and choosing varieties with a compact plant size can help prevent *P. capsici* fruit rot by avoiding contact with infested soil (Ando and

Grumet, 2006). Large-fruited *Cucurbita* sp. offer unique challenges that are difficult to address using cultural practices. Exploiting ARR to *P. capsici* fruit rot offers a valuable opportunity to improve disease management when integrated with other strategies.

Most winter squash and pumpkin cultivars reach full size by 20 to 24 dpp (Loy, 2004) and the development of ARR in many of the *Cucurbita* sp. cultivars tested coincides

with this period of growth (Krasnow and Hausbeck, 2015; Meyer and Hausbeck, 2013a). Similar to the results of experiments by Meyer and Hausbeck (2013a), the fruits of *Cucurbita maxima* cultivars in this study displayed a greater incidence of infection than the fruits of *Cucurbita pepo* and *Cucurbita moschata* cultivars. The *Cucurbita maxima* cultivars were the only *Cucurbita* sp. to develop *P. capsici* lesions at 56 dpp. Exocarp firmness of 'Golden Delicious' (*Cucurbita maxima*) and 'Dickenson Field' (*Cucurbita moschata*) processing squashes increased as the fruit matured, but firmness was not correlated with *P. capsici* lesion size on Golden Delicious, a cultivar highly susceptible to fruit rot (Meyer and Hausbeck, 2013a). In this study, there was no correlation between exocarp firmness and disease incidence among winter squash and pumpkin cultivars 22 dpp. Changes in surface wax as cucurbit fruit develop have been implicated as influencing resistance to *P. capsici* (Ando et al., 2009). *Cucurbita maxima* begins to accumulate epicuticular wax at 14 dpp (Sutherland and Hallett, 1993). Watermelon fruit also develop a thick wax layer at 14 dpp, which covers the fruit surface and stomat (Frankle and Hopkins, 1993). Fruits of *Cucurbita maxima* and *Citrullus lanatus* cultivars are susceptible to *P. capsici* at all maturity stages (Kousik et al., 2012; Krasnow and Hausbeck, 2015; Meyer and Hausbeck, 2013a), and changes in surface wax likely have a limited effect on ARR and fruit rot. Recent studies have identified *Cucurbita pepo* and *Citrullus lanatus* germplasm accessions with resistance to *P. capsici* fruit rot as early as 7 dpp during the period of fruit elongation (Kousik et al., 2012; Krasnow et al., 2014) providing additional evidence for the limited role of surface wax in resistance to fruit rot.

Biles et al. (1993) found that the cuticle of pepper increased in thickness as the fruit matured from green to red and developed resistance to *P. capsici* fruit rot. Similarly, the thicker cuticle and epidermal cells of the stem end of tomato were suggested to prevent infection of the fruit by *P. capsici* (Simonds and Kreutzer, 1944). The stylar end did not possess these characteristics and infection occurred within 70 to 90 min after inoculation. The exocarp of cucurbit fruit is likely the location where ARR is expressed as wounding the fruit before inoculation negates ARR. The surface of *Cucurbita* sp. contains trichomes and stomata (Barber, 1909; Sutherland and Hallett, 1993) and differences in the quantity and morphology of these structures may influence ARR to *P. capsici*. Zoospores were observed to accumulate preferentially over stomata of a *Cucurbita maxima* cultivar susceptible to *P. capsici*, but not a *Cucurbita moschata* cultivar with ARR (C. Krasnow and M. Hausbeck, unpublished data). Microcracks in the fruits surface also occur due to growth and water influx (Schaffer and Boyer, 1984) and may influence the susceptibility of winter squash and pumpkin cultivars to fruit rot.

Phytophthora fruit rot has long been a limiting factor in winter squash and pumpkin production. Cultivars that express ARR to *P. capsici* as early as 14 dpp could be selected as part of an integrated management program with fungicide sprays timed for the onset of fruit formation when protection is most needed. Winter squash and pumpkin may be stored postharvest before transporting and marketing. Infection and disease development of the fruit during postharvest storage are especially costly to growers due to the added expenses associated with disposing of the rotted produce. The use of cucurbit cultivars that express ARR may limit postharvest losses since ARR decreases the risk of fruit rot developing as the crop reaches maturity.

Literature Cited

Ando, K. and R. Grumet. 2006. Evaluation of altered cucumber plant architecture as a means to reduce *Phytophthora capsici* disease incidence on cucumber fruit. J. Amer. Soc. Hort. Sci. 131:491–498.

Ando, K., S. Hammar, and R. Grumet. 2009. Age-related resistance of diverse cucurbit fruit to infection by *Phytophthora capsici*. J. Amer. Soc. Hort. Sci. 134:176–182.

Anonymous. 2015. Vegetables summary 2015. U.S. Dep. Agr. Nat. Agric. Stat. Serv. 5 Feb. 2016. <http://usda.mannlib.cornell.edu/usda/current/VegeSumm/VegeSumm-02-04-2016.pdf>.

Babadoost, M. 2000. Outbreak of Phytophthora foliar blight and fruit rot in processing pumpkin fields in Illinois. Plant Dis. 84:1345.

Babadoost, M. and S.Z. Islam. 2003. Fungicide seed treatment effects on seedling damping-off of pumpkin caused by *Phytophthora capsici*. Plant Dis. 87:63–68.

Barber, K.G. 1909. Comparative histology of fruits and seeds of certain species of Cucurbitaceae. Bot. Gaz. 47:263–310.

Biles, C.L., M.M. Wall, M. Waugh, and H. Palmer. 1993. Relationship of Phytophthora fruit rot to fruit maturation and cuticle thickness of New Mexican-type peppers. Phytopathology 83:607–611.

Bird, G., H. Hausbeck, L. Jess, W. Kirk, Z. Szendrei, and F. Warner. 2014. Insect, disease and nematode control for commercial vegetables. Michigan State University Ext. Bull. E-312.

Cafe, A.C., J.M. Duniway, and R.M. Davis. 1995. Effects of the frequency of furrow irrigation on root and fruit rots of squash caused by *Phytophthora capsici*. Plant Dis. 79:44–48.

Foster, J.M. and M.K. Hausbeck. 2010. Managing Phytophthora crown and root rot in bell pepper using fungicides and host resistance. Plant Dis. 94:697–702.

Frankle, W. and D. Hopkins. 1993. Ingress of the watermelon fruit blotch bacterium into fruit. Plant Dis. 77:1090–1092.

Gadoury, D.M., R.C. Seem, A. Ficke, and W.F. Wilcox. 2003. Ontogenic resistance to powdery mildew in grape berries. Phytopathology 93:547–555.

Gerlach, W.W.P., H.A.J. Hoitink, and A.F. Schmitthenner. 1976. *Phytophthora citrophthora* on *Pieris japonica*: Infection, sporulation, and dissemination. Phytopathology 66:302–308.

Gevens, A.J., K. Ando, K.H. Lamour, R. Grumet, and M.K. Hausbeck. 2006. A detached cucumber fruit method to screen for resistance to *Phytophthora capsici* and effect of fruit age on susceptibility to infection. Plant Dis. 90:1276–1282.

Gevens, A.J., R.S. Donahoo, K.H. Lamour, and M.K. Hausbeck. 2007. Characterization of *Phytophthora capsici* from Michigan surface irrigation water. Phytopathology 97:421–428.

Hausbeck, M.K. and K.H. Lamour. 2004. *Phytophthora capsici* on vegetable crops: Research progress and management challenges. Plant Dis. 88:1292–1303.

Isakeit, T. 2007. Phytophthora blight caused by *Phytophthora capsici* on pumpkin and winter squash in Texas. Plant Dis. 91:633.

Jones, J.P. and R.J. McGovern. 1994. Effect of temperature and fungicides on the development of Phytophthora blight and fruit rot of squash. Proc. Fla. State Hort. Soc. 107:147–150.

Kennelly, M.M., D.M. Gadoury, W.F. Wilcox, P.A. Magarey, and R.C. Seem. 2005. Seasonal development of ontogenic resistance to downy mildew in grape berries and rachises. Phytopathology 95:1445–1452.

Kim, Y.J., B.K. Hwang, and K.W. Park. 1989. Expression of age-related resistance in pepper plants infected with *Phytophthora capsici*. Plant Dis. 73:745–747.

Koh, Y.J., B.K. Hwang, and H.S. Chung. 1987. Adult-plant resistance of rice to leaf blast. Phytopathology 77:232–236.

Kousik, C., J. Ikerd, and H. Harrison. 2014. Pre-and post-harvest development of Phytophthora fruit rot on watermelons treated with fungicides in the field. Plant Health Prog. 15:145–150.

Kousik, C., J. Ikerd, P. Wechter, H. Harrison, and A. Levi. 2012. Resistance to Phytophthora fruit rot of watermelon caused by *Phytophthora capsici* in US plant introductions. HortScience 47:1682–1689.

Kousik, C.S., M.L. Adams, W. Jester, R. Hassell, H. Harrison, and G. Holmes. 2011. Effect of cultural practices and fungicides on Phytophthora fruit rot of watermelon in the Carolinas. Crop Prot. 30:888–894.

Krasnow, C.S. and M.K. Hausbeck. 2015. Age-related resistance of *Cucurbita* spp. fruit to *Phytophthora capsici*. Phytopathology 106: S1.5 (abstr.).

Krasnow, C.S., R.P. Naegele, and M.K. Hausbeck. 2014. Evaluation of fruit rot resistance in Cucurbita germplasm resistant to *Phytophthora capsici* crown rot. HortScience 49:285–288.

Lamour, K.H. and M.K. Hausbeck. 2000. Mefenoxam insensitivity and the sexual stage of *Phytophthora capsici* in Michigan cucurbit fields. Phytopathology 90:396–400.

Lazarovits, G., R. Stossel, and E.W.B. Ward. 1981. Age-related-changes in specificity and glyceollin production in the hypocotyl reaction of soybeans to *Phytophthora megasperma* var. *sojae*. Phytopathology 71:94–97.

Loy, J.B. 2004. Morpho-physiological aspects of productivity and quality in squash and pumpkins (*Cucurbita* spp.). Crit. Rev. Plant Sci. 23:337–363.

McClure, T.T. and W.R. Robbins. 1942. Resistance of cucumber seedlings to damping-off as related to age, season of year, and level of nitrogen nutrition. Bot. Gaz. 103:684–697.

McGrath, M.T. 2000. Phytophthora fruit rot. APSnet Feature. 15 Mar. 2015. <http://www.apsnet.org/publications/apsnetfeatures/Pages/PhytophthoraFruitRot.aspx>.

Mellano, H., D. Munnecke, and R. Endo. 1970. Relationship of seedling age to development of *Pythium ultimum* on roots of *Antirrhinum majus*. Phytopathology 60:935–942.

Meyer, M.D. and M.K. Hausbeck. 2012. Using cultural practices and cultivar resistance to manage Phytophthora crown rot on summer squash. HortScience 47:1080–1084.

Meyer, M.D. and M.K. Hausbeck. 2013a. Age-related resistance to Phytophthora fruit rot in 'Dickenson Field' processing pumpkin and 'Golden Delicious' winter squash fruit. Plant Dis. 97:446–452.

Meyer, M.D. and M.K. Hausbeck. 2013b. Using soil-applied fungicides to manage Phytophthora crown and root rot on summer squash. Plant Dis. 97:107–112.

Newhall, A. and R. Wilkinson. 1949. Storage rots of squash in New York State. Plant Dis. Rep. 33:220–222.

Ppoyil, S.B.T. 2011. Effectiveness of mustard short-cycle cover crops for management of *Phytophthora capsici* and *Fusarium spp.* in cucurbits. MS Thesis. University of Illinois Urbana-Champaign, Champaign, IL.

Quesada-Ocampo, L.M. and M.K. Hausbeck. 2010. Resistance in tomato and wild relatives to crown and root rot caused by *Phytophthora capsici*. Phytopathology 100:619–627.

Schaffer, A.A. and C. Boyer. 1984. The influence of gene B on fruit development in *Cucurbita pepo*. J. Amer. Soc. Hort. Sci. 109:432–437.

Simonds, A.O. and W. Kreutzer. 1944. Infection phenomena in tomato-fruit rot caused by *Phytophthora capsici*. Phytopathology 34:813–817.

Sutherland, P. and I. Hallett. 1993. Anatomy of fruit of buttercup squash (*Cucurbita maxima* D.) surface, cuticle, and epidermis. N. Z. J. Crop Hort. Sci. 21:67–72.

Waterhouse, G.M. 1963. Key to the species of Phytophthora de Bary. Mycol. Pap. 92:1–22.